

Title: The Evolutionary History of Dogs in the Americas

Authors: Máire Ní Leathlobhair^{1*}, Angela R. Perri^{2,3*}, Evan K. Irving-Pease^{4*}, Kelsey E. Witt^{5*}, Anna Linderholm^{4,6*}, James Haile^{4,7}, Ophelie Lebrasseur⁴, Carly Ameen⁸, Jeffrey Blick^{9,†}, Adam R. Boyko¹⁰, Selina Brace¹¹, Yahaira Nunes Cortes¹², Susan J. Crockford¹³, Alison Devault¹⁴, Evangelos A. Dimopoulos⁴, Morley Eldridge¹⁵, Jacob Enk¹⁴, Shyam Gopalakrishnan⁷, Kevin Gori¹, Vaughan Grimes¹⁶, Eric Guiry¹⁷, Anders J. Hansen^{7,18}, Ardern Hulme-Beaman^{4,8}, John Johnson¹⁹, Andrew Kitchen²⁰, Aleksei K. Kasparov²¹, Young-Mi Kwon¹, Pavel A. Nikolskiy^{21,22}, Carlos Peraza Lope²³, Aurélie Manin^{24,25}, Terrance Martin²⁶, Michael Meyer²⁷, Kelsey Noack Myers²⁸, Mark Omura²⁹, Jean-Marie Rouillard^{14,30}, Elena Y. Pavlova^{21,31}, Paul Sciulli³², Mikkel-Holger S. Sinding^{7,18,33}, Andrea Strakova¹, Varvara V. Ivanova³⁴, Christopher Widga³⁵, Eske Willerslev⁷, Vladimir V. Pitulko²¹, Ian Barnes¹¹, M. Thomas P. Gilbert^{7,36}, Keith M. Dobney⁸, Ripan S. Malhi^{37,38}, Elizabeth P. Murchison^{1,a,§}, Greger Larson^{4,a,§} and Laurent A. F. Frantz^{4,39,a,§}

Affiliations:

- 1 Transmissible Cancer Group, Department of Veterinary Medicine, University of Cambridge, Cambridge, U.K.
- 2 Department of Archaeology, Durham University, Durham, U.K.
- 3 Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
- 4 The Palaeogenomics & Bio-Archaeology Research Network, Research Laboratory for Archaeology and History of Art, The University of Oxford, Oxford, UK.
- 5 School of Integrative Biology, University of Illinois, Urbana-Champaign, USA
- 6 Department of Anthropology, Texas A&M University, College Station, USA
- 7 Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark
- 8 Department of Archaeology, Classics and Egyptology, University of Liverpool, Liverpool, UK
- 9 Department of Government and Sociology, Georgia College and State University, USA
- 10 Department of Biomedical Sciences, Cornell University, Ithaca, USA
- 11 Department of Earth Sciences, Natural History Museum, London, UK
- 12 Department of Anthropology, University at Albany-SUNY, Albany, New York, USA
- 13 Pacific Identifications Inc., Victoria, Canada
- 14 Arbor Biosciences, Ann Arbor, USA.
- 15 Millennia Research Limited, Victoria, Canada
- 16 Department of Archaeology, Memorial University, Queen's College, St. John's, Canada
- 17 Department of Anthropology, University of British Columbia, Vancouver, Canada
- 18 The Qimmeq Project, University of Greenland, Nuussuaq, Greenland
- 19 Department of Anthropology, Santa Barbara Museum of Natural History, USA
- 20 Department of Anthropology, University of Iowa, Iowa City, USA
- 21 Institute for the Material Culture History, Russian Academy of Sciences, St Petersburg, Russia
- 22 Geological Institute, Russian Academy of Sciences, Moscow, Russia
- 23 Centro INAH Yucatán, Mérida, Yucatán, México
- 24 Department of Archaeology, BioArCh, University of York, York, UK
- 25 UMR 7209, Archéozoologie, Archéobotanique. Muséum national d'Histoire naturelle, Paris, France
- 26 Research and Collections Center, Illinois State Museum, Springfield, USA

27 Touray & Meyer Vet Clinic, Serrekunda, Gambia
28 Glenn A. Black Laboratory of Anthropology, Indiana University Bloomington, USA
29 Department of Mammalogy, Museum of Comparative Zoology, Harvard University, Cambridge,
MA, USA
30 Chemical Engineering Department, University of Michigan, Ann Arbor, USA.
31 Arctic & Antarctic Research Institute, St Petersburg, Russia
32 Department of Anthropology, Ohio State University, Columbus, USA
33 Natural History Museum, University of Oslo, Oslo, Norway
34 VNIIOkeangeologia Research Institute, 1 Angliiskiy Ave., St Petersburg, 190021, Russia
35 Center of Excellence in Paleontology, East Tennessee State University, Gray, USA
36 Norwegian University of Science and Technology, University Museum, Trondheim, Norway
37 University of Illinois at Urbana-Champaign Department of Anthropology, USA
38 University of Illinois at Urbana-Champaign Carl R. Woese Institute for Genomic Biology, USA
39 School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

* These authors contributed equally to this work

^a These authors co-supervised this work

[†] deceased

[§] Corresponding authors: Laurent A. F. Frantz – laurent.frantz@arch.ox.ac.uk ; Greger Larson – greger.larson@arch.ox.ac.uk ; Elizabeth P. Murchison - epm27@cam.ac.uk

Abstract (129 words): 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.

