Recommender (editor)

The manuscript “A novel lineage of the Capra genus discovered in the Taurus mountains of Turkey using ancient genomics” analyses the genomes of different ~14,000 year-old Capra specimens from an archaeological site in southern Turkey. The time and location of these remains are of interest because they can shed more light into the details behind the domestication process of domestic goats. Both reviewers have found that the manuscript makes relevant contributions in several fields. Reviewer one is particularly enthusiastic about the Dext statistic and suggests that this statistic is exposed in a more relevant manner.

There are however, several concerns that the two reviewers share. The first of them, is that the manuscript revolves around the claim of the novel finding of a lost Capra lineage. Beyond the difficulties surrounding the very definition of species and subspecies that Reviewer 1 raises and the possibility raised by Reviewer 2 of these specimen being a hybrid,

-both reviewers point to the current gap of knowledge that exists on the population structure of the modern Capra genus. The Discussion should be more explicitly framed acknowledging this gap of knowledge.

The Discussion now emphasises the limited amount of genomic data. Lines 233-235 of the revised manuscript reads: “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”. We also attempted to directly address the deficit in genomic data available for the genus by requesting access for east and west Caucasian Tur genomes from the Vargoats project. As these genomes have not been analyzed in a publication by the data generators, we include those samples in identity-by-state analyses only, and acknowledge the Vargoats consortia in the Acknowledgement. The overall structure of the phylogeny (Figure 1B) we report is consistent with the previously presented tree, with the Direkli4 clade falling as an outgroup to both Caucasian tur taxa. While we believe this strengthens our conclusion of a novel lineage in the Taurus Mountains, we state in the conclusion that “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” (lines 241-244).

The second concern is about the processing of the low coverage genomes. Some additional analyses are proposed to avoid mapping biases and to quantify the mismapping effects associated with the low coverage genomes. I also think it would be necessary to provide more information on the number of SNPs used in the different analyses.

We acknowledge that our data is of modest depth; as such we have presented SNP count numbers clearly for all analyses. These include: the SNP count underlying the IBS nj tree presented in the Figure 1 legend (lines 106-107), and for the sheep-aligned Figure S5 tree; all D statistic tests state their ABBA and BABA counts; the D statistics underlying Figure 2A are now shown in Table S5 and indicate in the caption (line 149); Treemix and OrientAGraph runs also have SNP counts indicated in their figure legend (S15 and S17). We have also taken on the reviewers' suggestions to include error rates as measured by "distance to the outgroup" (Figure S7) and using the ANGSD "perfect genome" approach (Table S1 and S3). In addition we have repeated several analyses using sheep aligned data, which is explained in detail to reviewer 2.

Something that the two reviewers do not comment on but I noticed is that in the legend of Figure 1B it is stated that the tree was done for genomes above 0.5x, but Tur2 is included and its genome is reported to be 0.02x.

Thank you for picking up on this. In the resubmitted manuscript we have added an additional low coverage sample, from the Taurasian tur lineage (Direkli16, 0.01X). The caption has been amended with: "and the lower coverage Tur2 (0.02X) and Direkli16 (0.01X) genomes using 625,495 transversion sites and pairwise IBS", lines 106-107.

I think that addressing these points would results in a significantly improved piece of work.

We thank the Recommender for their comments and suggestions. For ease of assessing the resubmission and for the reviewers, changes to the manuscript are listed below if not otherwise mentioned above:

- Abstract: lines 32-35 have been restructured for clarity
- All Identity-By-State analysis: with permission from the Vargoats consortia, three modern tur genomes (two West Caucasus tur and one East) have been included in IBS analyses (Figure 1B, S6, S7). Respecting that the data producers have not yet published an analysis of these genomes, we have not included these modern tur in other analyses, but note that our previous phylogeny holds with these additional genomes, supporting the finding of a sister group to both taxa.
- Figure 1B: colloquial species names have been added, with the binomial names for both tur species. An additional "Taurasian tur" genome has been added to the phylogeny (Direkli16, 0.01X). Site count has been added to the caption.
- MDS plot: new MDS plots (ancients+moderns, ancients/historics only) have been added on the suggestion of Reviewer 1 (Figure S6), and are described in Lines 116-120 of the main text. They show a clear affinity of the "Taurasian tur" specimen with tur, and the "European ibex" group in general
- Error: Figure S7 now shows "distance from the outgroup" as suggested by Reviewer 1. Tables S1 and S3 also now show errors as estimated by the ANGSD "perfect genome" approach. In both instances, the Direkli specimens do not show excessive error.
- Lines 175-177 suggest other circumstances in which the D_{ex} statistic would be of use: "Dex 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."
- Admixture graphs: following Reviewer 2's comments regarding an important parameter and the release of the ADMIXTOOLS2 preprint ("On the limits of fitting complex models of population history to genetic data", Maier et al 2022, Biorxiv), we have reconceptualized this analysis given the approach suggested by Maier & colleagues.

Briefly, we examined a subset of six genomes (limiting the scale of graph space explored) using an iterative approach. We find clear support for at least two admixture edges best fitting those six populations, with the Direkli wild goat modelled as admixed from the “Taurasian tur” clade in a majority of models (6/11). The full process is described in detail in the supplementary materials, with all “as-good-as” graphs available at https://osf.io/3ecqd/. We have updated the text (lines 216-222) to reflect these new results.

- The Discussion has been amended to include greater reference to Zheng et al (2020) and the relatively low amount of genomic data available for the *Capra* genus (lines 233-244).
- The Discussion places greater emphasis on the need for multi-disciplinary approaches to assign taxonomic status (lines 246-249)
- Supplementary Figures are clearly captioned.
- All instances of “pyrenica” have been amended to “Pyrenaica”.

Reviews

Reviewed by anonymous reviewer, 13 May 2022 10:03

In this article, the authors have sequenced multiple Capra ancient specimens from the Direkli and, in doing so, they have discovered one individual representing a tur-like novel lineage, Direkly 4, which might represent an extinct goat species (Taurasian tur) or subspecies highly related with Capra caucasica. Evidence of historical introgression of the Taurasian tur into ancient domestic goats is provided. It is a very interesting and relevant study, but several issues require further classification:

In the Introduction, the results obtained by Zheng et al. (Science Advances, DOI: 10.1126/sciadv.aaz5216) concerning the likely pre-domestication admixture between bezoars and tur-like species should be explained with more detail. In the light of these results, the placement of Direkli4 as sister to a clade of both Caucasian tur taxa would not be as unexpected as suggested in line 72. Indeed, Zheng et al indicate that among the 4 predomestication Anatolian bezoars 3 had a tur-like mitochondrial haplotype.

Given the relevance to Zheng et al to this manuscript as fairly pointed out by the reviewer, we have expanded in the Discussion section their inference of Tur-like ancestry in domestic goat.

Lines 235-244 now read: “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."

The authors used bwa aln to align ancient DNA reads to the goat reference genome. To mitigate the impact of reference bias (reads carrying the alternate allele are more difficult to map), which can have an adverse impact on the calculation of D-statistics, a variation-aware read aligner such as vg could be used instead.

While we agree that a variant aware approach for genotype calling would be ideal, we believe such a method is not suitable at this time due to the paucity of genomes available from across the genus and our understanding of across- and within-species variation. Such an approach should hopefully become a possibility when genus wide genomic datasets become available, such as the Vargoats project. Until then, our knowledge of known variants segregating across the genus are limited, and so an approach similar to vg would not be appropriate.

Acknowledging the reviewer's general point of reference bias and points raised by reviewer 2, we have repeated a large number of analyses using sheep aligned data. These consist of a subset of D statistic tests (Tables S7-S9), extended D calculations (S10 and S11), and bootstrapped IBS nj trees (Figure S5). While it would be preferable to repeat all analyses using sheep-aligned data, we are limited by the computational requirements of realignment. As such, analyses benefiting from population allele frequency estimates (e.g. Treemix, admixture graphs) remain calculated from goat-aligned, sheep-ascertained variants, as they are available for the largest number of samples. However, we believe are results are robust to reference bias given the high correlation between goat-aligned and sheep-aligned d statistic results we now calculate ($r > \sim 0.9$, see Supplementary Methods sections "D statistics " and "Extended D/Direkli4-specific alleles").

