ANCIENT DOG GENOMICS

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 contexts 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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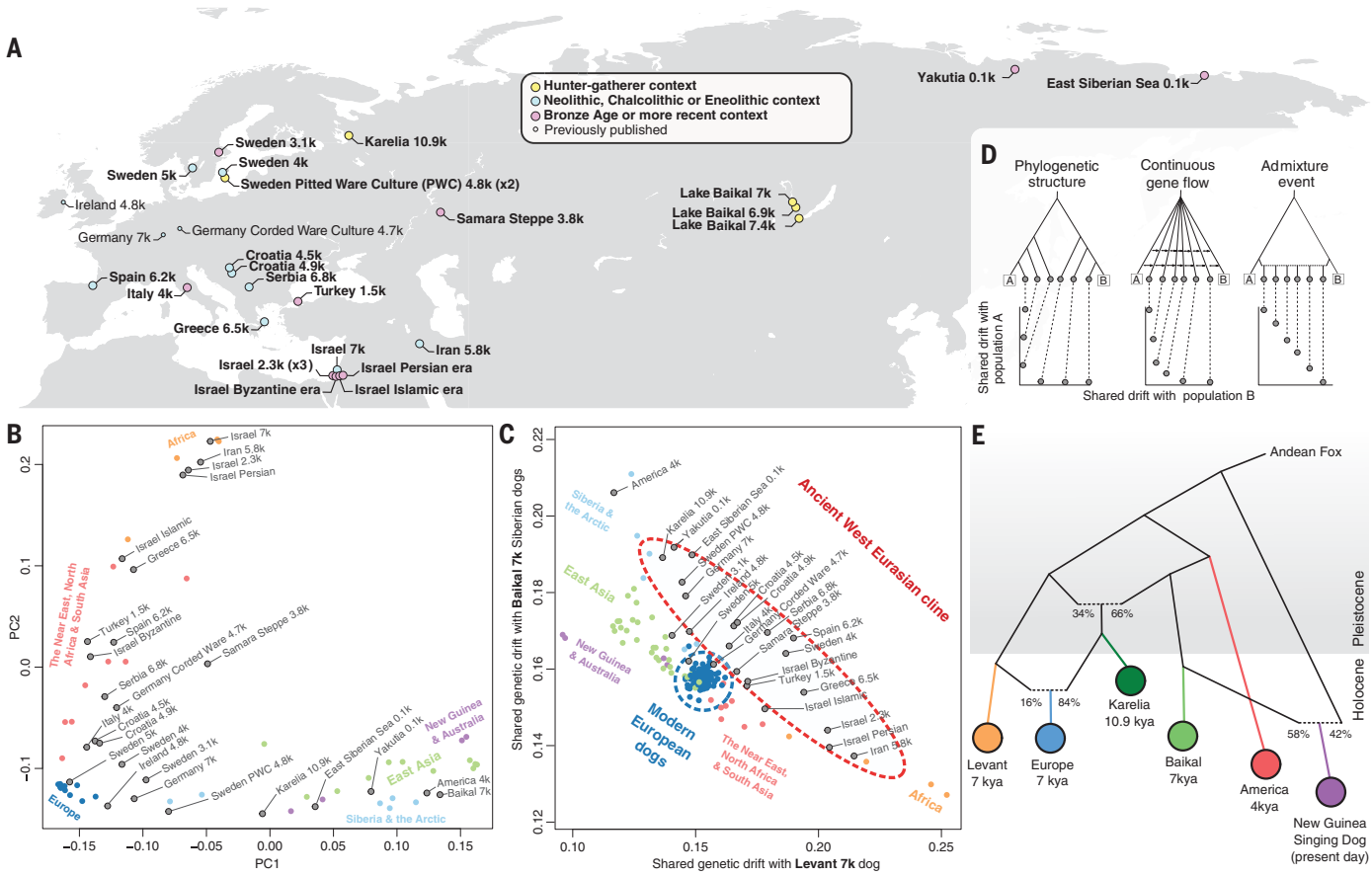

Fig. 1. Genomic structure of dogs dates to the Pleistocene. (**A**) Sampling locations of ancient dogs. k, 1000 years. (**B**) PCA results for all possible f_4-statistics among ancient dogs (gray) and a selection of worldwide modern dogs. (**C**) Outgroup f_3-statistics reveal a cline of Levant-related 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*).