Main Text (2362 words): 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 pre-contact 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 Paleo-Eskimo (~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). Regardless, modern American Arctic dog populations have complex histories with potential genetic contributions from both American and Eurasian Arctic dogs (3).

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 accommodate 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 f_4 ratios (Alaskan husky, Alaskan malamute and Greenland dogs; Table S10&S11; Supplementary Material). This result, however, could reflect ancient population substructure in Arctic dogs rather than genuine admixture (Supplementary Material). Our f_4 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.

References and Notes:

1. G. Larson *et al.*, Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 8878–8883 (2012).
2. A. Perri *et al.*, New evidence of the earliest domestic dogs in the Americas, *Am. Antiq.*, under review (2018).
3. See supplementary materials.
4. T. Goebel, M. R. Waters, D. H. O'Rourke, The late Pleistocene dispersal of modern humans in the Americas. *Science*. **319**, 1497–1502 (2008).
5. J. A. Leonard *et al.*, Ancient DNA evidence for Old World origin of New World dogs. *Science*. **298**, 1613–1616 (2002).
6. S. K. Brown, C. M. Darwent, E. J. Wictum, B. N. Sacks, Using multiple markers to elucidate the ancient, historical and modern relationships among North American Arctic dog breeds. *Heredity* . **115**, 488–495 (2015).
7. K. E. Witt *et al.*, DNA analysis of ancient dogs of the Americas: Identifying possible founding haplotypes and reconstructing population histories. *J. Hum. Evol.* **79**, 105–118 (2015).
8. B. van Asch *et al.*, Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs, confirmed by mtDNA analysis. *Proc. Biol. Sci.* **280**, 20131142

- (2013).
9. L. M. Shannon *et al.*, Genetic structure in village dogs reveals a Central Asian domestication origin. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 13639–13644 (2015).
 10. M. Raghavan *et al.*, Genomic evidence for the Pleistocene and recent population history of Native Americans. *Science*. **349**, aab3884 (2015).
 11. K. E. Graf, I. Buvit, Human Dispersal from Siberia to Beringia: Assessing a Beringian Standstill in Light of the Archaeological Evidence. *Curr. Anthropol.* **58**, S583–S603 (2017).
 12. J. V. Moreno-Mayar *et al.*, Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. *Nature*. **553**, 203–207 (2018).
 13. Z. Fan *et al.*, Worldwide patterns of genomic variation and admixture in gray wolves. *Genome Res.* **26**, 163–173 (2016).
 14. G.-D. Wang *et al.*, Out of southern East Asia: the natural history of domestic dogs across the world. *Cell Res.* **26** (2016), pp. 21–33.
 15. A. H. Freedman *et al.*, Genome sequencing highlights the dynamic early history of dogs. *PLoS Genet.* **10**, e1004016 (2014).
 16. L. A. F. Frantz *et al.*, Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science*. **352**, 1228–1231 (2016).
 17. B. M. Vonholdt *et al.*, Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature*. **464**, 898–902 (2010).
 18. J. K. Pickrell, J. K. Pritchard, Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genet.* **8**, e1002967 (2012).
 19. M. Raghavan *et al.*, The genetic prehistory of the New World Arctic. *Science*. **345** (2014).
 20. E. P. Murchison *et al.*, Transmissible dog cancer genome reveals the origin and history of an ancient cell lineage. *Science*. **343**, 437–440 (2014).
 21. A. Strakova *et al.*, Mitochondrial genetic diversity, selection and recombination in a canine transmissible cancer. *Elife*. **5** (2016), doi:10.7554/eLife.14552.
 22. C. A. Rebbeck, A. M. Leroi, A. Burt, Mitochondrial capture by a transmissible cancer. *Science*. **331**, 303 (2011).
 23. T. M. Anderson *et al.*, Molecular and evolutionary history of melanism in North American gray wolves. *Science*. **323**, 1339–1343 (2009).
 24. H. G. Parker *et al.*, Genomic Analyses Reveal the Influence of Geographic Origin, Migration, and Hybridization on Modern Dog Breed Development. *Cell Rep.* **19**, 697–708 (2017).
 25. M. Derr, *A Dog's History of America: How Our Best Friend Explored, Conquered, and Settled a Continent* (Farrar, Straus and Giroux, 2005).
 26. E. J. Lee *et al.*, Ancient DNA analysis of the oldest canid species from the Siberian Arctic and genetic contribution to the domestic dog. *PLoS One*. **10**, e0125759 (2015).
 27. S. Peterson, thesis (2010).
 28. G. Monaghan, C. Peebles, The construction, use, and abandonment of Angel Site Mound A: tracing the history of a Middle Mississippian town through its earthworks. *Am. Antiq.* **75**, 935–953 (2010).
 29. E. A. Bluhm, A. Liss, in *Chicago Area Archaeology* (Illinois Archaeological Survey, Urbana, 1961).
 30. P. W. Parmalee, A. A. Paloumpis, N. Wilson, Peoples occupying the Apple Creek Site, Illinois. *Illinois State Museum Reports of Investigations*. **23** (1972).
 31. P. W. Parmalee, A. A. Paloumpis, N. Wilson, “Animals Utilized by Woodland Peoples Occupying the Apple Creek Site, Illinois, Research Papers 5” (Illinois State Museum, Illinois

