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Origins and genetic legacy of prehistoric dogs

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Dogs were the first domestic animal, but little is known about their population history and to what extent it was linked to humans. We sequenced 27 ancient dog genomes and found that all dogs share a common ancestry distinct from present-day wolves, with limited gene flow from wolves since domestication but substantial dog-to-wolf gene flow. By 11,000 years ago, at least five major ancestry lineages had diversified, demonstrating a deep genetic history of dogs during the Paleolithic. Coanalysis with human genomes reveals aspects of dog population history that mirror humans, including Levant-related ancestry in Africa and early agricultural Europe. Other aspects differ, including the impacts of steppe pastoralist expansions in West and East Eurasia and a near-complete turnover of Neolithic European dog ancestry.

Wolves were the first animal with which humans formed a mutualistic relationship, eventually giving rise to dogs. Although there is little consensus regarding when (1–9), where (2, 8–13), and how many times (1, 8, 9, 14) domestication took place, the archaeological record (9, 15) attests to a long-term and close relationship to humans (9, 16–18). Modern dog genomes have revealed a complex population structure (5, 8, 10, 12, 19, 20), but because only six ancient dog and wolf genomes are currently available (4, 9, 14, 21), the process by which this structure emerged remains largely unknown.

Previous mitochondrial DNA (22–29) and genomic (9, 14, 21) studies have suggested an association between the genetic signatures of

dogs and their archeological context. However, dog and human genomes have not been quantitatively coanalyzed to assess the degree to which the population history of dogs was linked to that of humans—or may have been decoupled as a result of trade, human preference for particular types of dogs, variation in infectious disease susceptibility, or dogs moving between human groups.

To reconstruct dog population history, we sequenced 27 ancient dog genomes up to 10.9 thousand years (ka) old from Europe, the Near East, and Siberia (table S1) to a median of 1.5-fold coverage (range, 0.1- to 11-fold) (Fig. 1A and table S2) (30). To test the association with human population history, we compiled 17 sets of human genome-wide data (30) that matched the age, geographic location, and cultural con-

texts of the ancient dogs (table S4), and we directly compared genetic relationships within the two species.

Global dog population structure has its origins in the Pleistocene

To characterize the global population structure of ancient and modern dogs, we applied principal component analysis (PCA) to a matrix of all possible f_4 -statistics (30), alleviating differences in error rates and missing data. This approach recapitulates a major east–west axis of dog ancestry (PC1) (8, 9, 12), in which the western extreme comprises modern and ancient western Eurasian dogs and modern African dogs (Fig. 1B). The eastern extreme is represented by precontact North American dogs (21), three dogs from 7 ka ago from Lake Baikal in Siberia, and modern East Asian dogs, including New Guinea singing dogs and Australian dingoes. Similar results were obtained through standard model-based clustering (fig. S2).

All ancient and modern European dogs have greater affinity to eastern dog ancestry than ancient Near Eastern dogs have on the basis of f_4 tests (fig. S3), despite the overall east–west axis on PC1. Ancient European dogs are also distributed widely across a genetic cline between the East Eurasian and ancient Near Eastern dogs, which furthermore manifests as a linear cline along the diagonal when contrasting shared genetic drift with Baikal dogs and Levantine (Israel, 7 ka ago) dogs using outgroup f_3 -statistics (Fig. 1C). Simulations indicate that this linear, diagonal cline is difficult to explain with long-standing continuous gene flow or a tree-like history; instead, they suggest that the history of Mesolithic and Neolithic European dogs was marked by a major admixture episode (Fig. 1D) (30).

