# Title: Genomic evidence for the Holocene co-dispersal of dogs and humans across Eastern Eurasia

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**Abstract:**

As the first domestic species, dogs likely dispersed with different cultural groups during the Late Pleistocene and Holocene. To test this hypothesis, we analyzed 73 ancient dog genomes, including 17 newly sequenced individuals spanning nearly 10,000 years sampled from East Asia to the West Eurasian Steppe. Our results identify strong correlations between the ancestry of dogs and specific ancient human populations from Eastern Europe to Eastern Siberia, including Ancient Palaeo-Siberians, Eastern Hunter-Gatherers, East Asians, and Steppe pastoralists. We also identify multiple shifts in the ancestry of dogs that coincide with specific dispersals of hunter-gatherers, farmers, and pastoralists. Combined, our results reveal the long-term and integral role that dogs played in a multitude of human societies.

## Main Text:

## Introduction

While the timing and location of dog domestication remains elusive, genomic evidence indicates that domestic dogs were present in Europe during the Early Holocene, approximately 11,000 years before present (BP) (*1*, *2*), and in Eastern Siberia around 10,000 years BP (*3*). These dates, however, represent a minimum estimate for the emergence of domestic dogs. Recent genetic research suggests that dogs from Eastern and Western Eurasia had already diverged before the peopling of the Americas, which likely commenced during the Last Glacial Maximum around 20,000 years BP (*4–7*). It is therefore likely that other lineages, such as East Asian dogs or Arctic dogs, that make up a significant proportion of the ancestry of modern dogs, including dingoes (*8*, *9*), and spitz breeds (*2*), diversified during the Late Pleistocene or Early Holocene.

Given their early diversification and the different roles they played in past societies, including hunting, hauling and shepherding, it is possible that specific lineages of dogs formed part of the material, cultural and biological package that was disseminated during human migrations. In fact, recent work has highlighted multiple shared evolutionary trajectories between dogs and humans (*1*). However, distinguishing superficial similarities from those driven by co-dispersal events, remains a challenge due to a scarcity of ancient dog and human genomes from the same archaeological contexts. Despite this challenge, clear instances of co-dispersal events between dogs and humans have been identified, notably in the well-documented waves of peopling of the Americas (*4*, *5*, *10*). Ancestry shifts in dogs that mirror the spread of agriculture have also been suggested for populations in Europe, although lack of nuclear DNA from Mesolithic dogs from Europe has made it difficult to test this hypothesis (*1*, *11*, *12*).

Notably, recent analysis of genomes from Central and East Asia has revealed significant shifts in human ancestry linked to the spread of agriculture during the Neolithic and metalworking Bronze Age (*13–15*). Whether dogs accompanied these migrations, however, is unknown. To address whether dogs participated in these transformative societal and cultural shifts, we sequenced and analysed 17 ancient dog genomes (median depth 0.53x; 0.01–5.37X), ranging from Siberia and East Asia to the Central Eurasian Steppe (Fig. 1A-B, S1; Table S1).

The individual genomes were obtained from a ~9,700 years calBP individual sampled from East Siberia (Khatystyr Cave) and from eight archaeological sites in Xinjiang (Jirentaigoukou), the Gansu-Qinghai region (Haizang, Huoshiliang, Yabeili, and Jinchankou), Northeast China (Bayantala), and Kazakhstan (Botai and Kent), spanning the Neolithic to Historical periods (5,169-847 years calBP). These archaeological sites, which are located in Eastern Siberia, Central Asia's mid-latitude grassland and arid regions, and across the Hexi Corridor in Northwest China, witnessed multiple human migrations throughout the Holocene. As a result, they experienced important shifts in both human ancestry, and material culture (*13*, *15*, *16*). We co-analysed this data with 57 publicly available ancient dog genomes (Table S1) (*1–4*, *12*, *17*), as well as 160 publicly available modern domestic dog genomes which capture the extent of contemporary global dog diversity (Table S2).

## Early Holocene population structure in East Siberia

Genomic analyses of ancient humans from the Early Holocene (~8,500 years ago) in the trans-Baikal region (east of Lake Baikal) revealed genetic connections to Ancient Paleo-Siberians, a population also identified in Kolyma on the northeast Siberian coast around 10,000 years ago (*6*,

*18*). To investigate if these patterns are mirrored in ancient dogs, we analysed the genome of a ~9,700-year-old individual from Khatystyr Cave (Khatystyr1_9682) in Southeast Siberia (Aldan highlands, trans-Baikal; Figure 1A). Outgroup-f3 statistics showed that the Khatystyr dog shared more drift with the ancient Zhokhov dog (Zhokhov1_9515) than any other dog in our dataset (Fig. 1C, 2A; Table S3). Notably, the Zhokhov dog dates to the same period (~9,500 years BP) as the Kolyma human (10,000 years BP) and is from a similar region of Northeast Siberia (see Supplementary Material; Fig. 1A).

A *qpAdm* analysis, incorporating the ancient Zhokhov dog, a ~6,900-year-old dog from the Lake Baikal region (Baikal_6900), a modern Australian dingo (representing East Asian dogs), and a ~5,800-year-old dog from Tepe Ghela Gap in Iran (TepeGhelaGap1_5826; representing Western dogs)(*1*), revealed that the Khatystyr Cave dog's ancestry can be best modelled using the Zhokhov dog as the sole Eastern Eurasian source (Fig. S2; Table S4). This indicates a stronger genetic affinity with the contemporary, yet geographically distant, Zhokhov dog from an island off the coast of northeast Siberia, rather than the geographically closer, but ~2,000 years younger, Lake Baikal dogs (Fig. 1A&B). This pattern mirrors observations in ancient human populations ((*18*); Supplementary Material). This indicates that Zhokhov-like ancestry in dogs was associated with human populations possessing Ancient Paleo-Siberian-like ancestry, and that both dog and human ancestries extended all across Eastern Siberia, from Kolyma to the trans-Baikal region, in the Early Holocene.

Previous analyses of an ancient dog genome from the Early Holocene Lake Baikal region (Baikal_6900; Fig. 1) detected low levels of Western dog ancestry, which was attributed to potential issues with coverage (*2*). To address this issue we increased the coverage of a Late Mesolithic/Early Neolithic (Baikal_6900 in Fig. 1) dog genome from ~2x to >5x. D-statistics of the form D(Coyote, TepeGhelaGap1_5826, X, Baikal_6900), where X represents other ancient Arctic dogs (Zhokhov1_9515, Khatystyr1_9682, ShamankaII1_7400 and PadKalashkinova1_7000), all yielded non-significant values (Fig. S3; Table S5). This result indicates a lack of detectable gene flow between Western dogs (represented by TepeGhelaGap1_5826) and Baikal_6900 since its divergence from other contemporary Lake Baikal dogs (i.e., dogs from ShamankaII and PadKalashkinova; Table S1), or its divergence from the Zhokhov and Khatystyr Cave dogs.

## Early Bronze Age introduction of Arctic dog ancestry in China

Further south, ancient genomic data indicate that Early and Middle Neolithic human populations in present-day northern China possessed East Asian ancestry related to that of people living in China today (*14*). However, analyses of later human genomes identified an influx of Western ancestry via Siberia and the Steppe during the Late Neolithic and Early Bronze Age in the Hexi corridor and the Xinjiang province of Northwest China (*13*, *15*, *16*). We can assess whether this signal is mirrored in dogs since the ancestry of modern and ancient dogs can be broadly separated into two lineages that diverged during the Pleistocene: an Eastern lineage, primarily found in Arctic and East Asian dogs, and a Western lineage, encompassing dogs from Europe and the Near East (*1*, *12*). To do so, we calculated pairwise shared-drift (outgroup-f3 statistics) between each dog genome and an ancient representative individual from each lineage: a ~9,500 years BP dog from Zhokhov Island in Siberia (Zhokhov1_9515) representing the Eastern lineage (*3*), and a ~5,800 years BP dog from Tepe Ghela Gap in Iran (TepeGhelaGap1_5826) representing the Western lineage (*1*).

Based on the amount of shared drift with the Zhokhov and Tepe Ghela Gap dogs, newly sequenced ancient genomes from China could be separated into four groups (Fig. 1C). A similar pattern was observed in a Principal Components Analysis (PCA) (Fig. S4). The oldest group, which comprised dog genomes from the Gansu-Qinghai Region (Upper Yellow River), specifically the Late Neolithic site of Yabeili (Yabeili05_5035) and the Chalcolithic site of Jinchankou (Jinchankou03_3917, and Jinchankou04_3890; Qijia Culture, ~4,060–3,780 years BP), share a similar amount of drift with the Iranian dog (TepeGhelaGap1_5826) as present day Arctic and multiple south-east Asian dogs (Fig. 1A-C).

We then used a combination of *qpWave* and *qpAdm* to assess the support for admixture models (using genomes with >1x depth of coverage) involving between one and three ancestral sources: Arctic (represented by either the Zhokhov1_9515 or Baikal_6900), East Asian (represented by dingoes), and Western (represented by TepeGhelaGap1_5826; Supplementary Material; Fig. 3A, S2, S5; Table S6-7). Model selection was based on p-values, favouring simpler models with fewer sources when nested models, excluding one or more sources, yielded p-values exceeding 0.01. This analysis indicated that, with the exception of the 9,800-year-old Khatystyr Cave individual, the Baikal (Baikal_6900) individual consistently provided a superior fit (compared with Zhokhov1_9515) for the Arctic ancestry component and was therefore selected for all subsequent analyses.

Unlike most modern East Asian dog populations, our *qpAdm* modelling (Fig. 3A; Table S6) shows that a Neolithic dog from Yabeili (Yabeili05_5035) and a Chalcolithic dog from Jinchankou (Jinchankou03_3917) did not possess any detectable levels of Western dog ancestry. This result was also supported by a supervised *ADMIXTURE* analysis ((*19*); Fig. S5)). D-statistics of the form: D(Coyote, TepeGhelaGap1_5826; Dingo, Jinchankou/Yabeili) were, however, significantly negative for dogs at Jinchankou ($|Z|$= -5.0 and -4.1 respectively; $p<0.01$), but not Yabeili ($|Z|$=0.003; p=1; Fig. S6; Table S8). This discrepancy suggests that the Chalcolithic Jinchankou dogs may possess low levels of Western dog ancestry, which is further supported by the occurrence of the mitochondrial haplogroup C in dogs at the site, which is often associated with Western Eurasian dogs (*20*, *21*). Analyses of Bronze Age human genomes from the Upper Yellow River Basin, as well as Early Neolithic humans from China, however, revealed that people possessed mostly East Asian ancestry, with Western ancestry absent until the arrival of Bronze Age Steppe pastoralists (*16*, *22*, *23*). The potential Western dog ancestry at Jinchankou may therefore reflect the start of this expansion into East Asia.

Before the arrival of Western Eurasian ancestry, Qijia Culture humans of the Gansu-Qinghai Region received an influx of Northeast Asian ancestry related to Neolithic people (e.g., Lokomotiv, ~7,500 years BP) from the Baikal region (*16*, *22*, *23*). To assess whether this signal is mirrored in dogs, we tested for gene flow from Neolithic Baikal dogs (~6,900 years BP) into Late Neolithic Yabeili (Yabeili05_5035) and Chalcolithic Jinchankou dog genomes (Jinchankou03_3917, Jinchankou04_3890; Fig. 1A). We computed D-statistics of the form D(Coyote, Baikal_6900; Dingo, Jinchankou/Yabelli), using dingo genomes which lack recent European introgression as representatives of East Asian ancestry (Fig. S6-7; Table S8-9). Both D-statistics yielded significant results ($|Z|>3$; $p<0.01$) (Fig. S7; Table S9).

A *qpWave* analysis, however, could not reject a model in which the Yabelli dog from Neolithic China (~5,000 years) could be modelled as deriving its ancestry from a single source represented by dingoes (Fig. 3A; Table S6). This discrepancy indicates that the D-statistic result is likely driven by a small contribution from Arctic dogs (i.e. Baikal_6900), yet insufficient to reject a

single-source model in *qpWave* (Fig. 3A), which potentially is also due to the low coverage of this individual (Table S1). Higher coverage of Neolithic Chinese dogs will be useful to address when both Arctic and Western ancestry first arrived in Northwest China.

We could, however, reject a single source model for a Chalcolithic Jinchankou (Jinchankou03_3917) dog for which we generated enough coverage (>1x; Table S7). A *qpAdm* analysis indicated that this Jinchankou individual possessed between ~38-45% ancestry best modelled using a ~6,900-year-old dog from the Lake Baikal (Baikal_6900) region as a source and 62-55% dingo (East Asian) ancestry (Fig. 3A; Table S6). This result was further supported by significantly positive ($p<0.01$), D-statistics of the form D(Coyote, Baikal_6900, Dingo, Jinchankou) (see Fig. S7; Table S9). Since the Lake Baikal dog genome analysed here originated from a context where humans are known to possess Northeast Asian ancestry (Supplementary Material; Fig. 4), these results (*i.e.* both *qpAdm*/*qpWave* in Fig. 3A, and D-statistics in Fig. S7) imply that the movement of people with Northeast Asian ancestry into Northern China during the early Bronze Age was accompanied by a concomitant shift in local dog ancestry.

**Western ancestry in Steppe dogs prior to the Bronze Age**

The Bronze Age also witnessed major shifts across the Steppe. Earlier populations from these regions, characterized by predominantly Eastern Hunter-Gatherer and Northeast Asian ancestry, such as humans at the Eneolithic site of Botai (~5,500-5,000 years BP), were replaced by an influx of ancestry related to Iranian Neolithic farmers and Caucasus Hunter-Gatherers (*15*). To address whether this is mirrored in dogs, we first analysed a 4.2x genome obtained from a ~5,200-year-old dog from the Eneolithic Steppe site of Botai (Botai3_5169), which predates the arrival of Western Eurasian ancestry in humans in the Bronze Age (*15*).

Outgroup-f3 statistics showed that the Botai dog shared more affinity with the Zhokhov dog (Zhokhov1_9515, Siberia, Eastern) than with the ancient Tepe Ghela Gap (TepeGhelaGap1_5826, Iran, Western ancestry) dog (Fig. 1C; Table S3). D-statistics of the form D(Coyote, TepeGhelaGap_5826; Botai_5169, Zhokhov_9515) and D(Coyote, TepeGhelaGap_5826; Botai_5169, Baikal_6900), however, were significant (Z=-5.9 and -9.9 respectively; $p<0.01$) for gene flow from the Western Eurasian lineage, represented by an ancient Iranian dog (TepeGhelaGap1_5826) into Botai since its split with Zhokhov (Zhokhov1_9515; Fig. S8; Table S10). Modelling with *qpAdm* and F4ratio indicated that the ancestry of the Botai dog could be modelled as ~75% Arctic (Baikal_6900), and 25% Western (TepeGhelaGap_5826; Fig. 3A, S9; Table S6, S11).

To address whether Western ancestry increased in Steppe dogs during the Bronze Age, we analysed two previously published dog genomes from the Late Bronze Age Srubnaya culture (~3,800-3,200 years BP; Ishkinino1_3275 and Samara_3800; Fig. 1A-B) and a newly sequenced genome from a ~3,200-year-old dog from the later Begazy–Dandybai culture (Kent1_3150; Fig. 1A-B). Both dogs from Ishkinino and Samara were best modelled as possessing over ~60% Western ancestry, ~25% East Asian ancestry, and ~15% Arctic ancestry (Fig. 3A; Table S6). The slightly later dog from Kent instead was best modelled as possessing ~70% Western ancestry and ~30% Artic. High levels of Western Eurasian ancestry in Bronze Age Steppe dogs were confirmed by a supervised ADMIXTURE analysis (Fig. S5), and persisted in the Steppe until at least the Historical period, as demonstrated by a historical dog from Bolgar (Bolgar1_1000) with ~70% Western ancestry and ~30% Arctic ancestry (Fig. 3A; Table S6).

These results demonstrate that Western dog ancestry predates the arrival of Iranian Farmer and Caucasian Hunter-Gatherer (CHG) human ancestry in the region during the Bronze Age (*15*). Interestingly, Eastern Hunter-Gatherer (EHG) ancestry, which comprises the majority of the ancestry in humans from the Eneolithic site of Botai, is also found in Western Eurasia as far as Eastern Europe, including in people from the Veretye culture in Karelia (*24–26*). Notably, previous work has shown that 10,900-year-old dogs from the Veretye culture in Karelia possess both Western and Eastern ancestry (*1*, *2*). Outgroup-f3 statistics showed a closed genetic similarity between Botai and Veretye dogs (Veretye1_10930; Fig. 2B; Table S3). In addition, our *qpAdm* analysis showed that the ancestry of the Veretye dogs could also be modelled as ~65-75% Arctic (Baikal_6900) and ~35-25% Western (TepeGhelaGap1_5826), similar to that of the Botai dog (Botai3_5169; Fig. 3A; Table S6). This indicates that dogs accompanying EHG human populations across Eurasia, between 10,000–5,500 years BP possessed dogs with a similar genetic make-up. This suggests that the Western ancestry observed in the Botai dog could have been acquired through connections with EHG populations from Eastern Europe, while later influx of Western ancestry in the Bronze Age was likely the result of introduction of dogs that accompanied people with Iranian and Caucasian Hunter Gather ancestries (*15*).

