

0.08 and 0.10) give estimated ages of $13,000 \pm 3,000$ and $17,000 \pm 3,000$ years for clades B and C, respectively.

Thus, our mtDNA data suggest a first origin of domestic dogs either $\sim 40,000$ years ago, forming only clade A, or $\sim 15,000$ years ago, possibly involving all the three clades A, B, and C. However, the oldest subcluster of clade A in Europe (as determined from the mean genetic distance from haplotypes unique to the western part of the world to the nodal haplotype shared with East Asia; 0.39 substitutions, SD = 0.09) is estimated to be only $9,000 \pm 3,000$ years old (Fig. 2A). An origin of 40,000 years ago for clade A would therefore imply a long isolation in East Asia of dogs before they spread to the rest of the world. Circumstantial evidence therefore indicates a simultaneous origin in East Asia $\sim 15,000$ years ago for clades A and B, and possibly also clade C.

In the context of the archaeological record, this seems to be a probable scenario. There is no certain evidence for domestic dogs in late Paleolithic China, but in the earliest Neolithic, finds are numerous, dating back to 7,500 yr B.P. (4, 19). Considering the relatively limited amount of archaeological work done in East Asia, the lack of late Paleolithic finds does not exclude a much earlier origin of domestic dogs in East Asia. The earliest Southwest Asian finds dated at $\sim 12,000$ yr B.P. are from unspecified small canids (7, 8), and remains with typical dog morphology appear only by 9,000 yr B.P. (4, 11). The German find from 14,000 yr B.P. consists of a single jaw fragment (6), and there is a considerable temporal gap to later European finds, which appear by $\sim 9,000$ yr B.P. (4, 5, 12). The earliest North American finds are dated at 8,500 yr B.P. (4, 20). An East Asian origin is supported by a morphological feature of the jaw diagnostic of domestic dogs and also found in some Chinese wolves but generally not in other wolves (4, 10).

In conclusion, the archaeological record cannot define the number of geographical origins or their locations, but suggests the date at 9,000 to 14,000 yr B.P., while our mtDNA data indicate a single origin of domestic dogs in East Asia $\sim 15,000$ or 40,000 yr B.P. We conclude that a synthesis of available data points to an origin of the domestic dog in East Asia $\sim 15,000$ yr B.P. In this event, clade A would have had several origins from wolf haplotypes, and the first domestication of wolves would not have been an isolated event, but rather a common practice in the human population in question.

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Ancient DNA Evidence for Old World Origin of New World Dogs

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Mitochondrial DNA sequences isolated from ancient dog remains from Latin America and Alaska showed that native American dogs originated from multiple Old World lineages of dogs that accompanied late Pleistocene humans across the Bering Strait. One clade of dog sequences was unique to the New World, which is consistent with a period of geographic isolation. This unique clade was absent from a large sample of modern dogs, which implies that European colonists systematically discouraged the breeding of native American dogs.

The dog is the only domesticated species that was distributed across Eurasia and the Americas before the development of transoceanic travel during the 15th century. Genetic, morphologic, and behavioral studies (1–5) have

shown that domestic dogs derive from the gray wolf (*Canis lupus*), a species that has a holarctic distribution. Therefore, domestic dogs were either brought to the New World by late Pleistocene humans crossing the Bering Strait from Asia or were domesticated in the New World independently from gray wolves. A New World domestication of dogs is supported by morphological (1) and limited genetic data (6). Further, the antiquity of dog and human remains in the New World suggests independent Old and New World domestication events. The oldest dog remains in the New World, from Danger Cave, Utah (7), are dated from 9000 to 10,000 years before the present (yr B.P.) and compare with the earliest dates of about 12,000 to 14,000 yr B.P. for dog remains from archaeological sites in Germany, Israel, and Iraq (8–10). The arrival of humans in North America occurred by at least 12,000 to 14,000 yr B.P. (11, 12) and therefore was coincident with or predated the first appearance of dogs in the archaeo-

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1). Consequently, our phylogenetic analysis suggests that minimally, about five founding dog lineages (including the ancestor of clade *a*) invaded North America with humans as they colonized the New World. Further, the presence of the unique haplotype group (clade *a*) derived from New World haplotype D28 is consistent with a history of isolation (19).

Analysis of ancient sequences from New World dog remains from localities as distant as Peru and Alaska supports the hypothesis that ancient and modern dogs worldwide share a common origin from Old World gray wolves. Our results differ from those of a previous study (6) that reported sequences closely related to New World wolves in four

of five dog remains associated with native Americans in British Columbia. This finding could represent localized interbreeding between domestic dogs and North American wolves, as suggested by morphologic (20, 21) and historic (13, 21) data. However, our data suggest that widespread introgression of female wolf matriline into the native dog population occurred infrequently, because all sequences from ancient native dogs were well differentiated from those found in North American wolves. Similarly, extant North American gray wolves show no genetic evidence of interbreeding with dogs, despite the high concentration of dogs in many areas occupied by gray wolves (22). Hybridization is occasionally observed in Europe, where dogs are common and gray wolves are rare (23).