It would be useful to assess the error rates associated with sequencing by contrasting the genetic distance of ancient samples of species A to an outgroup (distance 1) vs genetic distances of high quality modern samples of species A to an outgroup (distance 2). An inflation of genetic distance 1 with regard to distance 2 would provide a conservative estimate of such error rate. Another measure of interest would be to count differences between the sequenced DNA fragments and regions of the goat genome that are highly conserved across Capra species.

We thank the reviewer for this very sensible suggestion. We include "distance from the outgroup" measures, derived from the sheep-aligned IBS calculations used in Figure S5, in the new Figure S7 and describe the results under "Error estimation" in the Supplementary Information. The majority of ancient Direkli specimens do not show excessive distance to the outgroup, with the highest distances being observed in historic and modern European (alpine and Iberian) ibex. A single Direkli wild goat / *Capra aegagrus* shows elevated distance to the outgroup relative to modern *Capra aegagrus* (0.240308), but all other Direkli specimens have unremarkable distance values.

We additionally report error values for ancient and historic Direkli & *Capra* genomes in Tables S1 and S3. Error rates were reasonable, with all falling below 0.5% and the highest reaching 0.3428%; the highest Direkli genome error was just 0.1947%. Together this lends confidence that this genomic data, while of low coverage, do not show excessive error and this does not drive out results.

In line 120, I find paradoxical that the combination "tur-like genome, tur-like mitochondria" is never observed in any of the specimens. Parental tur and bezoar populations should be larger than the population of hybrids, right? Hybridization between Capra species can happen, and without a doubt, has happened, but probably is not a very frequent event.

Yes this is not an intuitive result. We note we only have found 3 specimens from the Direkli with a Tur-like nuclear genome; additional sampling from Direkli Cave could establish if this extended to the entire population as suggested, but is beyond the scope of this study.

If I understand well, the Direkli 4 individual has a tur-like autosomal genome (Figure 1B) and a bezoar-like mitochondrial genome (Figure 2B), so could it be an hybrid between the two species, tur and bezoar, rather than a new Taurasian tur species (Capra taurensis) or subspecies (Capra caucasica taurensis)? Although mtDNA coalescent estimates suggest that this "Taurasian tur" may have diverged from the Caucasian lineages 130-200kya, this seems quite a short divergence time in terms of speciation (shorther than the Bos taurus/Bos indicus divergence time for instance). Indeed, in the paper authored by the same authors in Science (Daly et al. 2018), the predomestic radiation of the divergent bezoar/goat Levant population is assumed to have taken place 38,500 to 195,200 BP and it is not treated as a subspecies. There is even a more compelling example: the estimated time of divergence between Asian and Western pigs is 1 million years BP, and these two populations are not treated as different suid species. In summary, evidence that the new lineage discovered by the authors corresponds to a new species or subspecies is, in my view, not proved beyond a reasonable doubt.

Besides, how do we know that this divergent lineage is extinct in modern turs? I do not think that the variation of this species has been investigated in depth. It would be good to collect Capra genus modern sequences and construct a phylogenetic tree encompassing both modern and ancient Capra sequences to assess the variation of each species on a broader basis.

We appreciate the reviewer's insights from across artiodactyls and with *Capra*. It is challenging to make direct comparisons across groups as taxonomists of different animal orders apply different standards and reach different conclusions. Here our intention was to be consistent with (unsettled) designations and delimitations used within *Capra*. We hope that a future reassessment of the taxonomic assignments for the genus may be useful for evolutionary and conservation work in the genus similar to the *Felidae* (Kitchener A. C., Breitenmoser-Würsten...), perhaps using a unified species concept (De Queiroz 2007) and incorporating data from archaeozoological and palaeogenomic studies such as this one.

