Genetics and Material Culture Support Repeated Expansions into Paleolithic Eurasia from a Population Hub Out of Africa

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Abstract

The population dynamics that followed the Out of Africa (OoA) expansion and the whereabouts of the early migrants before the differentiation that ultimately led to the formation of Oceanian, West and East Eurasian macropopulations have long been debated. Shedding light on these events may, in turn, provide clues to better understand the cultural evolution in Eurasia between 50 and 35 ka. Here, we analyze Eurasian Paleolithic DNA evidence to provide a comprehensive population model and validate it in light of available material culture. Leveraging on our integrated approach we propose the existence of a Eurasian population Hub, where *Homo sapiens* lived between the OoA and the broader colonization of Eurasia, which was characterized by multiple events of expansion and local extinction. A major population wave out of Hub, of which Ust'Ishim, Bacho Kiro, and Tianyuan are unadmixed representatives, is broadly associated with Initial Upper Paleolithic lithics and populated West and East Eurasia before or around 45 ka, before getting largely extinct in Europe. In this light, we suggest a parsimonious placement of Oase1 as an individual related to Bacho Kiro who experienced additional Neanderthal introgression. Another expansion, started before 38 ka, is broadly associated with Upper Paleolithic industries and repopulated Europe with sporadic admixtures with the previous wave (GoyetQ116-1) and more systematic ones, whereas moving through Siberia (Yana, Mal'ta). Before these events, we also confirm Zlatý Kůň as the most basal human lineage sequenced to date OoA, potentially representing an earlier wave of expansion out of the Hub.

Key words: molecular anthropology, paleolithic Eurasia, ancient DNA, material culture.

Significance

We used an approach that integrates genetic with archaeological evidence to model the peopling of Eurasia by *Homo sapiens* after the Out of Africa (OoA); we infer the presence of an OoA population Hub from which multiple waves of expansion (chronologically, genetically, and technologically distinct) emanated to populate the new continent. We explain the East/West Eurasian population split as a longer permanence of the latter in the OoA Hub, and provide an explanation for the mixed East–West ancestry reported for paleolithic Siberians and, to a minor extent, GoyetQ116-1 in Belgium. We propose a parsimonious placement of Oase1 as an individual related to Bacho Kiro who experienced additional Neanderthal introgression and confirm Zlatý Kůň genetically as the most basal OoA human lineage sequenced to date, also in comparison to Oceanians and putatively link it with non-Mousterian material cultures documented in Europe 48–43 ka.

Introduction

Several layers of genetic, paleoanthropology, and paleoclimatology evidence point to 70–60 ka as the most likely time window for the major colonization of Eurasia by *Homo sapiens*. For several millennia, however, the human population OoA did not expand much from a demographic perspective, with the divergence between Eastern and Western Eurasian populations inferred not earlier than 45–40 ka from modern DNA data (Soares et al. 2012; Schiffels and Durbin 2014; Pagani et al. 2015, 2016; Malaspinas et al. 2016; Bergström et al. 2020; Choin et al. 2021). We can imagine that, after leaving Africa (Pagani 2019), the ancestors of all non-Africans lived somewhere on the new continent, interbred with Neanderthals (Green et al. 2010), and persisted as a single population for at least 15 thousand years (conservatively, the time between the OoA bottleneck and the split between European and East Asian populations, marking the beginning of a broader expansion) and later diffused from this "population Hub" ultimately colonizing all of Eurasia and further.

A simplistic interpretation would see this Hub as just a stopover after which the ancestors of contemporary East and West Eurasians would diverge to reach their respective homelands. Two recent studies, however, showed that the scenario is more complex than that: Prüfer et al. (2021) analyzed the genome of a paleolithic woman from Zlatý Kůň (Czech Republic) and determined that it belonged to a lineage basal to the split between later Eastern and Western Eurasian, who share some drift with respect to Zlatý Kůň. Whereas her radiocarbon dating has proved unreliable, Zlatý Kůň has been "dated genetically" and proved to be older than 45 kyr making her the oldest *H. sapiens* sequenced to date. In the second study, Hajdinjak et al. (2021) sequenced a handful of individuals recovered in the Bacho Kiro cave (Bulgaria) and dated around 45 ka showing that they are genetically closer to modern and ancient East Asians than they are to modern and ancient Europeans. On top of that, the Bacho Kiro individuals also have a higher than usual proportion of Neanderthal