**Bronze Age introduction of Western dog ancestry in Northwest China**

Additional ancestry shifts in people from East Asia during the Late Bronze Age (~3,300 years BP) were likely driven by the expansion of Western Steppe pastoralists (*13*, *27*, *28*). Previous studies showed that modern East Asian dogs possessed Western Eurasian ancestry (*1*, *29*, *30*), however, lack of ancient genomes from East Asia has made it difficult to assess whether this was the result of Bronze Steppe pastoralist expansion or due to later processes, particularly the influx of European breed dogs during the 20th century (*31*, *32*). Based on the detection of the C haplogroup in two ~4,000 years BP dogs from Jinchankou, previous ancient mitochondrial DNA studies proposed a Bronze Age arrival of Western dog ancestry in China (*20*, *21*). Relying on mitochondrial haplogroups as ancestry proxies in dogs, however, is challenging, given the presence of both A (higher frequency in Eastern Eurasia) and C (higher frequency in Western Eurasia) haplogroups in early Western dog populations, such as the ~10,000-year-old dogs from Veretye (*1*, *2*).

Interestingly, a newly sequenced dog genome from Jirentaigoukou (Jirentaigoukou02_3300, Late Bronze Age, ~3,300 years BP), situated at the eastern margin of the Eurasian steppe in Xinjiang, shared affinities with Western Eurasian dogs based on outgroup-f3 statistics (Fig. 1C; Table S3). F4ratio (Fig. S9) and *qpAdm* (Fig. 3A, S2) modelling indicated that this individual possessed ~50% Western ancestry and ~50% East Asian ancestry.

Analysis of an ancient human genome from the site of Jirentaigoukou indicated that the individual derived most of its ancestry from Western Steppe pastoralists (Andronovo/Sintashta lineage, ~3,300–3,100 years BP; (*33*)). High levels of Western Eurasian ancestry were similarly observed in ancient dog genomes associated with Steppe pastoralist cultures from Ishkinino (Ishkinino1_3275; ~3,300 years BP), Samara (Samara_3800; ~3,800 years BP), and Kent (Kent1_3150; ~3,100 years BP; Fig. 3A). Combined, our results indicate that the increase of Western ancestry in both humans and dogs in the Eastern Steppe and Xinjiang (*13*, *33*), was likely mediated by the expansion of Western Steppe pastoralists toward the East during the Bronze Age.

To the east of Jirentaigoukou, in the Hexi Corridor, ancient dogs from the Early Bronze Age sites of Haizang (Haizang05_3774, Haizang06_3676 and Haizang07_3772, Middle Period of the Qijia

Culture, ~3800–3550 years BP), and Huoshiliang (Huoshiliang09_3787, Huoshiliang10_3779, Huoshiliang11_3917, Xichengyi culture, ~4070–3650 years BP), also showed stronger genetic affinities with the ancient Iranian dog (Fig. 1C; Table S3) compared to a Late Neolithic dog from Yabeili (Yabeili05_5035) and a Chalcolithic dog from Jinchankou (Jinchankou03_3917). F4-ratio (Fig. S9; Table S11), *qpADM* (Fig. 3A, S2; Table S6), and supervised ADMIXTURE (Fig S5). analyses of genomes with >1x revealed that while the 3,900 calBP Jinchankou dog (Jinchankou03_3917) lacked Western ancestry, the Huoshiliang (Huoshiliang09_3787, Huoshiliang10_3779, Huoshiliang11_3917) and Haizang (Haizang05_3774, Haizang06_3676) dogs from Gansu Province possessed ~15–35% Western ancestry. This result was also supported by highly significant ($|Z|<-3$, $p<0.01$) D-statistics of the form D(Coyote, TepeGhelaGap1_5826, Haizang/Huoshiliang, Dingo) (Fig. S6; Table S8).

These results were further supported by an *AdmixtureBayes* analysis (*34*), based on genomes with >1x depth of coverage, which modelled the Huoshiliang dogs as a mixture between Western and East Asian ancestry with high support (>99% probability; Fig. 3B, S10). This admixture graph also indicated that the Western ancestry component in Huoshiliang dogs was more closely related to the Botai dog's Western ancestry component than to the ancient Iranian dog (TepeGhelaGap1_5826). Combined, these findings indicate that the Western Eurasian component in East Asia was disseminated via the Steppe, reaching Gansu Province (i.e. Huoshiliang and Haizang) by at least 3,900 calBP, during the Bronze Age. Admixture dating using *DATES* (31), based on genomes with >1x depth of coverage, further supports that Western dog ancestry was introduced in the region between ~3,800 and 4,000 years ago (Supplementary Methods; Fig. S11-12; Table S13).

In contrast to Huoshiliang and Haizang (Fig. 1A), the dog from Jinchankou (Jinchankou03_3917; Fig. 3A), situated a few hundred kilometres eastward, exhibited no detectable levels Western ancestry based on *ADMIXTURE*, *ADMIXTUREBAYES* and *qpAdm*. This result suggests that the dispersal of Western dog ancestry during the Bronze Age was not a homogeneous event throughout the area. Generating new genomic data from additional early Bronze Age dogs in these provinces will help clarify the geographic and temporal dynamics of Western ancestry and its relationship to the introduction of other domesticates and Bronze technologies. Western dog ancestry in ancient East Asian individuals reached ~40% in two ~850-year-old dogs from the Liao Dynasty (Bayantala12_847, and Bayantala13_859) in Inner Mongolia (Bayantala). These ancestry proportions are similar to those in contemporary Northern Chinese dogs (Fig. 3A).

Although our *qpAdm* models accurately represented the ancestry of pre-Bronze Age and Bronze Age Steppe and East Asian dogs ($p > 0.01$), they exhibited poor fit for Liao Dynasty and modern Asian dogs (Fig 3A). These results indicate that the Arctic, East Asian, and West Eurasian sources used in these analyses are insufficient to fully account for modern East Asian dog ancestry, suggesting an additional, unmodeled ancestral contribution within the last 850 years. Combined, our results indicate that while there are documented introductions of European dog breeds to China during the 20th century (e.g., (28, 29)), at least part of the Western Eurasian ancestry found in modern North Chinese dogs results from admixture beginning in the Bronze Age during the expansion of Western Steppe pastoralist, yet that this process likely continued at least until the Early Liao Dynasty.

**Concordance and discrepancies between human and dog ancestry in Asia**

Analyses of our newly generated ancient dog genome from Asia show generally good concordance between Eastern and Western Eurasian ancestry in dogs and humans, with Eastern human populations like Ancient Palaeo-Siberians, Northeast Asians, and East Asians associated with Eastern dogs of East Asian or Arctic ancestry, and Western human populations such as Iranian farmers/Caucasian Hunter-Gatherer, and Steppe pastoralists associated with the Western Eurasian dog lineage (Fig. 4). Interestingly, however, Eastern Hunter-Gatherers from Karelia (Veretye) and Botai, who are genetically closer to Western Eurasian humans than to Eastern Eurasians, were associated with dogs that possess mostly Eastern ancestry (i.e., Arctic dogs; Fig. 3A). To visualise this discrepancy we aligned PCA built from 17 human and 17 dog ancient genome data from similar location and time period (Fig. 4; Supplementary Material) using Procrustes transformation.

These analyses indicate a remarkable concordance between the two species, where the first principal component (PC1) differentiates both dogs and humans based on their Western and Eastern ancestries (Fig. 4C). The second principal component (PC2) separated both people and dogs roughly based on the latitude. Specifically, Eastern Hunter-Gatherers were separated from Iranian farmers/Caucasian Hunter-Gatherers along PC2, and Ancient Palaeo-Siberians were separated from Northeast Asians and East Asians (Fig. 4C). Similarly, East Asian and Arctic dogs are differentiated along PC2.

These analyses, however, highlighted several discrepancies. Firstly, while Eastern Hunter-Gatherers align more closely to Iranian farmers and Caucasian Hunter-Gatherers on PC1, dogs from the same context (i.e. Veretye and Botai) are shifted toward other Eastern (i.e., Arctic) dogs. Secondly, while ~7,000-year-old Northeast Asians from Lake Baikal align with East Asians on PC2, as expected (*15*), dogs from the same context are plotted with Arctic dogs from Khatystyr Cave and Zhokhov Island, located further north (Fig. 4C). This pattern suggests major population splits in both dogs and humans were not concurrent events, and/or that dogs, particularly those of Arctic ancestry, were likely exchanged between human communities of hunter gatherers in Northern Eurasia possessing different ancestry.

## Conclusions

Our results show that the shifts in dog ancestry across the Eurasian Steppe, East Asia, and Eastern Siberia often correlate temporally and spatially with migrations of hunter-gatherer, farming, and pastoralist communities. Dogs therefore likely dispersed alongside diverse cultural groups with varying subsistence strategies and ancestries, which suggest that dogs played an integral role in a multitude of human societies. Our analyses, however, also highlighted some discrepancies between the population splits of dogs and humans, suggesting that Early Holocene communities of hunter-gatherers in Northern Eurasia, possessing different ancestry, likely also exchanged dogs.

The greater antiquity of dogs, relative to all other domestic species, implies integration within a broader spectrum of communities across Eurasia, Africa, and North and South America during the late Pleistocene and Holocene. Consequently, dogs likely fulfilled a wider range of roles than other domesticates, encompassing hunting, hauling, and shepherding across disparate cultural contexts. Analyses of ancient dog genomes, from diverse archaeological contexts, will be essential to assess whether dogs participated in other human migrations, such as those associated with the dissemination of agricultural technologies in Europe and the Near East.

Co-dispersal of humans and domestic animals has been documented in other species, including livestock, which facilitated the establishment of agricultural communities (*35*), and horses, which significantly altered human mobility (*36*). Co-analysis of ancient animal and human genomes provides the opportunity to investigate co-dispersal events at the community level, rather than at the single-species level. This approach has the potential to transform our understanding of human-animal interactions in the past and the roles that specific species played within past societies.

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## Supplementary Materials

Materials and Methods

Figs. S1 to S15

References (*37–98*)

Data S1 to S15

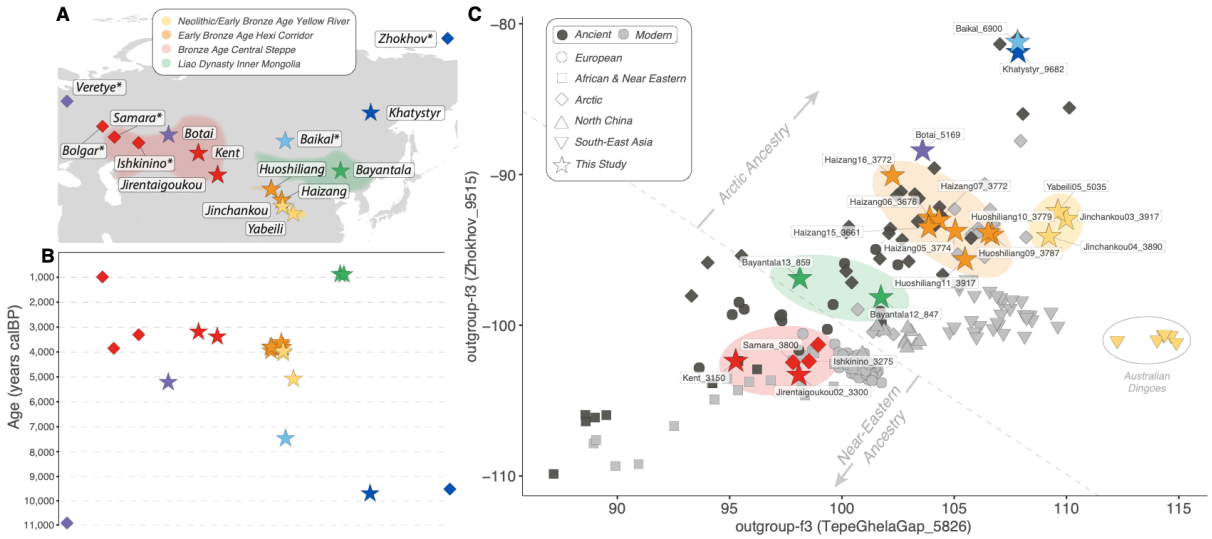


**Fig. 1. Location, age, and ancestry of the newly sequenced ancient dog genomes. (A)** Location of the ancient Eurasian published (diamonds*) and unpublished (stars) dog genomes analyzed in this study. Distributions of key human cultural complexes/periods are shown. Information for other ancient genomes from Western Eurasia and North America analyzed in this study can be found in Table S1. **(B)** Temporal distribution of ancient Eurasian samples in (A), based on either direct radiocarbon dates, or securely-dated contexts (Table S1). **(C)** Levels of shared drift (outgroup-f3) between ancient (dark grey) or modern dogs (light grey) and an ancient Near Eastern dog (Iran_5826; x-axis) and an Arctic dog (Zhokhov_9515; y-axis). The x-axis has been inverted to highlight geographic structure with respect to (A; i.e. an East-West ancestry cline). Samples are coloured based on shared ancestry, and both temporal and geographic proximity to the following human groups: Eastern Hunter-Gatherer (purple), Ancient Palaeo-Siberian (dark blue), Northeast Asian (light blue), Central Steppe (red), Neolithic (yellow) and Bronze Age (orange) Upper Yellow River, and Liao Dynasty Mongolia (green). Sample age is given in years before present as a suffix (e.g. Iran_5826). Coloured ellipses delineate four groups of newly sequenced Chinese dogs, classified largely by their Western Eurasian ancestry: Neolithic/Chalcolithic Yellow River samples (Yabeili and Jinchankou; yellow), Early Bronze Age Hexi Corridor samples (Huoshiliang and Haizang; orange), Bronze Age Central Steppe samples (Jirentaigoukou; red) that cluster with other Steppe dogs (Kent, Samara, and Ishkinino), and Liao Dynasty Inner Mongolian dogs (Bayantala; green).

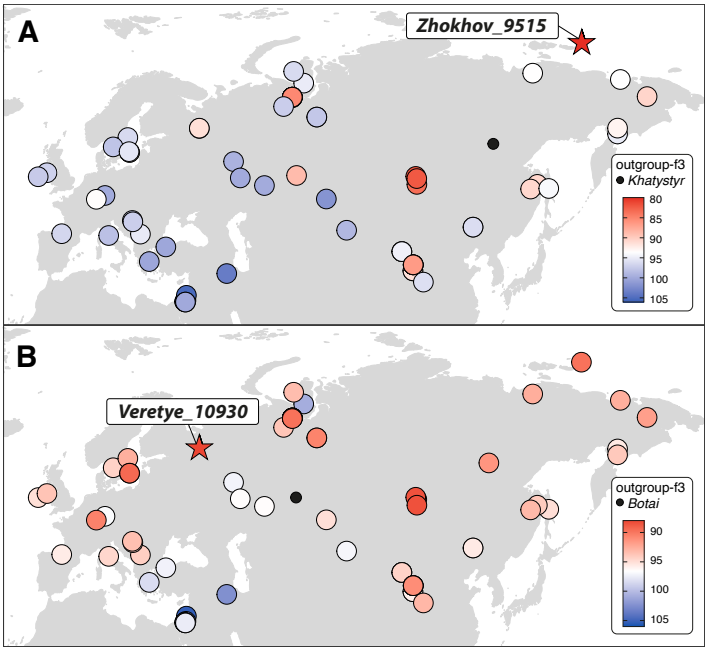


**Figure 2. Level of shared drifts between the newly sequenced Khatystyr cave (~9,682 years ago) and Botai (~5,169) dog genome and other ancient dogs.**

Levels of shared drift (outgroup-f3) between ancient Eurasian dogs and either **(A)** Siberian (Khatystyr_9682) or **(B)** central Eurasian steppe **(**Botai_5169) dogs. Labelled stars represent the individuals with the highest outgroup-f3 values (red) for each comparison, and black circles indicate the location of Khatystyr and Botai dogs, respectively. These results show that the closest individual to the Khatystyr cave genome (~9682) is the Zhokhov dog (also supported by our *qpAdm* results; see Figure 3A, S2) and that the closest individual to the Botai dog is the Mesolithic European Veretye dog genome.