On the subject of whether the Direkli4 lineage represent ”hybrids" or a new Taurasian taxa, we argue that our genetic results are most consistent with a taxonomic distinction between the lineage and wild bezoar goat, with some gene flow, rather than a recent Tur-bezoar hybrid scenario. Measuring derived allele sharing using the *D* statistic (Direkli1-2, Direkli4; X, Outgroup - see Figure 2A) shows that the “taurensis” Direkli specimen (Direkli16 and Direkli17) have an imbalance of ~0.88. Complimentary results are obtained when wild bezoar goat are used to define the derived allele (*D* ≃ -0.87, bottom of Figure 2A). These are not the pattern of derived allele sharing expected if the taurensis lineage was indeed a hybrid. F1 hybrids would, on average, have *D* values of ~0. Successive generations would produce *D* values gradually further from 0, in a direction dependent on the admixing populations.

Our expanded admixturegraph2 results (lines 215-222) indicate that the “taurasian tur” Direkli4 genome is not best modelled as a hybrid between bezoar and tur. As detailed in our response to Reviewer 2, we have followed an iterative procedure for testing graphs as recommended by the “On the limits of fitting complex models of population history to genetic data” Maier et al 2022 pre-print (and describe the process in the SI section “Graph-based modelling”). Selecting two admixture events as best, most parsimonious model fitting the data, a majority (6/11) “as-good-as” graphs model Direkli bezoar as being admixed from the “Taurasian tur” (median 1.5%). Only 1/11 graphs model the “Taurasian tur” Direkli4 as a mixture between Caucasian tur and *Capra aegagrus/hircus*. All of these 11 graphs are available at https://osf.io/3ecqd/, which is also provided in the supplementary materials.

We agree that with additional genomic sequencing of both living and deceased *Capra* specimens may reveal the history of lineage e.g. subsumination into other populations via admixture; extant in a specific locale etc. Indeed, in the submitted text we state “assumed” and “hypothesised extinction”. We now include text referring to the VarGoats consortia in the final line of the discussion, which will analyse three modern Tur genomes in consort with other *Capra* genomies. With permission from that consortia, we have included the three modern tur genomes in IBS nj tree analyses (Figure 1B, Figure S5-6) which recapitulate the phylogenetic structure reported originally and place the taurasian tur lineage as sister to both east and west caucasian tur. We look forward to both broader and deeper sequencing projects examining the *Capra* genus to determine a more complete evolutionary history.

We agree with Reviewer 2 (see below) that the focus on species designation within the *Capra* and tur groups may not have been helpful in communicating the substance of the lineage discovery. In our original text we aimed to be consistent with the designations used within *Capra* rather than other *Mammalia* groups. However, if we consider a species as a “separately evolving metapopulation lineage” (De Queiroz 2007), then our present study cannot determine if the Taurasian tur maintained a continuous range with the Caucasian tur in the Late Pleistocene. As such we have amended the Discussion text to emphasize our uncertainty and reduced the stress placed on the taxonomic status. Lines 233-249 now read:

“Based on the current, limited genomic data from the *Capra* genus, which we improve on here, this lineage appears to be an outgroup 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)"

A multivariate analysis of the data via MDS (only ancient and ancient + modern) wold be also advisable

Thank you for this suggestion, we have included these using sheep-aligned data as Figure S6. We find the two "Taurasian tur" lineage genomes (Direkli4 and Direkli16) with sufficient coverage for inclusion, group with but slightly apart from the historic and modern Caucasian tur samples, with a slight bias towards east Caucasian tur. From the MDS plot, there is no strong indication that these represent a hybrid population. To reflect these results, lines 116-118 now read "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.".

The results obtained by Zheng should be incorporated more broadly into the Discussion because they are strongly connected with the main findings of Daly and coworkers.

As detailed above, we have encorportated Zheng et al's results into our Discussion to a greater extent due to its relevance here (lines 239-244).

In the Supplementary Materials (media 1-file), each Figure should have the corresponding caption to facilitate its interpretation.