- Valley Archaeological Program, Springfield, I, 1972).
32. J. B. Griffin, Late prehistory of the Ohio Valley. *Handbook of North American Indians*. **15**, 547–559 (1978).
 33. F. Church, J. P. Nass Jr, J. P. Hart, C. B. Reith, Central Ohio Valley during the Late Prehistoric Period: Subsistence-Settlement Systems' Responses to Risk. *Northeast Subsistence-Settlement Change: AD 700--1300*, 11 (2002).
 34. W. C. Mills, *Explorations of the Baum prehistoric village site* (FJ Heer, 1906).
 35. J. B. Griffin, Fort Ancient Has No Class: The Absence of an Elite Group in Mississippian Societies in the Central Ohio Valley. *Archeological Papers of the American Anthropological Association*. **3**, 53–59 (1992).
 36. E. G. Squier, E. H. Davis, *Ancient Monuments of the Mississippi Valley: Comprising the Results of Extensive Original Surveys and Explorations* (Smithsonian Institution, 1848).
 37. F. W. Putnam, in *Additional Mounds of Duval and Clay Counties, Florida.*, C. B. Moore, Ed. (Journal of the Academy of Natural Sciences of Philadelphia, Philadelphia, 1896), pp. 26–27.
 38. D. F. Morey, Burying key evidence: the social bond between dogs and people. *J. Archaeol. Sci.* **33**, 158–175 (2006/2).
 39. K. Nolan, P. Sculli, Rejoinder to Sciulli and Purcell: Two Late Prehistoric Dogs from the Reinhardt Site (33PI880), Pickaway County, Ohio. *Pa. Archaeol.* **84**, 65–73 (2014).
 40. C. B. Moore, Aboriginal sites on the Tennessee river. *Journal of the Academy for Natural Sciences of Philadelphia*. **16**, 169–428 (1915).
 41. T. C. Rick, J. M. Erlandson, R. L. Vellanoweth, T. J. Braje, From pleistocene mariners to complex hunter-gatherers: The archaeology of the california channel islands. *Journal of World Prehistory*. **19**, 169–228 (2005).
 42. T. C. Rick *et al.*, Dogs, humans and island ecosystems: the distribution, antiquity and ecology of domestic dogs (*Canis familiaris*) on California's Channel Islands, USA. *Holocene*. **18**, 1077–1087 (2008).
 43. W. S. Webb, D. L. DeJarnette, "The Flint River Site, Museum Paper 23" (Geological Survey of Alabama, Tuscaloosa, Alabama, 1948).
 44. D. M. Warren, thesis (2004).
 45. W. D. Lipe, J. N. Morris, T. A. Kohler, *Dolores Archaeological Program: Anasazi Communities at Dolores: Grass Mesa Village* (USDI Bureau of Reclamation, Engineering and Research Center, Denver, 1988).
 46. J. M. Galloy, PART V : WOODLAND PERIOD The Janey B . Goode Site (11S1232): Highlights of Investigations at a Massive Late Prehistoric Site in the American Bottom. *Illinois Archaeology*. **22**, 529–552 (2010).
 47. Q. L. Borgic, J. M. Galloy, Domesticated Dog Remains from the Janey B. Goode Site (2004).
 48. G. L. Houart, Koster: a stratified Archaic site in the Illinois valley (1971) (available at <http://core.tdar.org/document/147855>).
 49. K. W. Butzer, Changing Holocene Environments at the Koster Site: A Geo-Archaeological Perspective. *Am. Antiq.* **43**, 408–413 (1978).
 50. J. E. Buikstra, in *The Archaeology of Death*, R. Chapman, I. Kinnes, K. Randsborg, Eds. (Cambridge University Press, 1981), pp. 123–132.
 51. E. R. Hajic, *Koster site archaeology I: stratigraphy and landscape evolution* (Center for Amer Archeology Pr, 1990).
 52. S. Struever, F. A. Holton, Koster: Americans in search of their prehistoric past (1979)