We modeled the genetic history underlying dog population structure for five populations that represent major ancestries and tested all 135,285 possible admixture graph models with up to two admixture events (30). Only one

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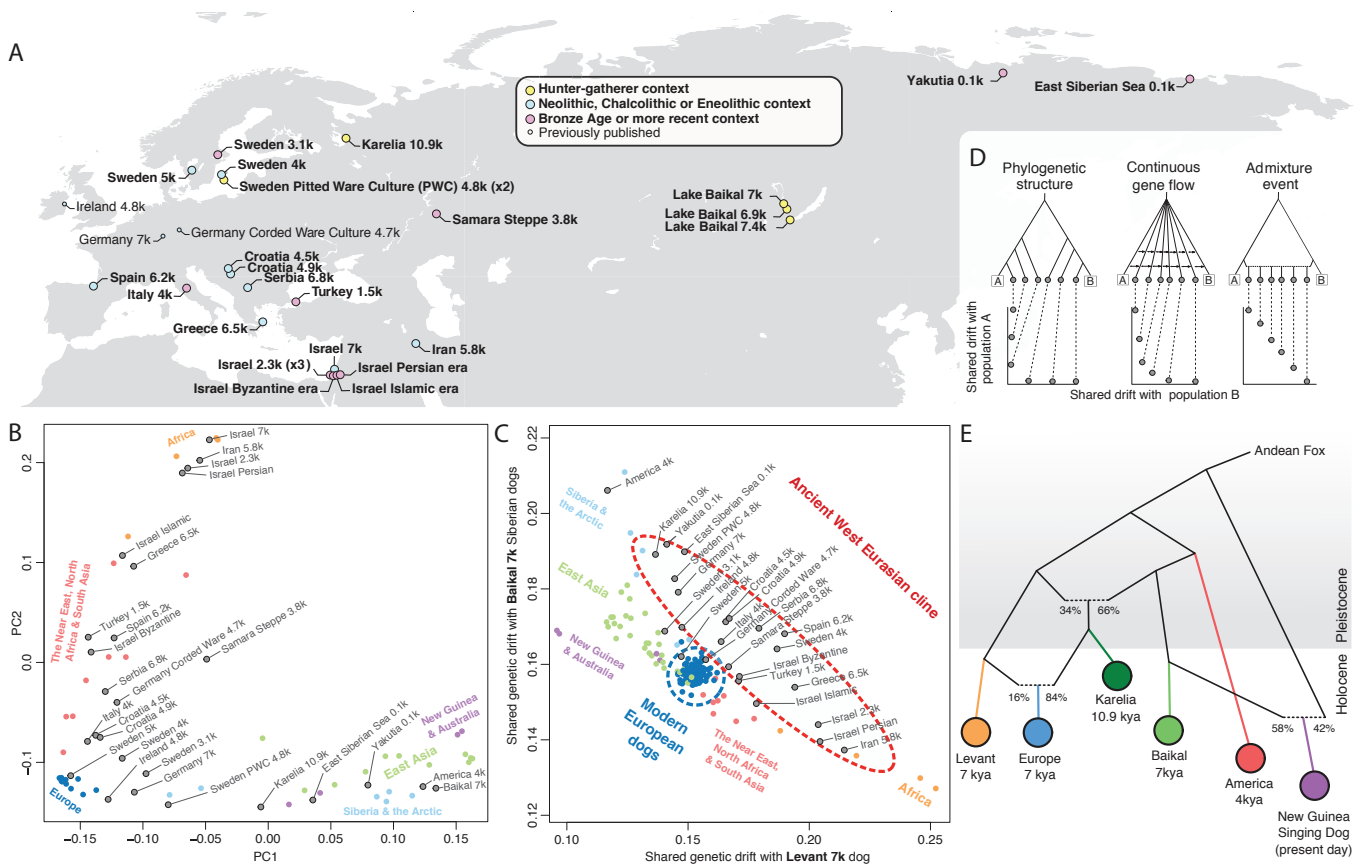


Fig. 1. Genomic structure of dogs dates to the Pleistocene. (A) Sampling locations of ancient dogs. k, 1000 years. (B) PCA results for all possible f_4 -statistics among ancient dogs (gray) and a selection of worldwide modern dogs. (C) Outgroup f_3 -statistics reveal a cline of Levant-related versus Baikal-related (horizontal and vertical axes, respectively) ancestry across ancient West Eurasian dogs, but not

among modern European dogs. (D) Coalescent simulations demonstrating that a diagonal f_3 cline as in (C) is consistent with an admixture event, but less so with continuous gene flow and not with phylogenetic structure alone. (E) An admixture graph that fits all f_4 statistics between major dog lineages. The European dog was grafted onto the graph identified through exhaustive testing. kya, 1000 years ago.

