A novel lineage of the *Capra* genus discovered in the Taurus Mountains of Turkey using ancient genomics.

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Abstract

Direkli Cave, located in the Taurus Mountains of southern Turkey, was occupied by Late Epipaleolithic hunters-gatherers for the seasonal hunting and processing of game including large numbers of wild goats. We report genomic data from new and published *Capra* specimens from Direkli Cave and, supplemented with historic genomes from multiple *Capra* species, find a novel lineage best represented by a ~14,000 year old 2.59X genome sequenced from specimen Direkli4. This newly discovered *Capra* lineage is a sister clade to the Caucasian tur species (*Capra cylindricornis* and *Capra caucasica*), both now limited to the Caucasus region. We identify genomic regions introgressed in domestic goats with high affinity to Direkli4, and find that West Eurasian domestic goats in the past, but not those today, appear enriched for Direkli4-specific alleles at a genome-wide level. This forgotten “Taurasian tur” likely survived Late Pleistocene climatic change in a Taurus Mountain refugia and its genomic fate is unknown.

Introduction

The genus *Capra* includes the domestic goat (*Capra hircus*) as well as a variety of wild mountain-dwelling goat/ibex species distributed across Eurasia and North Africa including several listed as endangered or vulnerable (Shackleton 1997; Pidancier et al. 2006). Nine species are currently recognized by the IUCN; however, taxonomic relationships are still under revision (Pidancier et al. 2006; Zheng et al. 2020). Among these, the status of the two species endemic to the Caucasus Mountains has been debated (Parrini, Cain, and Krausman 2009; Groves and Grubb 2011). The East Caucasian tur (*Capra cylindricornis*) has been considered either a species distinct from the West Caucasian tur (*Capra caucasica*) or they comprise a single species of two potentially-hybridizing populations (Heptner, Nasimovich, and Bannikov 1961). Moreover the bezoar (*Capra aegagrus*), progenitor of domestic goat, has also been reported to hybridize with both tur varieties with which it shares seasonal grazing territories in the Caucasus region (Pfitzenmayer 1915; Sarkisov 1953; P. J. Weinberg 2002). Interspecies *Capra* gene flow is well known (Manceau et al. 1999; Pidancier et al. 2006; Kazanskaia, Kuznetsova, and Danilkin 2007), and may explain discordant phylogenies across loci (Pidancier et al. 2006; Ropiquet and Hassanin 2006). Such admixture may have shaped the evolution of domestic goat; for example, the tur has been identified as a putative source of a *MUC6* allele driven to fixation in domestic populations and likely selected for gastrointestinal parasite resistance (Zheng et al. 2020; Grossen et al. 2020). Tur additionally shows differing affinity to domestic and wild goat genomes indicating a complex evolutionary history of the genus.

Although tur are currently restricted to the Caucasus region, ancient wild goat specimens recovered from Direkli Cave, a camp site used by Late Pleistocene hunters in the Central Taurus Mountains of southern Turkey (Figures 1A, S1 and S2) (B. S. Arbuckle and Erek 2012), were found to carry a tur-like mitochondrial lineage, designated T (Daly et al. 2018). Three of these four reported ancient *Capra* specimen fall within the bezoar autosomal diversity, but a fourth - Direkli4, dated to 12,164-11,864 cal BCE (Ramsey 2009; Reimer et al. 2020) and sequenced here to 2.59X mean genome coverage (Table 1) - shows an excess of ancestral alleles in *D* statistic tests (Green et al. 2010) when paired with domestic/bezoar goat (Figure S3, Table S2) implying Direkli4 carries ancestry basal to that clade. To explore this signal further we generated low coverage genomes from historic and rare *Capra* samples, including a 20th century CE zoo-born East Caucasian tur (Tur2), tur specimens from the Dariali-Tamara Fort archaeological site near Kazbegi, Georgia (Mashkour et al. 2020), a zoo-born Walia ibex, and supplemented with published modern and ancient *Capra* genomes (Table S1, S3, Figure S4) (Zheng et al. 2020; Grossen et al. 2020). Surprisingly, a neighbour joining tree from nuclear genome identity-by-state (IBS) information places Direkli4 as sister to a clade of both Caucasian tur taxa, a signal obtained using either goat- or sheep-aligned data (Figures 1B and S5). The Direkli4 genome thus suggests a previously-unrecognized *Capra* lineage sister to both Caucasian tur inhabited the Taurus Mountains ~14,000 years ago.

