RESEARCH ARTICLE

ANCIENT DNA

Ancient genomics and the origin, dispersal, and development of domestic sheep

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The origins and prehistory of domestic sheep (*Ovis aries*) are incompletely understood; to address this, we generated data from 118 ancient genomes spanning 12,000 years sampled from across Eurasia. Genomes from Central Türkiye ~8000 BCE are genetically proximal to the domestic origins of sheep but do not fully explain the ancestry of later populations, suggesting a mosaic of wild ancestries. Genomic signatures indicate selection by ancient herders for pigmentation patterns, hornedness, and growth rate. Although the first European sheep flocks derive from Türkiye, in a notable parallel with ancient human genome discoveries, we detected a major influx of Western steppe–related ancestry in the Bronze Age.

Numbering 1.2 billion worldwide (FAO, 2020), sheep were initially domesticated from the Asiatic mouflon (*Ovis gmelini*), which ranged from Türkiye to eastern Iran (*1*–*3*). Along with meat, skin, and fat, their lifetime (secondary) products, including milk (*4*) and dung (*5*), have played a major role in human societies. Wool, in particular, was a sought-after commodity and newly discovered source of warm, breathable, water resistant textiles, which was intertwined through the economies of early complex societies in fourth to third millennium BCE Southwest Asia and later in Bronze Age Europe (*6*, *7*).

The origins of sheep management and husbandry can be traced to the mid–ninth millennium BCE in the northern Fertile Crescent. Among Early Neolithic sites in the upper Euphrates basin and Central Türkiye, faunal remains reveal the emerging new relationship between humans and sheep through shifts in species composition, age profiles, diet, the occurrence of bone pathologies, evidence of fetal and neonatal deaths on site, and progressive size reduction compared with earlier hunted assemblages (*8*–*11*). One millennium later, caprine pastoralism was consolidated more widely across Southwest Asia with smaller, phenotypically domestic sheep populating landscapes well beyond the natural distribution of wild sheep (*12*–*14*).

To investigate the origins, dispersal and development of sheep, we analyzed 118 newly sequenced ancient sheep genomes spanning 12,000 years (Fig. 1A) with a mean coverage F1 of 0.85X (~0.01X to 5.38X; figs. S2 and S3 and tables S1 to S5), supplemented with five published ancient genomes (*15*, *16*). Their geographic range stretches from Mongolia to Ireland (fig. S1), with a particular focus on Southwest Asia (*N* = 70 xxx) (Fig. 1B). We analyzed these with 73 modern *Ovis* genomes (table S4), including 57 domestic *Ovis aries* from Asia, Europe, and Africa; 12 *O. gmelini* from Iran; and 4 Iranian urials (*Ovis vignei*).

Ancient wild genomes point away from domestication in the east of the Fertile Crescent

Eight of our ancient genomes are from wild *Ovis*. Three Iranian samples from Tappeh Sang-e Chakhmaq (~6000 BCE; Fig. 1) (*17*, *18*) are identifiable as urial (*O. vignei*) by their segregation with modern urials in principal components analysis (PCA; PC3 in fig. S4 and table S6), *D* statistics (fig. S5 and table S7), and their mitochondrial DNA (mtDNA) sequences (fig. S6 and table S1). Four specimens with genomic affinity with wild Eurasian mouflon (*O. gmelini*; fig. S4) derive Nachcharini Cave (Lebanon) and Körtik Tepe (Türkiye), dating to mid-10th