model fits the data, and features the Mesolithic Karelian dog (10.9 ka ago) as having received part of its ancestry from a lineage related to eastern dogs and part from the Levantine lineage (Fig. 1E) [two highly similar models nearly fit (fig. S4)]. The model can be extended to feature the earliest Neolithic European dog (7 ka ago) (14) as a mixture of the Karelian and the Levantine branches without loss of fit (fig. S5), supporting the dual ancestry model for European dogs suggested by the ancient ancestry cline (Fig. 1C). The observed phylogenetic structure implies that all five ancestry lineages (Neolithic Levant, Mesolithic Karelia, Mesolithic Baikal, ancient America, and New Guinea singing dog) must have existed by 10.9 ka ago (the radiocarbon date of the Karelian dog) and thus most likely existed prior to the transition from the Pleistocene to the Holocene epoch ~11.6 ka ago.

No detectable evidence for multiple dog origins or extensive gene flow from wild canids. Studies have suggested that wolf populations in Europe (3, 11), the Middle East (12), Central

Asia (10), Siberia (31), and East Asia (2, 8), or more than one of these (9), contributed to early dog diversity. One study, however, demonstrated that modern wolves and dogs are reciprocally monophyletic and suggested bidirectional gene flow (5). We corroborated that gene flow must have occurred by identifying widespread asymmetries between dogs in their affinity to wolves (Fig. 2, A and B, and fig. S7). However, the gene flow was likely largely unidirectional from dogs into wolves, as we also identified some gray wolves that are symmetrically related to all modern and ancient dogs (Fig. 2C). Past gene flow from wolves into specific dog populations would have manifested as an affinity to any member of the modern gray wolf lineage in these tests, so our results suggest that persistent gene flow into dogs has been so limited as to be undetectable at the current resolution of the data. Furthermore, this result is consistent with a scenario in which all dogs derive from a single ancient, now-extinct wolf population, or possibly multiple closely related wolf populations. Although it is still possible that other, thus-far-unsampled

ancient wolf populations were independently involved in early domestication (3, 9, 31), our data indicate that they did not contribute substantially to later dogs.

In contrast to the lack of wolf admixture into dogs, we identified dog admixture into almost all analyzed present-day wolves (Fig. 2B), with the strongest signals typically coming from dogs into geographically proximate wolf populations in Europe, the Near East, and East Asia (fig. S7). We also replicated affinities between ancient American dogs and coyotes (21) and between African dogs and African golden wolves (32), although the direction of gene flow in both cases is unclear and the small magnitude is unlikely to impact most analyses of dog relationships (table S5). We did not find genome-wide evidence for gene flow from Tibetan wolves into Tibetan dogs, despite evidence for wolf ancestry locally around the EPAS1 gene, which is associated with adaptation to altitude (33, 34). Dogs thus do not show similar evidence of wild introgression as has been found in pigs, goats, horses, sheep, and cattle (35–40).