ancestry, which resulted from an interbreeding that occurred just a few generations before they lived. Taken together, these studies show that sometimes before 45 ka, Europe was inhabited by a lineage basal to all other Eurasians (Zlatý Kůň), whereas around 45 ka it hosted a human population closer to ancient and contemporary East Asians than to Europeans (Bacho Kiro). These findings trigger the question of where and how the ancestors of Kostenki14, (Fu et al. 2016), the oldest (~38 ka) individual sequenced to date that shares more drift with Europeans with respect to East Asians, lived and accumulated genetic drift after splitting from Eastern Eurasians.

Furthermore, the time interval between ~50 and ~35 ka is characterized by the appearance and turnover across Eurasia of several techno-complexes which, based on technological characteristics, we divide into: (1) non-Mousterian and non-Initial Upper Paleolithic (IUP) technologies that appeared during the Middle to Upper Paleolithic transition, comprising Uluzzian, Châtelperronian, Szeletian, and Lincombian-Ranisian-Jermanowician (LRJ); (2) production of blades using volumetric and levallois methods here extensively defined as IUP(Boëda et al. 2013; Kuhn and Zwyns 2014; Kuhn 2019); (3) lithic industries characterized by the production of blades and bladelets often together with ornaments and bone tools and here inclusively defined as Upper Paleolithic (UP) (see Supplementary Section 1, Supplementary Material online for an in-depth definition of these material culture labels). Since only a few contexts present with both material culture and stratigraphically related human remains for which aDNA is available (table 1, fig. 2, Supplementary table S1, Supplementary Material online); this leads to many possible scenarios of association between cultural change and human migration, as well as with interspecific and intraspecific human interaction.

Therefore, an enhanced understanding of the population dynamics during the broader colonization of Eurasia is critical to explain the shaping of current *H. sapiens* genetic diversity OoA, and to understand if cultural change

Table 1.

List of paleolithic individuals used for the qpGraph analyses, see Supplementary table S1, Supplementary Material online for full details and fig. 2 for a map with the geographic position of the sites

Sample	Techno-complex	Country	Date (ka)	Reference
Zlatý Kůň	Szeletian/IUP[a]	Czech Republic	>45	Prüfer et al. (2021)
Ust'Ishim	IUP[a]	Russia	45	Fu et al. (2014)
Bacho Kiro	IUP	Bulgaria	45	Hajdinjak et al. (2021)
Oase1	IUP/UP[a]	Romania	40	Fu et al. (2015)
Tianyuan	IUP[a]	China	40	Yang et al. (2017)
Kostenki14	UP[a]	Russia	38	Fu et al. (2016)
GoyetQ116-1	UP[a]	Belgium	35	Fu et al. (2016)
Sunghir	UP	Russia	34	Sikora et al. (2017)
Yana	UP	Russia	32	Sikora et al. (2019)
BK1653	UP	Bulgaria	35	Hajdinjak et al. (2021)
Mal'ta	UP	Russia	24	Raghavan et al. (2014)

[a]Attribution based on nearby coeval sites.

documented in the archeological record can be attributed to population movements, human interactions, convergence, or any intermediate mechanism of biocultural exchange.

To address this crucial point, we set out to exploit the available genomes from ancient paleolithic individuals, interpreting the results in the light of archeological evidence to better elucidate the role of the Hub during the peopling of Eurasia and in the cultural changes that accompanied it.

Results

We reconstructed the relationship between the available paleolithic genomes (Supplementary Section 2, Supplementary Material online) using the software qpGraph, which based on the observed f-statistics computes the best-fitting admixture proportions and branch lengths relying on a user-specified topology. We first implemented the simple population tree proposed by Prüfer et al. (2021) and proceeded to add other samples step-wise, starting with Bacho Kiro and jointly analyzing the new samples for the first time.