Materials and methods

DNA from 7 postcranial bone elements from Direkli Cave and 13 historic *Capra* specimen was extracted via standard aDNA protocols (Yang et al. 1998), with a 0.5% sodium hypochlorite pre-wash (Korlević et al. 2015) performed for the Direkli material. Following uracil excision (Rohland et al. 2015) and dsDNA library construction (Meyer and Kircher 2010), libraries were subject to shotgun sequencing (Illumina HiSeq 2000 and NovaSeq 6000) or RNA-bait enrichment of mtDNA reads prior to shotgun sequencing. Additional sequencing data was also generated for specimen Direkli4.

Using bwa aln (Li, Ruan, and Durbin 2008) a relaxed alignment (-n 0.01 -o 2, Meyer et al. 2012) was performed against the goat reference ARS1 (Bickhart et al. 2017) or an outgroup genome (Oar_rambouillet_v1.0). Subsequent analyses were primarily performed in the ANGSD environment (Korneliussen, Albrechtsen, and Nielsen 2014) using single read sampling. A more detailed methodology is provided in the Supplementary Material, available at OSF (DOI 10.17605/OSF.IO/3ECQD).

Table 1: Sample provenance and sequencing summary.

Sample	Morphological Species	Origin	Age	Sex [b]	Nuclear Cov.[c]	mtDNA Cov.
Direkli4	*Capra spc.*	E4/8A, Direkli Cave, Turkey	12,164-11,864 cal BCE (2σ)	M	2.59	642.23
Direkli9	*Capra spc.*	B6/5, Direkli Cave, Turkey	Est. 12,100-8,900 BCE[a]	M	0.0003	9.5
Direkli12	*Capra spc.*	B13/4A, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	M	0.07	44.06
Direki13	*Capra spc.*	B13/7B, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	M	0.0055	76.99
Direkli14	*Capra spc.*	D3/7, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	M	0.0005	13.24
Direkli15	*Capra spc.*	B6/5, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	F	0.0002	24.21
Direkli16	*Capra spc.*	B8/7, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	F	0.01	15.11
Direkli17	*Capra spc.*	E5/5, Direkli Cave, Turkey	Est. 12,100-8,900 BCE	F	0.0001	0.0845
Caucasus1	*Capra caucasica*	Tamara Fort, Kazbegi, Georgia	4th-21st c. CE, probably 5th-15th c. CE	M	0.55	64.63
Caucasus2	*Capra caucasica*	Tamara Fort, Kazbegi, Georgia	4th-21st c. CE, probably 5th-15th c. CE	M	0.0021	379.71
Caucasus3	*Capra caucasica*	Tamara Fort, Kazbegi, Georgia	4th-21st c. CE, probably 5th-15th c. CE	M	0.004	464.51
Falconeri1	*Capra falconeri hepteneri*[d]	Unknown, via Parc de la Haute-Touche	20th Century CE	M	0.58	72.11
Falconeri2	*Capra falconeri*	Born at MNHN Zoo, Paris	20th Century CE	M	0.06	45.78
Ibex1	*Capra ibex*	Unknown	20th Century CE	F	3.93	179.03
Ibex2	*Capra ibex*	Pointe de Calabre, Savoie	20th Century CE	M	0.05	21.4
Sibirica1	*Capra sibirica*	Born at MNHN Zoo, Paris	20th Century CE	M	0.04	163.16
Sibirica2	*Capra sibirica*	Born at MNHN Zoo, Paris	20th Century CE	F	1.48	205.78
Tur2	*Capra cylindricornis*	Unknown, via Vincennes Zoo	20th Century CE	F	0.02	4.96
Walie1	*Capra walie*	Born at MNHN Zoo, Paris	20th Century CE	M	0.75	103.12
Pyrenaica2	*Capra pyrenaica*	Unknown	20th Century CE	M	0.16	51.2
Nubiana1	*Capra nubiana*	Unknown	20th Century CE	M	1.25	211.32

[a]Estimated ages for Direkli material is based on calibrated ages from the cave stratigraphy.
[b]M=Male, F=Female
[c]Cov. = coverage.
[d.]Falconeri1, a likely Barbary sheep (see Supplementary Methods).

