DOG DOMESTICATION

Genomic evidence for the Holocene codispersal of dogs and humans across Eastern Eurasia

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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 sampled from East Asia to the West Eurasian Steppe spanning nearly 10,000 years. Our results indicate correlations between the ancestry of dogs and specific ancient human populations from eastern Europe to Eastern Siberia, including Ancient Paleo-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.

While the timing and location of dog domestication remain elusive, genomic evidence indicates that dogs were present in Europe [~11,000 years calibrated before present (yr B.P.) (*1*, *2*)] and in Eastern Siberia [~10,000 yr B.P. (*3*)] during the Early Holocene. These dates, however, represent a minimum estimate for the emergence of domestic dogs. In fact, recent work indicates that major dog lineages, including Eastern (East Asian and Arctic) and Western (Europe and Near East) dog lineages, likely had already diversified during the Pleistocene, >20,000 years ago (*1*, *2*, *4*). Given their early diversification and the different roles they played in past societies, it is likely that specific lineages of dogs formed part of the material, cultural, and biological package that was disseminated during human migrations.

Recent analyses of genomes from Central and East Asia have revealed substantial shifts in human ancestry linked to the spread of agriculture during the Neolithic and metalworking Bronze Age (*5*–*7*). Whether these cultures acquired dogs locally or migrated with specific dog lineages during these transformative societal and cultural shifts, however, is unknown. To address this, we sequenced and analyzed 17 ancient dog genomes (median depth 0.53×; 0.01–5.37×) dated to between 9700 and 870 yr B.P. from Siberia, East Asia, and the Central Eurasian Steppe (Fig. 1, A and B; fig. S1; and table S1).

These archaeological sites, located in Eastern Siberia, Central Asia's mid-latitude grassland and arid regions, and across the Hexi Corridor in Northwest China, experienced important shifts in both human ancestry and material culture during the Holocene (*5*, *7*, *8*). We coanalyzed these data with 57 publicly available ancient dog genomes (median depth 1.8×; 0.01–28.0×; table S1) (*1*–*3*, *9*–*11*) as well as 160 publicly available modern domestic dog genomes that capture the extent of contemporary global dog diversity (table S2), along with 18 ancient human genomes (table S3).

Early Holocene population structure in Eastern Siberia

Genomic analyses of ancient humans from the Early Holocene (~8500 yr B.P.) 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 ~10,000 yr B.P. (*12*, *13*). To investigate whether these patterns are mirrored in ancient dogs, we analyzed the genome of an ~9700-year-old individual from Khatystyr cave (Khatystyr1_9682: 1.3×) in Southeast Siberia (Aldan highlands, trans-Baikal; Fig. 1A). Outgroup-f3 statistics showed that the Khatystyr dog shared the most drift with the Northeast Siberia ~9500 yr B.P. Zhokhov dog (Zhokhov1_9515; Fig. 2A), which is contemporaneous with the Kolyma human (10,000 yr B.P.; supplementary materials; Fig. 1A).

A *qpAdm* analysis, incorporating the ancient Zhokhov dog, an ~6900-year-old dog from the Lake Baikal region (Baikal_6900: 5.2×), a modern Australian dingo (representing East Asian dogs), and an ~5800-year-old dog from Tepe Ghela Gap in Iran [TepeGhelaGap1_5826; representing Western dogs (*1*)], revealed that the Khatystyr dog's ancestry can best be modeled using the Zhokhov dog as the sole Eastern Eurasian source (fig. S2 and table S5). 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 ~2000 years younger, Lake Baikal dogs (Fig. 1, A and B), which are associated with people possessing Northeast Asian ancestry (*7*).

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. Our study, however, did not find evidence of Western dog ancestry in the Lake Baikal dogs (fig. S3), which contradicts a previous study (*2*). This discrepancy is likely due to the higher coverage data generated in our current study (see supplementary materials).

Early Bronze Age introduction of Arctic dog ancestry in China

Farther south, ancient genomic data indicate that Early and Middle Neolithic human populations in present-day northern China had East Asian ancestry related to that of people living in China today (*6*). 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 (*5*, *7*, *8*). We assessed whether this signal is mirrored in dogs by calculating pairwise shared drift (outgroup-f3 statistics) between each dog in our dataset with ancient representatives of the Eastern (Zhokhov1_9515) and Western (TepeGhelaGap1_5826 from Iran) dog lineages (Fig. 1).