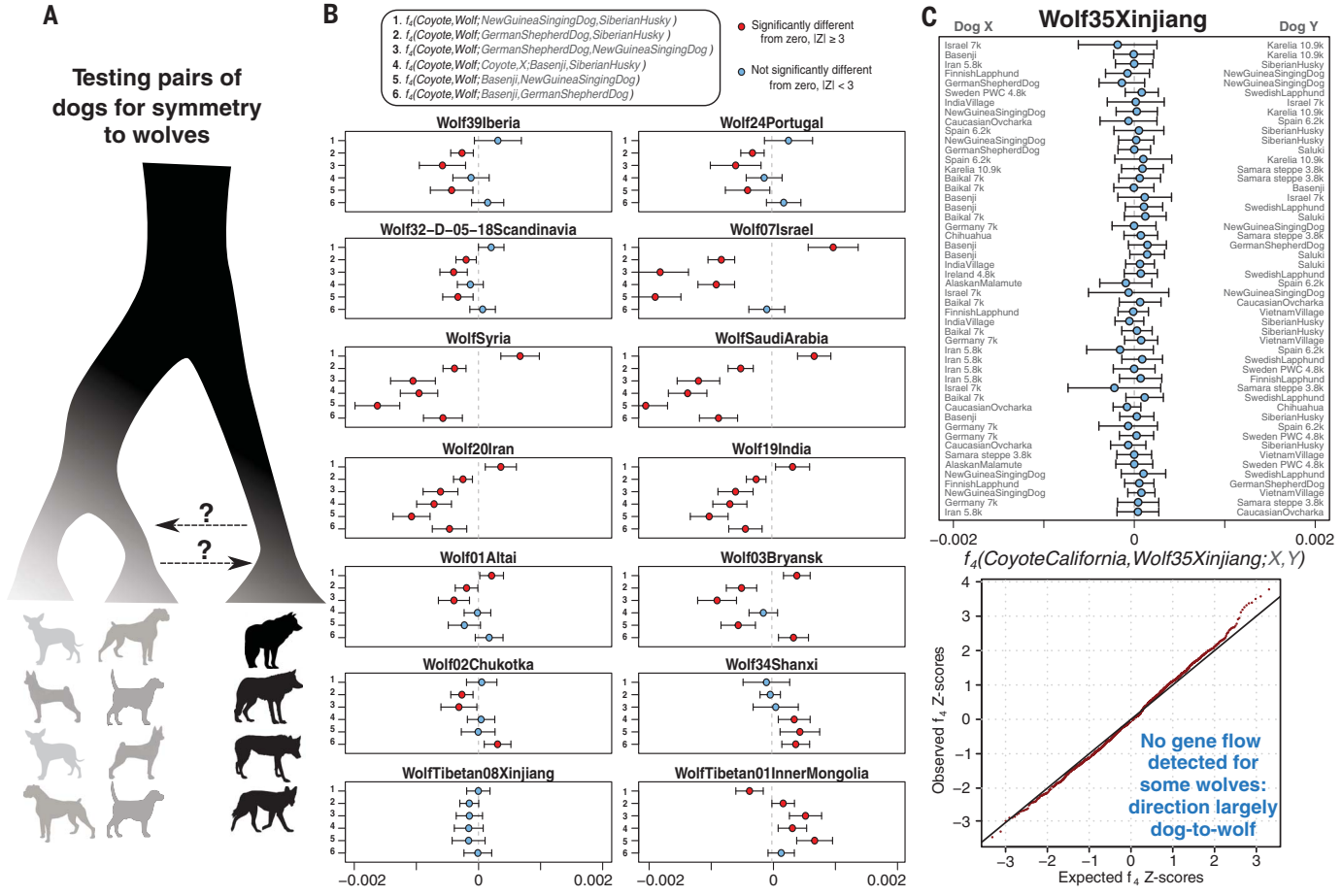

Fig. 2. All detectable gene flow is consistent with being unidirectional from dogs into wolf populations. (**A**) Illustration of asymmetry tests (f_4-statistics) comparing 35 Eurasian gray wolves to all pairs of 66 ancient and modern dogs. (**B**) Selected results using coyotes as outgroup. (**C**) 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 European 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