Six of 12 ancient Latin American haplotypes are grouped in clade *a* and include sequences found in dog remains from Bolivia, Peru, and Mexico (Fig. 1). No sequences from clade *a* have been found in samples from over 350 modern dogs (17). The upper bound of a 95% confidence limit for the frequency that sequences from clade *a* could have in this modern sample and be missed (an observed frequency of zero) is 1.0% (24). Consequently, the absence of clade *a* sequences from modern dogs suggests an extensive replacement of native American dogs by those introduced by Europeans. These lin-

Fig. 2. Statistical parsimony cladogram of precontact Latin American (gray), Alaskan (black), and modern (white) dog haplotypes from clade I (5). Modern sequences from (5) are labeled D, and other sequences from GenBank are labeled with their accession number. Each branch represents a 1-bp change or indel, and dots represent hypothetical haplotypes.

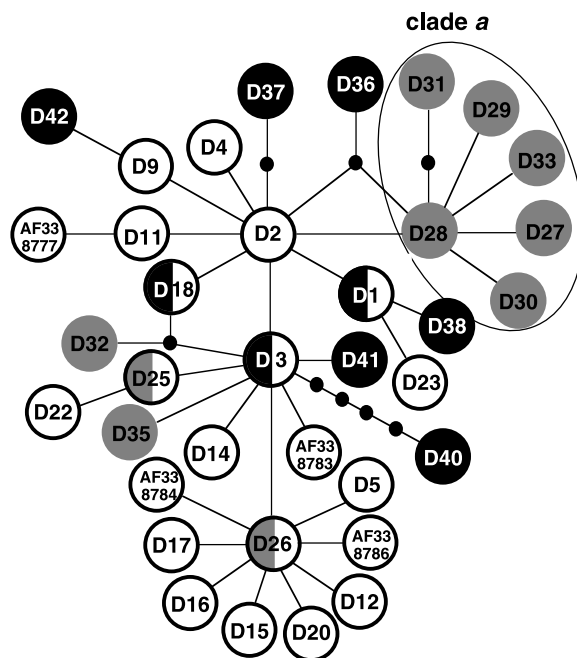


Table 1. Sample source, locality, age, and haplotype, based on a 257-bp segment of the mitochondrial control region (5). Haplotypes D1, D3, D6, D18, D25, and D26, shown in bold, have previously been reported (5), and all other haplotypes are novel. F:AM samples are from the American Museum of

Natural History, New York. The ages for Alaskan samples are radiocarbon dates from the NSF-Arizona Accelerator, Mass Spectrometry Facility. RYBP, radiocarbon years before the present; C.E., calendar year (common era). Radiocarbon years were converted to calendar years using the tables in (29).

ID	Haplotype	Source	Locality	Age	Reference number
Pre-Columbian					
JAL 330	D27	William Isbell	Iwawi, Bolivia	>1000 yr B.P.	
JAL 331	D28	William Isbell	Iwawi, Bolivia	>1000 yr B.P.	
JAL 332	D29	William Isbell	Iwawi, Bolivia	>1000 yr B.P.	
JAL 334	D28	William Isbell	Iwawi, Bolivia	>1000 yr B.P.	
JAL 337	D28	William Isbell	Iwawi, Bolivia	>1000 yr B.P.	
JAL 365	D26	Sonia Guillén	Chiribaja Baja, Peru	1000 yr B.P.	
PC 5	D30	Sonia Guillén	Chiribaja Baja, Peru	1000 yr B.P.	
PC 6	D31	Sonia Guillén	Chiribaja Baja, Peru	1000 yr B.P.	
PC 8	D25	Raúl Valadez	Teotihuacan, Mexico	1300 yr B.P.	
PC10	D32	Raúl Valadez	Texcoco, Mexico	800 yr B.P.	
PC 12	D33	Raúl Valadez	Tula (Hildago), Mexico	1400 yr B.P.	
PC 13	D6	Raúl Valadez	Tula (Hildago), Mexico	1400 yr B.P.	
PC 14	D35	Raúl Valadez	Tula (Hildago), Mexico	1400 yr B.P.	
Alaskan					
Perm597	D3	F:AM 67156	Fairbanks area, Alaska	430 ± 55 RYBP; 1455 C.E.	AA35220
JAL 27	D36	F:AM 67155A	Fairbanks area, Alaska	320 ± 50 RYBP; 1530 or 1640 C.E.	AA35229
JAL 42	D37	F:AM 30435	Fairbanks area, Alaska	228 ± 33 RYBP; 1665 C.E.	AA37619
JAL 43	D38	F:AM 30436	Fairbanks area, Alaska	349 ± 37 RYBP; 1520, 1600, or 1630 C.E.	AA42304
JAL 44	D3	F:AM 67154A	Fairbanks area, Alaska	222 ± 39 RYBP; 1675 C.E.	AA42305
JAL 45	D18	F:AM 70932	Fairbanks area, Alaska	307 ± 40 RYBP; 1640 C.E.	AA42306
JAL 46	D40	F:AM 67155	Fairbanks area, Alaska	265 ± 43 RYBP; 1655 C.E.	AA42307
JAL 49	D1	F:AM 68010	Fairbanks area, Alaska	220 ± 43 RYBP; 1675 C.E.	AA42309
JAL 53	D41	F:AM 97133	Fairbanks area, Alaska	278 ± 40 RYBP; 1650 C.E.	AA38450
JAL 59	D42	F:AM 30482	Fairbanks area, Alaska	401 ± 40 RYBP; 1475 C.E.	AA38451
JAL 62	D37	F:AM 70963C	Fairbanks area, Alaska	442 ± 35 RYBP; 1450 C.E.	AA42311