- (available at <http://core.tdar.org/document/117353/koster-americans-in-search-of-their-prehistoric-past>).
53. J. A. Brown, R. K. Vierra, *What happened in the Middle Archaic?: Introduction to an ecological approach to Koster Site Archaeology* (Academic Press Orlando, 1983).
 54. R. J. Jeske, R. Lurie, THE ARCHAEOLOGICAL VISIBILITY OF BIPOLAR TECHNOLOGY: AN EXAMPLE FROM THE KOSTER SITE. *MidCont. J. Archaeol.* **18**, 131–160 (1993).
 55. A. L. Boon, thesis, Indiana University of Pennsylvania (2013).
 56. E. R. Hajic, in *Encyclopedia of Geoarchaeology*, A. S. Gilbert, Ed. (Springer Netherlands, 2017), *Encyclopedia of Earth Sciences Series*, pp. 457–458.
 57. M. D. Wiant *et al.*, The archaic period in the lower Illinois river basin. *Archaic Societies: Diversity and Complexity across the Midcontinent*, 229–286 (2009).
 58. D. F. Morey, M. D. Wiant, Early Holocene Domestic Dog Burials From the North American Midwest. *Curr. Anthropol.* **33**, 224–229 (1992).
 59. F. C. Hill, *A Middle Archaic Dog Burial in Illinois* (Foundation for Illinois Archaeology, 1972).
 60. W. S. Webb, D. L. DeJarnette, “Little Bear Creek Site, Museum Paper 26” (1948).
 61. F. S. Barkalow Jr., Vertebrate Remains from Archaeological Sites in the Tennessee Valley of Alabama. *South. Indian Stud.* **24**, 3–41 (1972).
 62. C. P. Lope, M. A. Masson, T. S. Hare, C. Pedro, P. C. Delgado Ku, The Late Postclassic chronology of Mayapan: new radiocarbon evidence. *Ancient Mesoamerica.* **17**, 153–176 (2006).
 63. T. Proskouriakoff, in *Mayapan, Yucatan, Mexico, Carnegie Institute of Washington Publication 619* (1962), vol. 619, p. 87.
 64. A. L. Smith, in *Mayapan, Yucatan, Mexico, Carnegie Institute of Washington Publication 619* (1962), p. 619.
 65. M. A. Masson, C. P. Lope, Animal use at the Postclassic Maya center of Mayapan. *Quat. Int.* **191**, 170–183 (2008).
 66. A. E. Kane, C. K. Robinson, *Dolores Archaeological Program: Anasazi Communities at Dolores: McPhee Village* (USDI Bureau of Reclamation, Engineering and Research Center., Denver, 1988).
 67. M. L. Fowler, Modoc Rock Shelter: An Early Archaic Site in Southern Illinois. *Am. Antiq.* **24**, 257–270 (1959).
 68. P. W. Parmalee, “Appendix II: animals remains from the Modoc Rock Shelter site, Randolph County, Illinois” (Illinois State Museum, Springfield, Illinois, 1959), pp. 61–63.
 69. W. S. Webb, D. L. DeJarnette, The Perry Site, 1Lu25. *Geological Survey of Alabama, Alabama Natural History Museum Paper.* **25** (1948).
 70. E. Futato, Middle and Late Archaic Settlement at the Perry Site, 1LU25, Lauderdale County, Alabama. *Journal of Alabama Archaeology.* **48**, 80–92 (2002).
 71. J. A. Tuck, Archaic Indian Cemetery in Newfoundland. *Sci. Am.* **222**, 112–121 (1970).
 72. J. A. Tuck, An Archaic Cemetery at Port Au Choix, Newfoundland. *Am. Antiq.* **36**, 343–358 (1971).
 73. J. A. Tuck, *Ancient people of Port au Choix* (1976).
 74. B. C. Hood, The Maritime Archaic Indians of Labrador: Investigating Prehistoric Social Organization. *Newfoundland and Labrador Studies.* **9** (1993) (available at <https://journals.lib.unb.ca/index.php/NFLDS/article/view/940>).
 75. M. A. P. Renouf, Palaeoeskimo Seal Hunters at Port au Choix, Northwestern