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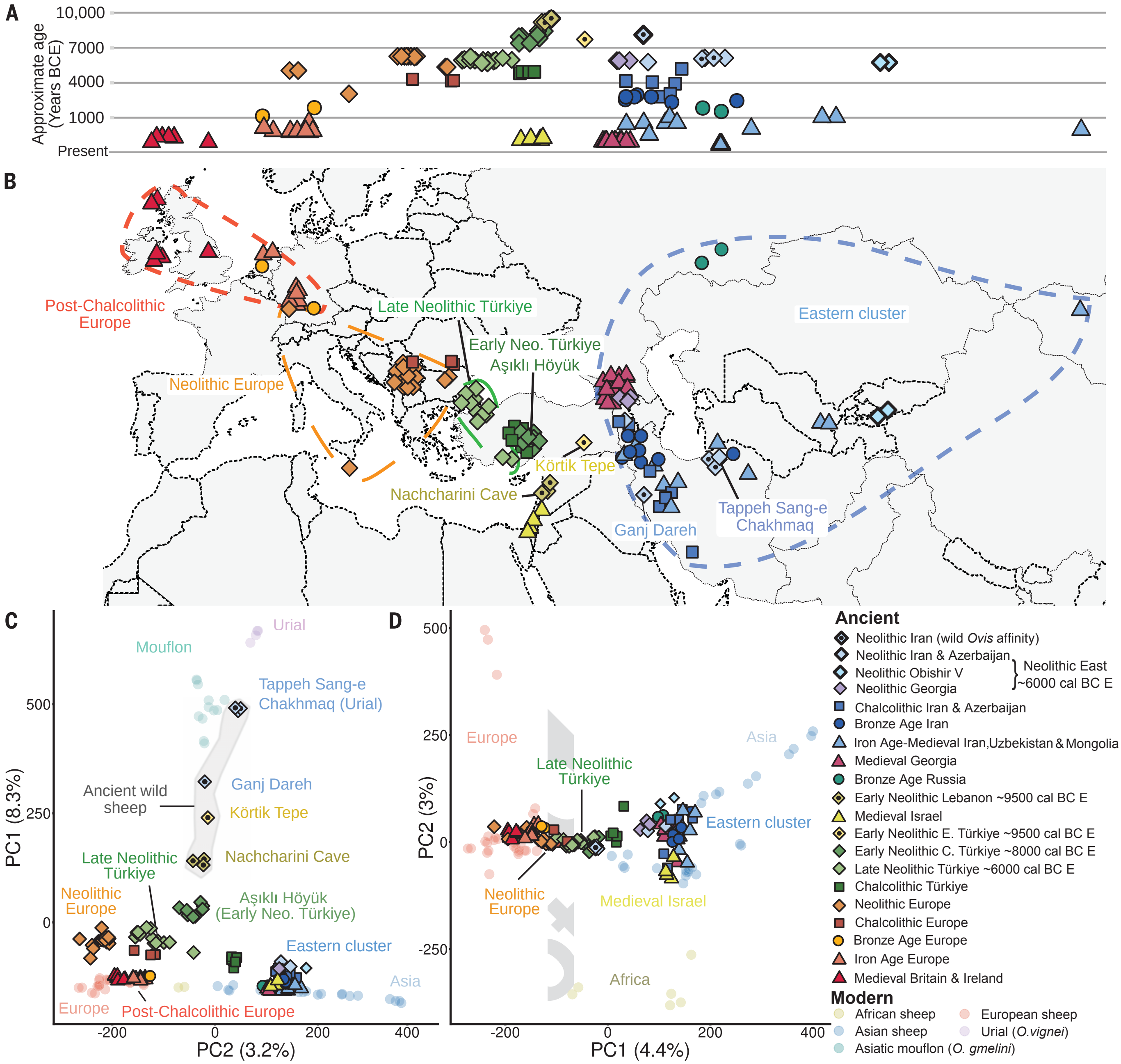

Fig. 1. Provenance and principal components analysis of 123 ancient wild and domestic sheep genomes (118 reported in this study) projected onto modern *Ovis* diversity. (**A**) Approximate sample date plotted versus (jittered) longitude [corresponding to positions in (B)]. Symbols with dots indicate ancient wild genomes. (**B**) Provenance and cultural period of sampled genomes. (**C**) Plot of PC1 and PC2 with symbol and color key as in the map; clear separations between hunted wild (samples from Tappeh Sang-e Chakhmaq, Ganj Dareh, Körtik Tepe, and Nachcharini Cave) and human-managed sheep and also between eastern and western locations are visible. The "Eastern cluster" designation encompasses ancient sheep from Georgia, Iran, Azerbaijan, Uzbekistan, Kyrgyzstan, and Mongolia. (**D**) Plot of PC1 and PC2 calculated with modern wild genomes removed, which shows geographic separation by continent. Cal, xxx; C., central; E., eastern.