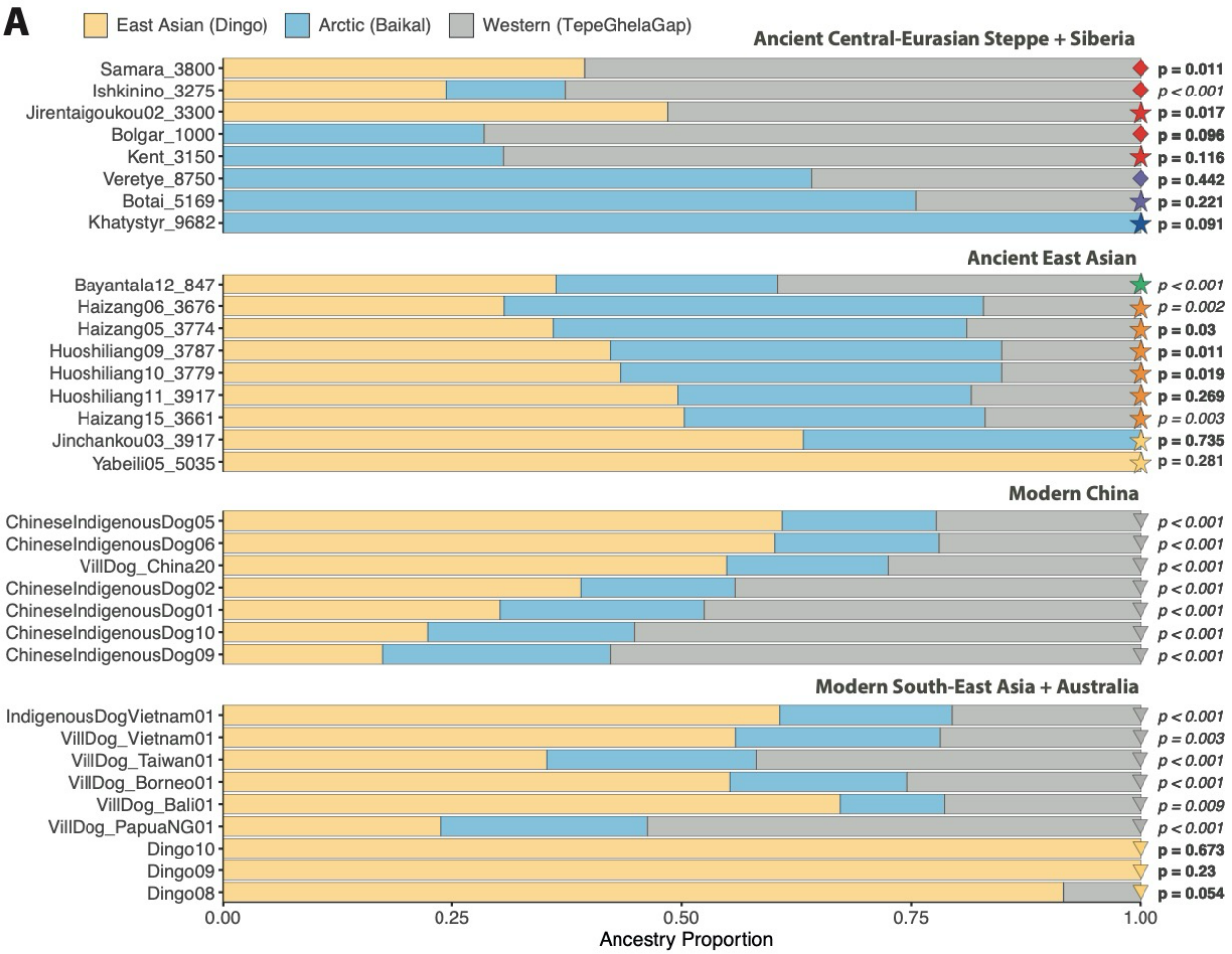
A
East Asian (Dingo)
Arctic (Baikal)
Western (TepeGhelaGap)
Ancient Central-Eurasian Steppe + Siberia
Samara_3800
Ishkinino_3275
Jirentaigoukou02_3300
Bolgar_1000
Kent_3150
Veretye_8750
Botai_5169
Khatystyr_9682
p = 0.011
p < 0.001
p = 0.017
p = 0.096
p = 0.116
p = 0.442
p = 0.221
p = 0.091
Ancient East Asian
Bayantala12_847
Haizang06_3676
Haizang05_3774
Huoshiliang09_3787
Huoshiliang10_3779
Huoshiliang11_3917
Haizang15_3661
Jinchankou03_3917
Yabeili05_5035
p < 0.001
p = 0.002
p = 0.03
p = 0.011
p = 0.019
p = 0.269
p = 0.003
p = 0.735
p = 0.281
Modern China
ChineseIndigenousDog05
ChineseIndigenousDog06
VillDog_China20
ChineseIndigenousDog02
ChineseIndigenousDog01
ChineseIndigenousDog10
ChineseIndigenousDog09
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
Modern South-East Asia + Australia
IndigenousDogVietnam01
VillDog_Vietnam01
VillDog_Taiwan01
VillDog_Borneo01
VillDog_Bali01
VillDog_PapuaNG01
Dingo10
Dingo09
Dingo08
p < 0.001
p = 0.003
p < 0.001
p < 0.001
p = 0.009
p < 0.001
p = 0.673
p = 0.23
p = 0.054
0.00
0.25
0.50
0.75
1.00
Ancestry Proportion
B
WEST
EAST
ARCTIC
EAST ASIA
TepeGhelaGap
TepeGhelaGap_5826
Baikal
Baikal_6900
Zhokhov
Zhokhov_9515
Botai
Botai_5169
Huoshiliang
Huoshiliang11_3917
Port-au-Choix
PortauChoix_4157
Khatystyr
Khatystyr_9682
Jinchankou
Jinchankou03_3917
Dingo
Dingo07

**Figure 3. Ancestry modelling of ancient and modern Eastern Eurasian dogs.**

(**A)** Proportion of West Eurasian (grey), Arctic (light blue) and East Asian (yellow) ancestries in ancient and modern East Eurasian published (diamonds*) and unpublished (stars) dog genomes estimated using *qpAdm* for the best model (1 to 3 sources). Model selection relied on p-values, with simpler models prioritized when nested models (excluding one or more sources) returned p-values greater than 0.01. For each individual, the ancestry proportions from the model with the highest p-value are presented, even in cases where the model was formally rejected ($p < 0.01$). While our *qpAdm* models, based on these three sources, adequately represent the ancestry of most ancient Steppe and East Asian dogs ($p > 0.01$), they often poorly fit modern Asian dogs, suggesting unmodeled ancestral contributions. (**B)** Consensus Bayesian topology based on AdmixtureBayes from high-coverage (1.65–19.6x) ancient dog genomes, with branches and admixture events that exceed the posterior probability threshold (99%) are shown. The graph shows two admixture events, a West Eurasian (TepeGhelaGap) into both Eneolithic Steppe (Botai) and in the Early Bronze Age Hexi Corridor (Huoshiliang). The single tree with the highest posterior probability, which contains all four estimated admixture events and their corresponding ancestry proportions (estimated in AdmixtureBayes), are shown in Fig. S10. Ancestry proportions (pie graphs) were estimated in AdmixtureBayes.

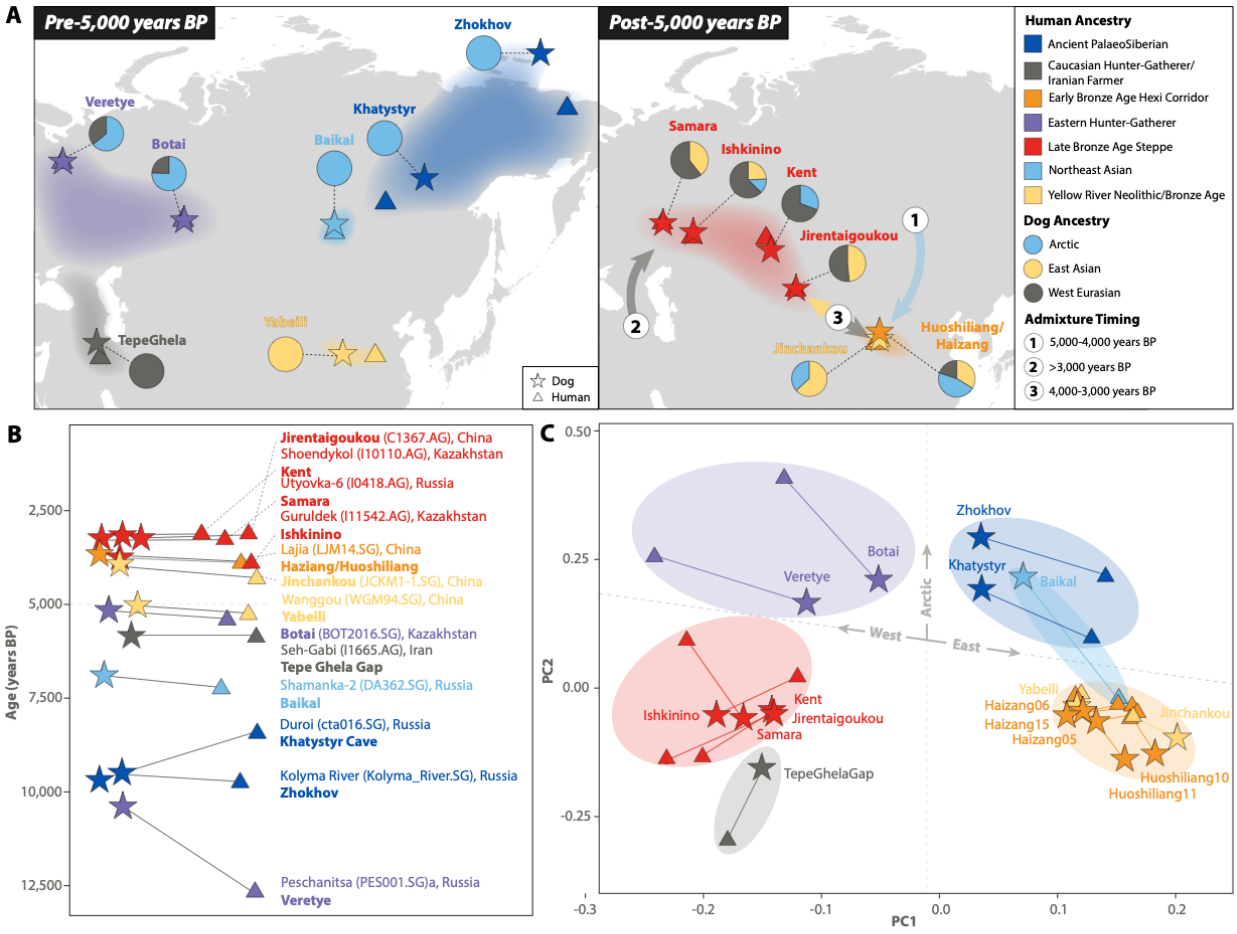


**Figure 4. Correspondence between human and dog ancestry in Eastern Eurasia.**

**(A)** Maps showing both human (triangle) and dog (star) ancestry in pre and post 5,000 years contexts (i.e. pre and post Bronze Age Steppe expansion). Pie charts represent mean ancestry proportions for each population estimated by *qpAdm* (see Fig. 3A, S2).The first map shows that the Western dog ancestry (gray in pie charts) is restricted to Western Eurasia, while the East Asian dog ancestry (yellow in pie chart) is restricted to Eastern Eurasia. In contrast, the Arctic dog ancestry exhibits a broader distribution across Northern Eurasia. The second map depicts post Bronze Age shifts in dog ancestry, associated with the following known human migrations: (1) eastward expansion of Arctic dog ancestry to Jinchankou during the Chalcolithic (5,000-4,000 years BP), associated with the documented influx of Northeast Asian ancestry in the region (*16, 22, 23*); (2) influx of Western Eurasian dog ancestry from the Caucasus into the Steppe region (>3,000 years BP), concomitant with well-characterized migrations of Caucasian hunter-gatherer ancestry (*15*); and (3) subsequent westward dispersal of this Western Eurasian dog ancestry from the Steppe into the Hexi Corridor (Haizang and Huoshiliang) during the early Bronze Age (~4,000-3,000 years BP), as well as the westward movement of East Asian dog ancestry, both of which coincide with known human migration patterns (*13, 27, 28*). **(B)** Concordance between the age of human (triangle) and dog (star) genomes depicted in panel A. **(C)** Principal components built from 17 human and 17 dog ancient genome data from similar locations and time periods (see panel A and B) and aligned using Procrustes rotation. The first principal component (PC1) differentiates both dogs and humans based on their Western and

Eastern ancestries. The second principal component (PC2) separated both people and dogs roughly based on the latitude, including East Asian and Arctic dogs.

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# Supplementary Materials for

## Genomic evidence for the Holocene co-dispersal of dogs and humans across Eastern Eurasia

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**The PDF file includes:**



**Other Supplementary Materials for this manuscript include the following:**

## Materials and Methods

### Archaeological site descriptions

*Jinchankou, Qinghai, China*

The Jinchankou Site (102.54°E, 36.92°N) is located on the second terrace of the south bank of Datong River, north of Jinchankou Village, Jiading Township, Huzhu County, Qinghai Province. Covering an area of approximately 0.8 hectares, it is a site from the Middle Period of the Qijia culture dating back to around 4060 to 3780 years BP (*37*, *38*). The Qinghai Provincial Institute of Archaeology excavated the site in 2012, unearthing pottery, bone tools, jade artefacts, and a large number of animal bones (*39*). Through systematic flotation and macrofossil identification, the Jinchankou Site yielded a significant amount of foxtail millet and also revealed the earliest remains of wheat in Qinghai Province. Additionally, findings included a hemp seed and seeds of grasses such as Poaceae and Setaria (*37*). In terms of zooarchaeology, domesticated animals such as pigs, dogs, yellow cattle, goats/sheep, as well as a variety of wild animals like deer, roe deer, muntjacs, musk deer, foxes, martens, bears, rabbits, and badgers were discovered (*39*). Combining the stable carbon and nitrogen isotope analysis of the site's prehistoric inhabitants and animal bone remains (*40*) suggests that the primary food source for the inhabitants of the Jinchankou Site was foxtail millet, supplemented by hunting herbivores and domestic animal husbandry. The presence of a minimal number of dogs indicates a likely role in hunting or guarding rather than being a significant food source (*40*). This study analysed two left mandibles of dogs from the Jinchankou Site to ensure they belonged to two different dogs. The sample numbers are Jinchankou03 and Jinchankou04.

*Haizang, Gansu, China*

The Haizang Site (102.62°E, 37.95°N) is located on the eastern terrace of the Haizang River, a tributary of the Shiyang River, in Sanpanmo Village, Jinyang Town, Liangzhou District, Wuwei City, Gansu Province. It is preliminarily identified as a settlement site engaged in jade processing. Based on stratigraphic deposits and unearthed artefacts, the Haizang Site can be divided into two periods: the Qijia culture and the Warring State period. Systematic dating of carbonized wheat remains unearthed from the lower layers indicates that the early dates mainly range from 3800 to 3550 years BP. In 2019, an excavation area of 1000 square meters yielded pottery, copper, stone, bone, jade artefacts, turquoise beads, and animal remains such as horse heads, sheep heads, horse hooves, and whole sheep found in sacrificial pits (*41*). This study obtained ancient DNA from five dogs at the Haizang Site. In the first batch of experiments, the right mandibles of three dogs were selected, while in the third batch, the left mandibles of two dogs were chosen, with no duplicate samples in each sample trace unit. The sample numbers for the two batches are Haizang05, Haizang06, Haizang07, and Haizang15, Haizang16.

*Huoshiliang, Gansu, China*

The Huoshiliang Site (99.24°E, 40.21°N) is located in Jinta County, Jiuquan City, Gansu Province, in the middle reaches of the Heihe River in the Jinta Basin. Based on the ceramic characteristics of unearthed pottery, the site is identified as belonging to the Xichengyi culture. Radiocarbon

dating of animal bone collagen from the site suggests an age range of 4070 to 3650 years BP (*42*, *43*). During excavations by the Gansu Province Institute of Cultural Relics and Archaeological Research in 2017, a large number of pottery, stone tools, bone tools, smelting slag, and animal bone remains were unearthed at the Huoshiliang Site. Plant remains such as foxtail millet, broomcorn millet, barley, and wheat were also identified through flotation (*44*). Analysis of the animal remains excavated at the Huoshiliang Site revealed a predominance of domestic animals such as sheep/goats, dogs, pigs, and cattle, as well as wild animals like deer, antelopes, wild rabbits, small rodents, and birds (*43*). Further stable carbon and nitrogen isotope analysis of animal bones indicated a diverse livestock feeding strategy at the Huoshiliang Site around 3850 years BP. After 3850 years BP, omnivorous livestock such as pigs and dogs primarily consumed C3 plants, while herbivorous livestock like sheep and cattle mainly consumed C4 plants (*42*). This study selected three samples from different layers at the Huoshiliang Site for analysis, including the left calcaneus, left ulna, and right calcaneus of dogs. The numbers are Huoshiliang09, Huoshiliang10, and Huoshiliang11.

*Yabeili, Gansu, China*

The Yabeili Site (105.65°E, 35.00°N) is located in the downstream terrace of the Hulu River basin in Qinan County, Tianshui City, Gansu Province. Excavated artefacts at the site include pottery, stone tools, bone tools, as well as human and animal bones. The animal bone remains at the site include Dog, Pig, Sika deer, Roe deer, Pheasant, Cattle, Horse, and Sheep/goat. Based on the characteristics of the unearthed artefacts, the temporal span of the Yabeili site is estimated to range from the Late Neolithic period to the Ming Dynasty (*45*). This study analysed the left maxilla of a domestic dog from the Yabeili site. The sample number is Yabeili05.

*Bayantala, Inner Mongolia, China*

The Bayantala Site (102.62°E, 37.95°N) is located in Bayantala Sumu, Balin Right Banner, Chifeng City, Inner Mongolia, and is an Early Liao Dynasty settlement site. The site covers an area of about 4200 square metres and was salvaged by the archaeology department of Chifeng university, Inner Mongolia in 2011. The unearthed artefacts at the site include pottery, porcelain, gold, iron, bone tools, glassware, and stone tools, as well as a large number of animal bone remains (*46*). Additionally, plant remains from the site were obtained through a flotation soil sample system, including crops such as millet, broomcorn millet, barley, cultivated barnyard grass, buckwheat, and hemp, as well as seeds of weed plants from the Fabaceae, Chenopodiaceae, Poaceae, Asteraceae, and Polygonaceae families (*47*). Furthermore, animal bone identification revealed that the animal remains at the Bayantala site mainly include Canidae, horses, Bovidae subfamily, Caprinae, Cervidae, Suidae, camels, small rodents, and small carnivores. This study obtained whole genome information from two domestic dog bones, one right mandible and one left maxilla. The sample numbers are Bayantala12 and Bayantala13.

*Jirentaigoukou, Xinjiang, China*

The Jirentaigoukou site (82.783375°E, 43.855°N) is located in the east of Qialegen Village, Kekehaote Ha'er Mongolian Township, Nieleke County, Xinjiang Uygur Autonomous Region, at the confluence of the middle reaches of the Kashgar River. The site dates back approximately 3600 to 3000 years BP (*48*), with the main remains from the Middle to Late Bronze Age (*49*). It is also where the earliest known coal usage traces in the world were found (*50*). The Jirentaigoukou site consists of a residential area and a burial area. Among these, Gaotai tombs, the high-level large tombs at the Jirentaigoukou site have radiocarbon dates mostly ranging from 1683 BCE to 1497 BCE (*51*). These tombs represent the largest, highest-grade, and most well-preserved stone burial structures from the prehistoric period so far discovered in Xinjiang and even across the Eurasian grasslands (*49*). The site has yielded a large quantity of animal bone remains including sheep, cattle, horses, dogs, gazelles, and red deer, with a predominance of sheep, horses, and cattle, indicating that the inhabitants primarily relied on these animals for meat consumption (*48*). Among the large plant remains recovered from the site, there were grains like foxtail millet of East Asian origin and wheat/barley domesticated in the West Asian Fertile Crescent (*48*), highlighting the Jirentaigoukou site as a microcosm of early global crop dissemination and an ideal area for studying cultural exchanges between East and West. This study focuses on a domestic dog's left mandible excavated from a high-level tomb at the Jirentaigoukou site, whose number is Jirentaigoukou02.