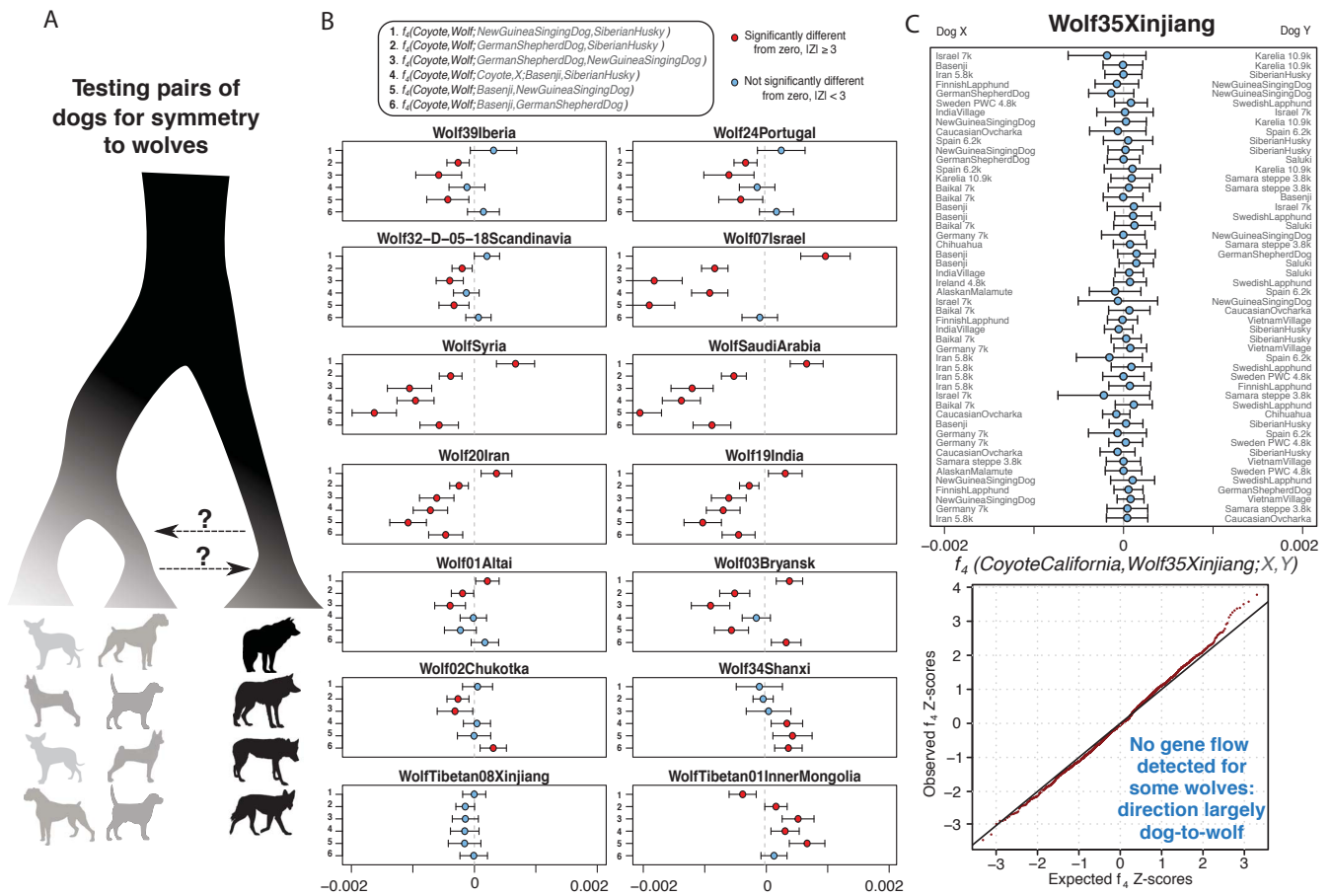


Fig. 2. All detectable gene flow is consistent with being unidirectional from dogs into wolf populations. (A) Illustration of asymmetry tests (f_4 -statistics) comparing 35 Eurasian gray wolves to all pairs of 66 ancient and modern dogs. (B) Selected results using coyotes as outgroup. (C) A wolf from Xinjiang, western China, is not closer to some dog populations

than to others, as the test statistics are consistent with being normally distributed around 0 (the quantile–quantile plot includes all 66 dogs). If there had been a substantial gene flow from some wolf population into some dog population, we would expect all wolf individuals to display asymmetric relationships.

Assessing the relationship between dog and human population histories
 We next quantitatively compared the population relationships observed in dogs with those of humans. First, using Procrustes rotation to align f_4 PCA results obtained on dog and human genomes matched in time and space (Fig. 3A) (30), we find that the population structures of the two species resemble each other (Procrustes correlation = 0.48, $P = 0.043$). However, there are also several cases where the matched dogs and humans cluster in different parts of the PCA space. The greatest differences (Fig. 3B) are observed for Chalcolithic Iran, in which the human population is different from the Neolithic Levant (41, 42) but the dogs in the two regions are similar. In Neolithic Germany and Ireland, the humans are more shifted toward the Levant (43, 44) but the dogs are shifted toward Northern European hunter–gatherer contexts. In the Bronze Age Steppe and in Corded Ware Germany, the humans are shifted away from the Neolithic Euro-