Newly sequenced ancient dogs from China could be separated into four groups on the basis of the amount of shared drift with the Eastern and Western dogs (Fig. 1C) as well as principal components analysis (PCA) (fig. S4). The oldest group (Fig. 1, A to C, yellow), which comprised dog genomes from the Gansu-Qinghai region (Upper Yellow River), specifically the Late Neolithic site of Yabeili (Yabeili05_5035: 0.1×) and the Chalcolithic site of Jinchankou (Jinchankou03_3917: 1.7×, and Jinchankou04_3890: 0.1×; Qijia culture, ~4060–3780 yr B.P.), share a similar amount of drift with the Iranian dog (TepeGhelaGap1_5826) as present-day Arctic and multiple Southeast Asian dogs (Fig. 1, A to C).

We used *qpWave* and *qpAdm* to test admixture models (for genomes with >1× depth of coverage) with one to three ancestral sources: Arctic (Zhokhov1_9515 or Baikal_6900), East Asian (dingoes), and Western (TepeGhelaGap1_5826) (supplementary materials; Fig. 3A; figs. S2 and S5; and tables S7 and S8). We selected the simplest models, favoring nested models with the fewest sources that returned P values

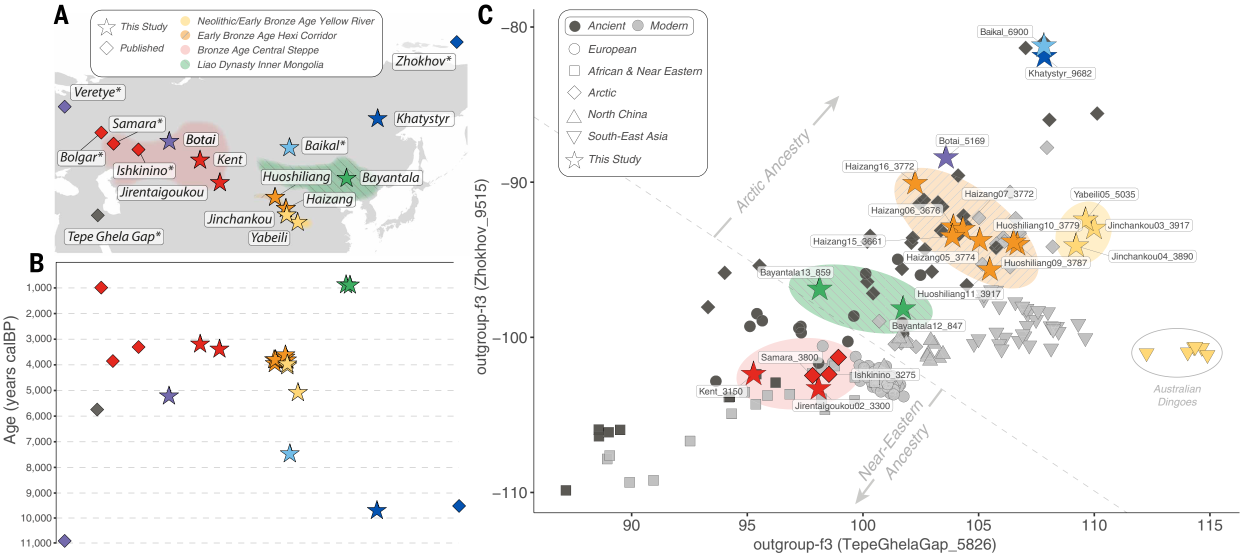

Fig. 1. Location, age, and ancestry of the newly sequenced ancient dog genomes. (**A**) Location of the ancient Eurasian published (indicated with diamonds) and unpublished (indicated with stars) dog genomes analyzed in this study. Distributions of key human cultural complexes or periods are shown. Information 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 gray) or modern dogs (light gray) and an ancient Near Eastern dog (TepeGhelaGap_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 colored according to shared ancestry and both temporal and geographic proximity to the following human groups: Eastern hunter-gatherer (purple), Ancient Paleo-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., TepeGhelaGap1_5826). Colored 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).

exceeding 0.01. This showed that, except for the Khatystyr dog, the Baikal dog consistently provided a better fit for the Arctic ancestry than the Zhokhov dog and was thus used in all subsequent analyses.