millennium BCE. Both assemblages lack demographic indicators of management (*13*, *19*) and predate evidence of sheep management (*2*, *20*). A final wild mouflon genome is from ~8000 BCE Ganj Dareh (Iran), where sheep (in contrast to contemporaneous herded goats) show a demographic profile typical of hunted populations (*21*). In PCA, when we project our ancient data on a framework of modern sheep and wild *Ovis* genomes (Fig. 1C, fig. S4, and tables S3 and S4), these ancient wild samples clearly separate from those representing managed, domestic assemblages on PC1; this, along with other analyses, were tested for robustness with respect to sequencing error and selection of variant sites (*22*).

Among the ancient wild sheep (Fig. 1, B and C), those which plot closest to domesticates on PC1 are the three more western mouflon genomes from Nachcharini Cave in Lebanon (~9700 to 9000 BCE), followed by those from Körtik Tepe [2σ (σ, standard deviation) C_{14} age: 9873 to 9453 BCE] in Southeast Türkiye, and then Ganj Dareh (2σ C_{14} age: 8279 to 7960 BCE) in the Iranian Zagros toward the eastern side of the wild *Ovis* range (Fig. 1C). This hierarchy within wild versus domesticated

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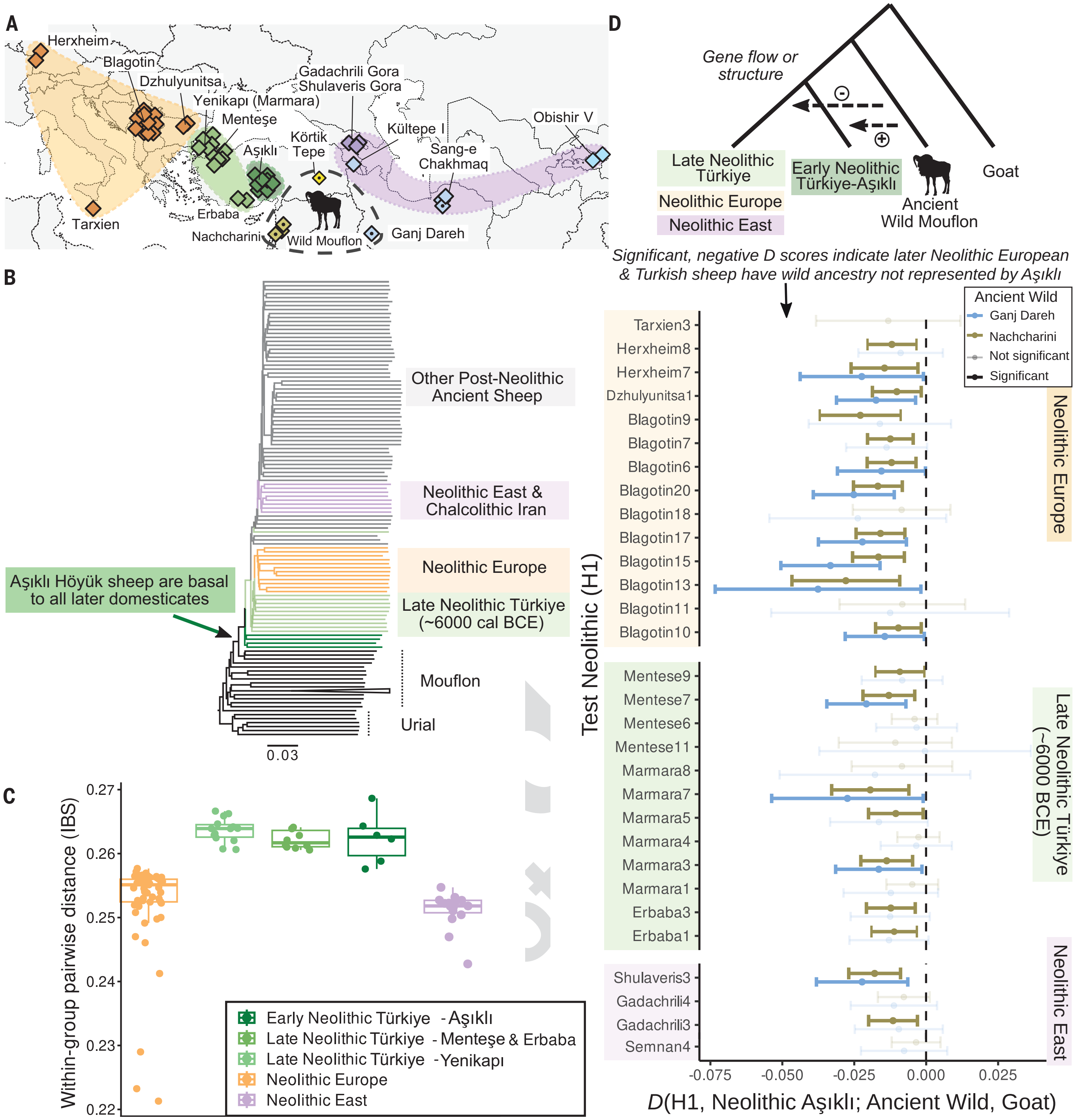