pean cluster (45, 46) in a manner not seen in dogs.
 Second, we evaluated if the admixture graph topologies that best fit the data for one species could also explain population relationships of the other. Although we found no graphs that fit the data perfectly for both species, graphs that fit or nearly fit dogs ranked among the 0.8 to 2.8% top-scoring graphs in the human search, and graphs that fit humans ranked among the 0.007 to 1.2% top-scoring graphs in the dog search (Fig. 3C and fig. S9). However, this analysis did not take into account the different time depth of the two species' population histories: The >40-ka-ago divergence of human East and West Eurasian ancestries (47) is markedly older than the earliest appearance of dog morphology in the fossil record, conservatively dated to 14.5 ka ago (48), although older (3, 31), disputed (49, 50) specimens have been claimed.
 Third, we found that the sign (positive or negative) of f_4 -statistics in dogs matched the

sign in humans in 71% of 31,878 tests (null expectation is 50%) across 24 matched dog–human pairs, although this decreased to 58% when restricted to dogs and humans from Europe. We identified specific f_4 -statistics that exemplify both concordance and discrepancy between the species (Fig. 3D). Whereas it is not known what degree of concordance would be expected between the histories of two species on the basis of biogeographical factors alone, the results of these three analyses demonstrate that ancestry relationships in dogs and humans share overall features but are not identical over space and time, and there are several cases where they must have been decoupled.
 Recurrent population histories
 One notable example of concordance is that both humans and dogs in East Asia are closer to European than to Near Eastern populations, which in both humans (43) and our best-fitting graph (Fig. 1E) is best modeled by European ancestry being a mixture of