Unlike most modern East Asian dog populations, our *qpAdm* modeling based on genomes with >1× depth (Fig. 3A and table S7), as well as supervised *ADMIXTURE* analysis (*14*) (fig. S5), shows that dogs from the Neolithic Yabeili and Chalcolithic Jinchankou cluster (Fig. 1, A to C, yellow) did not have any detectable levels of Western dog ancestry. D-statistics of the form D(Coyote, TepeGhelaGap1_5826; Dingo, Jinchankou/Yabeili) were, however, significantly negative for Jinchankou dogs ($|Z| = -5.0$ and -4.1, respectively; $P < 0.01$) but not for the Yabeili dog ($|Z| = 0.003$; $P = 1$; fig. S6 and table S9). This discrepancy suggests that the Jinchankou dogs may have low levels of Western dog ancestry, not detectable by *qpAdm*, which is further supported by the occurrence of the mitochondrial haplogroup C in dogs at the site, often associated with Western Eurasian dogs (*15*, *16*). Analyses of Bronze Age human genomes from the Upper Yellow River Basin as well as Early Neolithic humans from China, however, revealed that people had mostly East Asian ancestry, with Western ancestry absent until the arrival of Bronze Age Steppe pastoralists (*8*, *17*, *18*). The potential Western dog ancestry detected in the Chalcolithic 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 from the Baikal region (*8*, *17*, *18*). To assess whether this signal is mirrored in dogs, we tested

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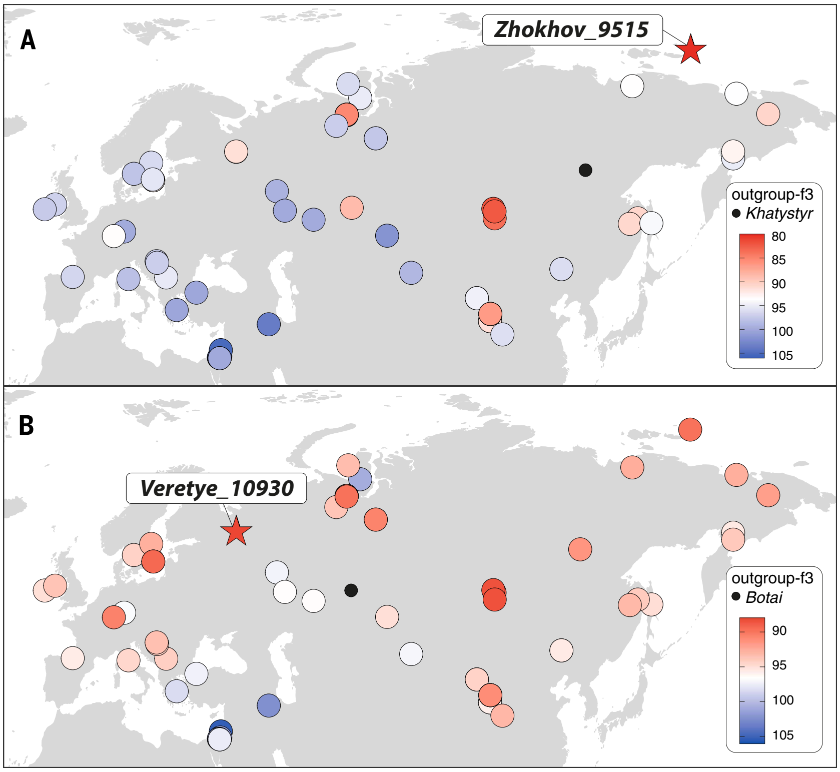

Fig. 2. Level of shared drift between the newly sequenced Khatystyr cave (~9682 yr B.P.) and Botai (~5169 yr B.P.) dogs and other ancient dogs. Levels of shared drift (outgroup-f3) between ancient Eurasian dogs and either (**A**) Siberian (Khatystyr_9682) or (**B**) central Eurasian steppe (Botai_5169) dogs. Labeled 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 Fig. 3A and fig. S2) and that the closest individual to the Botai dog is the Mesolithic European Veretye dog genome.