We tried to add Bacho Kiro in all plausible positions without invoking additional admixture events, with the exception of the extra Neanderthal introgression already documented for the Bacho Kiro samples (Hajdinjak et al. 2021) (Supplementary fig. S1 and Section 3, Supplementary Material online). To allow the likely European Neanderthal population that admixed with the ancestors of Bacho Kiro to be different from the Neanderthal population that admixed with the ancestors of all non-Africans shortly after the OoA, we designed it as a different node closer to the Neanderthal from Vindija (Croatia); if it was indeed the same Neanderthal population the total inferred drift in all edges between the two Neanderthal nodes admixing with Eurasians would be 0. Additionally, to avoid our results to be driven by later

population interaction between Eurasia and Western Africa (Chen et al. 2020) or by the putative admixture of Mbuti pygmies with an archaic ghost hominin (Hammer et al. 2011; Hsieh et al. 2016; Lipson et al. 2020) we used four ancient South African hunter-gatherers (Schlebusch et al. 2017; Skoglund et al. 2017) (Supplementary table S1, Supplementary Material online) instead of Mbuti, and found the best placement of Bacho Kiro as a sister group of Tianyuan (Supplementary fig. S1C and Section 3.2, Supplementary Material online). This placement is different from the one proposed by Hajdinjak et al. (2021) and we found no support for a treeplacing Bacho Kiro as an early branch among the OoA lineage (Supplementary fig. S1A, Supplementary Material online) when immediately accounting for its higher Neanderthal ancestry, possibly also thanks to the availability of Zlatý Kůň, who may provide good guidance to the basal OoA genetic landscape. After adding Kostenki14 as a key ancient European sample, we found that the 45 kyr old Ust'Ishim would fit better as a basal split along the branch leading to Tianyuan and Bacho Kiro (Supplementary Section 3.3, Supplementary Material online) (Supplementary fig. S2, Supplementary Material online). As noted in Supplementary Section 3.3, Supplementary Material online, however, alternative configurations are compatible with a trifurcation between Kostenki14, Ust'Ishim and the branch leading to Tianyuan and Bacho Kiro, despite the total score obtained when placing Ust'Ishim together with Tianyuan and Bacho Kiro seems to point to a small albeit nonnegligible evolutionary path shared among these three samples.