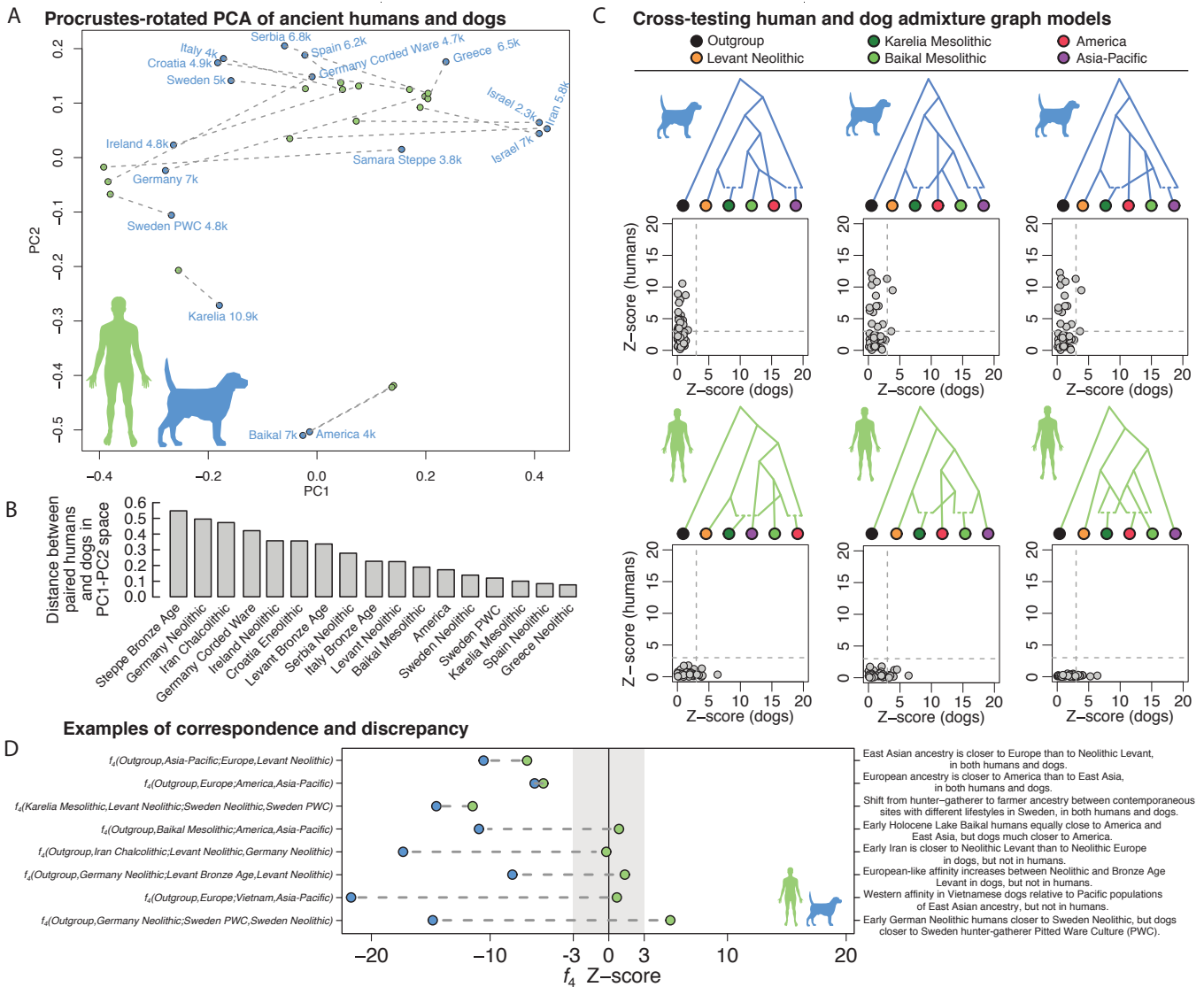


Fig. 3. Quantitative comparisons between dog and human population genomic structures. (A) PCA results for all possible f_4 -statistics on ancient dogs (blue), overlaid through Procrustes transformation by the corresponding analysis performed on ancient humans matched in time, space, and cultural context to the dogs (green). Dashed lines connect each matched pair. (B) Euclidean residuals

between the Procrustes-rotated human and dog coordinates. (C) The three admixture graphs that fit for one species and provide the smallest error for the other. Scatter plots show absolute Z-scores for the difference between observed and predicted f_4 -statistics. (D) Examples of f_4 -statistics that reveal similarities and differences between humans and dogs (far right text).

ancestry related to the Near East and East Asia. However, the divergence of Near Eastern "Basal Eurasian" ancestry in humans was likely >45 ka ago (43), suggesting that dog population dynamics may have mimicked earlier processes in humans. A second example is that all European dogs have a stronger affinity toward American and Siberian dogs than they have to New Guinea singing dogs, which likely represent a type of unadmixed East Asian dog ancestry, mirroring a circumpolar affinity between humans in Europe and the Americas (Fig. 3D) (51). Human groups at Lake Baikal 24 to 18 ka ago had western Eurasian affinities and contributed to Native

American ancestry (51) but were largely replaced by the Holocene (52). Although the dogs at Lake Baikal dated to 7 ka ago constitute a similar link between the Americas and Europe (Fig. 1, C and E), this link occurred >10 ka later (Fig. 3D). Thus, shared circumpolar ancestry through northern Eurasia is an important feature of both human and dog population structures, though this likely did not result from the same migration episodes.

Neolithic expansion into Europe
Ancient human genomes have revealed a major ancestry transformation associated with

the expansion of Neolithic agriculturalists from the Near East into Europe (43, 45, 53), and a study of ancient dog mitochondria suggested they were accompanied by dogs (27). We hypothesized that the genomic cline we observe across ancient European dogs (Fig. 1C) could be, at least in part, due to admixture between dogs associated with Mesolithic hunter-gatherers and incoming Neolithic farmers. Three observations support this: First, the hypothesized hunter-gatherer end of the cline is occupied by the 10.9-ka-old Mesolithic Karelian dog and dogs from a 4.8-ka-old hunter-gatherer Pitted Ware Culture site in Sweden. Second, relative to the Swedish