414 Newfoundland. *Newfoundland and Labrador Studies*. **9** (1993) (available at
 415 <https://journals.lib.unb.ca/index.php/NFLDS/article/view/941>).
 416 76. E. J. Guiry, V. Grimes, Domestic dog (*Canis familiaris*) diets among coastal Late Archaic
 417 groups of northeastern North America: A case study for the canine surrogacy approach. *Journal of*
 418 *Anthropological Archaeology*. **32**, 732–745 (2013).
 419 77. A. Perri, in *Economic Zooarchaeology: Studies in Hunting, Herding and Early Agriculture*,
 420 P. Rowley-Conwy, D. Serjeantson, P. Halstead, Eds. (Oxbow, 2017).
 421 78. G. M. Allen, *Dogs of the American aborigines* (Museum [of Comparative Zoology], 1920),
 422 vol. 63.
 423 79. W. A. Ritchie, An Early Site in Cayuga County, New York. *Research Records*. **7** (1945).
 424 80. M. Eldridge, A. Parker, C. Mueller, S. Crockford, “Archaeological investigations at Ya
 425 asqalu’i/Kaien Siding, Prince Rupert Harbour” (Millennia Research Limited for CN, 2014).
 426 81. A. Parker, M. Eldridge, in *Proceedings of the 42nd Annual Conference on Computer*
 427 *Applications and Quantitative Methods in Archaeology*, F. Giligny, F. Djindjian, L. Costa, P.
 428 Moscati, S. Rober, Eds. (Archaeopress, Oxford, 2014), pp. 114–122.
 429 82. S. J. Crockford, “Analysis of the vertebrate fauna from neighbouring Prince Rupert Harbour
 430 sites GbTo-54 and GbTo-13: prehistoric mountain goat capital of North America” (Pacific
 431 IDentification for Millenia Research Limited, 2014).
 432 83. K. C. Nolan, Distributional Survey of the Reinhardt Site (33PI880), Pickaway County,
 433 Ohio: A Strategy for Deciphering the Community Structure of a Fort Ancient Village. *MidCont. J.*
 434 *Archaeol.* **36**, 105–130 (2011).
 435 84. K. C. Nolan, Archaeological Survey of the Reinhardt Tract Property through a Certified
 436 Local Government (CLG) Grant on behalf of the City of Columbus in Harrison Township,
 437 Pickaway County, Ohio, Volume I: Survey Results. *Report Submitted to the Ohio Historic*
 438 *Preservation Office, Columbus, OH* (2009) (available at
 439 http://www.academia.edu/download/464862/Reinhardt_Tract_CLG_reportVolI_Final-web.doc).
 440 85. K. C. Nolan, R. A. Cook, An evolutionary model of social change in the Middle Ohio
 441 Valley: Was social complexity impossible during the late woodland but mandatory during the late
 442 prehistoric? *Journal of Anthropological Archaeology*. **29**, 62–79 (2010/3).
 443 86. J. E. Kerber, NATIVE AMERICAN TREATMENT OF DOGS IN NORTHEASTERN
 444 NORTH AMERICA: ARCHAEOLOGICAL AND ETHNOHISTORICAL PERSPECTIVES.
 445 *Archaeology of Eastern North America*. **25**, 81–95 (1997).
 446 87. R. A. Cook, DOGS OF WAR: POTENTIAL SOCIAL INSTITUTIONS OF CONFLICT,
 447 HEALING, AND DEATH IN A FORT ANCIENT VILLAGE. *Am. Antiq.* **77**, 498–523 (2012).
 448 88. M. A. Potter, R. S. Baby, Hopewellian Dogs. *Ohio J. Sci.* **64**, 36–40 (1964).
 449 89. W. D. Frankforter, G. A. Agogino, The Simonsen Site: Report for the Summer of 1959.
 450 *Plains Anthropol.* **10**, 65–70 (1960).
 451 90. G. A. Agogino, W. D. Frankforter, A Paleo-Indian Bison-Kill in Northwestern Iowa. *Am.*
 452 *Antiq.* **25**, 414–415 (1960).
 453 91. J. C. Equihua, Proyecto Salvamento Arqueológico Tizayuca 2006. Informe. Secuencias
 454 estratigráficas y conjuntos arquitectónicos, tomo I. Technical report submitted to the INAH (2008).
 455 92. A. Manin, thesis, Muséum National d’Histoire Naturelle (2015).
 456 93. A. Hrdlička, *The Anthropology of Kodiak Island* (Wistar Institute of Anatomy and Biology,
 457 1944).
 458 94. R. F. Heizer, G. W. Hewes, A. Hrdlicka, nd Archaeology of the Uyak Site, Kodiak Island,
 459 Alaska (1956) (available at <http://www.jstor.org/stable/pdf/277048.pdf>).