The scenario emerging from our proposed tree (fig. 1A, Supplementary fig. S2B, Supplementary Material online) depicts Zlatý Kůň as a population basal to all subsequent splits within Eurasia. Downstream of Zlatý Kůň, the separation of Ust'Ishim and other genetically East Asian ancient samples (Bacho Kiro and Tianyuan, red in fig. 1A) from the branch eventually leading to Kostenki and Sunghir (genetically
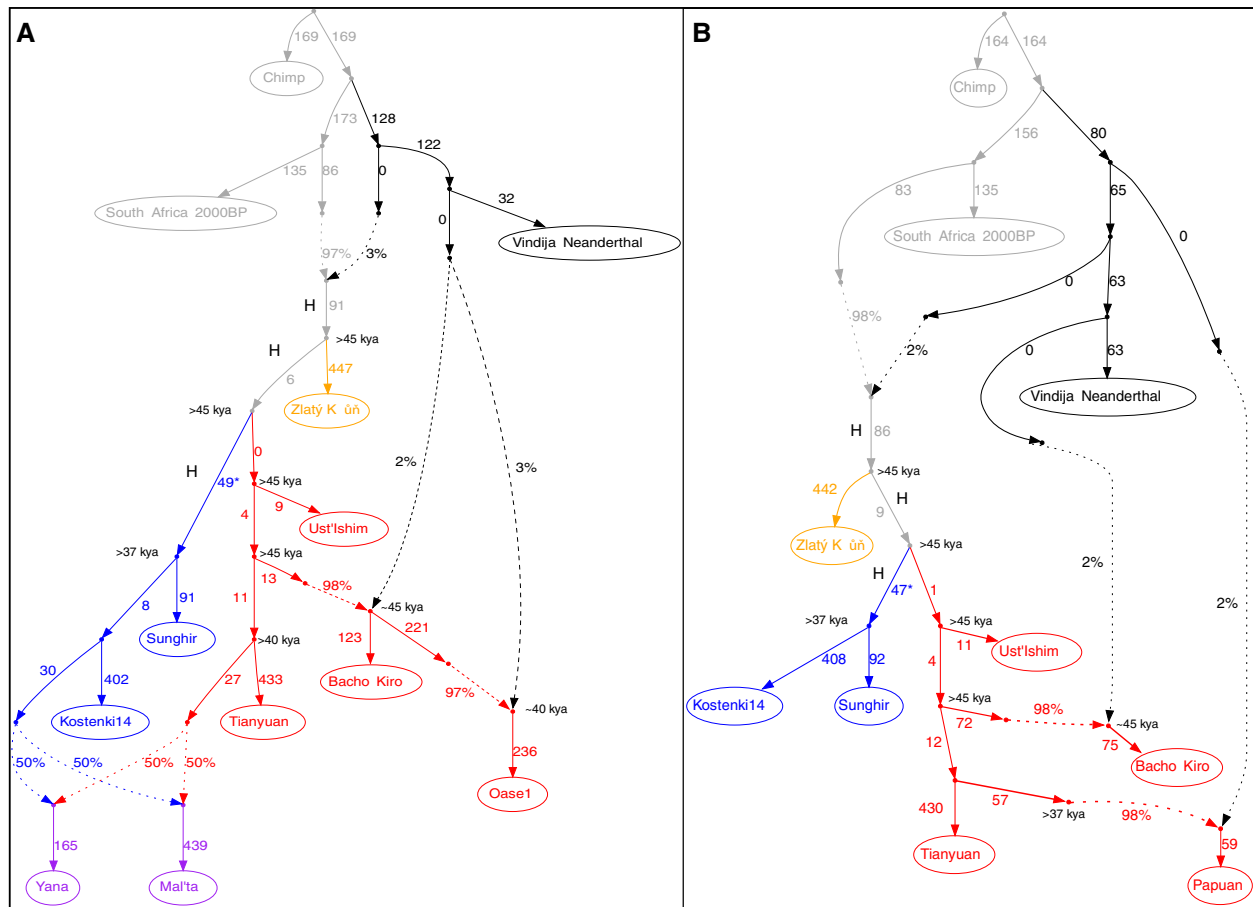
Fig. 1.—qpGraph trees for Paleolithic Eurasia. (A) Best fit population tree that recapitulates the major population streams from an OoA Hub, colored according to the most parsimonious lithic culture affiliation (IUP or non-Mousterian/non-IUP: yellow; Initial Upper Paleolithic, IUP: red; Upper Paleolithic, UP: blue - cultural affiliation for each sample are extensively reported in Table 1 and Supplementary Table S1). See Supplementary Sections 1 and 3, Supplementary Material online for more details on the qpGraph generation and on the material culture labels. The tree proposed here is based on 71,853 SNPs due to the presence of Oase1, but its significance holds with a greater number of SNPs (303,651) when Oase1 is removed (Supplementary fig. S5C, Supplementary Material online), which also yields a nonzero branch upstream of Ust'Ishim. (B) Modern Papuans can be added as a terminal branch of the Paleolithic expansion that was associated with IUP in Eurasia. Such a tree, based on 418884 SNPs, is just one of the six acceptable possibilities we identified (Supplementary fig. S7, Supplementary Material online) and is reported here just on the basis of its parsimonious nature. Nodes labeled with "H" represent population differentiation inferred to have happened inside the population Hub OoA. Asterisks indicate genetic drift putatively occurred inside the Hub, which differentiates the West and East Eurasian genetic components.