Fig. 2. Patterns of Neolithic sheep diversity. (**A**) The groupings of Neolithic samples compared in (B), with sampled sites also indicated. (**B**) Neighbor-joining tree based on IBS data of ancient and modern *Ovis*. Asikli Hoyuk sheep are basal to all later domesticates. The Late Neolithic Türkiye sample grouping apart from others (Marmara8) is an outlier with regards to eastern ancestry (see Fig. 3B). Neolithic East refers to genomes from ~6000 BCE Iran, Azerbaijan, Georgia, and Kyrgyzstan, highlighted in purple in (C). The outgroup goat is not shown, and a clade of modern Iranian mouflon is collapsed; see fig. S9 for individually labeled phylogeny. Pie10 and Pie11 were excluded owing to higher sequencing error rates (table S1). (**C**) Comparative plots of diversity among Neolithic groups using within-group pairwise IBS distance. (**D**) Error-corrected *D* statistics testing whether the pairing of Early Neolithic Central Turkish (Aşıklı Höyük) and individuals from Late Neolithic (~6000 BCE) sites retains integrity when ancient wild sheep groups are considered as introgressors; group level tests are presented in table S7, and tests with Aşıklı individuals, in fig. S16.

affinity is supported by identity-by-state phylogenetic analysis, where the Lebanese mouflon form the closest ancient outgroup to all domesticate genomes, and Ganj Dareh, the most distant (fig. S6). Additionally, later Iranian domestic sheep cannot be modeled (qpWave; table S10) as stemming from the Ganj Dareh mouflon genome. This evidence points away from a core area of sheep domestication at the east of