*Kent, Kazakhstan*

The settlement of Kent (75.56269927°E, 49.12116196°N) is located in Central Kazakhstan and dates back to the 15th–11th centuries BCE (*52*). Kent is one of the most studied sites of the Begazy-Dandybai culture (Sargary-Alekseyevka), occupying an area of approximately 30 hectares (*52*). Kent was a major cultural and economic centre, comprising six smaller settlements with residential houses, economic buildings, craft (metallurgical) quarters, and ceremonial sites for public gatherings and religious rituals, as well as extensive agricultural regions. Material culture indicates a high level of militarization, with imported ceramics suggestive of a multi-ethnic population with extensive intercultural connections (*52*). The economic basis for the existence of Kent society was migratory livestock breeding and long-distance metal trade. While the zooarchaeological assemblage at Kent was dominated by domestic animals, such as sheep (~52%), cattle (~27%), and horses (~18%), wild animals including aurochs (*Bos cf. primigenius*), goitered gazelle (*Gazella subgutturosa*), saiga (*Saiga tatarica*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), elk (*Alces alces*), and kulan (*Equus hemionus*) were also present. Human diet at Kent was primarily meat and dairy based, with residues of milk from ruminant animals have been found in vessels. Stone plates for grinding plant products, grain grinders, and bronze sickles for harvesting crops and preparing fodder for domestic animals also indicate a reliance on plants. The dog specimen studied here was part of a collective burial of six young male dogs (14th century BCE) buried in two distinct tiers (*53*). As the individuals were purposefully oriented north-south, the burial is interpreted as an apotropaic complex (*53*).

*Botai, Kazakhstan*

The site of Botai (67.645786°E, 53.303942°N) is an Eneolithic settlement in northern Kazakhstan dating back to ~3,500 BCE, and associated with the eponymous Botai Culture (*54*). The site

consists of a substantial number of semi-subterranean pit houses, with associated pits and middens and a potential corral structure (*55*). The Botai subsistence economy relied heavily upon horse management with archaeological (*56*), organic residue (*57*) and genetic evidence (*36*) suggesting that Botai horses were domesticated, but not the direct ancestors of modern domesticated horses (*55*). Botai-type horses were replaced in the region with the modern domestic lineage (DOM2) after the migration of Sintashta/Petrovka and later descendent Andronovo Culture peoples into the region after ~ 2,000 BCE (*58*). The dog specimen included in this study was the rear portion of a cranium that came from excavations conducted in 2018. The find site was located 20 - 40 cm below the ground surface, within a pit cut into the eastern margin of an abandoned pit house, with associated deposits otherwise including many butchered horse bones. The greatest breadth of the dog's occipital condyle, measurement 25 (*59*), was 40.38 mm.

*Khatystyr Cave, East Siberia*

The cave (grotto) Khatystyr is located on the right bank of the Aldan River, 2 km from the village of Khatystyr (125.1025°E, 58.5507°N) (Yakutia, East Siberia, Russian Federation) and is a limestone cavern formed in place of a deep crack. The cave with finds was first accidentally discovered back in 1962 by the foreman of the Aldan timber industry enterprise A. Ivanov (*60*). In the cave, not far from the entrance, he found a human skeleton lying directly on the surface of the cave floor near the wall. Nearby were the remains of a fire, and further deep inside the cave, an accumulation of brown bear, wolf and fox bones was discovered. In the 1970s, the human skeleton, on the initiative of B.S. Russanov, was dated to 9,800 years ago (*60*). Later, among the animal bone remains collected there, G.G. Boeskorov identified the bones of a brown bear (*Ursus arctos*) and a domestic dog. In 2017, the bone remains from the cave, which also included the dog bones under study, were dated at the Institute of Accelerator Analysis Ltd. in Japan (*61*). The dates obtained from the Khatystyr cave were between10,200–9,500 years calBP, which coincides with the early stage of the Sumnagin Mesolithic culture, dated to 9400–5900 years BP (10700–6800 cal. BP).

### *Radiocarbon Dating*

We generated radiocarbon dates for 15 dogs (Table S1). Sample preparation and measurements were carried out in either the Key Laboratory of Western China's Environmental Systems (MOE), Lanzhou University, the Radiocarbon Dating Laboratory at Lund University, or Beta analytics. Raw dates were calibrated (see Table S1) using the IntCal20 curve correction (*62*) in the Oxcal 4.4 online program.

### *Ancient DNA extraction, library preparation, and sequencing*

#### *Kunming Institute of Zoology, Chinese Academy of Sciences*

For Chinese samples (n = 14; Fig. S1), laboratory work was conducted in a dedicated ancient DNA facility at the Kunming Institute of Zoology, Chinese Academy of Sciences. All samples were UV-irradiated, and freshly collected bone powder (~100 mg) was washed with 0.5% NaClO and nuclease-free (NF) water to minimize contamination. DNA was extracted using a modified version

of the protocol (*63*): specifically, bone powder was digested with a solution containing EDTA, Tween-20, and proteinase K at 37°C with constant shaking for 39 hours. The supernatant was purified using the High Pure Extender Assembly (from High Pure Viral Nucleic Acid Large Volume Kit, Roche Diagnostics GmbH) with PB buffer, 5M sodium acetate, and Tween-20, washed twice with PE buffer, eluted in 110 µl TET buffer, and stored at -20°C.

Double-stranded libraries were constructed from purified extracts using the NEBNext® Ultra™ II DNA Library Prep Kit (New England BioLabs). End repair was performed through incubation of NEBNext Ultra II End Prep Enzyme Mix and Reaction Buffer at 20°C for 30 minutes, followed by 65°C for 30 minutes. Adapter ligation was then conducted using either the NEBNext® Adapter (n = 9; LZA03, LZA04, LZA05, LZA06, LZA07, LZA09, LZA10, LZA11 and LZC02) or the KAPA Universal Adapter (n = 5; LZC05, LZC12, LZC13, LZC15 and LZC16) incubated with NEBNext Ultra II Ligation Master Mix and Ligation Enhancer at 20°C for 15 minutes.

For samples prepared with the NEBNext® Adapter we performed uracil-DNA glycosylase (UDG) treatment using USER® Enzyme, which was incubated at 37°C for 15 minutes after ligation. This USER-treatment serves to excise uracil, and is likely responsible for obscuring the expected damage pattern at the 5' end (see Fig. S1), which has also been documented in other studies (*3*, *64*, *65*).

Adapter-ligated DNA was then purified using Qiagen MinElute columns, and eluted in 40 µl NF water. PCR amplification was performed with unique dual-indexes using AMPLITAQ GOLD 360 MASTER MIX, with Index Primer and Universal PCR Primer, followed by purification using SPRIselect. Libraries were sequenced on an Illumina NovaSeq S4 platform (paired-end, 2×150 bp) at Annoroad Gene Technology, Beijing.

***University of Oxford***

Laboratory work for central Eurasian samples (*i.e.,* Kent and Botai; n = 2) was carried out in an ultra-clean laboratory facility at the University of Oxford (Oxford, UK). Powder was generated from tooth/petrous samples using a Dremel® diamond drill at a low-speed to avoid overheating. DNA was then extracted from ~50mg of bone powder using a protocol optimised for the recovery of ultra-short DNA molecules (*66*), and converted into double-stranded DNA libraries using the blunt-end single-tube (BEST) protocol (*67*). Purified libraries were then dual-indexed through the addition of unique 6 bp barcodes to 5'/3' ends (*68*), with PCR amplification optimised through qPCR to reduce clonality and maximise complexity. Concentration, and fragment size distribution of purified, amplified libraries were estimated on a Qubit™ 3 Fluorometer using high-sensitivity dsDNA standards, and an Agilent 2200 TapeStation using the high-sensitivity D1000 marker, respectively. Libraries were purified using SPRIselect, and deep sequenced on a NovaSeq S4 platform (2×150 bp) at Novogene.

***University of Copenhagen***

At the cleanlab facilities of the Globe Institute in Copenhagen (Copenhagen, Denmark), a petrous bone was extracted from the Khatystyr Cave sample (Khatystyr1_9682; n = 1), and a new DNA extract was generated from the previously-extracted (*1*) Lake Baikal dog rib (Baikal_6900; n=1).

Both extractions were performed on bone subsamples with an overnight digestion in EDTA µL (0.5M, pH8), Urea µL (1M), and Proteinase K µL (10ng/µL) according to (*69*). Subsequently, single stranded Illumina libraries were built with the Santa Cruz Reaction Protocol (v3.1.1) (*70*) and purified with Monarch columns. The libraries were then amplified and indexed using KAPA HiFi HotStart (1 U/µL) and 15 PCR cycles. Two separate pairs of Illumina index sequences were used for each sample of dual for multiplexing. Sequencing was performed on the libraries with Illumina's NovaSeq Platform at the The GeoGenetics Sequencing Core.

***Ludwig Maximilian University (LMU), Munich***

Additional laboratory work for the Botai individual was performed in ultra-clean facilities of the Department of Veterinary Science at Ludwig Maximilian University, Munich. A petrous bone was sectioned into fragments using a hand drill, pulverized using a mechanical press, and finely ground using a Retsch MM400 (Retsch, Germany) swing mill. To minimize contaminant DNA, samples were subjected to a pre-lysis bleaching step (*71*, *72*), specifically a 15-minute incubation in 1mL bleach (0.25% NaOCl), followed by two washes (vortexed and centrifuged at 3,000 rpm for 2 minutes) in 900µl HPLC-grade water, and one final wash in 700µl of 0.5M EDTA (pH 8.0). DNA was then extracted from the remaining powder using 975µl of extraction buffer (0.45M EDTA, 0.05% Tween-20) and 25µl of Proteinase K (0.25mg/ml; Thermo Scientific™), incubated at 37°C for 48 hours, with a final 2-hour incubation at 56°C.

Downstream DNA extraction procedures were performed semi-automatically using a Hamilton Microlab StarLet IV liquid handler (Hamilton, Germany) following a modified (*63*) protocol. Specifically, 150µl of lysate was combined with 1560µl of binding buffer (5M GuHCl, 40% 2-propanol, 0.12M sodium acetate, 0.05% Tween 20; (*66*)) and 10µl of washed silica-coated magnetic beads (G-Biosciences). After a 15-minute binding step, the beads were pelleted on a magnet, the supernatant discarded, and the beads washed three times with PE buffer (Qiagen) and air-dried for 3 minutes. DNA was then eluted twice by incubating 30µl of TET buffer (1mM EDTA, 10mM Tris-HCl, 0.05% Tween-20) at room temperature for 5-minutes, with eluate combined for a total extract volume of ~50µL. Two negative controls were included in each extraction round.

Double-stranded Illumina sequencing libraries were prepared from 32µl of each DNA extract using a modified (*68*) protocol. Blunt-end repair was performed by adding T4 DNA Ligase buffer, dNTPs, T4 PNK, and T4 DNA Polymerase, followed by incubation at 20°C for 30 minutes and 65°C for 30 minutes. Products were purified with silica-coated beads and washing buffer PB (Qiagen) with minor volume adjustments to the (*73*) protocol. After washing with PE buffer and air-drying, DNA was eluted with 21µl of TET buffer. Illumina P5 and P7 sequencing adapters were ligated by incubating 20µl of the purified blunt-end product with T4 DNA Ligase buffer, PEG-4000, T4 DNA Ligase, and adapters at 20°C for 30 minutes and 65°C for 10 minutes. Clean-up was performed on a Hamilton Microlab StarLet IV using Sera-Mag SpeedBeads™ (Cytivia) and 80% ethanol washes, followed by elution with 21µl of TET buffer. The libraries were finalized with a fill-in reaction using Isothermal amplification buffer, dNTPs, and BST 2.0 Polymerase, incubated at 65°C and 80°C for 20 minutes each.

Unique dual indices (UDIs) were added to 10µl (out of 30µl) of the library reaction for multiplex sequencing using AmpliTaq Gold™ DNA Polymerase. The amplification protocol included an

initial denaturation at 95°C for 10 minutes, 15 cycles of 95°C for 30 seconds, 60°C for 30 seconds, and 72°C for 1 minute, followed by a final extension at 72°C for 7 minutes. Three library amplifications were obtained and subsequently pooled at equimolar concentrations for shotgun whole genome sequencing (PE, 60bp) on a NextSeq 2000 at the Laboratory for Functional Genome Analysis (LAFUGA), LMU, Munich.

### *Ancient DNA authentication and genotyping*

Paired-end reads were collapsed, and adapters trimmed in LeeLom v.1.2.15 (*74*), with reads shorter than 30 bp discarding using seqkit v.2.3.0 (*75*). Filtered reads were then mapped against the CanFam3.1 dog reference genome (*76*) using the Burrows-Wheeler Aligner (BWA) algorithm v.0.7.17-r1188, specifying the following parameters: *bwa aln -l 16500 -n 0.01*. Mapped reads were sorted, and filtered to exclude PCR duplicates, as well as reads with low mapping quality (Phred <30). DNA damage patterns were then assessed using mapDamage v.2.1.0 (*77*), to authenticate sequences as ancient (Fig. S1).

We combined our ancient data (ranging between 0.01–5.37x) with publicly-available genomes from 57 ancient dogs (Table S1), as well as 160 modern canids (Table S2). Modern genome data was obtained from the National Institute of Health's dog project VCF: https://research.nhgri.nih.gov/dog_genome/data_release/index.shtml, which were genotyped using GATK standard practices (*78*). Ancient BAMs were processed using ANGSD v.0.937 (*79*), with pseudohaploid genotype calls generated using a custom script. Specifically, for each site a random base (with Phred >20) was selected at random, excluding variants within the first/last 5bp of each reads, and limiting variants called in ancient individuals to those represented in the modern reference panel.

To reduce the impact of DNA damage, we used PLINK v1.90b6.21 (*80*) to restrict our dataset to transversion sites, and filtered for sites with low minor allele frequency (--maf 0.01) and strong linkage disequilibrium (--indep-pairwise 10kb 1 0.5). This resulted in a final dataset of 2,030,128 transversions.

### *Principal component analysis*

Principal Component Analysis (PCA) was performed using smartpca (EIGENSOFT v.8.0.0; (*81*)), with ancient samples projected onto eigenvectors constructed from high-quality modern samples (''lsqproject: YES'') (Fig. S4). The outgroup (*i.e.,* coyote) was excluded. To assess population structure across Eurasia, we calculated outgroup-f3 statistics using struct-f4 package (*82*) for every possible comparison of ancient and modern dog, and both TepeGhelaGap_5826 (West Eurasian) and Zhokhov_9515 (Arctic) (Fig. 1C), as well as the Botai_5169 and Khatystyr_9682 dogs (Fig. 2A–B), with the Coyote used as an outgroup.

### *D-statistics and F4-ratio*

We tested for specific gene flow events using D-statistics as implemented in admixr. Significance was determined using p-values derived from Z-scores, after adjusting for multiple tests (i.e., Benjamini Hochberg adjustment), at a threshold of 0.01. We first tested for gene flow between

ancient East Asian/Steppe dogs using D-statistics of the form: D(Coyote, X, Y, Z); where X = either TepeGhelaGap_5826 (West Eurasian; Fig. S13; Table S14) or Zhokhov_9515 (Arctic; Fig. S14; Table S15), Y = ancient East Asian/Steppe dogs, and Z = published ancient West Eurasian dog genomes (see Table S1 for population labels). Significantly negative D-statistics indicate an excess of allele sharing between either West Eurasian or Arctic dogs, and the East Asian/Steppe dog being compared. To quantify the proportion of West Eurasian ancestry in Steppe and East Eurasian (both modern and ancient Arctic and East Asian) dogs we performed f4-ratio analysis in admixr, where A = Basenji, B = TepeGhelaGap_5826, X = ancient East Eurasian dog, C = Zhokhov_9515 or Baikal_6900, and O= Coyote (Fig. S9; Table S11).

We also tested for West Eurasian gene flow into exclusively ancient East Asian dogs and dingoes using D-statistics of the form: D(Coyote, TepeGhelaGap_5826, X, Y), where X = ancient East Asian, and Y = a pre-European contact dingo (dated to between 802-870 years calBP) from the Nullarbor Plain in southern West Australia (*8*). Dingoes are thought to contain varying levels of West Eurasian ancestry due to post-colonial gene flow with introduced European dogs (*8*). With the exception of Dingo08, all dingoes were non-significant, indicative of "pure" East Asian ancestry (Fig. S6; Table S8).

Next, we tested for gene flow from Baikal Arctic and Eneolithic Steppe dogs into Neolithic East Asian dogs using D-statistics of the form: D(Coyote, X, Y, Jinchankou/Yabeili); where X = Arctic dog lineages, specifically PadKalashkinova_7000, ShamankaII_7400, and Baikal_6900, and Y = dingoes without European dog ancestry (Fig. S7; Table S9)

We also tested for gene flow from Western Eurasian dogs into Botai using D-statistics of the form: D(Coyote, X, Botai, Zhokhov); where X represents ancient Western dogs (Fig. S8; Table S10). Here, significantly negative D-statistics (Z-score > 3) indicate gene flow from West Eurasia into the central Eurasian steppe.