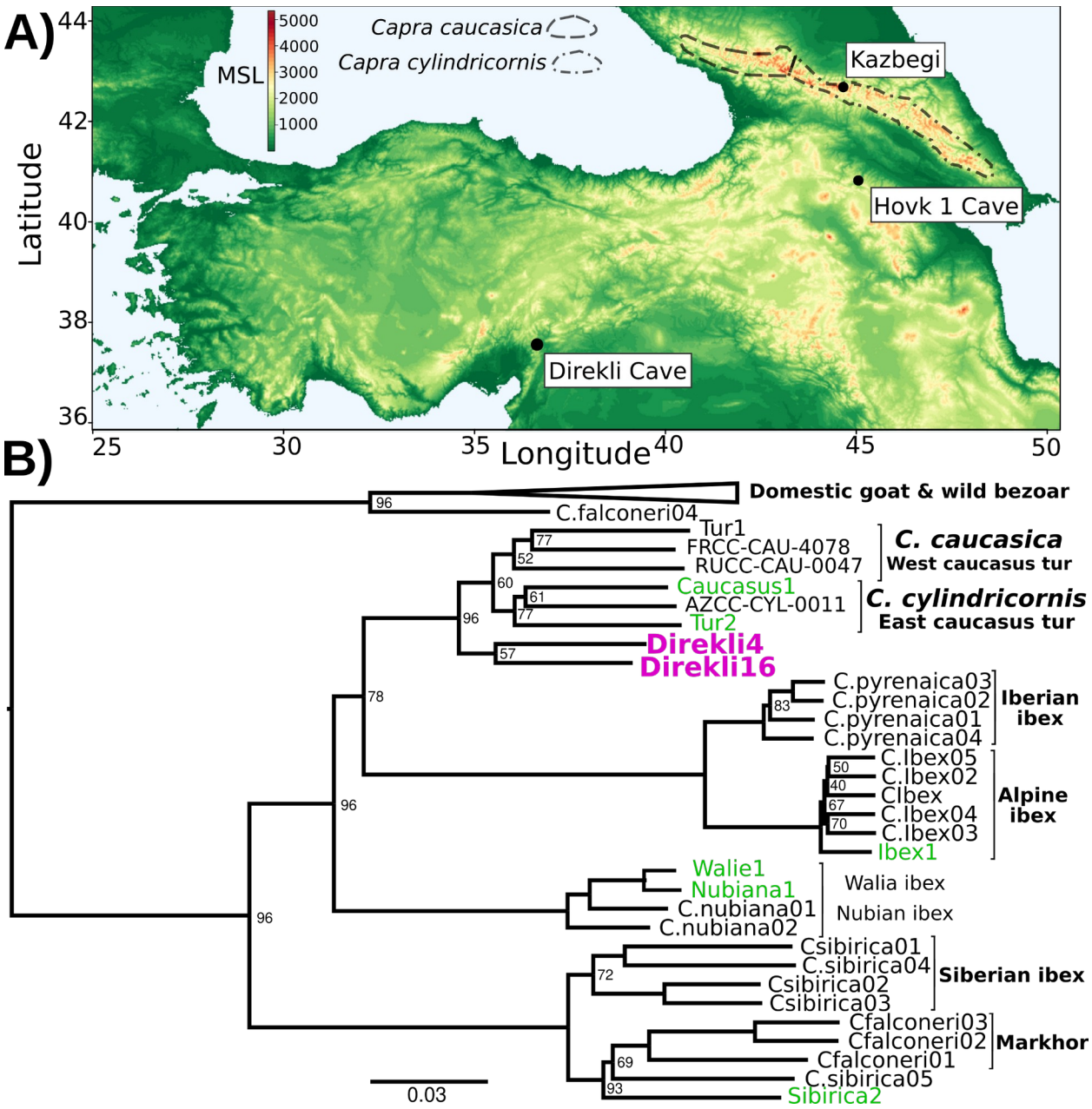

Figure 1: A) Elevation map of southwest Asia. Key sites are indicated, with *C. caucasica* and *C. cylindricornis* distributions from (Gavashelishvili et al. 2018) displayed. MSL=metres above mean sea level. B) Neighbour joining phylogeny of genomes >0.5X and the lower coverage Tur2 (0.02X) and Direkli16 (0.01X) genomes using 625,495 transversion sites and pairwise IBS, rooted on Sheep (not shown, as well as a likely Barbary Sheep sample Falconeri1, see Supplementary Methods). Node support from 100 replicates using 50 5Mb regions sampled without replacement shown when <100. Pink=Direkli4, green=other genomes first reported here.