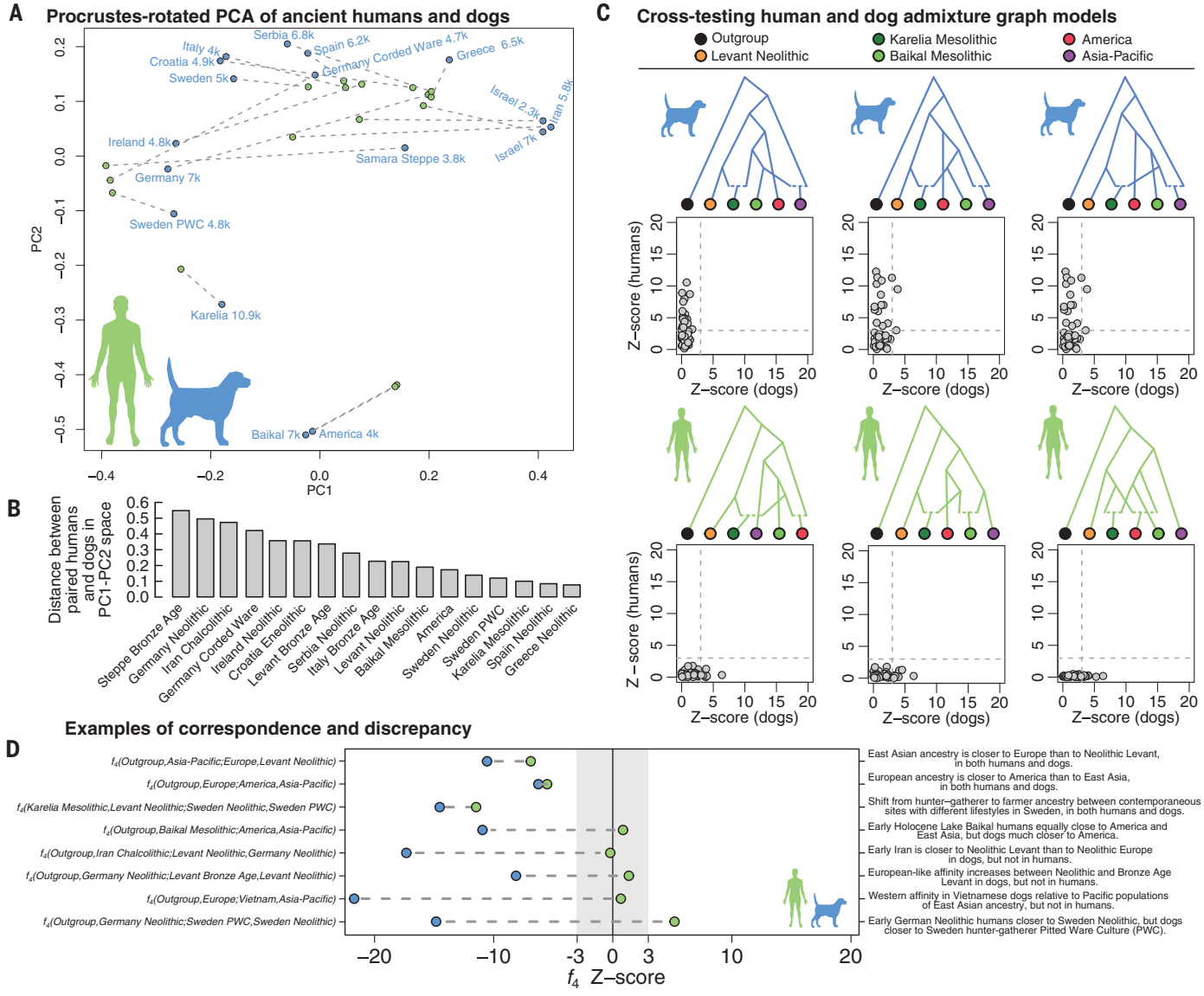

Fig. 3. Quantitative comparisons between dog and human population genomic structures. (**A**) PCA results for all possible f_4-statistics on ancient dogs (blue), overlaid through Procrustes transformation by the corresponding analysis performed on ancient humans matched in time, space, and cultural context 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 ancestry 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

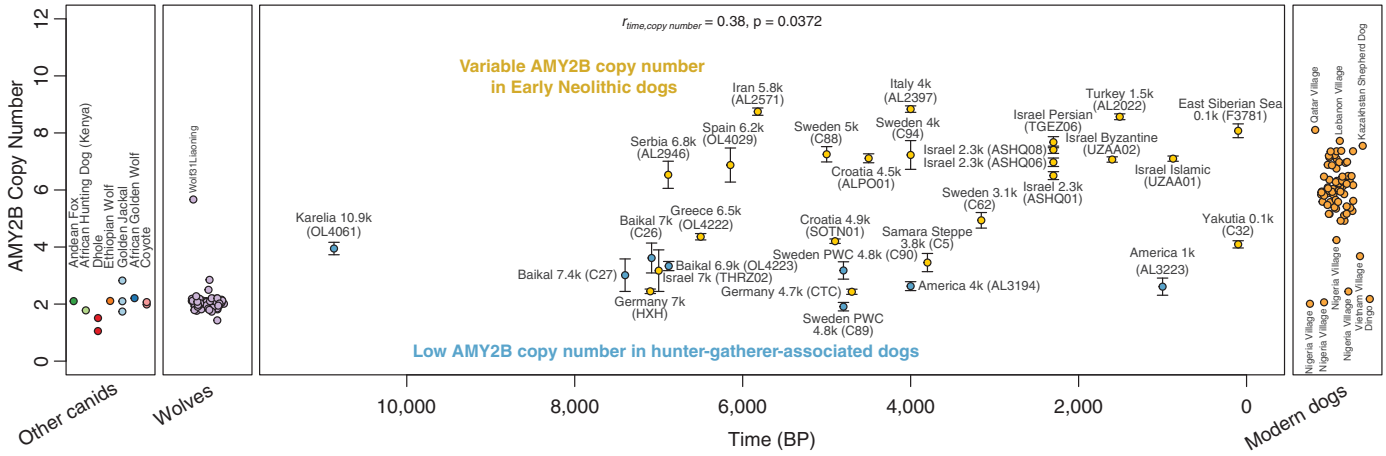

Fig. 4. Expansion of copy number in the *AMY2B* pancreatic amylase gene largely occurred after the transition to agriculture. Ancient dogs are plotted against their age, with blue color indicating dogs from likely hunter–gatherer human contexts. Bars denote 95% binomial confidence intervals around the ratio of the number of reads mapping to the copy number variable region to those mapping to control regions throughout the genome.

hunter–gatherer dogs, a contemporaneous dog from a Swedish Neolithic agricultural context is shifted toward the Levantine end of the cline, mirroring humans at the same sites (*41*, *53*, *54*) (Fig. 3, A and D, and fig. S10D). Third, Neolithic Levantine affinity increases toward the south (P = 0.0196, linear regression), consistent with a range expansion alongside Neolithic human groups. Whereas dogs clearly associated with Mesolithic continental "Western hunter–gatherer" (*43*) human groups have yet to be identified, our results suggest that such dogs would have strong affinity toward the Siberian end of the European cline. Overall, these results indicate that the Neolithic expansion of farmers into Europe was also associated with an ancestry transformation for dogs.