95. A. F. Steffian, Fifty years after Hrdlicka: Further excavation of the Uyak site, Kodiak Island, Alaska. *Contributions to the anthropology of southcentral and southwestern Alaska*, 141–164 (1992).
96. C. F. West, K. N. Jarvis, Osteometric Variation in Domestic Dogs (*Canis familiaris*) from the Kodiak Archipelago, Alaska. *Int. J. Osteoarchaeol.* **25**, 289–298 (2015).
97. G. M. Allen, Dog Skulls from Uyak Bay, Kodiak Island. *J. Mammal.* **20**, 336–340 (1939).
98. G. R. Scott, Affinities of Prehistoric and Modern Kodiak Islanders and the Question of Kachemak-Koniag Biological Continuity. *Arctic Anthropol.* **29**, 150–166 (1992).
99. D. W. Clark, Contributions to the Later Prehistory of Kodiak Island, Alaska. National Museum of Man Mercury Series, No. 20. *National Museums of Canada: Ottawa* (1974).
100. C. F. West, C. A. France, Human and Canid Dietary Relationships: Comparative Stable Isotope Analysis From the Kodiak Archipelago, Alaska. *J. Ethnobiol.* **35**, 519–535 (2015).
101. C. P. Groves, The advantages and disadvantages of being domesticated. *Perspectives in Human Biology.* **4**, 1–12 (1999).
102. P. Tacon, C. Pardoe, Dogs make us human (2002) (available at <http://www98.griffith.edu.au/dspace/handle/10072/16675>).
103. F. J. Simoons, *Eat Not this Flesh: Food Avoidances from Prehistory to the Present* (Univ of Wisconsin Press, 1994).
104. L. B. Gregory, The Hatch site: A preliminary report. *Virginia Archeological Society, Quarterly Bulletin.* **34**, 239–248 (1980).
105. E. S. Gregory, Weyanoke Old Town. *Archeological Society of Virginia Quarterly Bulletin.* **41**, 49–71 (1986).
106. J. P. Blick, The Archaeology and Ethnohistory of the Dog in Virginia Algonquian Culture as Seen from Weyanoke Old Town. *Algonquian Papers-Archive.* **31** (2000) (available at <https://ojs3.library.carleton.ca/index.php/ALGQP/article/view/849>).
107. C. F. Feest, *The Virginia Indian in Pictures, 1612-1624* (Smithsonian Institution, 1967).
108. B. C. McCary, *Indians in Seventeenth-Century Virginia* (University Press of Virginia, Charlottesville, 1957).
109. J. P. Blick, A preliminary report on the osteometric analysis of some aboriginal dogs (*Canis familiaris*) from Weyanoke Old Town, 44 PG 51, Prince George County, Virginia. *Bull. Am. Assoc. Hist. Nurs.* **43** (1988).
110. H. C. Rountree, *Pocahontas's People: The Powhatan Indians of Virginia Through Four Centuries* (University of Oklahoma Press, 1990).
111. R. Beverley, *The History and Present State of Virginia* (The University of North Carolina Press, Chapel Hill, 1705).
112. C. F. Feest, *Virginia Algonquians* (Smithsonian Institution, 1978).
113. W. A. Ritchie, *The Archaeology of New York State* (Knopf Doubleday Publishing Group, 1965).
114. J. A. Strong, Late Woodland dog ceremonialism on Long Island in comparative and temporal perspective. *The Bulletin of the Journal of the New York State Archaeological Association.* **91**, 32–38 (1985).
115. A. Perri, thesis, Durham University (2013).
116. W. D. Wallis, *The Micmac Indians of Eastern Canada* (U of Minnesota Press, 1955).
117. J. E. Kerber, A. D. Leveillee, R. L. Greenspan, AN UNUSUAL DOG BURIAL FEATURE AT THE LAMBERT FARM SITE, WARWICK, RHODE ISLAND: PRELIMINARY OBSERVATIONS. *Archaeology of Eastern North America.* **17**, 165–174 (1989).

118. T. Harriot, *A Brief and True Report of the New Found Land of Virginia* (digitalcommons.unl.edu, London, 1588).
119. W. Strachey, *The History of Travel into Virginia Britannia* (Hakluyt Society, London, 1612).
120. J. Smith, *The Generall Historie of Virginia, New-England, and the Summer Isles* (1624).
121. J. Brereton, *True Relation of the Discoveries of the North Part of Virginia* (1602).
122. P. Hulton, *America 1585: The Complete Drawings of John White* (1984) (available at <http://www.tandfonline.com/doi/abs/10.1080/00377996.1985.9958273>).
123. K. A. Kuckelman, The Archaeology of Yellow Jacket Pueblo (Site 5MT5): Excavations at a Large Community Center in Southwestern Colorado (2003), (available at <http://www.crowcanyon.org/yellowjacket>).
124. V. V. Pitulko, A. Kasparov, Ancient Arctic Hunters: Material Culture and Survival Strategy. *Arctic Anthropol.* **33**, 1–36 (1996).
125. V. V. Pitulko, A. K. Kasparov, Archaeological dogs from the Early Holocene Zhokhov site in the Eastern Siberian Arctic. *Journal of Archaeological Science: Reports.* **13**, 491–515 (2017/6).
126. J. Dabney *et al.*, Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 15758–15763 (2013).
127. P. B. Damgaard *et al.*, Improving access to endogenous DNA in ancient bones and teeth. *Sci. Rep.* **5**, 11184 (2015).
128. M. Meyer, M. Kircher, Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb. Protoc.* **2010**, db.prot5448 (2010).
129. K. E. Witt *et al.*, DNA analysis of ancient dogs of the Americas: Identifying possible founding haplotypes and reconstructing population histories. *J. Hum. Evol.* **79**, 105–118 (2015).
130. M. E. Allentoft *et al.*, Population genomics of Bronze Age Eurasia. *Nature.* **522**, 167–172 (2015).
131. S. Lindgreen, AdapterRemoval: easy cleaning of next-generation sequencing reads. *BMC Res. Notes.* **5**, 337 (2012).
132. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics.* **25**, 1754–1760 (2009).
133. M. Schubert *et al.*, Improving ancient DNA read mapping against modern reference genomes. *BMC Genomics.* **13**, 178 (2012).
134. M. Kircher, Analysis of high-throughput ancient DNA sequencing data. *Methods Mol. Biol.* **840**, 197–228 (2012).
135. R. E. Green *et al.*, A draft sequence of the Neandertal genome. *Science.* **328**, 710–722 (2010).
136. P. Skoglund *et al.*, Genomic insights into the peopling of the Southwest Pacific. *Nature.* **538**, 510–513 (2016).
137. W. Haak *et al.*, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature.* **522**, 207–211 (2015).
138. L. A. F. Frantz *et al.*, Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science.* **352**, 1228–1231 (2016).
139. H. Jónsson, A. Ginolhac, M. Schubert, P. L. F. Johnson, L. Orlando, mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics.* **29**, 1682–1684 (2013).
140. B. Bai *et al.*, DoGSD: the dog and wolf genome SNP database. *Nucleic Acids Res.* **43**,