Results

Our additional screening of Direkli Cave *Capra* remains identified seven with surviving DNA (Table S4); two genomes show greater affinity to Direkli4 than bezoar from the same site (Figure 2A, Table S5). An MDS plot of IBS distances (Figure S6) places two Direkli samples with sufficient coverage (Direkli4 and Direkli16) close to East and West Caucasian tur genome clusters, with a slight bias to the former. This tur affinity is unlikely to be driven by error as Direkli specimens have low error rates (0.026-0.195%, Table S1 and S3) and do not show inflated distance-to-the-outgroup relative to modern genomes (Figure S7). A total of three out of the eleven Direkli Cave *Capra* specimens therefore are assigned to the tur-related clade, implying that while less numerous than bezoar, members of this clade were not rare in the region in the Late Pleistocene. Nuclear genome types (tur-like or bezoar) do not necessarily co-associate with mitochondrial lineages (tur T and bezoar F), with all combinations except “tur-like genome, tur-like mitochondria” observed (Figure 2B, Figures S8 and S9, Table S5), establishing that there was gene flow between these lineages. Additionally, there is little variation among Direkli T mtDNA (average 4.07 pairwise differences, compared to 67 among Direkli F mtDNA), suggesting a limited population size for this Direkli tur-like matrilineage.

A tur-like population in the Taurus Mountains is consistent with the high variability in body size of the *Capra* material at Direkli Cave where extremely large *Capra* remains have been reported alongside smaller bezoar-size individuals (Figure S10). Extant tur exhibit body weights 20-50% larger than bezoar (Masseti 2009; Castelló, Huffman, and Groves 2016) and it is plausible that the ‘large’ *Capra* from Direkli represent tur-lineage animals. Although there are clear differences between bezoar and tur horn morphologies (Pidancier et al. 2006), unfortunately, diagnostic horncore remains have not been recovered from Direkli. The cave was initially inferred to be occupied primarily during summer months (B. S. Arbuckle and Erek 2012), with subsequent discoveries of architectural remains and zooarchaeological analyses indicating more intensive use (Benjamin S. Arbuckle 2019). The presence of tur-related goats may reflect use of the cave in the winter months when, based on Caucasian analogs (Gavashelishvili 2009), tur would be expected to descend from the higher elevations surrounding the cave (>2000m above sea level).

Given the Direkli4 genome was recovered together with bezoar specimens, the two lineages of *Capra* likely had proximate ranges and hybridised. We use *D* statistics (Green et al. 2010) to