Increased copy number of the *AMY2B* gene, which is involved in starch digestion, has been linked to dietary adaptations of dogs during the agricultural transition (*6*, *55*, *56*). The paralogous *AMY1* gene has been under adaptive evolution in humans (*57*), though this does not seem clearly linked to agriculture (*58*). We observe low copy numbers in dogs from human hunter–gatherer contexts (Fig. 4), although the Mesolithic Karelian dog may already have possessed an elevated number relative to wolves. Several Neolithic dogs have as many copies as present-day dogs, as early as in 5.8-ka-old Iranian and 6.2-ka-old Spanish dogs, but others display low numbers (*14*, *56*), e.g., the 7-ka-old Levantine individual. These results suggest that selection for increased *AMY2B* copy number did not take place during the early stages of domestication, and in contrast to humans (*58*) it was not advanced in Mesolithic hunter–gatherer contexts but was variable in early agricultural populations and did not become widespread until several thousand years after the first appearance of starch-rich agricultural lifestyles.

Africa and the Near East

The clustering of modern African dogs with ancient dogs from the Levant and Iran, especially the oldest individual, dating to 7 ka ago, suggests a Near Eastern origin (Fig. 1, B and C, and fig. S2). Western (Anatolia and the Levant) and eastern (Zagros mountains of Iran) human groups in the Fertile Crescent were highly genetically differentiated (*41*), and the western groups were the primary source of gene flow into Europe and Africa (*41*, *59*) during the Neolithic. A source of African dog ancestry from the Levant (7 ka ago) is a better fit than Iran (5.8 ka ago) (Fig. 5A), mirroring the human history, as well as that of cattle (*40*). In contrast, we are unable to distinguish whether the Levant or Iran is the better source for Neolithic dog ancestry in Europe. Our results suggest a single origin of sub-Saharan African dogs from a Levant-related source (Fig. 5B), with limited gene flow from outside the continent until the past few hundred years.

In contrast to Africa, the 7-ka-old Neolithic Levantine population does not appear to have contributed much, if any, ancestry to present-day dogs in the Near East. Instead, 2.3-ka-old dogs in the Levant can be modeled as having 81% Iran-related and 19% Neolithic Europe–related ancestry (data file S1). By this time in the Levant, there was also human gene flow from Iran (*41*) and transient gene flow from Europe (*60*). However, our results suggest a more complete replacement of dog ancestry in the Levant by 2.3 ka ago (Fig. 5B). Later, modern Near Eastern dogs are best modeled as mixtures of the 2.3-ka-old Levantine and modern European sources (data file S1).

Steppe pastoralist expansions

Expansions of steppe pastoralists associated with the Yamnaya and Corded Ware cultures into Late Neolithic and Bronze Age Europe transformed the ancestry of human populations (*43*, *45*, *46*). To test whether dog ancestry was similarly affected, we analyzed a 3.8-ka-old dog from the eastern European steppe associated with the Bronze Age Srubnaya culture. Although its ancestry resembles that of western European dogs (Fig. 1C and fig. S10), it is an outlier in the center of PC1–PC2 space (Fig. 1B). A Corded Ware–associated dog (4.7 ka ago) from Germany, hypothesized to have steppe ancestry (*14*), can be modeled as deriving 51% of its ancestry from a source related to the Srubnaya steppe dog and the rest from a Neolithic European source (data file S1) (*30*). We obtain similar results for a Bronze Age Swedish dog (45%; 3.1 ka ago), but not a Bronze Age Italian dog (4 ka ago).