This has been done and we apologize for the lack of captions previously.

I have found very few typos, but some additional revision is advised to eliminate all of them. For instance:Table 1 should be provenance or provenience, but not providence that has a different meaning (an intersting discussion can be found in: https://www.merriam-webster.com/words-at-play/usage-of-province-providence-provenience-provenance). In Table 1, but also in other places, Pyrenica should be Pyrenaica (Capra pyrenaica).In page 8 of the suppl file," were are" seems incorrect. In page 9, Caucuasian is also

These have been completed, thank you.

Reviewed by Torsten Günther, 10 May 2022 09:55

This is a review of the preprint by Daly et al entitled “A novel lineage of the Capra genus discovered in the Taurus mountains of Turkey using ancient genomics”. In Direkli Cave in the Taurus mountains of modern-day Turkey, they found ~14,000 year old remains that appear to belong to an unknown lineage of the genus Capra, closely related to Caucasian tur species. This lineage is specifically represented by the genome of Direkli4. The authors created a broad dataset of many different ancient Capra genomes. While this study had a pretty specific focus, we are sure that this data could become handy for many other projects in the future. All sequence data is already available through public databases.

Additionally, the authors present an extended D statistic, Dex, to infer gene flow from a specific source population (by conditioning on all other potential outgroups/sources are ancestral). In this particular study, the method is used to detect allele sharing between the tur lineage and ancient (but not modern) European domestic goats. Code for the method is available through GitHub. This method could be useful in similar scenarios. Something that comes to mind are anatomically modern humans and archaic hominins, where “ghost” admixture can affect D statistic results and, for instance, Neandertal admixture can influence tests where only Denisovans and modern populations are used in the test itself. The utility of Dex for other studies could actually be stressed further by explaining in what cases one can apply it.

We thank the reviewers for this comment, and have added the following text to lines 175-177 “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, but where known variant sites are lacking.”

We generally think that this study represents a very interesting example that highlights the power of archaeogenomics to gain surprising insights into past distributions of species and genera. We have some comments below but none of them should systemically affect the major finding of an unknown tur population in the Taurus Mountains.

Definition of a new species:

The manuscript is strongly trying to assign some taxonomic status to the Direkli lineage, even potential species and subspecies names are proposed. As population geneticists, we usually do not have a strong opinion on what should be considered a (sub-)species. These populations were able to produce fertile offspring and interfertility seems to be common within the Capra genus. We simply believe that an attempt to define a mammalian species only based on a low coverage genome and without much morphological information has the potential to trigger some discussion and draw attention from the general quality of this research and the aspects of this finding that highlight the potential of ancient DNA research. The authors have found a tur population that seems to be extinct (within the limitations of the available data, see also below), so it represents a great example on how ancient DNA can help to uncover past distribution of species/taxa and how past climate change and other factors did influence the extinction of populations. Demographic reconstructions often require "ghost populations" to fit but we are struggling to place these in time and space. In this case, the Direkli lineage may actually represent one of these ghost populations that were suspected from previous results.

The fact that the "extinction" of this lineage must have taken place within the range of aDNA also highlights the possibility for follow up studies to specifically search for genetic traces of this group in modern Capra populations as well as archaeological material from Anatolia, the Caucasus and the Zagros mountain range. A discussion largely revolving around the taxonomic status of the lineage could distract from these findings and there are probably good arguments for different classifications that us geneticists may not even have in mind at this point. The mitochondrial divergence between the groups would fall into a range that is still considered one species in other systems. The exact status of this "Taurasian tur" could also have implications for the two Caucasian (sub-)species as well as local conservation efforts.