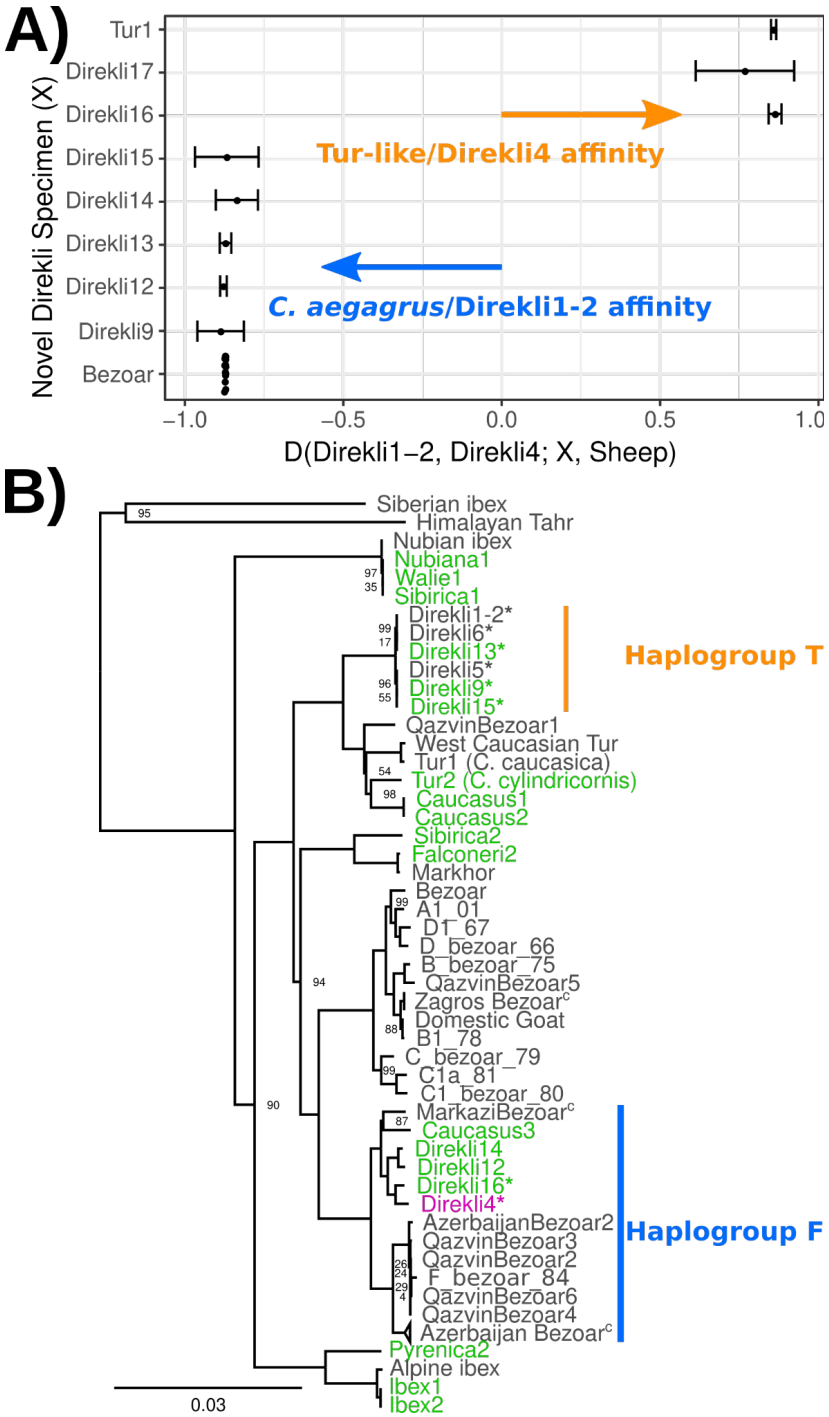

Figure 2: A) *D* statistic test of affinity using specimens from Direkli Cave and a historic *C. caucasica* individual for reference. Positive values indicate sample X has greater affinity with the Tur-like Direkli4 genome; negative values indicate greater affinity with the *C. aegagrus* Direkli1-2. Error bars represent 3 standard errors, underlying site counts are presented in Table S5. B) ML phylogeny of mtDNA, abbreviated. Bootstrap node support values (100 replicates) are displayed when <100. The complete phylogeny including likely Barbary sheep Falconeri1 is displayed in Figure S8. T haplogroup is as defined by (Daly et al. 2018) Low coverage sample Direkli17 is displayed in a highly reduced phylogeny Figure S9, C=collapsed. *=Direkli sample with discordant mtDNA and nuclear genome affinity.

measure Direkli4 derived allele sharing relative to either a likely-hunted (Table S7) or likely-herded (Table S8, Pearson's r >0.99) ~10,000 year old goat from the Zagros Mountains. A Late Pleistocene wild goat from the Armenian Lesser Caucasus, Hovk1, shows highest affinity with Direkli4 (Figure S11). Bezoar goats from Direkli Cave also show high Direkli4 allele sharing, mirroring affinity measures with west Caucasian tur (Zheng et al. 2020). While directionality is uncertain, these statistics imply gene flow between the tur-like lineage and wild bezoar.

Examining domestic goats we find that Neolithic genomes from Europe show greater affinity to Direkli4 (Figure S11), but Neolithic Iranian goats do not, echoing the distribution of Direkli bezoar-related ancestry in West Eurasian populations (Daly et al. 2018). We account for possible gene flow from Caucasian tur into modern European goat using the statistic D(Tur1, Direkli4; X, Sheep) to compare relative affinity with Tur1 and Direkli4 (Table S9). With the exception of two other tur samples, all examined domestic/bezoar goats show either a bias towards Direkli4 or gave a non-significant result, consistent with Direkli4-related admixture or a more complicated genetic history.