West Eurasians with a deep shared genetic drift - 49 units -, in blue in fig. 1A) defines the first major subdivision of Eurasian genetic components. We note that, on one hand, due to the peculiarities of the qpGraph tree construction and accretion, this represents only one among other unexplored and potentially supported trees, on the other hand, its topology is broadly matched by the spatiotemporal distribution of material cultural evidence at a cross-continental scale, according to the present state of archeological knowledge. From a chronological point of view the right branch (red) of fig. 1A presents samples dated ∼45/40 ka, whereas the left (blue) one is instead characterized by a younger date of the Kostenki and Sunghir samples (38 and 34 ka, respectively). The structure emerging from genetic distances is also

supported and confirmed by technological evidence. The earlier, red branch is consistently populated by contexts either directly showing or surrounded by geographic and temporal proxies exhibiting IUP technology (Supplementary tables S1 and S2, Supplementary Material online). The latter, blue branch is instead predominantly characterized by contexts with UP technology (Supplementary tables S1 and S2, Supplementary Material online). Finally, the basal Zlatý Kůň is coeval to Eastern European sites exhibiting Mousterian, non-Mousterian, and IUP technologies (Supplementary tables S1 and S3, Supplementary Material online).

Notably, Oase1, which has so far been regarded as a lineage unrelated to extant Eurasians (Fu et al. 2015), can be described as an additional admixture between the Bacho
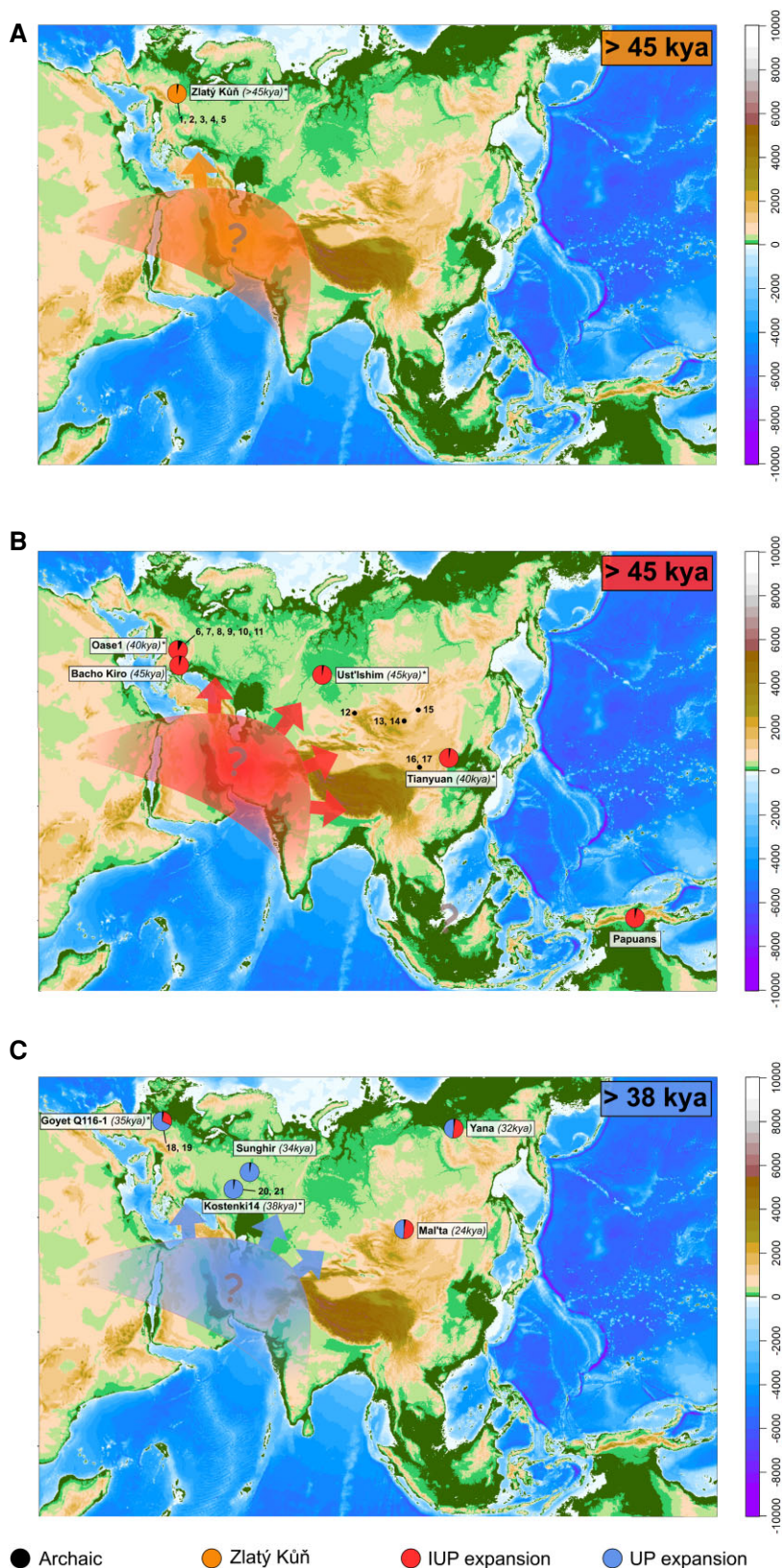
FIG. 2.—Subsequent expansions into Eurasia from a population Hub OoA. (A) Zlatý Kůň can be described as a putative early expansion from the population formed after the major expansion OoA and hybridization with Neanderthals, and could be linked with non-Mousterian and non-IUP cultures found in Europe 48–45 ka or with IUP. (B) Representative samples dated between 45 and 40 ka across Eurasia can be ascribed to a population movement with uniform