***qpAdm and qpWave analyses***

We used *qpAdm* and *qpWave* to test ancestry models and estimate ancestry proportions. We used the allsnps option (allsnps: YES) to maximize the number of SNPs used in overlapping for each combination of f-statistics. We first ran models with four sources: TepeGhelaGap_5826 (representative of Western ancestry), Dingo07 (representative of East Asian ancestry), Baikal_6900 (representative of Arctic ancestry in southern Siberia), Zhokhov_9515 (Arctic ancestry in Northern Siberia).

We used an ancient Iranian dog genome (TepeGhelaGap_5826) as the source for Western ancestry for these analyses for several reasons: 1) its geographical proximity to the region of Caucasian Hunter-Gatherer (CHG) ancestry, which constitutes the majority of Western human ancestry in Steppe pastoralists (*83–85*); 2) its superior coverage compared to other available ancient, early, Near Eastern genome (i.e. TelHreiz1_7000); 3) as opposed to Mesolithic/Neolithic European dog genomes, it does not possess any Arctic dog ancestry (*2*). Substituting the 2,300 years old dogs from Ashkelon (Ashkelon1_2300, Ashkelon2_2300, Ashkelon3_2300) instead of the TepeGhelaGap_5826 in our *qpAdm* analysis led to very consistent estimation of ancestry proportion across all ancestries (Fig. S15).

We used a "pure" dingo (Dingo07) as representative of East Asian ancestry as previous studies have shown they represent an early offshoot of the East Asian population which, as a result of its isolation in Australia for the majority of its history, was not affected by admixture from Arctic or Western dogs ((Souilmi et al. 2024); see above). Outgroup-f3 analyses also show that dingoes represent the closest individual to early East Asian dogs in our dataset (i.e. a Neolithic dog from Yabelii). Lastly the Zhokhov and Baikal dogs were used as a source of Arctic ancestry as in previous studies (*1–3*).

We used the following genomes as reference populations: Coyote08 (California coyote), Basenji, PortAuChoix_4500, a Greenland dog, and Skoteini_6544 (ancient greek genome; see (*1*)). We used *qpWave* for models with one source (Table S7). We found evidence for Zhokhov_9515 ancestry solely in Khatystyr_9682 and Bolgar_1000. Given the prevalence of Baikal_6900 like ancestry as a source we thus simplified our model removing Zhokhov_9515 as a source and kept Baikal_6900 as the only source for arctic ancestry (Table S6). For each dog we ranked the model based on their p-value, prioritizing a simpler model, with fewer sources i.e. if the p-value for the nested model when one or more sources was dropped was higher than 0.01.

### *ADMIXTUREBAYES*

We then tested models of admixture in a Bayesian framework using AdmixtureBayes (*34*). First, we generated TreeMix format allele frequencies (which AdmixtureBayes requires as input) using the plink2treemix.py script (https://github.com/thomnelson) and the following populations: Arctic (Baikal_6900, Botai_5169, Khatystyr_9682, PortAuChoix_4500, and Zhokhov_9515), East Asia (Dingo, Jinchankou03_3917, Huoshiliang11_3917), Western (TepeGhelaGap_5826), and an outgroup (Coyote). We ran *runMCMC.py* with 10 chains (*--MCMC_chains* 10) and 500,000 iterations (*--n* 500000) for 4 admixture events (*--max_admixes*). To evaluate convergence of the Markov Chain Monte-Carlo sampler, we utilized the *EvaluateConvergence.R* script (with convergence reached at ~200,000 iterations for each chain). We then analysed the output of the Markov chain using *analyzeSamples.py*, with 50% of the run discarded as burn-in (*--burn_in_fraction* 0.5), and thinning to every 10th run (*--thinning_rate* 10). The filtered output was then used to generate the topology with the highest posterior probability and branch estimates for each number of admixture events (*--top_trees --estimates*) (Fig. S10), as well as a consensus topology (*--consensus_trees*) that contained only branches and admixture events with >99% posterior probability (*--consensus_thresholds* 0.99), with admixture proportion and confidence reported for both (*--write_rankings*). Despite allowing four admixture events, we found that two: one from Western (TepeGhelaGap_5826) into Bronze Age Northwest Chinese (Huoshiliang11_3917) and Eneolithic Steppe (Botai_5169) dogs, respectively; was the most parsimonious (Fig. 3B).

### *DATES*

To estimate the timing of admixture events, we utilized the Distribution of Ancestry Tracts of Evolutionary Signals (DATES) algorithm (*33, 86*) (Fig. S11-12). For both Bronze Age Northwest Chinese (Haizang and Huoshiliang) and Eneolithic Steppe (Botai) dogs, we used the following two reference ancestries: East (ancient Baikal_6900, Jinchankou03_3917, Khatystyr1_9682,

PortAuChoix_4500, and Zhokhov_9515, as well as contemporary "pure" Dingoes and a Greenland dog), and West (ancient TepeGhelaGap_5826 and Basenji) Eurasian. Alongside the default parameters, we specified a starting genetic distance of 0.45 centimorgans ("lovalfit: 0.45"), and enabled block jackknife estimation of standard error across chromosomes ("jackknife: YES"). Estimates of admixture timing were then converted into years assuming the 3 year generation time widely used for dogs (*76*), as well as years BP through adding the mean calibrated radiocarbon age. With the exception of Huoshiliang11_3917, results for all Bronze Age Northwest Chinese dogs were significant (Z>3) and visual inspection of the exponential distribution fitted to the covariance decay curve suggested a good fit (Fig. S12). The exponential distribution did not fit well to the covariance decay curve in the case for the Botai or Jirentaigoukou Steppe dogs (Fig. S12) suggesting that either the TepeGhelaGap_5826 does not provide a suitable proxy for the component of West Eurasian ancestry found in these dogs, or that too many generations have elapsed since admixture.

### *ADMIXTURE analysis*

We ran a supervised ADMIXTURE analysis using ADMIXTURE v.1.3 (*19*) with the same input file as for the PCA. We modelled two distinct ancestries (K = 2), West (Ashkelon1_2300, Ashkelon2_2300, Ashkelon3_2300, TepeGhelaGap_5826) and East (Dingo04, Dingo07, Dingo10, Zhokhov_9515, PortauChoix_4157 and Baikal_6900) Eurasian. The proportion of Western ancestry in Eastern Eurasian individuals was similar to the estimate obtained by qpAdm (Fig. S5), except for Khatystyr_9682, which was inferred to possess ~45% Western ancestry by ADMIXTURE. This is likely to be an artefact of ADMIXTURE given that D-statistics of the form D(Coyote, TepeGhelaGap_5826, Khatystyr_9682, Zhokhov_9515) were not significant (|Z| = -1.599; p-value = 1.0; Table S11), and ADMIXTUREBAYES did not find evidence of admixture from Western populations in this sample.

### *Shared Dog-Human Population Histories*

To assess similarities in population structure between dogs and humans, we utilised genome-wide data for 18 ancient humans (*6*, *13*, *15*, *18*, *22*, *25*, *33*, *87–89*) from the AADR database (*90*) that correspond to similar (and in most cases the same) cultural, geographic and temporal archaeological contexts (see section below on expected human ancestry and Fig. 4). We performed PCA using emu v.0.9 (*91*) for both the dog and human datasets independently. The results were then standardized (scale() function), and aligned to each other using procrustes transformation (procrusted function in vegan package) in R.

### *Expected human ancestry*

***Baikal region***. The earliest ancient human genome in the region is from the Mal'ta boy (~24,000 years BP; (*92*)), which belongs to the Ancient North Eurasian (ANE) lineage, which was recently renamed Ancient North Siberian (ANS) due to its close relationship with a 30,000 years BP individual from Yana RHS in Northeast Siberia (*6*). ANS ancestry persisted in the region at least until 18,000 years BP in Afontova Gora (*93*). Later genomes from the Mesolithic/Neolithic period

(~7,000 years old) from Shamanka and Lokomotiv possess Northeast Asian ancestry (*15*). As the Baikal dog was recovered from a Mesolithic/Neolithic hunter-gatherer context (~7,000 years BP), a few hundred km from Shamanka and Lokomotiv (Pad Kalashnikova, Fig. 1 in (*94*)), we infer the ancestry of the associated humans was largely Northeast Asian (Fig. 4).

***Zhokhov Island***. The closest archaeological sites with early human genomic data from the island of Zhokhov are: (1) Yana RHS (~30,000 years old) which is ~800 km Southwest of Zhokhov Island near the North East Siberian coast, and (2) Kolyma (Duvanny Yar, ~10,000 years old) which is ~900 km Southeast of Zhokhov island, also near the North East Siberian coast. Humans at Yana carried Ancient North Siberian (ANS) ancestry, whereas those at Kolyma carried Ancient Palaeo-Siberian (APS; (*6*)) ancestry. Sikora et al. 2019, suggest that there was an ancestry turnover in the region before 10,000 years ago where ANS ancestry carrying human populations were replaced by incoming APS populations. Given that the Zhokhov dog is ~9,500 years old, we infer that the ancestry of people living on Zhokhov island likely carried APS ancestry (Fig. 4).

***Khatystyr Cave***. The closest archeological site with ancient human genomic data from this time period (~9,700 years BP) is Dzhylinda in Buryatia (trans-Baikal region), ~400km Southwest of Khatystyr Cave (*18*). The Dzhylinda-1 individual dating back to ~8500 years BP shared strong genetic affinity with the Kolyma individual (see above), which carried Ancient Palaeo-Siberian (APS) ancestry (*6*).

***Port au Choix, (North America)***. See (*4*) and (*5*) for details on dog-human movement into the Americas. Gene flow between ANS and APS formed the basal American ancestry (*6*). Following a period of isolation, possibly in western Beringia or northeast Asia, this population moved into North America, and diversified into the Ancient Beringians (AB) and Ancestral Native Americans (ANA) individuals (*95*). As the Port Au Choix dog is descended from the first wave of dogs which colonized the Americas over 20,000 years BP, we use the AB ancestry from a ~9,000 years BP individual recovered from Trail Creek Cave on the Alaskan Peninsula as a representative of early Native Americans (*96*).

***Botai.*** Analysis of 3 Copper Age human individuals (~5500–5300 years BP) at the site of Botai indicated they possessed Eastern Hunter-Gatherer (EHG) ancestry (*15*). These individuals form part of an ancestry cline towards Neolithic hunter-gatherers of central Asia, which are all a continuation of the ANS population (i.e. Mal'ta boy and Yana RHS). As the Botai dog was recovered from the same context, we infer EHG ancestry for the associated human population.

***Veretye***. Multiple studies have analysed the genome of hunter-gatherer individuals from Karelia that are contemporary with the Veretye dogs, all of which possess Eastern Hunter-Gatherer ancestry (*24–26*), referred to as Sidelkino ancestry in (*24*).

***Gansu Province (Jinchankou and Haizang).*** During the Early Neolithic (9,500–7,500 years BP), populations in the Upper Yellow River possessed both Northeast Asian and local Neolithic farmer ancestries (*14*), with later contribution (~3,900 years BP) from ancestries linked to the northward spread of rice agriculture from southern China (*22*, *97*). This mix of Northeast Asian and East Asian ancestries is found in the humans at Jinchankou. Later, during the Iron Age (~3,000–2,000 years BP), populations in the Gansu and Qinghai regions were connected to those in the Xinjiang Province through the Hexi Corridor, which led to an increase in Western Eurasian Steppe-related ancestry (*13*, *16*). The closest Iron Age archaeological site to the Haizang dogs was the Upper Yellow River site of Dacaozi (*22*).

***Xinjiang Province (Jirentaigoukou).*** Middle to Late Bronze Age (~3,000 years BP) human populations in Xinjiang (e.g. Jirentaigoukou) possess ancestry characterized by Andronovo and Sintashta steppe pastoral cultures, which differ from Early Bronze Age herders due to an increased proportion of Anatolian farmer-related ancestry (*13*).

***Iranian Farmers.*** The genetic composition of Europe shifted during the Neolithic due to the spread of farmers from the Zagros region of Iran (*98*). We selected an adult male human from the central Zagros site of Wezmeh Cave (~9,300 years BP) as the closest human population to the Tepe Ghela dog (*98*).

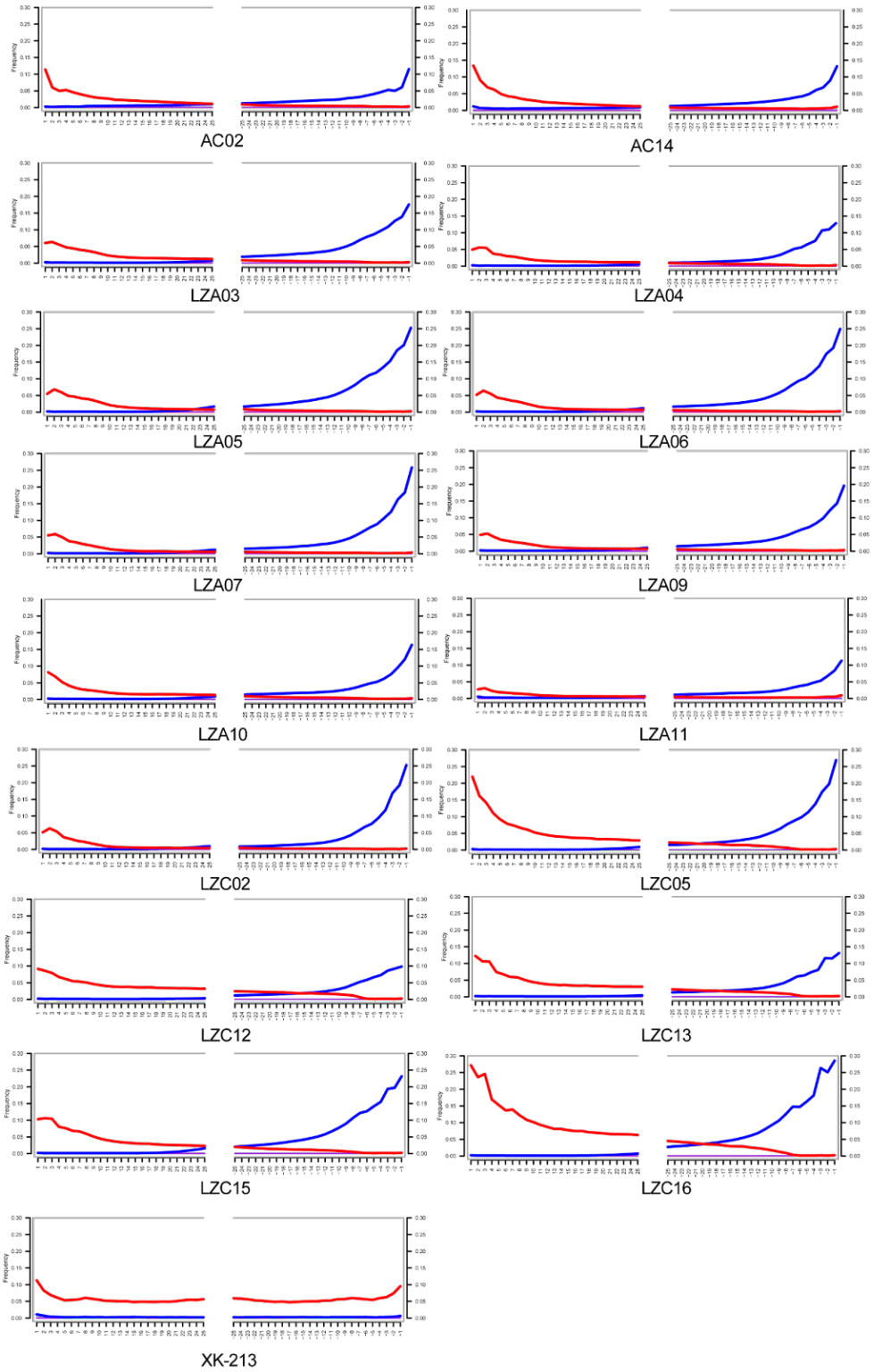



**Fig. S1.**

C-to-T (left, red) and G-to-A (right, blue) substitution frequencies estimated for ancient DNA libraries in MapDamage2. All samples (Table S1) show a characteristic excess of 5' C-to-T and 3' G-to-A substitutions at the start and end of reads respectively, authenticating the DNA as ancient.