for gene flow from the Baikal dog into the Yabeili and Jinchankou dogs (Fig. 1A). We computed D-statistics of the form D(Coyote, Baikal_6900; Dingo, Jinchankou/Yabeili), using dingo genomes that lack recent European introgression as representatives of East Asian ancestry (figs. S6 and S7 and table S10). Both D-statistics yielded significantly positive results ($|Z| > 3$; $P < 0.01$) (fig. S7 and table S10). A *qpWave* analysis, however, could not reject a single-source dingo ancestry model for the Yabeili dog. This discrepancy suggests a small Arctic dog contribution by the Late Neolithic (~5000 yr B.P.), insufficient for *qpWave* to reject a single source, possibly because of the Yabeili individual's low coverage.

We could, however, reject a single source model for the Chalcolithic Jinchankou dog with >1× depth of coverage (Jinchankou03_3917). A *qpAdm* analysis indicated that this individual had between ~38 and 45% Arctic (Baikal_6900) and 55 and 62% East Asian (modern dingo) ancestry (Fig. 3A and table S7). Significantly positive D-statistics of the form D(Coyote, Baikal_6900; Dingo, Jinchankou) ($P < 0.01$, fig. S7; table S10) further supported this result. Given that the Baikal dog originated from a context where humans have Northeast Asian ancestry (supplementary materials; Fig. 4), our results indicate that the movement of people with Northeast Asian ancestry into northern China during the Early Bronze Age was likely accompanied by a concomitant shift in local dog ancestry.

Western ancestry in Steppe dogs before the Bronze Age

The Bronze Age Steppe also witnessed major population shifts, as earlier groups (e.g., Eneolithic Botai, ~5500 to 5000 yr B.P.), primarily of Eastern hunter-gatherer and Northeast Asian ancestry, were partially replaced by people with Iranian Neolithic farmer and Caucasus hunter-gatherer related ancestry (*7*). To assess whether this is mirrored in dogs, we analyzed an ~5200-year-old Eneolithic dog from Botai in Kazakhstan (Botai3_5169: 4.2×; Fig. 1), which predates this human ancestry influx (*7*).

Both *qpAdm* and *F4-ratio* indicated that the ancestry of the Botai dog could be modeled as ~75% Arctic (Baikal_6900) and 25% Western (TepeGhelaGap_5826; Fig. 3A, fig. S9, and tables S7 and S11). Outgroup-f3 statistics showed that the Botai dog shared more affinity with the Zhokhov dog than with the Tepe Ghela Gap dog (Fig. 1C and table S4), and D-statistics of the form D (Coyote, TepeGhelaGap_5826; Botai_5169, Zhokhov_9515) and D(Coyote, TepeGhelaGap_5826; Botai_5169, Baikal_6900) were both significantly negative ($Z = -5.9$ and -9.9 respectively; $P < 0.01$), confirming the *qpAdm* and *F4-ratio* results.

To address whether Western ancestry increased in Steppe dogs during the Bronze Age, we analyzed two previously published dog genomes from the Late Bronze Age Srubnaya culture (~3800–3200 yr B.P.; Ishkinino1_3275 and Samara_3800; Fig. 1, A and B) and a newly sequenced genome from an ~3200-year-old dog from the later Begazy-Dandybai culture (Kent1_3150: 0.1×; Fig. 1, A and B). Dogs from Ishkinino and Samara were best modeled as possessing more than ~60% Western ancestry, ~25% East Asian ancestry, and ~15% Arctic ancestry (Fig. 3A, table S7, and fig. S5). Despite being farther east, the slightly later dog from Kent lacked East Asian ancestry and was instead best modeled as possessing ~70% Western ancestry and ~30% Arctic (Fig. 3A, table S7, and fig. S5). High levels of Western Eurasian ancestry in Steppe dogs persisted until at least 1000 yr B.P., as demonstrated by a medieval dog from Bolgar (Bolgar1_1000) with ~70% Western ancestry and ~30% Arctic ancestry (Fig. 3A and table S7).