Kiro population, or a closely related one, and Neanderthals. The tree displayed in fig. 1A accommodates Oase1 in such a position, yielding no outlier f2 and f4 values and being supported by a stepwise design as described in Supplementary Section 3.4, Supplementary Material online. This result is coherent from a geographical and chronological perspective, being Oase1 dated to around 5 kyr later with respect to Bacho Kiro and being located just a few hundred kilometers away. Incidentally, the proposed placement of Oase1 on the graph provides support for the claim made in the original Oase1 publication (Fu et al. 2015) about an additional pulse of Neanderthal admixture experienced by the Oase1 ancestors between the one shared by all non-Africans and the one that occurred 4–6 generations before it lived. We here propose that such an event may be shared with the Bacho Kiro population or with a closely related one, which could be seen as ancestral to Oase1. To rule out the possibility that Oase1 attraction to Bacho Kiro is driven by the excess of Neanderthal ancestry they share, we masked the most recent Neanderthal introgressed segments of Oase1 and rerun the analysis: Oase1 holds its position and needs no further Neanderthal contribution, hence confirming its affinity with Bacho Kiro is genuine and not a simple attraction introduced by the extra Neanderthal component present in both individuals (Supplementary fig. S3D and Section 3.4, Supplementary Material online). Finally, this placement for Oase1 is consistent with the reported East Asian genetic affinities for another sample from the same site (Oase2, Supplementary Section 3.4, Supplementary Material online).

The scenario inferred by genetic data and supported by material culture, would then explain Ust'Ishim as the result of early IUP movements toward Siberia (Zwyns et al. 2019; Zwyns 2021), and the presence of Bacho Kiro-like populations in Europe at least from 45 ka as part of a broader peopling event that reached as far East as Tianyuan ~40 ka with little or no interaction with preexisting Zlatý Kůň-like groups (Supplementary fig. S4 and Section 3.5, Supplementary Material online) but with occasional contacts with Neanderthals (Fu et al. 2015; Hajdinjak et al. 2021). The UP branch would have then emerged from a putative OoA population Hub well after 45 ka, a scenario that

finds support in previous hypotheses on the appearance of UP techno-complexes (e.g. Aurignacian) in Europe, although the role of migrations and exchange between Europe, Western Asia, and the Levant is still debated (Conard 2002; Mellars 2006; Teyssandier 2006; Davies 2007; Hoffecker 2009; Le Brun-Ricalens et al. 2009; Nigst et al. 2014; Zilhão 2014; Hublin 2015; Bataille et al. 2020; Falcucci et al. 2020). The origin and spatiotemporal development of later UP techno-complexes (e.g. Gravettian) are also still debated, and are currently interpreted as the outcome of mixed processes involving regional adaptation, functional convergence, and exchange between populations that took place in Europe (Pesesse 2010; Moreau 2012; Otte 2013, 2017; Kozłowski 2015) after the putative split from the OoA Hub. As far as Northern Asia and the reported Ancestral Northern Eurasian ancestry is concerned, the UP legacy may be responsible for the West Eurasian components already reported in ancient Siberian samples dated between 34 (Salkhit [Massilani et al. 2020]), 31 (Yana1 [Sikora et al. 2019]), and 24 ka (Mal'ta [Raghavan et al. 2014]). A tree featuring admixture events in varying proportions between sister groups of Kostenki14 and Tianyuan is supported, and can indeed explain this observation (fig. 1A, purple leaves; Supplementary fig. S5 and Section 3.6, Supplementary Material online). This is further supported by the younger chronology for these two sites which is compatible with a stepwise arrival of West Eurasian components in Siberia following the UP exit from the Hub sometimes before 38 ka. The lack of West Eurasian components in Tianyuan and in subsequent East Asian individuals may provide clues on the resistance of those groups to the incoming UP population movements, or on subsequent reexpansion from a genetically IUP-like population reservoir.