Despite this potential link between the steppe and the Corded Ware dog, most later European dogs display no particular affinity to the Srubnaya dog. Modern European dogs instead cluster with Neolithic European dogs (Fig. 1B) and do not mirror the lasting ancestry shift seen in humans after the pastoralist expansion (Fig. 3A). Earlier and additional steppe dog genomes are needed to better understand this process, but the relative continuity between Neolithic and present-day individuals suggests that the arrival of steppe pastoralists did not result in persistent large-scale shifts in the ancestry of European dogs.

Although steppe pastoralists also expanded east, they do not appear to have contributed much ancestry to present-day people in East Asia (*46*, *52*). Many modern Chinese dogs display unambiguous evidence [negative f_3 tests (*30*)] of being the product of admixture between a population related to the New Guinea singing dog (and the Australian dingo) and a West Eurasian–related population (table S6). A recent study also found a mitochondrial turnover in Chinese dogs in the last few thousand years (*61*). The best-fitting models involve not only ancestry from modern European breeds

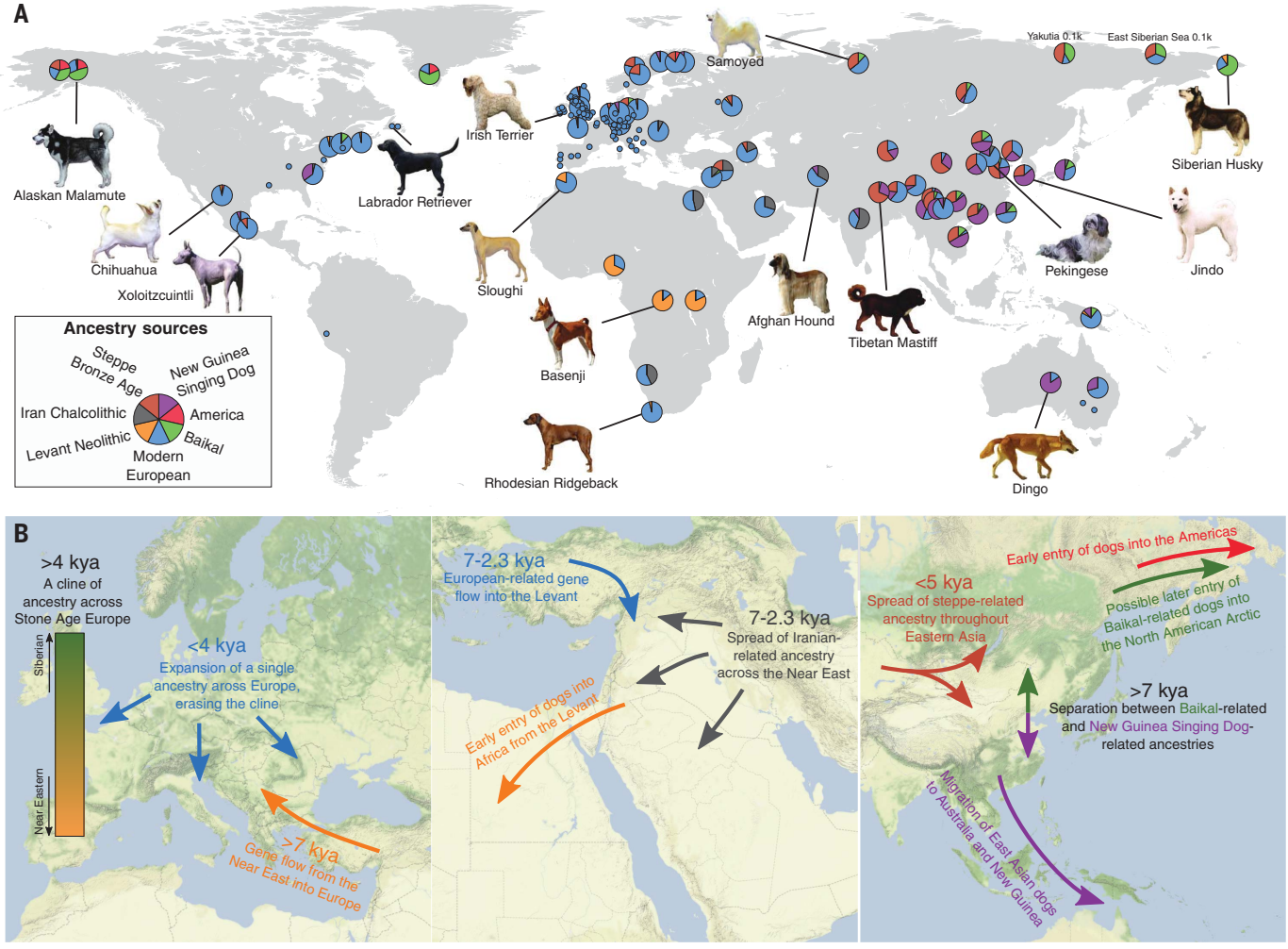

Fig. 5. Ancestry of global dogs today. (**A**) For each present-day population, the ancestry proportions estimated by the best-fitting qpAdm model, restricted to models containing up to four of seven selected sources, are displayed. Populations for which a single component accounts for ≥98% of the ancestry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

science.sciencemag.org/content/370/6516/557/suppl/DC1
Materials and Methods
Figs. S1 to S13
Tables S1 to S6
References (*62–150*)
Data File S1
MDAR Reproducibility Checklist

View/request a protocol for this paper from *Bio-protocol*.

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Science