The fact that the Botai dog had Western dog ancestry demonstrates that its arrival predates the arrival of Iranian farmer and Caucasian hunter-gatherer human ancestry in the region during the Bronze Age (*8*). Notably, Eastern hunter-gatherer ancestry, prevalent in Eneolithic Botai humans, is also found in humans from eastern Europe's Veretye culture (*19*–*21*), whose 10,900 yr B.P. dogs also show both Western and Eastern (Arctic) ancestry (*2*). Outgroup-f3 statistics showed a close genetic similarity between the Botai and Veretye dogs (Veretye1_10930; Fig. 2B and table S4), and our *qpAdm* analysis showed that the ancestry of the Veretye dogs was similar to that of Botai (i.e., ~65 to 75% Arctic and ~35 to 25% Western; Fig. 3A and table S7). This similarity suggests that dogs accompanying Eastern hunter-gatherer human populations across Eurasia (10,000 to 5500 yr B.P.) had similar genetic makeup. The Western ancestry in the Botai dog thus likely originated from connections with Eastern hunter-gatherer populations from eastern Europe, whereas later Bronze Age Western ancestry stemmed from dogs accompanying people with Iranian farmer and Caucasian hunter-gatherer ancestry (*7*).

Bronze Age introduction of Western dog ancestry in Northwest China

Analyses of ancient human genomes from East Asia also showed an influx of Western ancestry during the Late Bronze Age (~3300 yr B.P.), likely driven by the expansion of Western Steppe pastoralists into the region (*5*, *22*, *23*). Previous mitochondrial DNA studies suggested that Western dog ancestry also arrived in China by the Bronze Age, on the basis of the detection of haplogroup C in two ~4000 yr B.P. dogs at Jinchankou (*15*, *16*). Using mitochondrial haplogroups as ancestry