- D777–D783 (2014).
141. A. R. Quinlan, I. M. Hall, BEDTools: a flexible suite of utilities for comparing genomic features. *Bioinformatics*. **26**, 841–842 (2010).
 142. E. P. Murchison *et al.*, Transmissible [corrected] dog cancer genome reveals the origin and history of an ancient cell lineage. *Science*. **343**, 437–440 (2014).
 143. P. Skoglund, E. Ersmark, E. Palkopoulou, L. Dalén, Ancient Wolf Genome Reveals an Early Divergence of Domestic Dog Ancestors and Admixture into High-Latitude Breeds. *Curr. Biol*. **25**, 1515–1519 (2015).
 144. H. Li *et al.*, The Sequence Alignment / Map (SAM) Format and SAMtools 1000 Genome Project Data Processing Subgroup. *Data Processing*, 1–2 (2009).
 145. O. Thalmann *et al.*, Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*. **342**, 871–874 (2013).
 146. K. Katoh, G. Asimenos, H. Toh, in *Bioinformatics for DNA Sequence Analysis*, D. Posada, Ed. (Humana Press), *Methods in Molecular Biology*, pp. 39–64.
 147. K. Katoh, D. M. Standley, MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780 (2013).
 148. A. Stamatakis, RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*. **22**, 2688–2690 (2006).
 149. B. van Asch *et al.*, Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs, confirmed by mtDNA analysis. *Proc. Biol. Sci.* **280**, 20131142 (2013).
 150. A. Strakova *et al.*, Mitochondrial genetic diversity, selection and recombination in a canine transmissible cancer. *Elife*. **5** (2016), doi:10.7554/eLife.14552.
 151. J.-F. Pang *et al.*, mtDNA data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Mol. Biol. Evol.* **26**, 2849–2864 (2009).
 152. S. Björnerfeldt, M. T. Webster, C. Vilà, Relaxation of selective constraint on dog mitochondrial DNA following domestication, 990–994 (2006).
 153. Z. Hao, Q. Zhang, B. Qu, The complete mitochondrial genome of the Chinese indigenous dog. *Mitochondrial DNA A DNA Mapp Seq Anal.* **27**, 88–89 (2016).
 154. K. M. Webb, M. W. Allard, Mitochondrial genome DNA analysis of the domestic dog: identifying informative SNPs outside of the control region. *J. Forensic Sci.* **54**, 275–288 (2009).
 155. J.-H. Zhao, W. Liu, The complete mitochondrial genome of the Simao Chinese indigenous dog. *Mitochondrial DNA A DNA Mapp Seq Anal.* **27**, 545–546 (2016).
 156. M. W. Pedersen *et al.*, Postglacial viability and colonization in North America’s ice-free corridor. *Nature*. **537**, 45–49 (2016).
 157. A. J. Drummond, M. A. Suchard, D. Xie, A. Rambaut, Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969–1973 (2012).
 158. R. Lanfear, P. B. Frandsen, A. M. Wright, T. Senfeld, B. Calcott, PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Mol. Biol. Evol.* **34**, 772–773 (2017).
 159. A. J. Drummond, A. Rambaut, B. Shapiro, O. G. Pybus, Bayesian coalescent inference of past population dynamics from molecular sequences. *Mol. Biol. Evol.* **22**, 1185–1192 (2005).
 160. C. Drögemüller *et al.*, A mutation in hairless dogs implicates FOXI3 in ectodermal development. *Science*. **321**, 1462 (2008).
 161. N. Patterson, A. L. Price, D. Reich, Population structure and eigenanalysis. *PLoS Genet.* **2**, e190 (2006).