Genetic exchange between bezoar and the ancestors of Direkli4 could confound these measures of shared variation among domestic populations. We identified variants specific to Direkli4, conditioned on ancestral allele fixation in a range of defined groups (Figure 3A, Supplementary). Using this we calculate a statistic analogous to the D statistic, here termed the extended D or D_{ex}. D_{ex} measures the relative degree of allele sharing, derived specifically in a selected genome or group of genomes, and may have some utility in genera with complex admixture histories or admixture from ghost lineages. Relative to Neolithic Zagros goats, ancient domestic genomes from western Eurasia have an excess of Direkli4-specific variants (Figure 3B, Figure S12, Table S10). This “Direkli4-specific” allele sharing signal is absent in ancient goats from Iran-eastwards, and in all tested modern goat (Figure 3C). To control for possible reference biases, we calculated D_{ex} ascertaining on variants segregating in sheep (Table S11) and recovered similar results (Pearson’s r = 0.9935). Repeating the analysis using other ancient/historic *Capra* “specific” alleles shows somewhat correlated results (Table S12), but the distinct patterns of allele sharing (Figure S13, Table S13) imply that Direkli4 ancestry in domestic goat varies temporally and geographically.

We next identify alleles derived in Direkli4 also at a low frequency (>0%, ≤10%) in other *Capra* and bezoar, and then measure their abundance in domestic goats. The west Caucasian tur