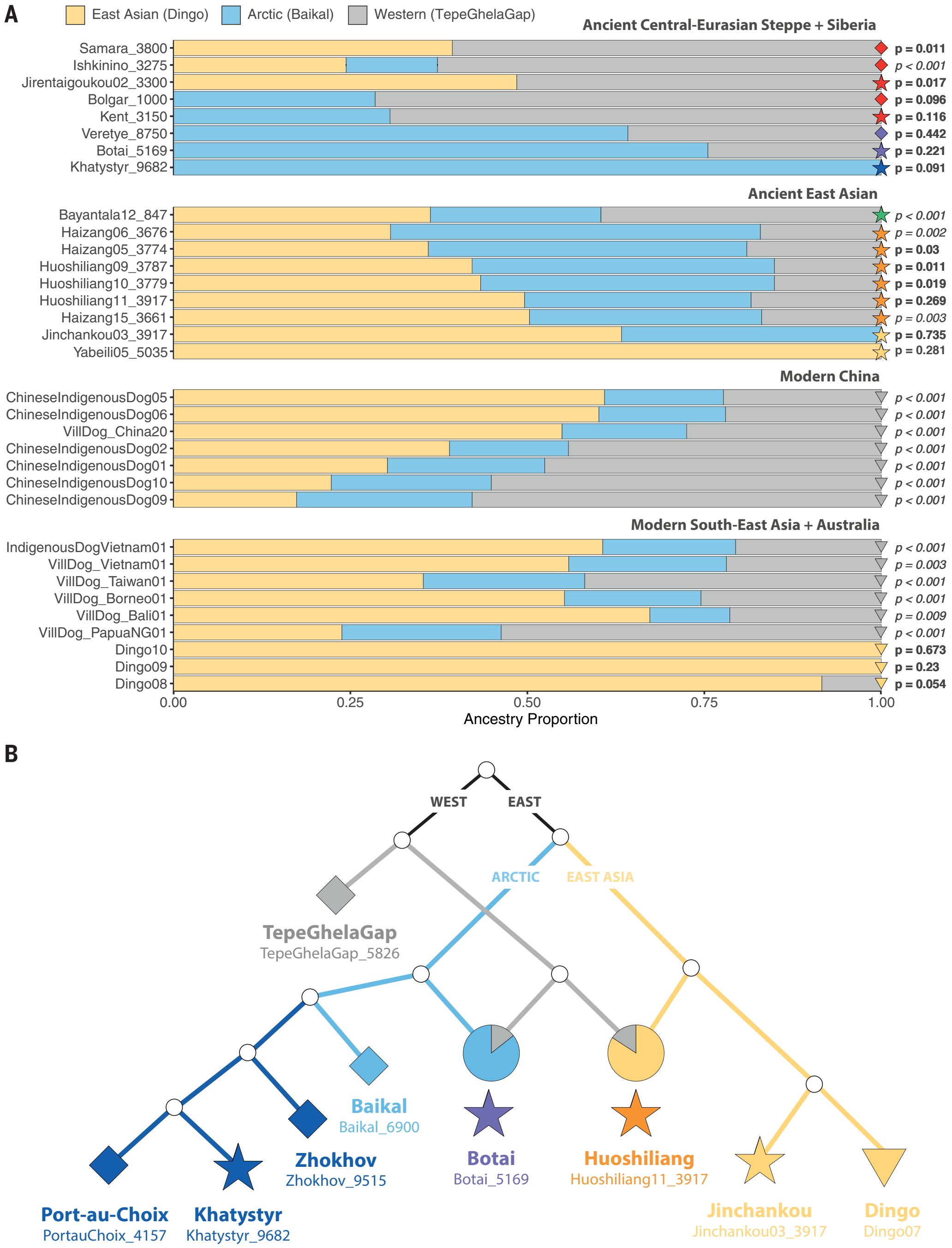

Fig. 3. Ancestry modeling of ancient and modern Eastern Eurasian dogs. (**A**) Proportion of West Eurasian (gray), Arctic (light blue), and East Asian (yellow) ancestries in ancient and modern East Eurasian published (indicated with diamonds) and unpublished (indicated with stars) dog genomes estimated using *qpAdm* for the best model (one to three 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 ($P < 0.01$). Although 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 to 19.6×) ancient dog genomes, with branches and admixture events that exceed the posterior probability threshold (99%) shown. The graph shows two admixture events, a West Eurasian (Tepe Ghela Gap) 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*), is shown in fig. S10. Ancestry proportions (pie charts) were estimated in *AdmixtureBayes*.

proxies in dogs, however, is challenging, as early Western dog populations, including the ~11,000-year-old Veretye dogs, have both Eastern-prevalent A and Western-prevalent C haplogroups (*1*, *2*).

F4-ratio (fig. S9) and *qpAdm* (Fig. 3A and fig. S2) modeling indicated that a Late Bronze Age (~3300 yr B.P.) dog from Jirentaigoukou (Jirentaigoukou02_3300: 0.1×), situated at the eastern margin of the Eurasian steppe in Xinjiang, had ~50% Western ancestry and ~50% East Asian ancestry, similar to other Bronze Age Steppe pastoralist dogs (i.e., Ishkinino1_3275 and Samara_3800; Fig. 3A). Genomic analyses showed that people from Jirentaigoukou derived most of their ancestry from Western