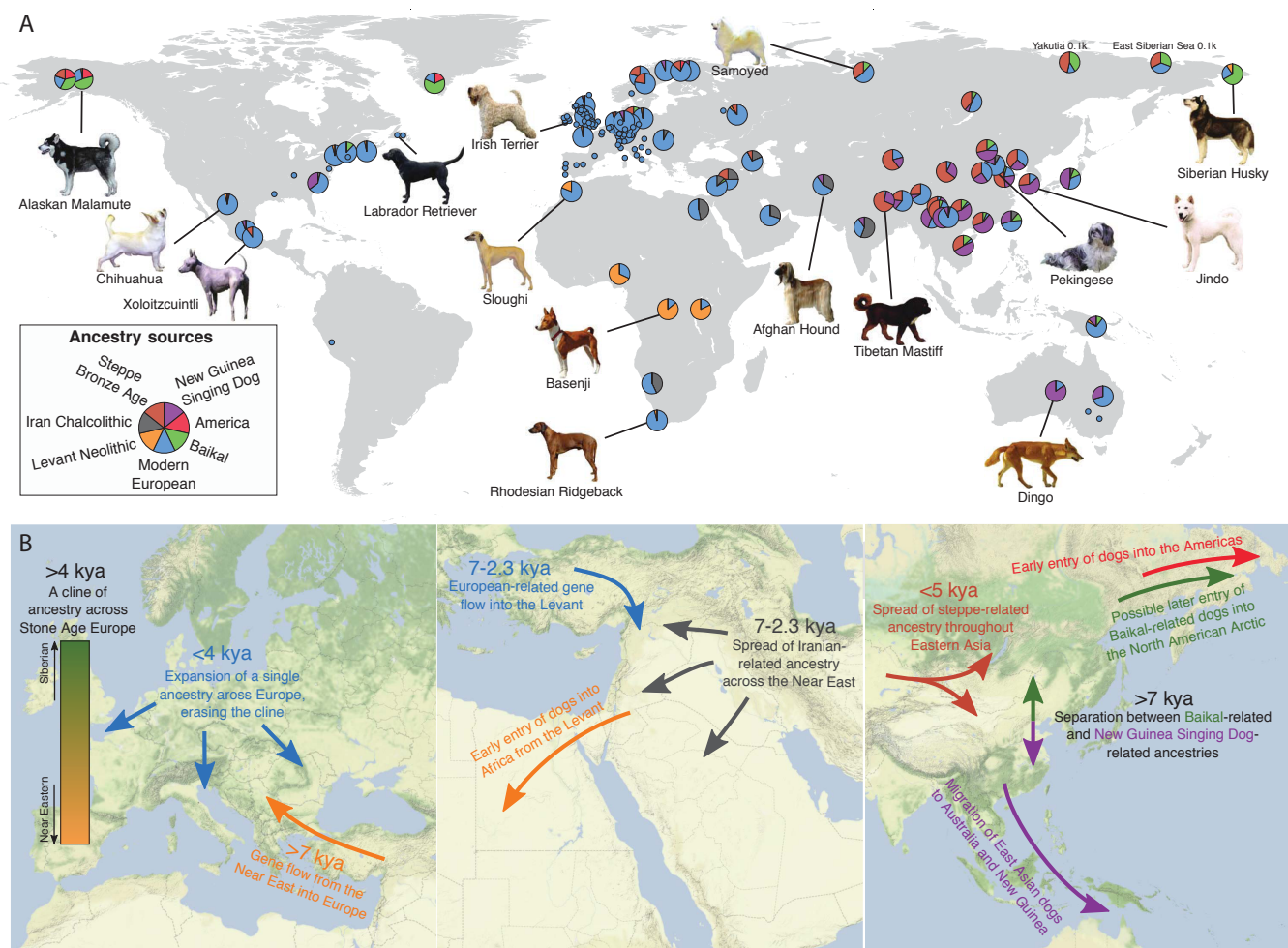


Fig. 5. Ancestry of global dogs today. (A) For each present-day population, the ancestry proportions estimated by the best-fitting qpAdm model, restricted to models containing up to four of seven selected sources, are displayed. Populations for which a single component accounts for $\geq 98\%$ of the ancestry

are collapsed to smaller circles. Dog pictures were obtained from Wikimedia under the CC BY-SA 3.0 license (<https://commons.wikimedia.org/wiki/Special:ListFiles/Desaix83>). (B) Illustrations of inferred population histories in three regions of the world.