West Eurasian IUP populations, on the other hand, likely declined and ultimately disappeared, as suggested by the fact that our population tree is compatible with the arrival in Europe of UP groups who experienced no further admixture with preexisting IUP or Neanderthals, with only two exceptions, both dated around 35 ka: the younger BK1653 individual from Bacho Kiro site (Hajdinjak et al. 2021) and GoyetQ116-1 (Fu et al. 2016). Whereas, the former can

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genetic features and material culture consistent with an IUP affiliation and which can also explain Oase1 after allowing for additional Neanderthal contributions; modern Papuans may be genetically seen as an extreme extension of this movement. (C) Following local genetic differentiation, a subsequent population expansion could explain the genetic components found in ancient samples <38 ka which contain it in unadmixed form (Kostenki14, Sunghir) or admixed with preexisting IUP components (Goyet Q116-1, Yana1, Mal'ta). The dates at the top right of each map provide a lower bound, based on the C14 of the earliest available sample for the inferred population wave. * indicate sites for which material culture was not available in direct association. For these sites, the nearest spatio-temporal proxies were used, as indicated in Supplementary table S1, Supplementary Material online. Numbers on the map refer to the position of relevant proxies: 1: Szeleta (S); 2: Pod_Hradem (S); 3: Moravský_Krumlov_IV (S); 4: Stranska_Skala_III-IIIc (IUP); 5: Brno-Bohunice (IUP); 6: Bacho_Kiro_IUP_layer_11 (IUP); 7: Ořechov_IV_–_Kabáty (IUP); 8: Brno-Bohunice (IUP); 9: Românesti-Dumbravita (UP); 10: Cosava (UP); 11: Tincova (UP); 12: Kara_Bom_OH_5_OH6 (IUP); 13: Tolbor-4_layer_4-5-6 (IUP); 14: Tolbor-16_layer_6 (IUP); 15: Kamenka_A (IUP); 16: Suindonggou_1 (IUP); 17: Suindonggou_2 (IUP); 18: Maisières-Canal (UP); 19: Spy_Ossiferous_Horizon_2 (UP); 20: Kostenki_12_Vokov (UP); 21: Kostenki_1 (UP).

be simply described as a member of the UP expansion that admixed with a population related to the older IUP Bacho Kiro individuals, the East Asian component carried by the latter needs to be explained as an interaction between pre-existing Bacho Kiro-like and incoming UP groups in West Europe with an additional Tianyuan-like component. Such a variegated East Asian substrate found in the otherwise West Eurasian GoyetQ116-1 sample may account for yet undescribed complexities within the IUP population branch (Supplementary fig. S6 and Section 3.7, Supplementary Material online). Interestingly, the fade of the IUP populations in Europe coincides with the extinction of the last Neanderthals (Hajdinjak et al. 2018).