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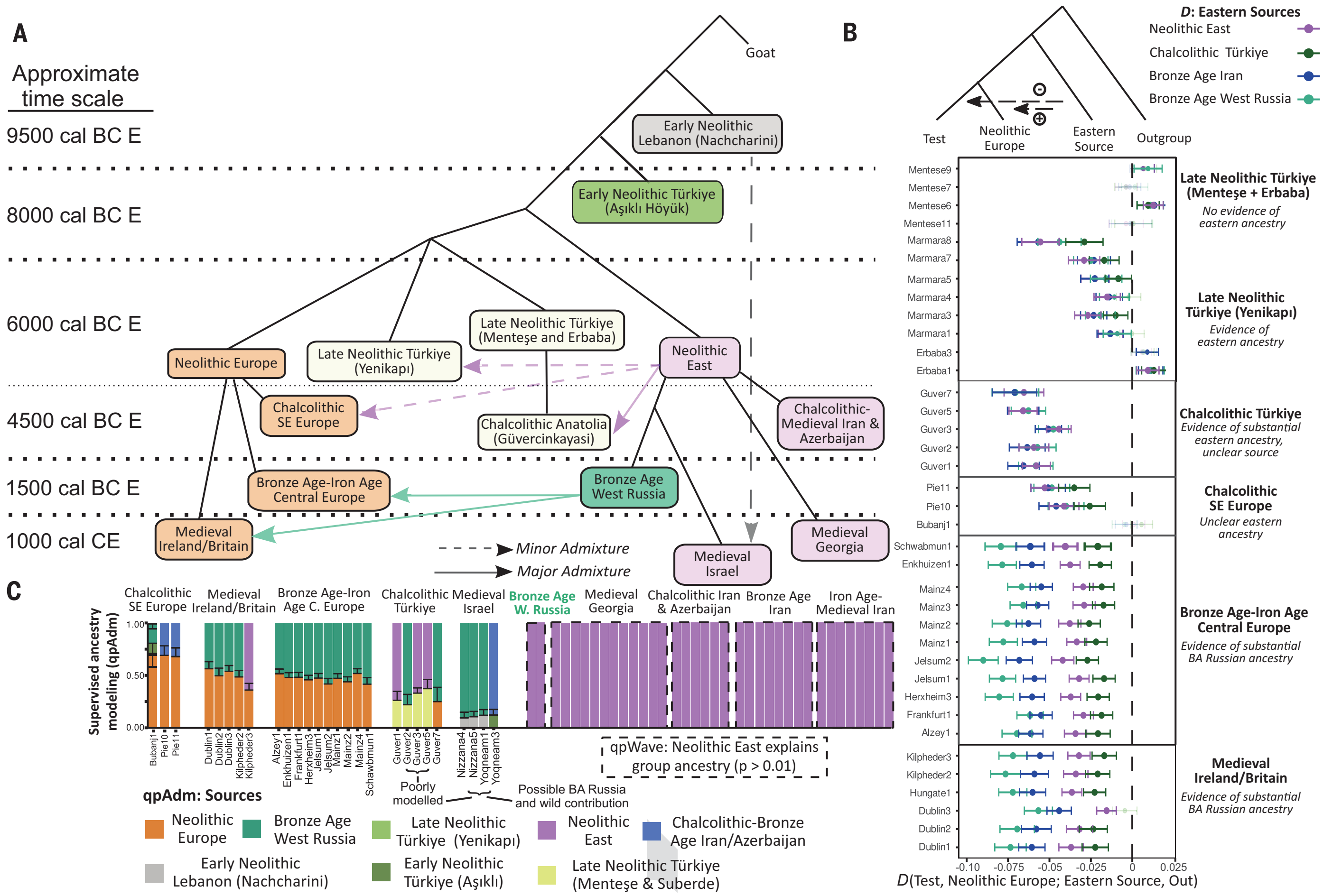

Fig. 3. An admixture history of domestic sheep. (**A**) Phylogenetic scheme based on recurrent features emerging in Admixtools2 exploration, with topology supported by a Treemix analysis (figs. S12 and S15). Dashed arrows denote minor (<25%) and solid arrows show major (>25%) secondary admixtures. Vectors involving the Medieval Israel, Medieval Georgia, and (combined for illustration) Chalcolithic-Medieval Iran-Azerbaijan groups were grafted to the model based on qpWave, qpAdm, and Treemix results. (**B**) Error-corrected *D* statistics testing for admixture from different eastern sources (see color key) with Neolithic European genomes as a reference. The strongest introgression signals are from a Neolithic East–related source in earlier time periods, with stronger signals from Bronze Age West Russia in later Europeans. Non–error-corrected group and individual tests are shown in figs. S20 and S21. (**C**) Supervised ancestry modeling of post-Neolithic genomes; the color key denotes the potential sources considered. Models with the highest *P* values are shown (*35*), with alternative fitting models in table S11. Fitting models for Chalcolithic Türkiye samples always comprise western and eastern mixture, but a range of alternate eastern sources are accepted, suggesting that their source is not well represented in our data; we similarly fit a range of models for the Medieval Israel sheep.

the mouflon range in the Zagros and accords with an origin in the western range of south-
F2 west Asia. It also aligns with the archaeofaunal record evidencing that domestic sheep phenotypes and management occurred later in that region, around 7000 BCE (*12*, *23*). By contrast, by around 8000 BCE, goats in Iran had already begun a demographic and genetic transition toward the domesticated state (*21*), indicating uncoupled early domestication processes in the two small livestock species in the eastern arc of the Fertile Crescent.