eages could be surviving in some unsurveyed modern Native American breeds or local dog populations (14, 25). However, genetic analysis of a diverse sample of 19 Mexican hairless dogs (xoloitzcuintle), a distinct ancient breed that has been present in Mexico for over 2000 years (25), only revealed mtDNA sequences previously observed in dogs of Eurasian origin (26). The absence of ancient North and South American dog haplotypes from a large diversity of modern breeds, including the Mexican hairless, illustrates the considerable impact that invading Europeans had on native cultures.

Our data strongly support the hypothesis that ancient American and Eurasian domestic dogs share a common origin from Old World gray wolves. This implies that the humans who colonized America 12,000 to 14,000 yr B.P. brought multiple lineages of domesticated dogs with them. The large diversity of mtDNA lineages in the dogs that colonized the New World implies that the ancestral population of dogs in Eurasia was large and well mixed at that time. Consequently, dogs, in association with humans or through trade, spread across Europe, Asia, and the New World soon after they were domesticated. Alternatively, if domestication was a more ancient event, as suggested by previous genetic results (5), human groups that first colonized the subarctic mammoth steppe of Siberia may have had dogs with them 26,000 to 19,000 yr B.P. (11). If the archaeological date of 12,000 to 14,000 yr B.P. for first domestication is accepted, the dog, as an element of culture, would have had to be transmitted across Paleolithic societies on three continents in a few thousand years or less. This would imply extensive intercultural exchange during the Paleolithic (27, 28). Regardless, the common origin of New and Old World dogs demands a reconsideration of the relationship between humans and dogs in ancient societies.

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Whole-Genome Analysis of Photosynthetic Prokaryotes

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The process of photosynthesis has had profound global-scale effects on Earth; however, its origin and evolution remain enigmatic. Here we report a whole-genome comparison of representatives from all five groups of photosynthetic prokaryotes and show that horizontal gene transfer has been pivotal in their evolution. Excluding a small number of orthologs that show congruent phylogenies, the genomes of these organisms represent mosaics of genes with very different evolutionary histories. We have also analyzed a subset of "photosynthesis-specific" genes that were elucidated through a differential genome comparison. Our results explain incoherencies in previous data-limited phylogenetic analyses of phototrophic bacteria and indicate that the core components of photosynthesis have been subject to lateral transfer.

Photosynthesis is an essential biological process in which solar energy is transduced into other forms of energy that are available to all life. Primary production by photosynthetic organisms supports all ecosystems, with the noted exceptions of deep-sea hydrothermal vents and subsurface communities. Oxygen, one of the by-products of photosynthesis by cyanobacteria and their descendants (including algae and higher plants), transformed the Precambrian Earth and made possible the development of more complex organisms that use aerobic metabolism (1, 2). Understanding the origin and evolution of the process of photosyn-

thesis is, therefore, of considerable interest.

All available evidence suggests that (bacterio)chlorophyll-based photosynthesis arose within the bacterial domain of the tree of life and was followed by subsequent endosymbiotic transfer into eukaryotes. Accurate dates for appearance of the first photosynthetic organisms are not known. Substantial information, including biomarkers, stromatolites, and paleosols, as well as data from molecular evolution studies, indicates that oxygenic (oxygen-evolving) photosynthesis arose by 2500 million years ago (2–5). On the basis of phylogenetic analyses and the well-detailed complexity of the photosynthetic machinery, mechanistically simpler anoxygenic (non-oxygen-evolving) photosynthesis almost certainly preceded and was ancestral to oxygenic photosynthesis (1, 6). Therefore the cyanobacteria, as ancient as they appear to be, were probably preceded by a diverse group of more primitive phototrophs. The supposed progeny of those early phototrophs are still

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