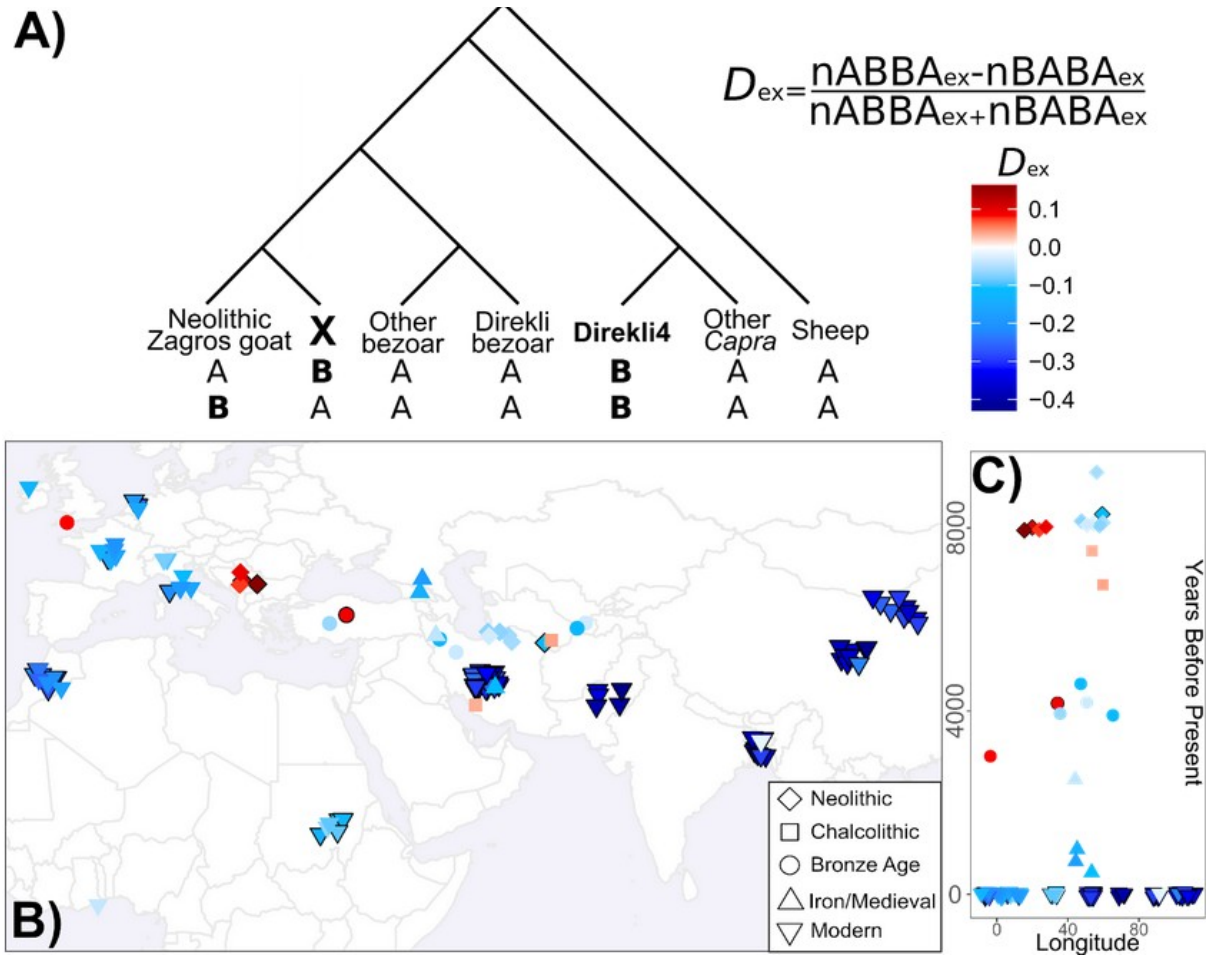

Figure 3: A) Extended *D* statistic. To control for gene flow with the *Capra* genus, we condition on variants derived in Direkli4 (H3) and a genome X (H2), but ancestral in other populations (here: Sheep, non-bezoar *Capra* genomes, bezoar from Direkli Cave, and other bezoar). Values are calculated relative to a set of Neolithic goat from the Zagros Mountains, and normalized similarly to the *D* statistic. B) Extended D statistic values for Direkli4 using transversions, C) plotted through time. Each symbol is a test genome, with shape denoting time period. Black borders indicates a |Z| score ≥ 3, using 1000 bootstrap replicates and 5Mb blocks.

(Tur1) most frequently shares derived alleles with Direkli4 and domestic goat (Figure S14, consistent with their cladal relationship (although this measure is sensitive to genome depth, Supplementary Methods). Ancient European domestic goats share a higher proportion of alleles with both Direkli4 and the high-coverage bezoar from Direkli Cave, Direkli1-2. In comparison, Modern European and African goats carry variation present in Direkli4 plus one of the two Caucasian tur (Tur1 and Caucasus1). This discrepancy could be explained by either gene flow from domestic goats into tur during the last 8,000 years, or alternatively an increase in tur-Direkli4 related ancestry in European populations over time.

Investigating gene flow events within *Capra*, automated tree-based model exploration (Pickrell and Pritchard 2012) detects admixture between the Direkli4/Tur lineage and the ancestors of the Late Pleistocene bezoar Hovk-1 (Figure S15). Residuals of this graph point to unmodelled affinity between Direkli4 and both Direkli Cave bezoar and with Neolithic Serbian domestic goat (Figure S16). Modern European goat do not show unmodeled Direkli4 affinity, supporting the interpretation that Direkli4-related ancestry has declined with time in west Eurasian goats. A reduced set of populations explored using ML network orientation (Molloy, Durvasula, and Sankararaman 2021) reiterates the Tur1/Direkli4 and Direkli bezoar lineages admixture, and also between Direkli bezoar and domestic goat (Figure S17). Investigating admixture graph space (Supplementary Methods, (Maier et al. 2022)) we find 2 admixture events best explain how a subset of populations (Sheep, Tur1, Direkli4, Direkli bezoar, Neolithic East Iran, and Neolithic Serbia) can be modelled. A majority (6/11) of graphs model Direkli bezoar as containing ancestry related to Direkli4 (median 1.5%, mean 5.2%; best fitting graph is shown in Figure S18), with a single graph modelling the opposite (2% Direkli bezoar ancestry). While the graph space explored is limited, these results suggest a greater degree of “Direkli4 to Direkli bezoar” gene flow than “Direkli bezoar to Direkli4”.

We finally identify 3 out of 112 regions introgressed from other *Capra* species to domestic goat (Zheng et al. 2020) which show high affinity with Direkli4 (Figures S18-20, S31-32, Supplementary Data Files 1 and 2). A further 7 regions appear to have most affinity with the Direkli4-tur clade (Figures S22-30), including a locus encompassing *MUC6*, a target of selection in domestic goats during the last 10,000 years (Zheng et al. 2020), implicating the Direkli4 lineage in the makeup of domestic goat gene pool.