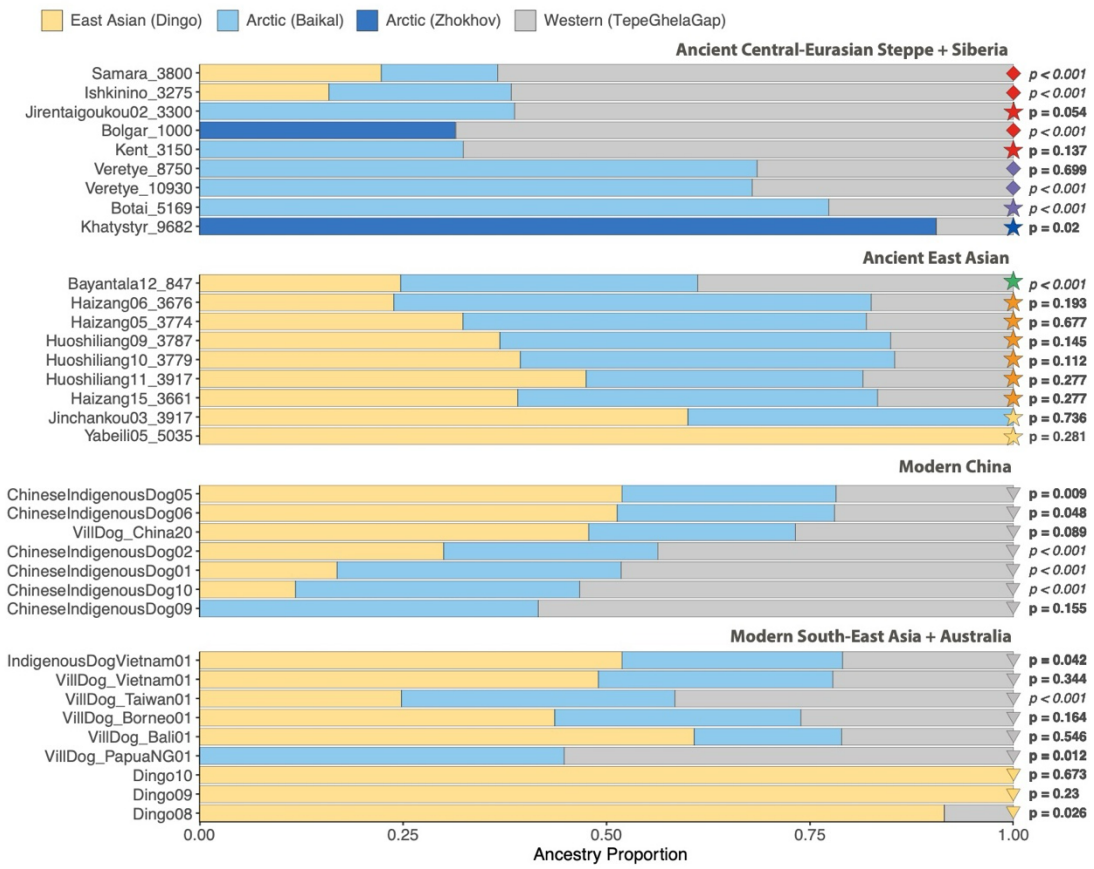



**Fig. S2.**

Proportion of West Eurasian (grey), Basal Arctic (dark blue), Arctic (light blue) and East Asian (yellow) ancestries in ancient and modern East Eurasian dogs estimated using qpAdm for the best model (1 to 4 sources).Ancient samples with <1% genome-wide coverage were excluded. Model selection relied on p-values, with simpler models prioritized when nested models (excluding one or more sources) returned p-values greater than 0.01. For each individual, the ancestry proportions from the model with the highest p-value are presented, even in cases where the model was formally rejected ($p < 0.01$).

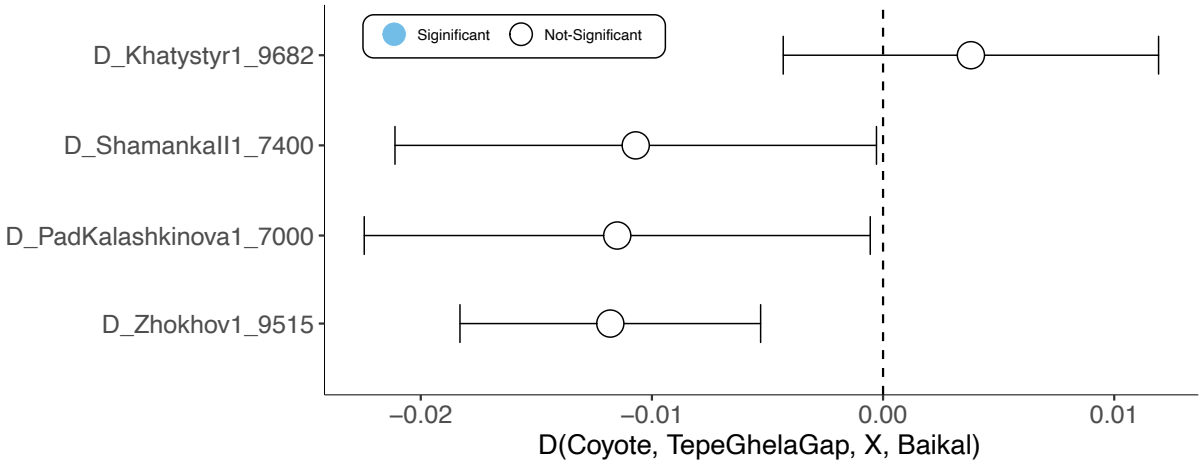
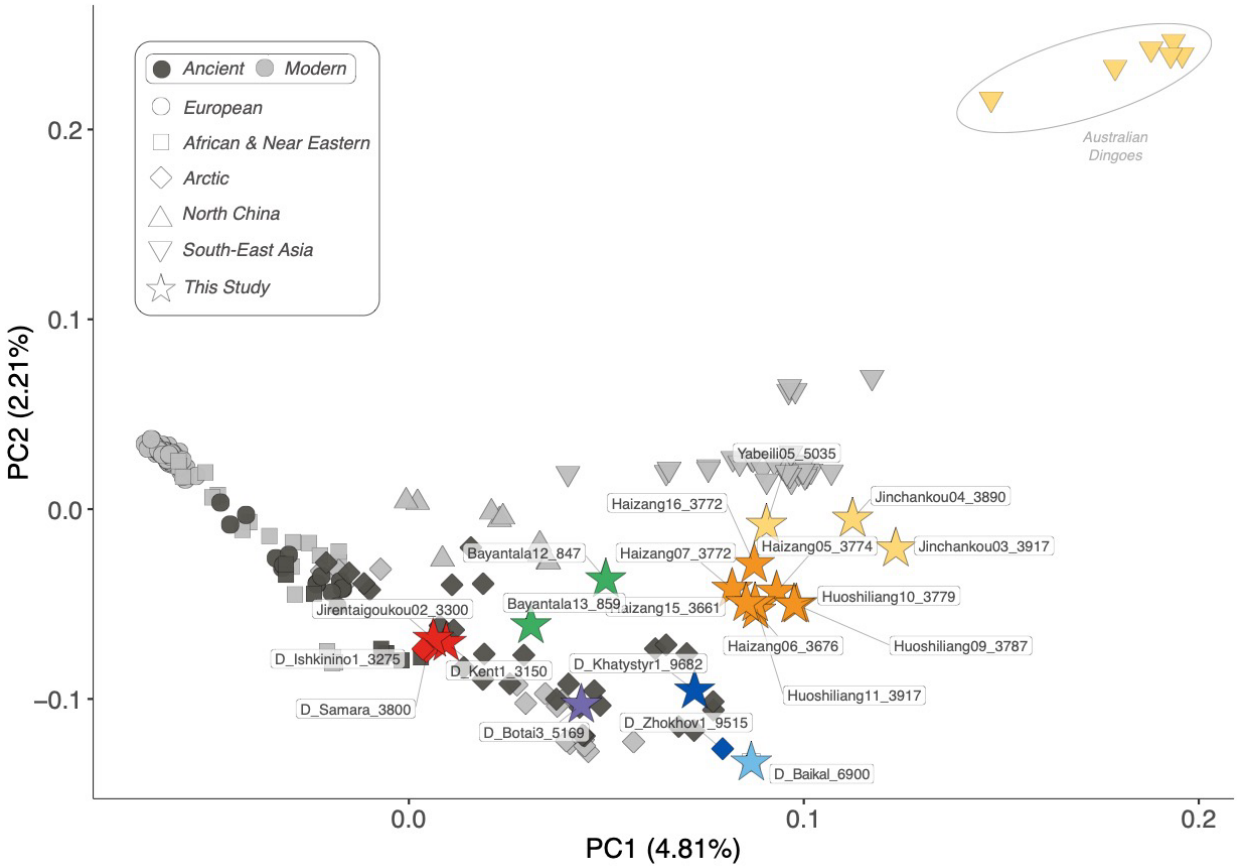



**Fig. S3.**

D-statistics of the form: D(Coyote, TepeGhelaGap_5826, X, Baikal_6900), where X represents ancient Arctic dogs (y-axis). All tests were non-significant (adjusted p-value > 0.01), which indicates the Baikal dog is free of Western dog ancestry.




526

527 **Fig. S4.**

528 Principal component analysis of ancient and modern dogs constructed using smartpca. Ancient
529 samples were projected (see methods). Samples are coloured based on shared ancestry, and both
530 temporal and geographic proximity to the following human groups: Eastern Hunter-Gatherer
531 (purple), Ancient Palaeo-Siberian (dark blue), Northeast Asian (light blue), Central Steppe (red),
532 Neolithic (yellow) and Bronze Age (orange) Upper Yellow River, and Liao Dynasty Mongolia
533 (green). Sample age is given in years before present as a suffix (e.g. Iran_5826).

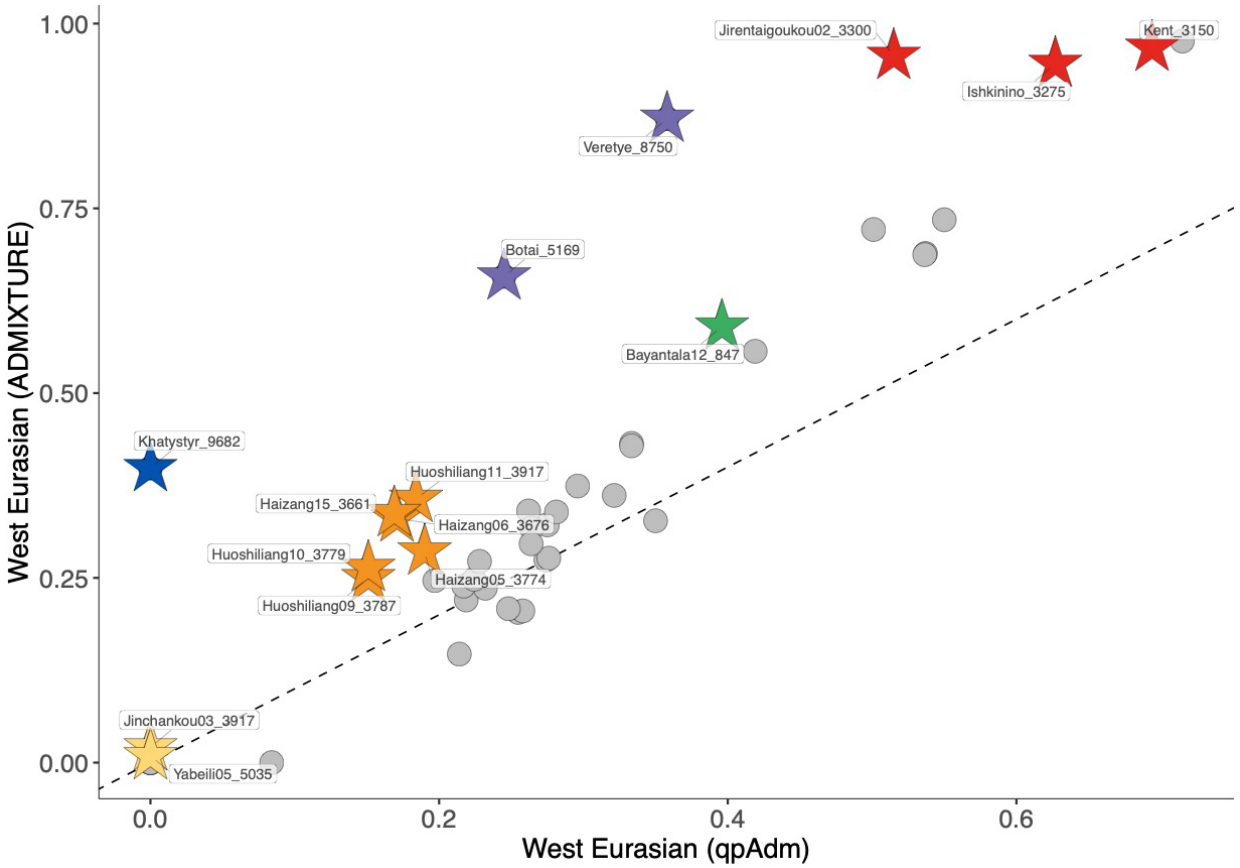



**Fig. S5.**

Comparison of the proportion of West Eurasian ancestry estimated using qpAdm (i.e., Fig. 3B) and supervised ADMIXTURE (K = 2). ADMIXTURE appears to overestimate the proportion of West Eurasian ancestry in the majority of ancient Steppe and East Asian dogs.

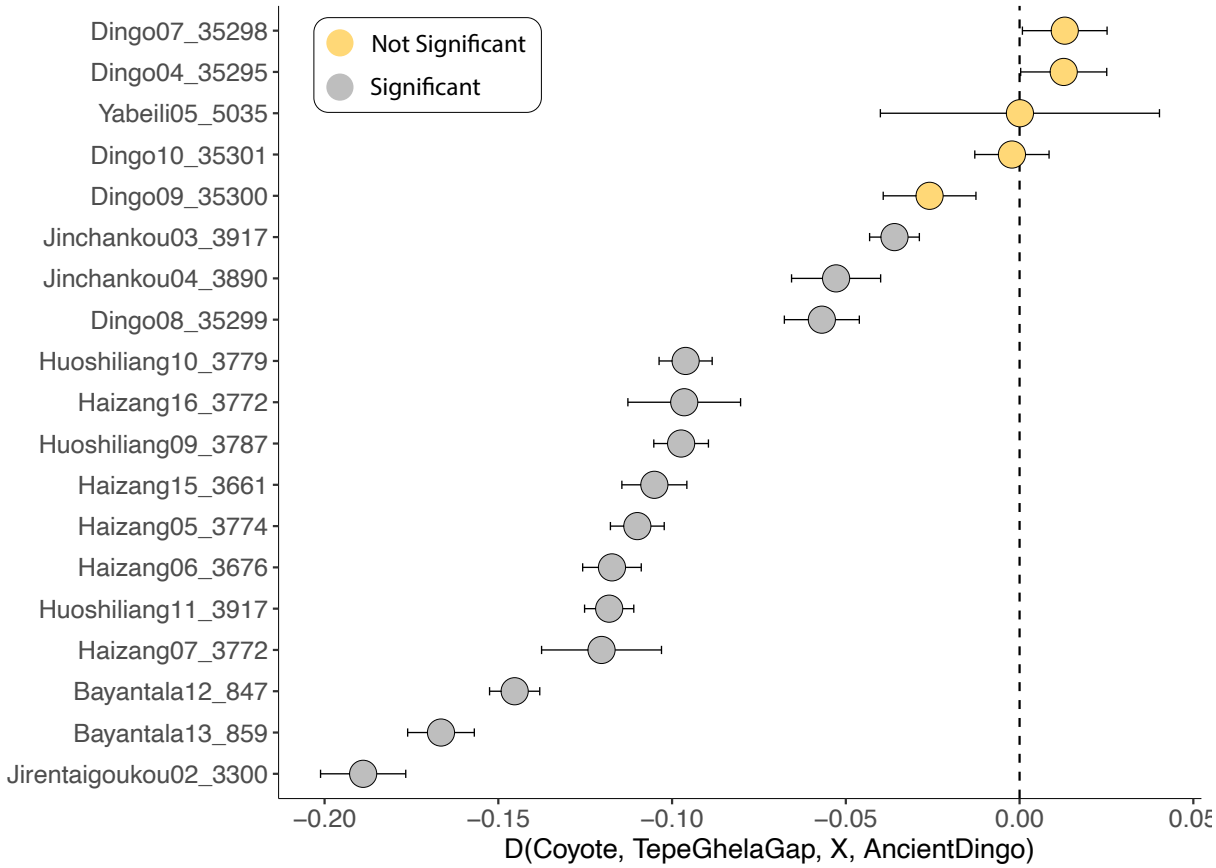



**Fig. S6.**

D-statistics of the form: D(Coyote, TepeGhelaGap_5826, X, AncientDingo) to test for the presence of West Eurasian ancestry in dingoes (X). We used a pre-European contact dingo (dated to between 802-870 years calBP) from the Nullarbor Plain (southern West Australia) as a representative of pure East Asian ancestry. Negative values are expected for dingoes with a component of West Eurasian ancestry, derived through post-colonial gene flow with European dogs. All dingoes except Dingo08 were below the significance threshold (i.e. Z-score <-3), which supports the results of both ADMIXTURE and qpAdm. We therefore excluded this individual from analyses.

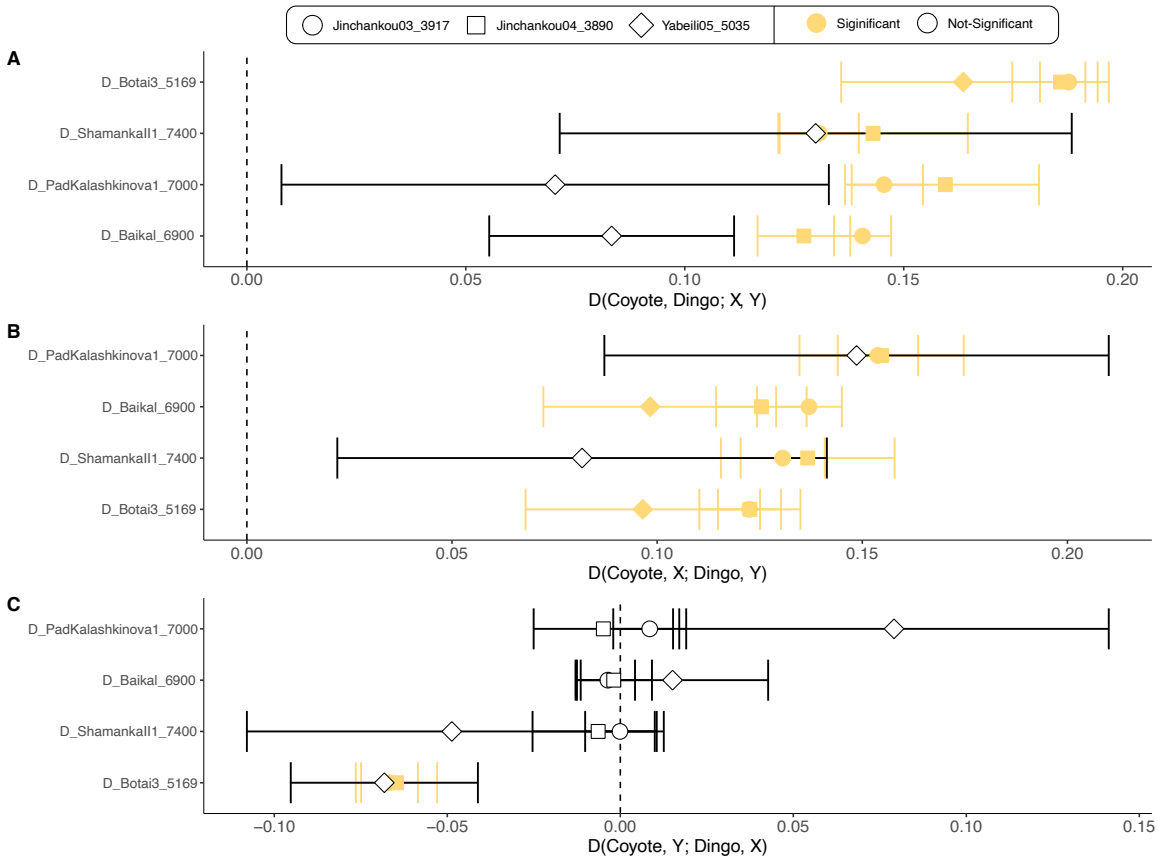



**Fig. S7.** D-statistics of the form: **(A)** D(Coyote, Dingo; X, Y), **(B)** D(Coyote, Y; Dingo, X), and **(C)** D(Coyote, X, Dingo, Y), where Y represents Arctic dog lineages (on the y-axis), and X represents Jinchankou and Yabeili. Filled shapes represent comparisons which exceed the significance threshold ($p<0.01$).