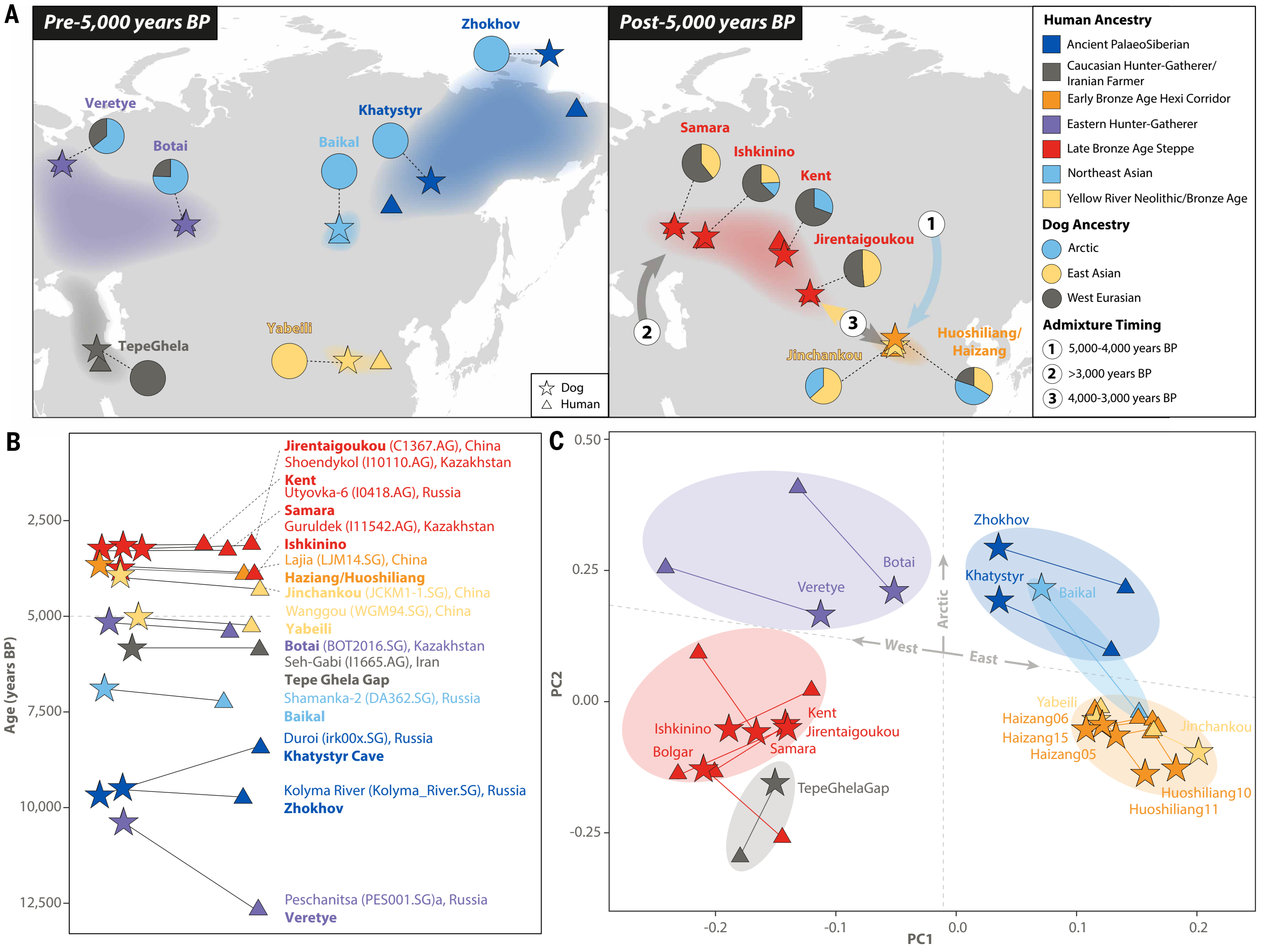

Fig. 4. Correspondence between human and dog ancestry in Eastern Eurasia. (**A**) Maps showing both human (indicated with triangles) and dog (indicated with stars) ancestry in pre- and post-5000-yr-B.P. contexts (i.e., pre– and post–Bronze Age Steppe expansion). Pie charts represent mean ancestry proportions for each population estimated by *qpAdm* (see Fig. 3A and fig. S2).The left map shows that the Western dog ancestry (gray in pie charts) is restricted to Western Eurasia, whereas 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 right 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 (5000 to 4000 yr B.P.), associated with the documented influx of Northeast Asian ancestry in the region (*8*,*17*,*18*); (2) influx of Western Eurasian dog ancestry from the Caucasus into the Steppe region (>3000 yr B.P.), concomitant with well-characterized migrations of Caucasian hunter-gatherer ancestry (*7*); 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 (~4000 to 3000 yr B.P.) as well as the westward movement of East Asian dog ancestry, both of which coincide with known human migration patterns (*5*,*22*,*23*). (**B**) Concordance between the age of human (triangle) and dog (star) genomes depicted in (A). (**C**) Principal components built from 18 human and 18 dog ancient genomes from similar locations and time periods [see (A) and (B)] and aligned using Procrustes rotation. The first principal component (PC1) differentiates both dogs and humans on the basis of their Western and Eastern ancestries. The second principal component (PC2) separates both people and dogs roughly on the basis of latitude, including East Asian and Arctic dogs.

Steppe pastoralists [Andronovo/Sintashta lineage, ~3300 to 3100 yr B.P. (*24*)]. Combined, our results indicate that the Western ancestry in dogs from the Eastern Steppe and Xinjiang (*5*, *24*) was 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: 0.1×, Haizang06_3676: 0.7×, and Haizang07_3772: 0.02×; Middle Period of the Qijia culture, ~3800 to 3550 yr B.P.) and Huoshiliang (Huoshiliang09_3787: 1.7×, Huoshiliang10_3779: 1.1×, Huoshiliang11_3917: 5.4×, Xichengyi culture, ~4070 to 3650 yr B.P.) also had ~15 to 35% Western ancestry per *F4-ratio* (fig. S9 and table S12), *qpADM* (Fig. 3A, fig. S2, and table S7), supervised *ADMIXTURE* (fig. S5), and D-statistics of the form D(Coyote, TepeGhelaGap1_5826; Dingo, Haizang/Huoshiliang) (fig. S6 and tables S9 and S13).