Early Neolithic Aşıklı Höyük are a basal population but do not fully represent domestic ancestry

PC1 also distributes samples of herded populations in order of archaeological age (Fig. 1C), stretching from Early Neolithic Aşıklı Höyük (8300 to 7500 BCE) through later Neolithic genomes (Fig. 2A) and subsequent periods to medieval and, lastly, modern genomes. The Aşıklı Höyük genomes, represented by a mixture of shotgun and whole-genome enrichment data (we restrict key analyses to shotgun data only), are from close in time to the beginnings of sheep domestication. There, herd management is reflected in the culling of young males, slaughtering near habitations, and accumulation of dung and urine in sediments, indicating the stabling of livestock on site (*8*, *24*). However, sheep at this time did not yet have the reduced size and altered morphology typical of later domesticates (*25*). When we modeled the ancient sheep phylogeny using either individuals with identity by state (Fig. 2B and fig. S9) or admixture graph exploration with genomes grouped into the major geographic-temporal PCA clusters (Fig. 3A, figs. S10 to S15, and F3
tables S8 and S9), Aşıklı Höyük holds a basal position among domesticates [inferred by using shotgun but excluding genome-enriched sequencing data (*22*)]. This is consistent with that population being genetically proximal to the origins of domestic sheep.

However, our Late Neolithic samples (here defined as ~6000 BCE) are likely not a simple derivation of this early Central Turkish diversity. *D* statistics with either the wild Ganj Dareh or Nachcharini sheep as outgroups to test the integrity of Aşıklı Höyük–Late Neolithic genome clade pairings point toward the latter having a broader wild ancestry than the flocks raised at Aşıklı Höyük (Fig. 2D and fig. S16; although

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tests with different Asikli individuals produce a mixture of positive, indeterminate, and negative results, fig. S17). Moreover, these later populations cannot be modeled as deriving from the Aşıklı sheep alone (by using qpWave to evaluate the fit of single ancestry streams, table S10). This could arise from local wild genomes being incorporated in their population histories after a common origin (*26*). Alternatively, a broader mosaic of wild diversity gave rise to the founder herds, not all of which are represented in our Aşıklı Höyük sample. Genomic sampling of additional ninth millennium BCE assemblages within the natural habitat of the mouflon, including from the Northern Levant and upper Euphrates basin in the center of the Fertile Crescent, would distinguish these scenarios.

Migrations and admixture shaped ancient sheep populations

In PC space, western Neolithic sheep appear highly structured (Fig. 1C). There are distinct clusters of genomes deriving from Turkish and European Neolithic sites. By contrast, ~6000 BCE Neolithic sheep genomes which are geographically dispersed among Georgia, Azerbaijan, eastern Iran and Kyrgyzstan sites (*15*) cluster tightly genetically; we refer to this group as "Neolithic East" in subsequent analyses. Relative homogeneity of these eastern genomes is supported by pairwise identity-by-state (IBS) values (Fig. 2C) and a cladal relationship (along with Chalcolithic Iran) in an IBS-based phylogeny (Fig. 2B).

When we calculated PC1 and PC2 without modern wild genomes, three poles of variation, marked by trends in ancient and modern European, Asian, and African animals (Fig. 1D), became apparent. Ancient Turkish sheep trend toward the European pole, Iranians toward the Asian population, and, although less pronounced, medieval genomes from Israel toward Africans, implying roles in the foundations of the respective continental herds. Supported by *D* statistics and qpAdm modeling (fig. S18 and tables S7 and S11), these separate continental affinities of the three corners of the Fertile Crescent have parallels in ancient goat and cattle genomes (*27*, *28*). However, there are additional complexities in the trajectories of these sheep populations.