Origins and genetic legacy of prehistoric dogs

Anders Bergström, Laurent Frantz, Ryan Schmidt, Erik Ersmark, Ophelie Lebrasseur, Linus Girdland-Flink, Audrey T. Lin, Jan Storå, Karl-Göran Sjögren, David Anthony, Ekaterina Antipina, Sarieh Amiri, Guy Bar-Oz, Vladimir I. Bazaliiskii, Jelena Bulatovic, Dorcas Brown, Alberto Carmagnini, Tom Davy, Sergey Fedorov, Ivana Fiore, Deirdre Fulton, Mietje Germonpré, James Haile, Evan K. Irving-Pease, Alexandra Jamieson, Luc Janssens, Irina Kirillova, Liora Kolska Horwitz, Julka Kuzmanovic-Cvetkovic, Yaroslav Kuzmin, Robert J. Losey, Daria Loznjak Dizdar, Marjan Mashkour, Mario Novak, Vedat Onar, David Orton, Maja Pasaric, Miljana Radivojevic, Dragana Rajkovic, Benjamin Roberts, Hannah Ryan, Mikhail Sablin, Fedor Shidlovskiy, Ivana Stojanovic, Antonio Tagliacozzo, Katerina Trantalidou, Inga Ullén, Aritza Villaluenga, Paula Wapnish, Keith Dobney, Anders Götherström, Anna Linderholm, Love Dalén, Ron Pinhasi, Greger Larson and Pontus Skoglund

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Dog domestication was multifaceted

Dogs were the first domesticated animal, likely originating from human-associated wolves, but their origin remains unclear. Bergstrom *et al.* sequenced 27 ancient dog genomes from multiple locations near to and corresponding in time to comparable human ancient DNA sites (see the Perspective by Pavlidis and Somel). By analyzing these genomes, along with other ancient and modern dog genomes, the authors found that dogs likely arose once from a now-extinct wolf population. They also found that at least five different dog populations ~10,000 years before the present show replacement in Europe at later dates. Furthermore, some dog population genetics are similar to those of humans, whereas others differ, inferring a complex ancestral history for humanity's best friend.

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