Discussion

Our results indicate that a lineage related to the Caucasian tur existed in the Taurus Mountains during the Late Pleistocene, as late as the 12th millennium cal BCE. Based on the current, limited genomic data from the *Capra* genus, which we improve on here, this lineage appears to be a sister group to the tur *C. caucasica* and *C. cylindricornis*. Similar to other mammalian groups (Gopalakrishnan et al. 2018; Palkopoulou et al. 2018; Zheng et al. 2020), admixture likely occurred among *Capra* lineages; the population reported here carries bezoar-associated mtDNA and a possible small amount of bezoar nuclear genome ancestry (2% from 1/12 graphs). The Taurasian tur population is itself a possible candidate for the source of Tur-like ancestry present in domestic goats, including an introgressed *MUC6* allele fixed in modern

populations which increases gastrointestinal parasite resistance (Zheng et al. 2020). Given the relative paucity of *Capra* genomic data available compared to other mammalian groups, additional genomes from the genus will help refine the history of divergences and gene flow events which shaped the group's evolution.

We suggest this novel "Taurasian tur" lineage be designated *Capra taurensis* following IUCN convention (P. Weinberg and Lortkipanidze 2020) or *Capra caucasica taurensis* under a subspecies classification (Wilson and Reeder 2005) if and when sufficient multi-disciplinary data allows for taxonomic delimitation (De Queiroz 2007). The Taurasian tur may have diverged from the Caucasian lineages 130-200kya based on mtDNA coalescent estimates (Bouckaert et al. 2014; Daly et al. 2018). The current distribution of *Capra* species is mostly discontinuous and is suggestive of climate-induced fragmentation (Shackleton 1997). The ancestors of Caucasian tur likely extended over a broader range in Eurasia during the Late Pleistocene but may have been poorly captured by the fossil record (Uerpmann 1987; Crégut-Bonnoure 1991; P. J. Weinberg 2002). The large variability and high upper size range of *Capra* remains are consistent with both smaller-bodied bezoar and larger-bodied tur-relatives being present within the faunal assemblage at Direkli as well as other sites in the central Taurus and Lebanese mountains (Üçagızlı cave, Ksar Akil, Saaide II), but not in the western Taurus where only bezoar are evident (Figure S10) (B. S. Arbuckle and Erek 2012). *C. taurensis* could have survived the Last Glacial Maximum within the central Taurus Mountains, a plausible refugia for *Capra* species in addition to the Pontic and Anti-Taurus ranges (Gavashelishvili et al. 2018) while experiencing a severe matrilineal bottleneck (Figure 2B). *C. taurensis* appears to have produced fertile offspring with other members of the *Capra* genus; the traces of shared ancestry in ancient bezoar and likely managed goat (Figure 3B) may be the consequence of direct gene flow or secondarily via admixed bezoar. Gene flow between early managed goats and Anatolian bezoar carrying *C*. *taurensis* ancestry could partially explain the divergence between Zagros and more westerly herds.

Given the tremendous pressure on *Capra* species via Anthropocene over-hunting and habitat disruption (Shackleton 1997), it is assumed that *C. taurensis* is extinct, with its existence only now revealed via palaeogenomics. The Caucasian tur's preference for snowier habitats (Gavashelishvili et al. 2018) combined with the lower altitude of the Taurus Mountains relative to the Caucasus (Figure 1A) may have rendered the lineage vulnerable to climatic change via Holocene warming and interspecific competition with bezoar, which are still found in the Taurus

mountains (Naderi et al. 2008; Gavashelishvili 2009), leading to its hypothesised extinction. As the history of *C. taurensis* following the Late Pleistocene is still unknown, further genomic surveys of Holocene *Capra* remains and present-day populations, such as the VarGoats project (Denoyelle et al. 2021), from this and adjacent regions may illuminate its genetic legacy.

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Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

Data, script and code availability

Raw sequencing reads, aligned QCed final bam files, and mitochondrial fasta files have been deposited in ENA under the project accession PRJEB51668. Admixture graphs "as good as" the best fitting graph are available at https://osf.io/3ecqd/. Capra taurensis has been registered under the Zoobank LSID urn:lsid:zoobank.org:act:1261A42B-B0C0-4571- 87F4-8EC3B5381A88. Scripts for extended D calculation/disentangling derived allele sharing are available at https://github.com/Xevkin/direkli_caprid_extended_ds/tree/main.

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