162. S. Purcell *et al.*, PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559–575 (2007).
163. E. Paradis, J. Claude, K. Strimmer, APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics.* **20**, 289–290 (2004).
164. F. Ronquist, J. P. Huelsenbeck, MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics.* **19**, 1572–1574 (2003).
165. H. E. L. Lischer, L. Excoffier, PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics.* **28**, 298–299 (2012).
166. P. O. Lewis, A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* **50**, 913–925 (2001).
167. N. Patterson *et al.*, Ancient admixture in human history. *Genetics.* **192**, 1065–1093 (2012).
168. T. M. Anderson *et al.*, Molecular and evolutionary history of melanism in North American gray wolves. *Science.* **323**, 1339–1343 (2009).
169. D. Reich, K. Thangaraj, N. Patterson, A. L. Price, L. Singh, Reconstructing Indian population history. *Nature.* **461**, 489–494 (2009).
170. D. H. Alexander, J. Novembre, K. Lange, Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009).
171. G. Larson *et al.*, Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences*, 1203005109– (2012).
172. A. Eriksson, A. Manica, Effect of ancient population structure on the degree of polymorphism shared between modern human populations and ancient hominins. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 13956–13960 (2012).
173. C. Murgia, J. K. Pritchard, S. Y. Kim, A. Fassati, R. A. Weiss, Clonal origin and evolution of a transmissible cancer. *Cell.* **126**, 477–487 (2006).
174. C. A. Rebbeck, R. Thomas, M. Breen, A. M. Leroi, A. Burt, Origins and evolution of a transmissible cancer. *Evolution.* **63**, 2340–2349 (2009).
175. A. Rimmer *et al.*, Integrating mapping-, assembly- and haplotype-based approaches for calling variants in clinical sequencing applications. *Nat. Genet.* **46**, 912–918 (2014).
176. A. McKenna *et al.*, The Genome Analysis Toolkit: A MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303 (2010).
177. B. Decker *et al.*, Comparison against 186 canid whole-genome sequences reveals survival strategies of an ancient clonally transmissible canine tumor. *Genome Res.* **25**, 1646–1655 (2015).
178. A. Vaysse *et al.*, Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLoS Genet.* **7**, e1002316 (2011).
179. K. Lindblad-Toh *et al.*, Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature.* **438**, 803–819 (2005).
180. G. Ha, A. Roth, D. Lai, A. Bashashati, J. Ding, Integrative analysis of genome-wide loss of heterozygosity and monoallelic expression at nucleotide resolution reveals disrupted pathways in triple-negative breast *Genome* (2012) (available at <http://genome.cshlp.org/content/22/10/1995.short>).
181. C. Fraley, A. E. Raftery, T. B. Murphy, L. Scrucca, mclust Version 4 for R: Normal Mixture Modeling for Model-Based Clustering, Classification, and Density Estimation. 2012. *University of Washington: Seattle*.
182. P. Concannon, S. Whaley, D. Lein, R. Wissler, Canine gestation length: variation related to time of mating and fertile life of sperm. *Am. J. Vet. Res.* **44**, 1819–1821 (1983).
183. A. C. Okkens, T. W. Hekerman, J. W. de Vogel, B. van Haaften, Influence of litter size and

breed on variation in length of gestation in the dog. *Vet. Q.* **15**, 160–161 (1993).

184. B. B. Gavrilovic, K. Andersson, C. Linde Forsberg, Reproductive patterns in the domestic dog--a retrospective study of the Drever breed. *Theriogenology*. **70**, 783–794 (2008).

185. L. B. Alexandrov *et al.*, Clock-like mutational processes in human somatic cells. *Nat. Genet.* **47**, 1402–1407 (2015).

186. D. P. Blaine, *A Domestic Treatise on the Diseases of Horses and Dogs* (T. Boosey, 1810).

187. S. M. Waszak *et al.*, Germline determinants of the somatic mutation landscape in 2,642 cancer genomes. *bioRxiv* (2017), p. 208330.

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; Supplementary Material) 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.

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

Muséum national d'Histoire naturelle. K.E.W. and R.S.M were supported by a National Science Foundation grant (BCS-1540336) and a Wenner-Gren grant. V.G. was supported by a Social Sciences and Humanities Research Council Insight Grant. V.V.P., E.Y.P., and P.A.N. were supported by Russian Science Foundation project N16-18-10265-RNF. We thank the staff of the Danish National High-Throughput Sequencing Centre for assistance in data generation and the Illinois State Museum Society for funding. **Author contributions:** L.A.F.F, G.L. and E.P.M conceived the project and designed research; A.P., K.D. and G.L. coordinated the archaeological analyses and sampling collection efforts with input from R.P.M, C.A., A.B-H and K.E.W.; A.P., 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., 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., S.B., A.D. E.A.D., J.E., J-M. R., M-H.S.S. conducted the ancient laboratory work with input from 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 samples; M.N.L. and Y-M.K. conducted the CTVT analyses with input from E.P.M., K.G., and 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., 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 all other authors. **Competing interests:** A.D., J.E, and J-M.R. are employees of Arbor Biosciences which provided target enrichment kits used in this study. J-M.R. is also a founder of Arbor Biosciences. **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.

Supplementary Materials:

Material and Methods

Figs. S1 to S28

Tables S3 to S8, and S12 to S16

Captions for Tables S1, S2, S9 to S11

References 26-187

Other Supporting Online Material for this manuscript includes the following:

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