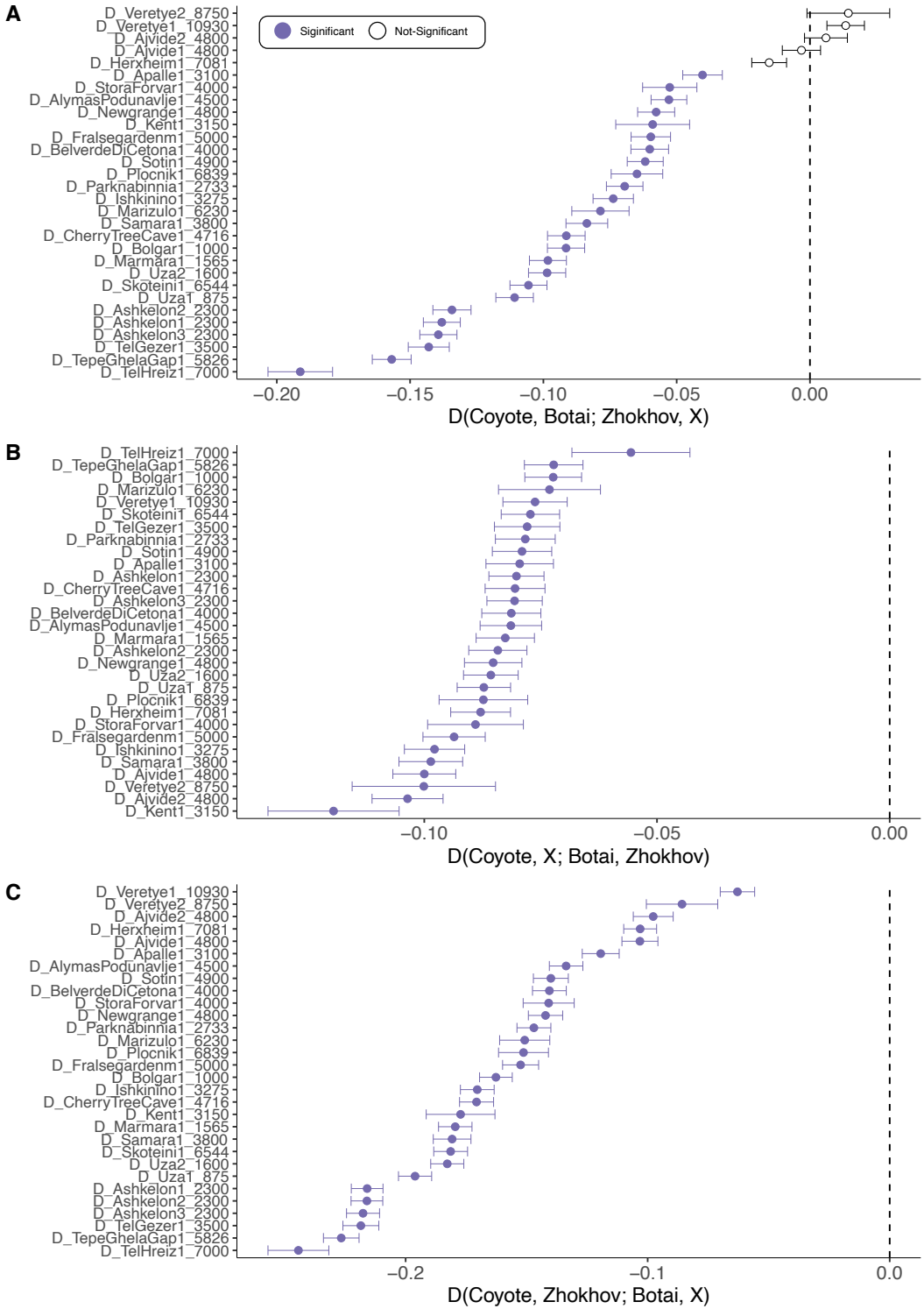



**Fig. S8.**

D-statistics of the form: **(A)** D(Coyote, Botai, Zhokhov, X), **(B)** D(Coyote, X, Botai, Zhokhov), and **(C)** D(Coyote, Zhokhov,Botai, X), where X represents ancient Western dogs, and pre-contact American dogs. Filled shapes represent comparisons which exceed the significance threshold (Z-score > 3). Zhokhov shares more ancestry with Botai compared to other Western dogs (A,C), however, Botai does possess Western ancestry (B).

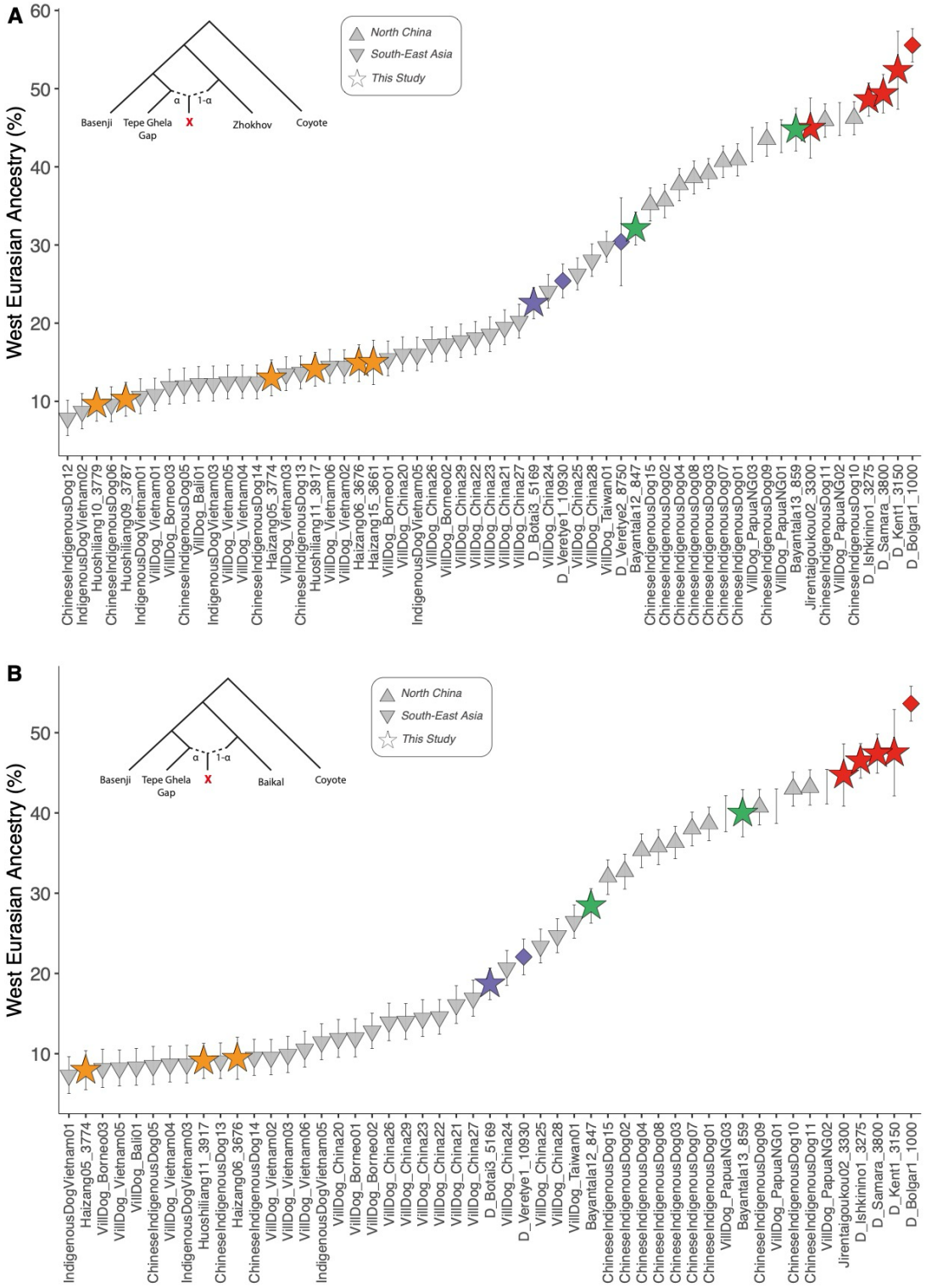



**Fig. S9.**
Proportion of West Eurasian ancestry in East Asian/Steppe dogs estimated using f4-ratio, where A = Basenji, B = Iran_5826, X = Ancient East Eurasian Dog, C = Zhokhov_9515 **(A)** or Baikal_6900 **(B)**, and O= Coyote.

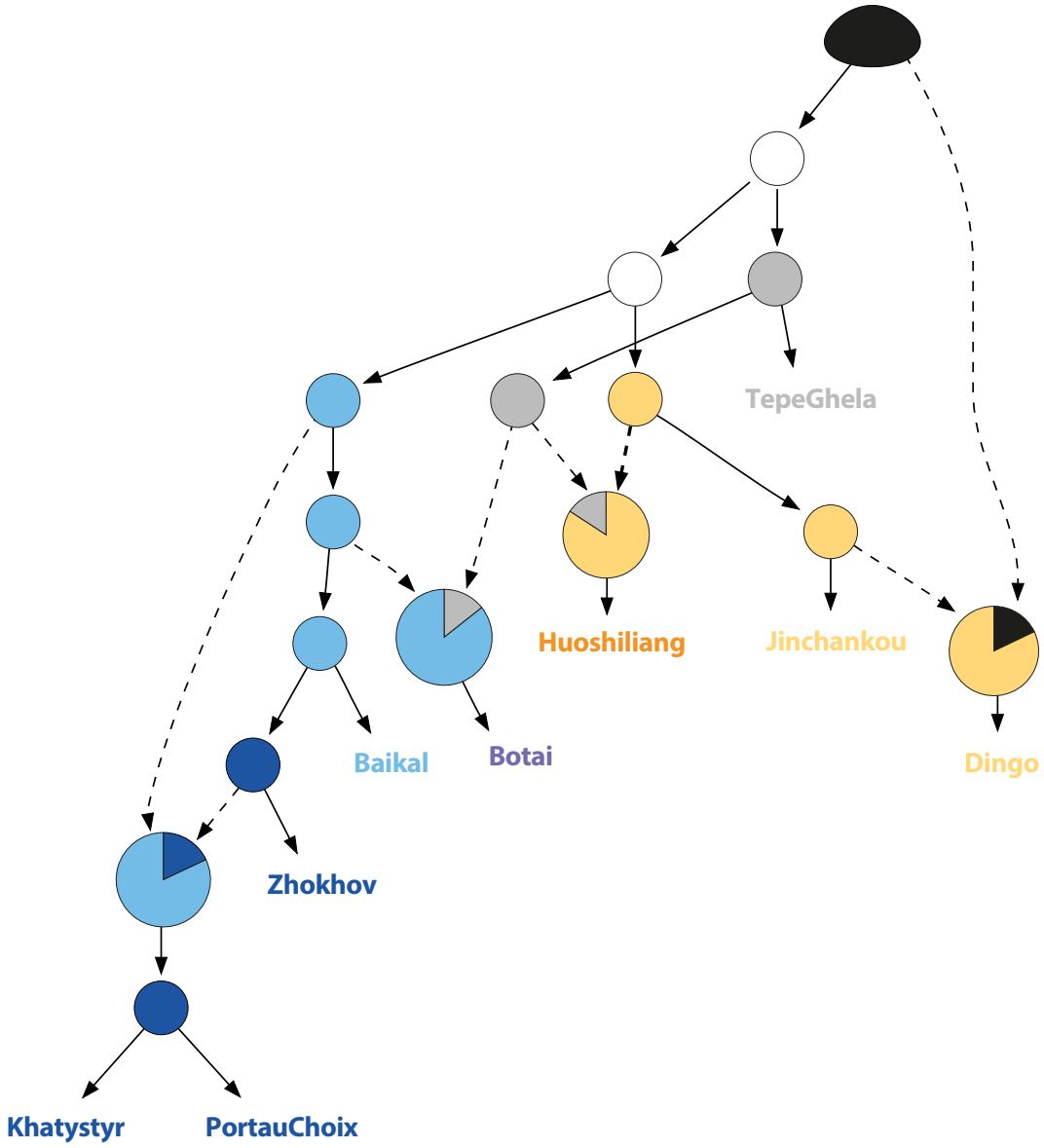



**Fig. S10.**
Topology with highest posterior probability (68.0%) estimated in AdmixtureBayes from high-coverage (1.65–19.6x) ancient dog genomes. The graph shows four admixture events: a basal component (black) into dingoes, a West Eurasian (TepeGhelaGap) into both Eneolithic Steppe (Botai) and in the Early Bronze Age Hexi Corridor (Huoshiliang), and a basal Arctic component into pre-contact American (Port-Au-Choix) and Khatystyr Cave dogs. Ancestry proportions (pie graphs) were estimated in AdmixtureBayes. The consensus topology (i.e. branch and admixture events >99%) is shown in Fig. 3B.

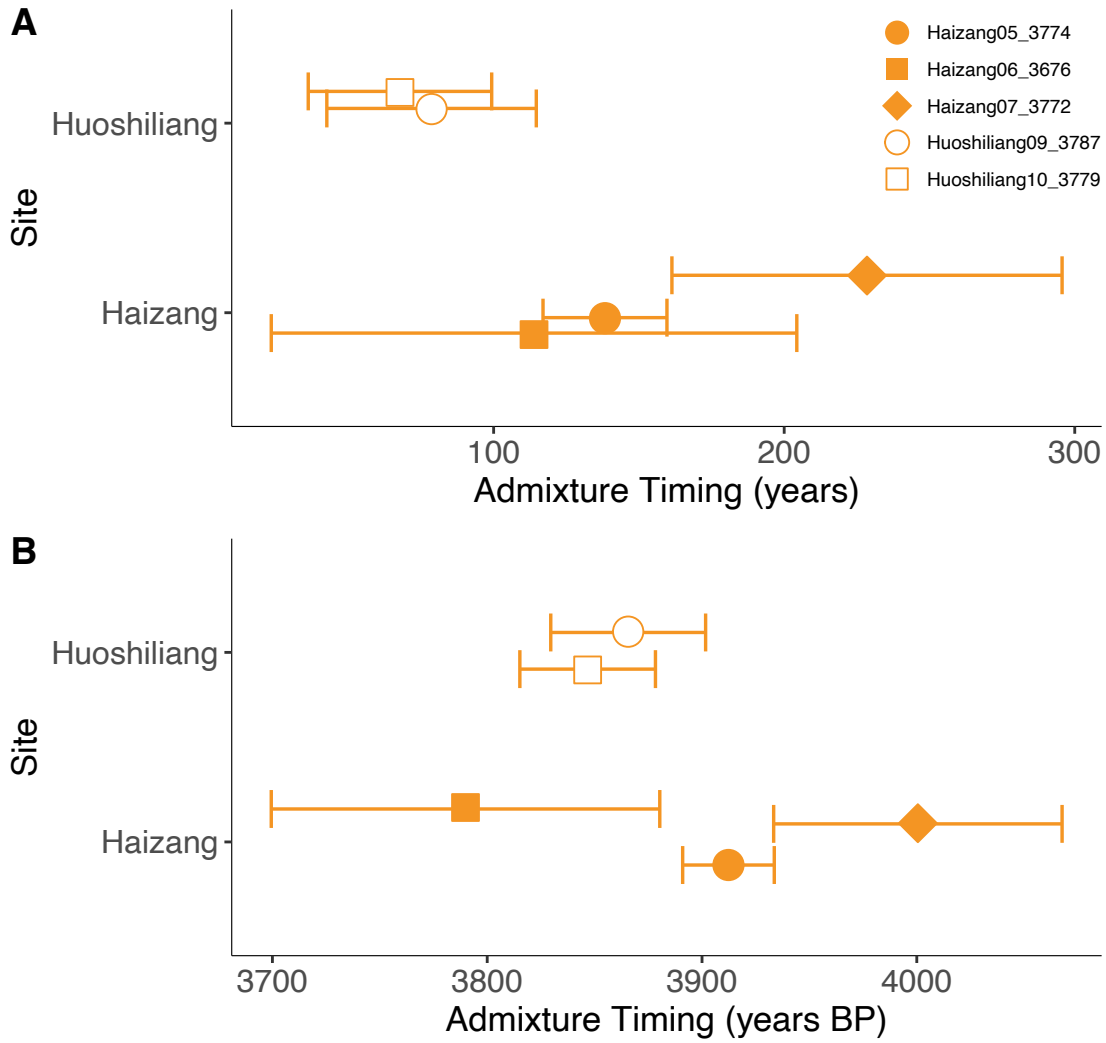



**Fig. S11.** Admixture timing estimates (mean ± standard error based on jackknife) between Bronze Age Northwest Chinese and West Eurasian dogs given in **(A)** years before present, and **(B)** years since admixture.