We thank the reviewers for this fair and nuanced assessment of the manuscript, and are glad that the commentary might be made available under the open review system. We agree that a single data type (in this instance genomic) is not sufficient to establish if a lineage should be designated as a distinct species. Acknowledging this we have amended the Discussion text to place less emphasis on the assignment of any particular designation (which we intended to do in the original text but may have failed in execution), but rather suggest binomial nomenclature if a taxonomic level can eventually be assigned. Lines 246-248 now reads: "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)"

We hope this manuscript will lead to multi-disciplinary investigations of mammalian assemblages in the Taurus and nearby mountain regions such as the Pontic or Anti-Taurus. Indeed, the absence of horn cores at the site of Direkli is a pity (albeit an intriguing observation - were horn cores moved off-site as trophies?), as horn morphologies are used within the *Capra* genus for species delimitation.

Writing of the text:

In general, the text is well written but there are some inconsistencies within the text that leave the feeling that it was at least partly written in a rushed way. For example, Introduction and Discussion seem quite strongly aiming at defining the new genome as a new (sub-) species while abstract and results seem more nuanced. There are also some seemingly contradictory statements, as e.g. (from the abstract): "West Eurasian domestic goats in the past, but not those today, appear enriched for Direkli4-specific alleles, and we further identify genomic regions introgressed in domestic goats with high affinity to Direkli4." – this sentence refers to two completely different results/analyses which is clear after reading the main text, but maybe not at this point.

The supplementary material could also take some work, e.g. making sure all display items are described (figure legends) and referenced in the text, maybe even move the supplementary figures closer to the corresponding text bits.

We appreciate the reviewers' thoughtful comments on the writing of the text. We agree that as-written the abstract line was contradictory, if not in substance. As the reviewers likely appreciate, the "Direkli4-specific" allele sharing is measured relative to a population of Aceramic Neolithic Zagros goat; this does not preclude European goats carrying Direkli4-lineage variants, or for some of those variants to have been fixed by selection. To help clarify this, lines 32-35 have been restructured and now read: "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".

We apologize for the structure of the SI and the Supplementary Figures; these were formatted for submission to a specific journal rather than for ease of review. All Supplementary Figures clearly have an associated caption. We have also ensured that all figures and tables are mentioned in the text.

The dataset and its limitations:

We believe that it should be made clearer that all conclusions are drawn with respect to the available data. The genus Capra seems to be understudied, so only a handful of full MT genomes are available and some species are only represented by relatively low quality aDNA nuclear genomes. This is especially true for the Caucasian tur species for which only 5 individuals are available. Furthermore, Direkli4 itself seems to be a hybrid as it carries a bezoar MT lineage. This means that a lot of the diversity of these species and within the genus itself is unknown. Adding that interbreeding seems to be quite common, this should be taken into account when discussing the species status of the new genome.

We agree with the reviewers that genomic data from across *Capra* are limited and that this raises concerns about the power and robustness of our findings. As such we have obtained permission from the VarGoats consortia to include three modern tur genomes (two western, one eastern) in IBS nj tree analyses (Figures 1B and S5) which recapitulate the phylogenetic structure reported originally and place the Taurasian tur lineage as sister to both east and west Caucasian tur. We look forward to both broader and deeper sequencing projects examining the *Capra* genus to determine a more complete evolutionary history. In the meantime, we have added text reflecting the current state of understanding of *Capra* genomics (see below), and referenced the VarGoats project (Line 277-278: “such as the VarGoats project (Denoyelle et al. 2021)”) which will take some steps to rectify this deficit.

We have expanded on our description of the genomic paucity across the genus in the Discussion. Lines 233-244 reads: ”Based on the current, limited genomic data from the Capra genus, which we improve on here, this lineage appears to be an outgroup 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.”

Ascertainment and reference bias:

The authors seem concerned that their results could be driven by certain biases. To avoid or mitigate them, they chose two approaches: mapping the reads to the sheep genome or using only sites that also segregate in sheep. While the first approach should reduce the effect of mapping/reference bias, the latter should avoid ascertainment bias. Most analyses are verified with the sheep ascertained variants but only the IBS tree is based on the sheep mapped data. We would be concerned that the goat mapped but sheep ascertained results of allele sharing analyses (e.g. Dex) could be influenced by mapping bias. Our recommendation would be to repeat these analyses with the sheep mapped data and sheep ascertained data to avoid both biases.