An *AdmixtureBayes* analysis (*25*), based on genomes with >1× depth of coverage, also modeled the Huoshiliang dogs as a mixture between Western (related to Botai dogs) and East Asian ancestry with high support (>99% probability; Fig. 3B and fig. S10). 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 3900 yr B.P., during the Bronze Age. Admixture dating using *DATES* (*26*) indicates that the Western dog ancestry was introduced in the region between ~3800 and 4000 years ago (supplementary methods, figs. S11 and S12, and table S14).

In contrast to Huoshiliang and Haizang (Fig. 1A), the dog from Jinchankou (Fig. 3A), situated a few hundred kilometers eastward, exhibited no detectable levels of Western ancestry per *ADMIXTURE*, *AdmixtureBayes*, and *qpAdm* (Fig. 3, A and B, and figs. S2, S10, and S15).

This result suggests that the dispersal of Western dog ancestry during the Bronze Age was not a homogeneous event throughout the area. Eventually, Western dog ancestry in ancient East Asia reached ~40% in two ~850-year-old dogs from the Liao Dynasty (1034 to 825 yr B.P.; Bayantala12_847: 0.1×, and Bayantala13_859: 0.02×) in Inner Mongolia (Bayantala), similar to present-day northern Chinese dogs (Fig. 3A). Our *qpAdm* models, however, exhibited poor fit for Liao Dynasty and modern Asian dogs (Fig. 3A), suggesting additional, unmodeled ancestral contribution(s) within the past 850 years to East Asian dogs.

Concordance and discrepancies between human and dog ancestry in Asia

Analyses of our newly generated ancient dog genomes from Asia show generally strong concordance between Eastern and Western Eurasian ancestry in dogs and humans. Eastern human populations such as Ancient Paleo-Siberians, Northeast Asians, and East Asians were associated with dogs of East Asian or Arctic ancestry, and Western human populations such as Iranian farmers, Caucasian hunter-gatherers, and Steppe pastoralists were associated with the Western Eurasian dog lineage (Fig. 4). However, Eastern hunter-gatherers from Veretye and Botai, who are genetically closer to Western Eurasian humans than to Eastern Eurasians, were associated with dogs that had largely Eastern ancestry (i.e., Arctic dogs; Fig. 3A). To visualize this discrepancy, we aligned PC analysis built from 18 human and 18 dog ancient genomes from similar locations and time periods (Fig. 4; supplementary materials) using Procrustes transformation.

These analyses indicate concordance between the two species, where PC1 differentiated both dogs and humans on the basis of their Western and Eastern ancestries (Fig. 4C). PC2 separated both people and dogs roughly on the basis of latitude. Specifically, Eastern hunter-gatherers were separated from Iranian farmers and Caucasian hunter-gatherers along PC2, and Ancient Paleo-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. First, although 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. Furthermore, whereas ~7000-year-old Northeast Asians from Lake Baikal align with East Asians on PC2, as expected (*7*), dogs from the same context are plotted with Arctic dogs from Khatystyr cave and Zhokhov Island, located farther north (Fig. 4C). This pattern suggests that 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 ancestries.

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 suggests that they played a role in a multitude of human societies. Our analyses also highlighted some discrepancies between the population splits of dogs and humans, suggesting that Early Holocene communities of hunter-gatherers in Northern Eurasia, having different ancestry, likely also exchanged dogs.

Codispersal of humans and domestic animals has been documented in other species, including livestock, which facilitated the establishment of agricultural communities (*27*), and horses, which majorly altered human mobility (*28*). Coanalysis of ancient animal and human genomes provides the opportunity to investigate codispersal 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

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Materials and Methods; Figs. S1 to S15; Tables S1 to S16; References (*29*–*91*);
MDAR Reproducibility Checklist

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