Ancient DNA Evidence for Old World Origin of New World Dogs

Jennifer A. Leonard,‡ Robert K. Wayne, Jane Wheeler, Raúl Valadez, Sonia Guillén, Carles Viñà

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 predates the first appearance of dogs in the archaeo-

References and Notes


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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 predates the first appearance of dogs in the archaeo-
logical record. Consequently, native American
dogs are likely to have derived from
American wolves.

Modern New World dogs are of questionable
use in determining their origin, because
native American dogs likely interbred with
dogs brought by European colonists and ul-
timately may have been replaced by them (13,
14). Consequently, we extracted DNA from
bones of 37 dog specimens from archaeolog-
ical sites in Mexico, Peru, and Bolivia that
were deposited before the arrival of Colum-
bus in the New World (15). We have success-
fully amplified 425 base pairs (bp) of the
mitochondrial DNA (mtDNA) control region
from 13 of them (Table 1). Further, we have
analyzed sequences from 11 dog remains
from Alaska, deposited before the first arrival
of European explorers (15) (Table 1). We
found 12 different haplotypes in 13 samples
from pre-Columbian dogs from Latin Amer-
ica. The two identical sequences originated
from the same locality [JAL 332 and JAL
334 from Bolivia (Table 1)]. The haplotypes
differed by 1 to 12 bp (0.2 to 3.1% diver-
gence). To compare our sequences to those
from previous studies, we focused on a 257-
bp fragment of the control region that was
homologous to sequences from 140 dogs ob-
tained from 67 diverse dog breeds (5) and to
sequences from 259 wolves obtained from 30
localities worldwide (16). When just this
fragment was considered, the ancient Latin
American sequences defined 11 haplotypes.
Twenty-five additional homologous dog se-
quences were found in GenBank, which
yielded five new haplotypes. Almost all mod-
dern dogs were sampled in the Old World, and
most corresponded to breeds originating
there. The few sequences from breeds of New
World origin (the Eskimo dog, Mexican hair-
less, Alaskan husky, Newfoundland, and
Chesapeake Bay retriever) and from Oceania
(the Australian dingo and the New Guinea
singing dog) were indistinguishable from
those of Eurasian dogs (5).

A phylogenetic tree based on the 257-bp
sequences (15) (Fig. 1) showed that the an-
cient American dog sequences clustered
within two of the four previously defined dog
clades (5). Ten of the pre-Columbian Amer-
ican dog haplotypes were clustered in clade I,
and one sequence from Tula, Mexico [PC 13
(Table 1)], was clustered in clade IV. Clade I
is the most diverse clade of dog sequences
and comprises about 80% of dog haplotypes,
including the Australian dingo, the New
Guinea singing dog, the African basenji, the
greyhound, and other ancient breeds. Ameri-
can gray wolf sequences (Fig. 1, lu28 to lu33
in blue) are not clustered with those from
dogs and differ by 3 to 13 bp from the ancient
American dog sequences. Three of the an-
cient sequences are identical to those ob-
served in Eurasian dogs, and none differs by
more than 5 bp (Fig. 1). However, when the
sequence of the entire 425-bp segment from
ancient samples is compared to over 350
modern dog sequences of different lengths
(17), only the pre-Columbian sequence from
sample PC13 is identical to one found in
modern dogs (haplotype D6). These results
suggest that New and Old World dogs are
derived from Eurasian wolves.

Our pre-Columbian samples were from
Latin America, where gray wolves are rare or
absent. Consequently, we obtained remains
from the permafrost deposits of Alaska,
where gray wolves were abundant in the past
and could provide a source for domestication
and interbreeding (1). These deposits often
yield relatively well-preserved DNA from
specimens as old as 50,000 years (18). How-
ever, the 11 dog remains that we tested dated
between 1450 and 1675 C.E., and thus most
postdate the first arrival of European colo-
nists in the New World (Table 1). Neverthe-
less, all of these dog remains were deposited
before the first sighting of Alaska by Euro-
peans (by Vitus Bering and Aleksey Chirikov
in 1741) and thus should represent pure na-
tive American dogs. Based on the 257-bp
sequence, we found 8 haplotypes in 11 sam-
ple. Five are unique, whereas three are
shared with modern domestic dogs [D1, D3,
and D18 (Fig. 1)]. All ancient Alaskan dog
sequences possess clade I haplotypes (Fig. 1,
green).