but also substantial contributions from the 3.8-ka-old Srubnaya steppe dog (Fig. 5A and data file S1). Some populations, especially those in Siberia, additionally require a fourth source related to the 7-ka-old Lake Baikal dogs, but no or minimal New Guinea singing dog-related ancestry. Our results thus raise the possibility that the eastward migrations of steppe pastoralists had a more substantial impact on the ancestry of dogs than humans in East Asia (Fig. 5B).

Later homogenization of dog ancestry in Europe

The extensive range of ancestry diversity among early European dogs is not preserved today, as modern European dogs are all symmetrically related to the ancient dogs in our dataset (Fig. 1C, fig. S13, and data file S1) (30). This suggests little to no contribution of most local Mesolithic and Neolithic populations to present-day diversity in Europe. Instead,

we found that a single dog from a Neolithic megalithic context dated to 5 ka ago at the Frälsögården site in southwestern Sweden can be modeled as a single-source proxy for 90 to 100% of the ancestry of most modern European dogs, to the exclusion of all other ancient dogs (fig. S13 and data file S1). This implies that a population with ancestry similar to this individual, but not necessarily originating in Scandinavia, replaced other populations and erased the continent-wide genetic cline (Fig. 5B). This ancestry was in the middle of the cline (Fig. 1C), and so present-day European dogs can be modeled as having about-equal proportions of Karelian- and Levantine-related ancestries [54 and 46%, respectively, for German shepherd on the basis of the admixture graph (Fig. 1E)].

The Frälsögården dog is also favored as a partial ancestry source for a 4-ka-old Bronze Age dog from Italy, a 1.5-ka-old dog from Turkey and Byzantine and Medieval, but not earlier

dogs in the Levant (data file S1), providing some constraints on the timing of this ancestry expansion. However, the circumstances that initiated or facilitated the homogenization of dog ancestry in Europe from a narrow subset of that present in the European Neolithic, including the phenomenal phenotypic diversity and genetic differentiation of modern breeds (12, 19, 20) (Fig. 1C), remain unknown.

More recently, this modern European ancestry has dispersed globally and today is a major component of most dog populations worldwide (Fig. 5A). Our ancestry models, however, reveal that some precolonial ancestry does survive in breeds such as the Mexican chihuahua (~4%) and Xoloitzcuintli (~3%) and the South African Rhodesian ridgeback (~4%) (data file S1).

Discussion

The diversification of at least five dog ancestry lineages by the onset of the Holocene was

followed by a dynamic population history that in many ways tracked that of humans, likely reflecting how dogs migrated alongside human groups. However, in several instances, these histories do not align, suggesting that humans also dispersed without dogs, dogs moved between human groups, or that dogs were cultural and/or economic trade commodities.

Certain aspects of genetic relationships between dog populations, such as an east–west Eurasian differentiation, circumpolar connections, and possible basal lineages in the Near East, resemble features of human population history that were established before the earliest estimated dates of dog domestication. This superficial mirroring between the species may therefore instead point to recurrent population dynamics due to biogeographic or anthropological factors that remain to be understood. A key question is how dogs spread across Eurasia and the Americas by the Holocene, since no major human population movements have been identified after the initial out-of-Africa expansion that could have driven this global dispersal.

We find that the modern and ancient genomic data are consistent with a single origin for dogs, though a scenario involving multiple closely related wolf populations remains possible. However, in our view, the geographical origin of dogs remains unknown. Previously suggested points of origin based upon present-day patterns of genomic diversity (2, 8, 10) or affinities to modern wolf populations (12) are sensitive to the obscuring effects of more recent population dynamics and gene flow. Ultimately, integrating DNA from dogs and wolves even older than those analyzed here with archaeology, anthropology, ethology, and other disciplines is needed to determine where and in which environmental and cultural context the first dogs originated.

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SUPPLEMENTARY MATERIAL

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