To explore the role of gene flow in the development of ancient sheep, we explored phylogenetic relations using admixture graph exploration and Treemix (fig. S12) and constructed a summary schema (Fig. 3A). This retained the most frequent features within best-fitting solutions [(*22*); tables S8 and S9] and explicitly modeled inferred population mixtures with qpAdm (Fig. 3B and table S11). The primary divide in the Late Neolithic (~6000 BCE) and subsequent periods is between east and west (Figs. 1, C and D, and 3A). The earliest admixture between these involves sheep from Late Neolithic Yenikapı on the western shore of the Bosphorus, showing additional minor eastern ancestry relative to neighboring sheep populations (qpAdm: 17 to 20% with one outlier, Marmara8, at 53 ± 16%; fig. S19 and table S11). Late Neolithic Turkish populations have been noted to exhibit reduced mtDNA diversity, which is modeled as the result of a population bottleneck occurring as founder flocks migrated from the region of domestication (*29*, *30*). mtDNA diversity does not similarly decline in the Neolithic East (table S1). Although we saw reduced autosomal diversity (assessed as levels of pairwise allele sharing; Fig. 2C) in the Neolithic European and Eastern populations, this was not the case in our Late Neolithic Turkish sheep. This contrast between maternal and whole genome patterns may be at least partly explained by secondary directional admixture (mediated largely by choice of sires), which, in herded stock, can leave mtDNA diversity unchanged (*28*). There were distinct routes and events during dispersal from the initial domestication region throughout coastal and inland Türkiye (*26*, *31*), with likely ongoing exchange of animals within Neolithic Southwest Asia.

We found little evidence of discontinuity after the foundation of the eastern population: sheep from the Chalcolithic and later periods can be modeled entirely by the Neolithic East group (qpWave, table S10) according with their close clustering in PCA and despite a wide geographical provenance. Conversely, both the European and Central Turkish Chalcolithic show differences relative to their Neolithic counterparts, clearly indicated by *D* statistics (Fig. 3B and figs. S19 to S23) and unsupervised ancestry modeling (fig. S24). Within central Türkiye, in a discontinuity with Neolithic genomes, Chalcolithic Güvercinkayası sheep are a mix of western and eastern ancestry (57 to 70%, from all fitting group-level qpAdm models with a range of possible eastern sources; table S11). At Güvercinkayası, decorated pottery, stamped seals, and seal impressions point to connections to Mesopotamian Ubaid culture sites (*32*), which were known to practice large-scale, mobile sheep pastoralism (*33*). Notably, the signals of east-to-west gene flow in Southwest Asian sheep have resonance with a wider recurring pattern of westward movements from the Caucasian, Iranian, or northern Mesopotamian cultural sphere that is paralleled in both material culture and human genetics (*34*). Substantial Iranian or Caucasus ancestry influx into Anatolian and Mediterranean human populations also occurred in the Chalcolithic and has been postulated to correlate with the spread of Anatolian languages basal to Indo-European tongues (*35*). Eastern input extends into Southeast European Chalcolithic sheep (18.7 to 32.3% for best-fitting models, but qpAdm allows several possible sources; table S11), according with multiple postulated cultural shifts between the Early Neolithic Starčevo horizon (represented here by the Blagotin assemblage, Fig. 2A) and the Chalcolithic period [fig. S1, (*36*)].

Steppe-related sheep migration to Europe

The most dramatic east to west genome introgression, both in distance traversed and extent of influence, is that which transformed Bronze Age and subsequent European sheep. Supervised ancestry modeling, likelihood-based graph exploration [Treemix (*37*); figs. S12 to S15), and *D* statistics (Fig. 3B; variation in *D* scores were observed by using individual Neolithic European sheep rather than groups; see fig. S21 and table S6) favor Late Bronze Age sheep sampled from the Russian Volga–Ural steppe as the best-fitting source. With qpAdm, we estimate that that 44 to 61% of the individual ancestry of European sheep from the Bronze Age onwards derives from Western steppe–related admixture (Fig. 3C). Post-Neolithic translocations of steppe sheep into Europe fit studies of modern genetic markers (*38*) and are hinted at by ancient mtDNA data (*39*).