To better visualize the relationship of
modern and ancient dog sequences from
clade I, we created a statistical parsimony
network where haplotypes can occupy nodes
and where each branch represents a single
nucleotide substitution or an insertion or de-
letion (15) (Fig. 2). This network shows that
haplotype D28, found in ancient samples from
Bolivia, is ancestral to a clade of unique
New World haplotypes and differs from them
by one or two substitutions. Haplotypes D36,
found in ancient Alaskan dogs, or D2, a com-
mon haplotype in Old World dogs, are puta-

tively ancestral to this endemic New
World clade that we designate as clade a (Fig.
2). The statistical parsimony network sug-
ests that the remaining ancient sequences
might be derived from the common haplo-
types D2, D3, D9, and D26 (Fig. 2) (5). Fur-
ther, an additional lineage must be de-

![Fig. 1. Neighbor-joining tree of sequences from precontact dogs from Latin America (purple) and Alaska (green) and modern dogs (black, pre-
fix D, for sequences from [5], or GenBank ac-
cession numbers), Eur-
asian wolves (black, pre-
fix Lu, from [16]), and
American wolves (blue, pre-
fix Lu, from [16]).
Coyotes [black, prefix La,
from (16)] are used as an
group. Previously de-

fined clades of dogs (5)
are indicated with red
branches. Clade a refers
to a group of dog se-
quences unique to the
New World. Haplotypes
shared between modern
and ancient dogs are
marked with an asterisk.

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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 haplotypes 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-

![Diagram](image)

Fig. 2. Statistical parsimony cladogram of precontact Latin American (gray), Alaskan (black), and modern (white) dog haplotypes from clade 1 (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).