We agree with the reviewers that sheep-aligned, sheep-ascertained data would be the ideal in this study. While we were limited by the computational burden of realigning >1500X total fold coverage of modern data, plus ancient genomes, we realigned a representative subset (46, indicated in Table S3 and not including those in Table S1), including the modern tur specimen given access to us by the Vargoat consortia for the IBS analyses.

Using the sheep aligned data, we repeated a subset of *D* statistic tests (Tables S7-9) and found high correlation with the goat-aligned test results ($r > 0.9$ for Tables S7 and S8; $r = \sim 0.49$ for S9 however the directionality and large *D* values observed are consistent between sheep and goat aligned tests).

We also include two sheep-aligned IBS nj trees (Figure S5) and MDS plots (Figure S6), with node support values for the former. We again find that the “Taurasian tur” genomes fall close to

Caucasian tur groups, with no evidence the taurasian tur falling on a hybrid cline with domestic goat.

Given the lower number of sheep-aligned genomes available, we did not rerun analyses dependent on population allele frequencies (e.g. Treemix, Orientagraph, admixturegraph). We hope in the future a full exploration of *Capra* lineage evolution can be performed with this approach and using a dataset fully representative of the genus' diversity (e.g. using pangeomic approaches). However, we repeated the key D_{ex} tests involving Direkli4 as H3 (i.e. that underlie Figure 3B), with sheep-aligned/sheep-aligned+ascertained values reported in Tables S10 and S11. A note of caution is that the D_{ex} absolute values are dependent on the genomes included e.g. an additional modern tur or bezoar with tur ancestry could substantially reduce the number of alleles defined as "Direkli4-specific". As such absolute values and nABBAA/nBABAA are expected to vary between the goat-aligned (many genomes) and sheep-aligned (fewer) tests.

As detailed in the Supplementary Information, we found high correlation between goat-aligned and sheep-aligned tests (r= ~ 0.9 for un-ascertained and sheep-ascertained SNP sets). We hope that, given the computational requirements of re-aligning the full breadth of genomes used elsewhere in the paper, the high correlation between sheep- and goat-aligned results lend confidence to our conclusions.

Minor comments:

- Line 123: Considering that all these individuals carrying this T lineage so far were found in the same place, it may be difficult to conclude how many actual introgression events took place. There could be multiple closely related events or further distant in the past or other possibilities.

We agree that these scenarios are also possible and have changed the text on line 128 (new line number) to "suggesting a limited population size for this Direkli tur-like matrilineage".

- Please add the species names to Figure 2B.

Done

- Line 246: One could probably test those demographic scenarios with this dataset. That might be beyond the scope of this article but it would certainly add relevant information.

We agree and look forward to future studies which have the genomic data to do this.

- Please list non default parameters instead of just writing "relaxing parameters (Meyer et al 2012).

Done, for Line 87 and the supplementary material.

- Was the auto_only option set to FALSE in admixtools2? By default, the package assumes human data, i.e. it ignores all chromosomes after chr22.

Thank you for pointing this out, as auto_only was left on its default value of TRUE. Rather than repeat the previous analysis with the correct auto_only parameter choice, we applied an iterative approach as suggested by “On the limits of fitting complex models of population history to genetic data”, Maier et al 2022 preprint. This is described above in the response to reviewer 1 and extensively in the supplementary material (under “Graph-based modelling”). Briefly, we performed 50 iterations of different complexity classes (admixture events) using a reduced set of 6 populations to limit admixture space exploration. Two admixture events well fit the data, and after filtering graphs we found 11 “as-good-as” models, which are available at https://osf.io/3ecqd/. The majority (6/11) of these graphs model the Direkli bezoar as admixed from the Direkli “Taurasian tur” (median 1.5%, mean 5.17%), with only 1/11 showing the Direkli4 genome as admixed from Direkli bezoar (2% Direkli bezoar ancestry).

While the graph space explored is limited, we believe that this iterative approach improves on what was performed in the previous version of the manuscript, and we thank the reviewer for their diligence in checking parameter choice.