One of the most substantial findings from ancient human genomics is strong evidence for a massive steppe-derived population turnover in Europe around 3000 to 2700 BCE (*40*, *41*). We infer that, in the frame of this cultural process, sheep populations were transformed by a translocation from the steppe into central and western Europe by the mid–second millennium BCE. This was likely motivated by the lifeways and dietary preferences of the third millennium BCE Yamnaya culture, i.e., primarily sheep-herding, migratory pastoralists of the Pontic-Caspian steppe that depended on small livestock for dairy products (*42*, *43*).

Ancient signals of selection and sheep production traits

To test which traits may have undergone selection in prehistory, we focused on the two clusters of genomes in our data with the best sampling and genome coverage (Fig. 1C): Neolithic southeast Europe (restricted to genomes from the ~6000 BCE assemblage of Blagotin-Poljna, Serbia) and Bronze Age–to–medieval European sheep (pooled across assemblages dating to ~1400 BCE to ~1100 CE). We used these two groups comprising 6 (mean 1.37X coverage) and 13 genomes (mean 1.69X coverage) and compared them with 17 modern wild sheep genomes (*44*) to calculate pairwise xxxxxxx in genome-wide windows. This is summarized in population branch statistics (*45*) within which we identified 50-kb windows with excessive divergence and located these signals on the respective trajectories of the Neolithic or post-Chalcolithic groups (fig. S25).

On the branch leading to the ~6000 BCE Neolithic population, it is notable that, within the 10 most-elevated signal peaks, a majority contain genes with prior evidence for phenotype consequence and/or selection history in

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modern sheep. The strongest genome-wide peak is adjacent to the genes *PDGFRA* and *KIT* [a locus implicated in selection and coat color, e.g., piebaldism, in multiple species (*27*, *46*); fig. S25]). The fourth-ranked region contains *MC1R*, which has also had variation linked to coloration in multiple studies (*47*, *48*). This suggests that, within the first two millennia of sheep husbandry and mirroring results from ancient goat genomes (*27*), herders had strong preferences for coat colors and patterns. This may have aided identification within communally herded flocks, resulted from pleiotropy with behavior (*49*), or reflected value for decoration or textile production, although systemic use of animal-based textiles does not occur until later periods (*50*). Alternately, domestic animals possess strong symbolic and aesthetic value, and it is possible that herders simply favored the beautiful and unusual. Other outlier Neolithic signals contain genes suggesting early selection for growth rate [*GHR* (*51*)], wool morphology [*SHCBP1* (*52*)], and climate adaptation [*TBC1D12* (*53*)].

Selection in later ancient Europe

By the Bronze Age, sheep began to play a more central economic role in Europe, demonstrated by the appearance of larger breeds, higher proportions of polled (i.e., hornless) animals and wool as a key textile and traded commodity (*54*, *55*). In the post-Chalcolithic European branch, the strongest signals include *RXFP2*, the major determinant of horn shape and the polled trait (*56*). We did not find strongly outlying signals associated with wool trait loci, although the occurrence of several within the top 1% of genome windows may concord with a more diffuse selection process (table S12). These include *IRF2BP2*, which has a 3′ untranslated region–derived variant associated with fleece fiber (*57*) that shows an increase from 50 to 91% (P = 0.012, binomial test) between our Neolithic European sheep and those bred in the Iron Age and medieval periods (fig. S26).

We have shown that herds in the wool-enriched economies of Bronze Age and later Europe were transformed by a major influx from the Western steppe. Within these, we see some indication of selection at fleece-related genes. However, as coarse yarns continued to be used for textiles, the adoption of wool was probably a spatially and temporally heterogeneous process, rendering human exploitation of this lifetime product more akin to an evolution than a revolution (*55*).

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SUPPLEMENTARY MATERIALS

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