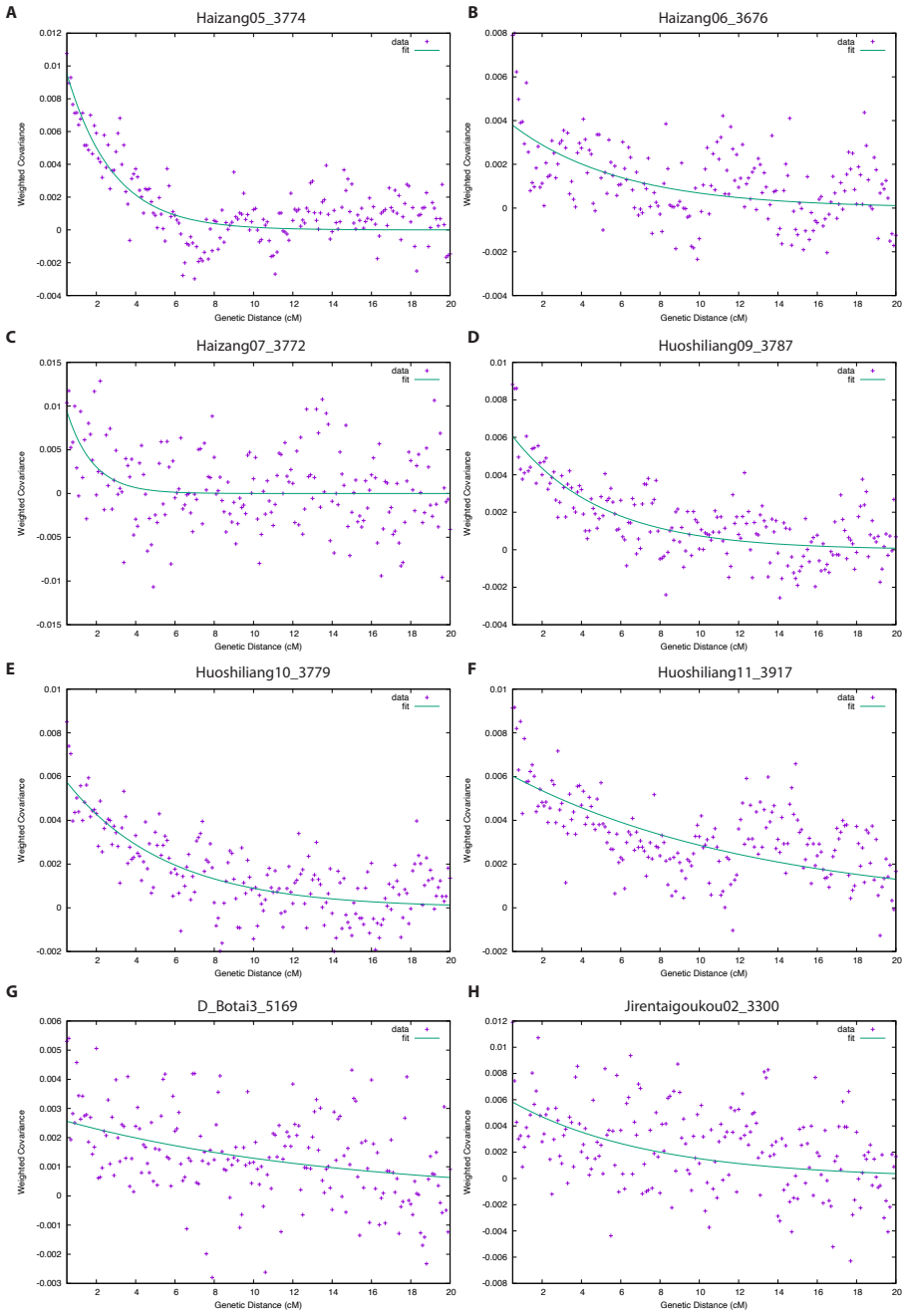



**Fig. S12**.

Coancestry curves for DATES. Results were considered significant at first if Z-score > 2 and normalized root-mean-square deviation (NRMSD) < 0.7. As all of the Bronze Age Northwest Chinese and West Eurasian dogs tested had NRMSD > 0.7 (see Table S13), we then performed visual inspection of the covariance decay curve. This showed that the exponential distribution fitted the decay curve for the majority of **(A–F)** Bronze Age Northwest Chinese dogs (with the exception of Huoshiliang11_3917), which suggested a good fit. In contrast, the **(G)** Botai and **(H)** Jirentaigoukou dogs showed no evidence for covariance decay, which indicates either the TepeGhelaGap_5826 does not provide a suitable proxy for the component of West Eurasian ancestry, or that too many generations have elapsed since admixture.

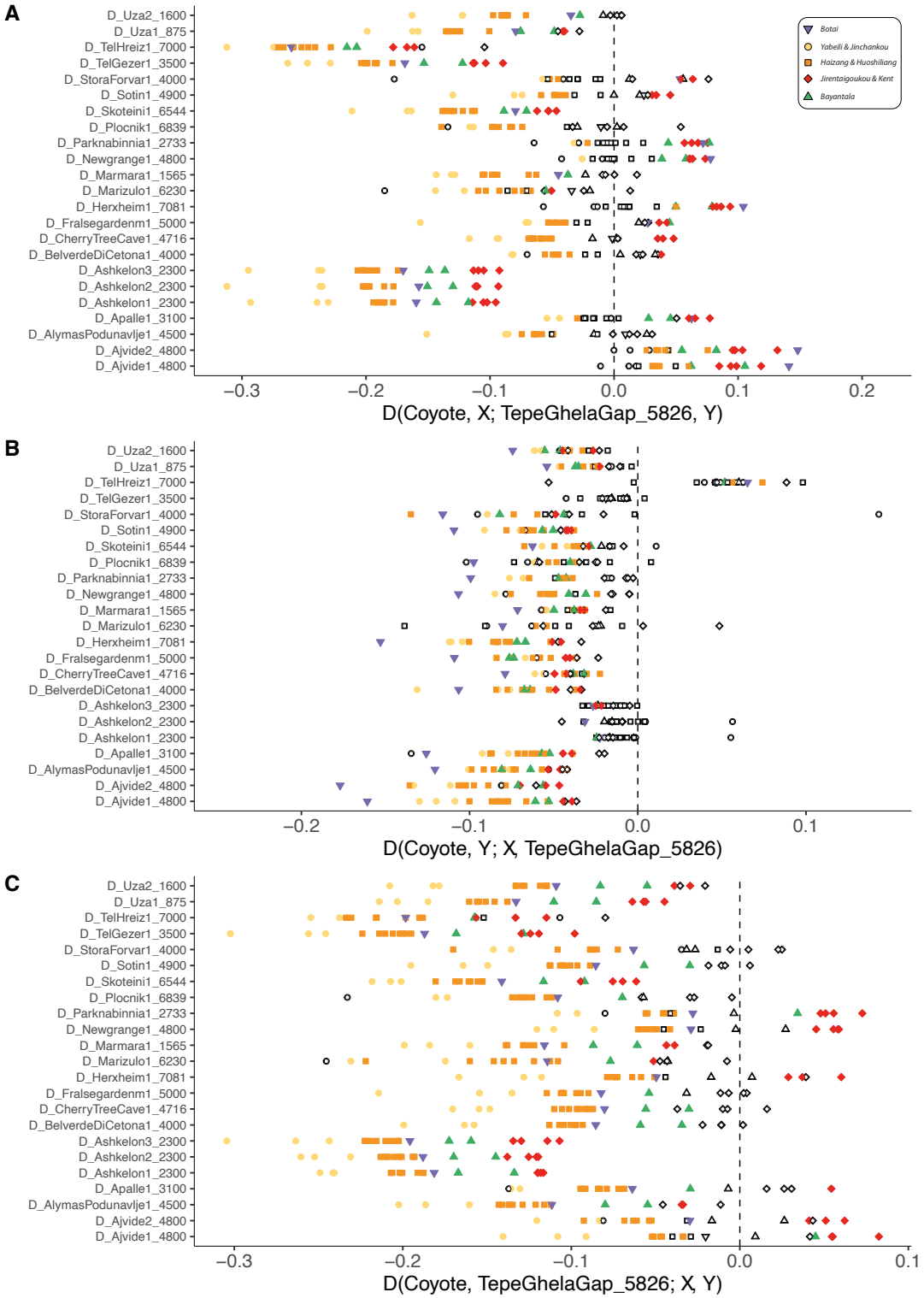



**Fig. S13.**

D-statistics of the form: **(A)** D(Coyote, X, TepeGhelaGap, Y), **(B)** D(Coyote, Y, X, TepeGhelaGap), and **(C)** D(Coyote, TepeGhelaGap, X, Y), where Y represents ancient East Asian and central Eurasian steppe dogs (see inset in A), and Y represents ancient West Eurasian dogs (y-axis).

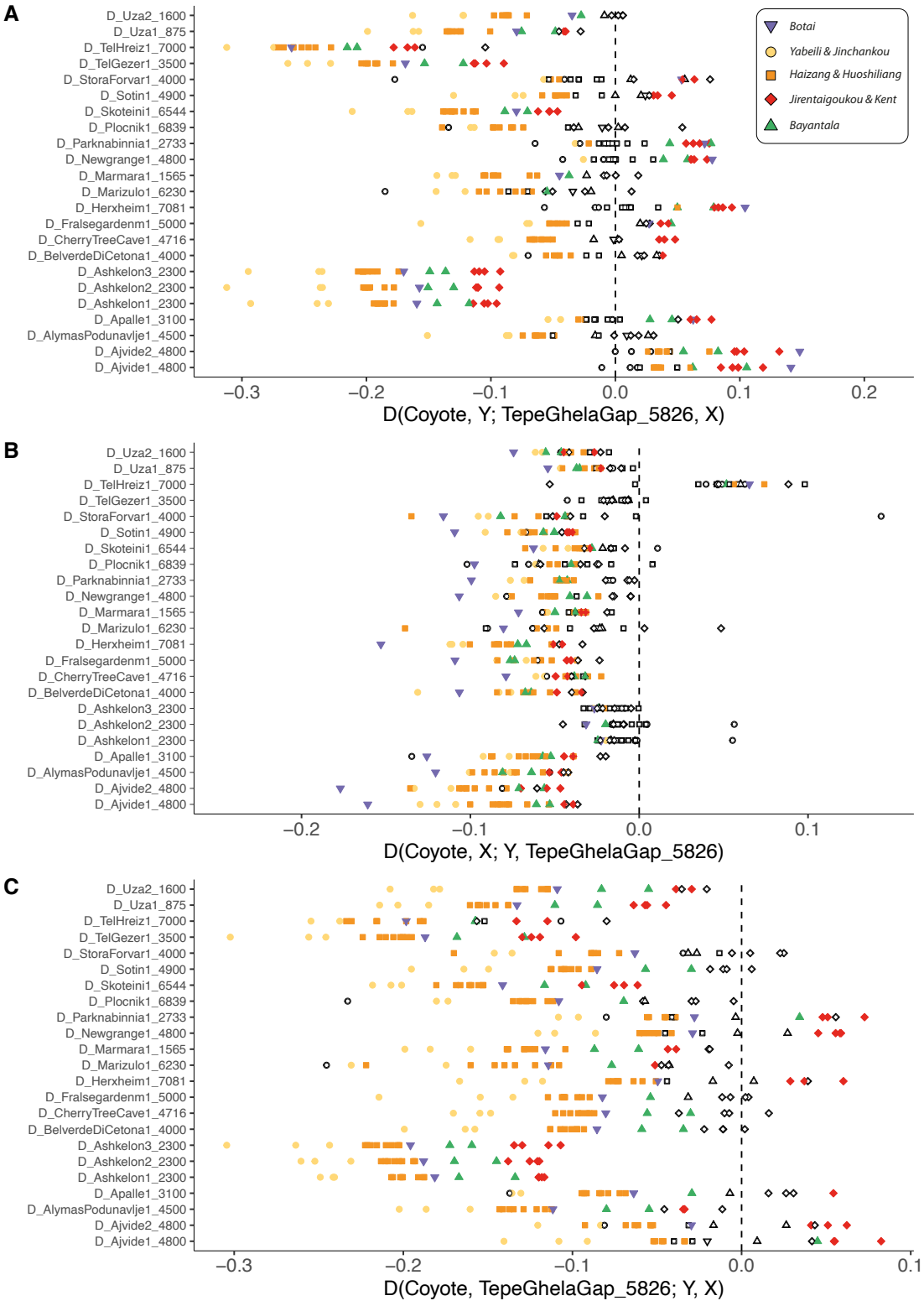



**Fig. S14.**

D-statistics of the form: **(A)** D(Coyote, X, Zhokhov, Y), **(B)** D(Coyote, X, Y, Zhokhov), and **(C)** D(Coyote, Zhokhov, Y, X), where X represents ancient East Asian and central Eurasian steppe dogs (see inset in C), and Y represents ancient West Eurasian dogs (y-axis).

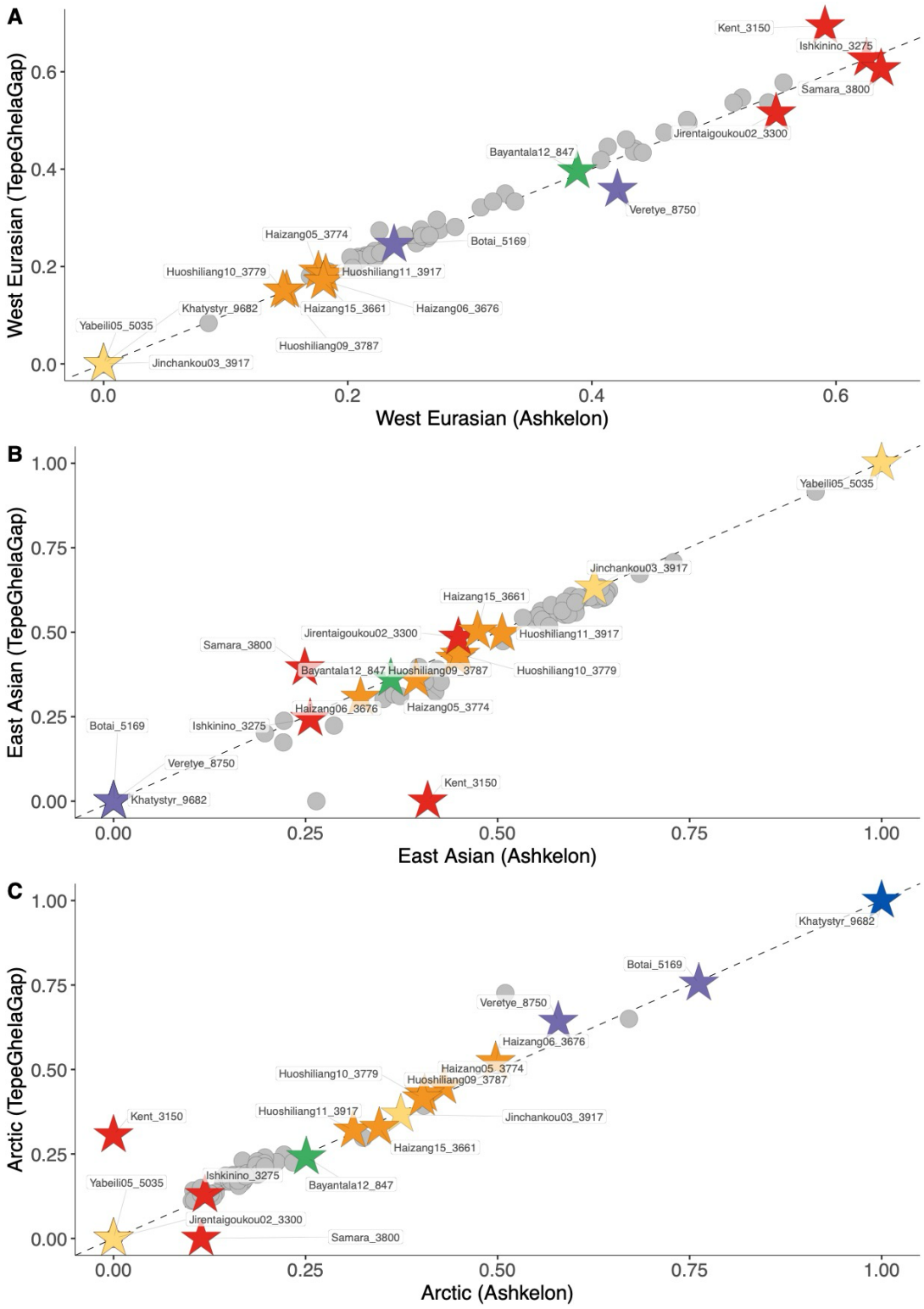



**Fig. S15.**

Comparisons of the proportion of **(A)** West Eurasian, **(B)** East Asian, and **(C)** Arctic ancestries estimated in ancient and modern East Eurasian dogs where the Near Eastern source was either Askelon1_2100, Askelon2_2100, Askelon3_2100 (x-axis) or TepeGhelaGap_5826 (y-axis).

**Data S1. (separate file)**

Type or paste caption here.