<table>
<thead>
<tr>
<th>ID</th>
<th>Haplotype</th>
<th>Source</th>
<th>Locality</th>
<th>Age</th>
<th>Reference number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-Columbian</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>JAL 330</td>
<td>D27</td>
<td>William Isbell</td>
<td>Iwawi, Bolivia</td>
<td>&gt;1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>JAL 331</td>
<td>D28</td>
<td>William Isbell</td>
<td>Iwawi, Bolivia</td>
<td>&gt;1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>JAL 332</td>
<td>D29</td>
<td>William Isbell</td>
<td>Iwawi, Bolivia</td>
<td>&gt;1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>JAL 334</td>
<td>D28</td>
<td>William Isbell</td>
<td>Iwawi, Bolivia</td>
<td>&gt;1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>JAL 365</td>
<td>D30</td>
<td>Sonia Guílén</td>
<td>Chiribaja Baja, Peru</td>
<td>1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>PC 5</td>
<td>D30</td>
<td>Sonia Guílén</td>
<td>Chiribaja Baja, Peru</td>
<td>1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>PC 6</td>
<td>D31</td>
<td>Sonia Guílén</td>
<td>Chiribaja Baja, Peru</td>
<td>1000 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>PC 8</td>
<td>D25</td>
<td>Raúl Valadez</td>
<td>Teotihuacan, Mexico</td>
<td>1300 yr B.P.</td>
<td></td>
</tr>
<tr>
<td>PC 10</td>
<td>D32</td>
<td>Raúl Valadez</td>
<td>Texcoco, Mexico</td>
<td>800 yr B.P.</td>
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<tr>
<td>PC 12</td>
<td>D33</td>
<td>Raúl Valadez</td>
<td>Tula (Hidalgo), Mexico</td>
<td>1400 yr B.P.</td>
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</tr>
<tr>
<td>PC 13</td>
<td>D6</td>
<td>Raúl Valadez</td>
<td>Tula (Hidalgo), Mexico</td>
<td>1400 yr B.P.</td>
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<tr>
<td>PC 14</td>
<td>D35</td>
<td>Raúl Valadez</td>
<td>Tula (Hidalgo), Mexico</td>
<td>1400 yr B.P.</td>
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<tr>
<td>Alaskan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perm397</td>
<td>D3</td>
<td>F:AM 67156</td>
<td>Fairbanks area, Alaska</td>
<td>430 ± 55 RYBP;</td>
<td>AA35220</td>
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<tr>
<td>JAL 27</td>
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<td>F:AM 67156A</td>
<td>Fairbanks area, Alaska</td>
<td>320 ± 50 RYBP;</td>
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<td>Fairbanks area, Alaska</td>
<td>228 ± 33 RYBP;</td>
<td>AA37619</td>
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<td>D38</td>
<td>F:AM 30436</td>
<td>Fairbanks area, Alaska</td>
<td>349 ± 37 RYBP;</td>
<td>AA42304</td>
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<tr>
<td>JAL 44</td>
<td>D3</td>
<td>F:AM 67154A</td>
<td>Fairbanks area, Alaska</td>
<td>222 ± 39 RYBP;</td>
<td>AA42305</td>
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<td>Fairbanks area, Alaska</td>
<td>307 ± 40 RYBP;</td>
<td>AA42306</td>
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<td>JAL 46</td>
<td>D40</td>
<td>F:AM 67155</td>
<td>Fairbanks area, Alaska</td>
<td>265 ± 40 RYBP;</td>
<td>AA42307</td>
</tr>
<tr>
<td>JAL 49</td>
<td>D1</td>
<td>F:AM 68010</td>
<td>Fairbanks area, Alaska</td>
<td>220 ± 43 RYBP;</td>
<td>AA42309</td>
</tr>
<tr>
<td>JAL 53</td>
<td>D41</td>
<td>F:AM 97133</td>
<td>Fairbanks area, Alaska</td>
<td>278 ± 40 RYBP;</td>
<td>AA38450</td>
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<tr>
<td>JAL 59</td>
<td>D42</td>
<td>F:AM 30482</td>
<td>Fairbanks area, Alaska</td>
<td>401 ± 40 RYBP;</td>
<td>AA38451</td>
</tr>
<tr>
<td>JAL 62</td>
<td>D37</td>
<td>F:AM 70963C</td>
<td>Fairbanks area, Alaska</td>
<td>442 ± 35 RYBP;</td>
<td>AA42311</td>
</tr>
</tbody>
</table>
eagles could be surviving in some unsurveyed modern Native American breeds or local dog populations (J4, 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 Southern 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. (J1). 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.

References and Notes
6. B. F. Koop, M. Burbidge, A. Byun, U. Rink, S. J. Crockett, in Dogs Through Time: An Archaeological Perspective, S. J. Crockett, Ed. (British Archaeological Reports, Oxford, 2000), pp. 271–285. Two of the five ancient remains studied were dated to 1938 and 1940; the rest were designated as “prehistoric” by the authors.

15. Supporting material is available on Science Online.
17. The 350 modern dog sequences are from over 250 dogs corresponding to 124 haplotypes with sequenc- es deposited in GenBank, and 100 dogs from 20 different breeds (C. Vilà, data not shown).
24. J. H. Zarr, Biostatistical Analysis (Prentice Hall, Upper Saddle River, NJ, ed. 4, 1999); the calculation is made according to example 24.5.
30. We thank R. Tedford (American Museum of Natural History, New York) and W. Isbell (Department of Anthropology, State University of New York at Binghamton) for samples. This research was supported by grants from the University of California Institute for Mexico and the United States and NSF (grant OPP-9817937). We thank C. Anderung, J. Brantingham, A. Götterström, B. Van Valkenburgh, and M. Zeder for comments on the manuscript.

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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 photosynthesis is, therefore, of considerable interest. All available evidence suggests that (bacteria) 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