Given the relatively simple population tree needed to explain the post-OoA Eurasian population movements using aDNA samples available to date, and benefiting from the basal position of Zlatý Kůň, we tried to add Oceanian populations (using modern Papuans from Skoglund et al. 2015) within the emerging picture to resolve a long-lasting debate on their topological position with respect to East and West Eurasians. Starting from the topologies proposed in Malaspinas et al. (2016) and Choin et al. (2021), we first tried to place Papuans as the most basal branch along with the non-African subtree, allowing for the documented Denisova admixture (Reich et al. 2011; Meyer et al. 2012). We avoided including the sampled Denisova aDNA within the population tree to eliminate attractions from yet uncharacterized, deep splits along the hominin branch (Hajdinjak et al. 2021), and opted for letting qpGraph infer Denisova as a basal split along the archaic human lineage. Simply placing Papuans in a basal position (either before or after the split of Zlatý Kůň) was rejected and highlighted a notable attraction between them and Tianyuan. We then tried to describe Papuans as a sister of Tianyuan (fig. 1B, Supplementary fig. S7A, Supplementary Material online) (Wall 2017), a solution that yielded only one marginal outlier that could be resolved when taking all the single nucleotide polymorphism (SNPs) into account (Supplementary Section 3.8, Supplementary Material online). This topology could be further improved, with the resolution of all marginal outliers, when allowing for a contribution of a basal lineage, whose magnitude decreased the deeper was its position along and beyond the OoA tree: 94% as the ancestor of Bacho Kiro and Tianyuan (Supplementary fig. S7B, Supplementary Material online) or 42% as the most basal IUP lineage (Supplementary fig. S7C, Supplementary Material online), 26% before the West/East Eurasia split (Supplementary fig. S7D, Supplementary Material online), 2% before the Zlatý Kůň lineage, along the OoA path (Supplementary fig. S7E, Supplementary Material online), and 1% as an earlier, otherwise extinct OoA (xOoA, Supplementary fig. S7F, Supplementary Material online) as proposed by Pagani et al. (2016). Notably, all the acceptable solutions for the placement of Papuans within the broader OoA tree encompass a Denisova contribution and confirm Zlatý Kůň as the most basal human genome among the ones ever found OoA. Taken together with a lower bound of the final settlement of Sahul at 37 ka (the date of the deepest population splits estimated by Malaspinas et al. 2016), it is reasonable to describe Papuans as either an almost even mixture between East Asians and a lineage basal to West and East Asians occurred sometimes between 45 and 38 ka, or as a sister lineage of East Asians with or without a minor basal OoA or xOoA contribution. We here chose to parsimoniously describe Papuans as a simple sister group of Tianyuan, cautioning that this may be just one out of six equifinal possibilities.

To somewhat lessen the bias that might be introduced by qpGraph being a supervised method reliant on the operator's assumption and to improve the robustness of our inference, we also performed an unsupervised analysis of the individuals comprising our core model using OrientAGraph (Molloy et al. 2021), which implements a Maximum Likelihood Network Orientation algorithm in Treemix (Pickrell and Pritchard 2012), improving its performances. We only specified chimp as an outgroup and the additional gene flow from Neanderthals experienced by Bacho Kiro. The best-fitting tree we obtained running OrientAGraph/Treemix (Supplementary fig. S8, Supplementary Material online) matches the one we identified as most supported using qpGraph in Supplementary fig. S2B, Supplementary Material online: with Zlatý Kůň as the most basal Eurasian lineage, Bacho Kiro and Tianyuan as sisters, and Ust'Ishim splitting early from that branch (IUP), just after the split from the branch that would lead to Kostenki14 and Tianyuan (UP).

Discussion

With our work, we leveraged the concept of a post OoA population Hub to infer at least three expansions that recapitulate the major genetic components observed in Paleolithic Eurasia to date. This emerging scenario provides a scaffold that elegantly accommodates available information on the most likely associated cultural assemblies for the most representative ancient human remains available to date between 60 and 24 ka (fig. 2, Supplementary Section 4, Supplementary Material online).

Zlatý Kůň may represent an early expansion, which left little to no traces in subsequent Eurasians and occurred before or around 45 ka (fig. 2A). We speculate this population movement might be linked either to IUP (Tostevin 2003; Richter et al. 2008) or to non-Mousterian and non-IUP lithic techno-complexes that appeared in Central and Eastern Europe between 48 and 44 ka (e.g., Szeletian, LRJ) (Svoboda 2000; Nejman et al. 2017).

A subsequent expansion (linked to IUP in Eurasia) can be dated earlier than 45 ka as proposed by Zwyns et al. (2019),

and here we propose it to be a wider phenomenon that populated the broad geographic area between Mediterranean Levant (Marks and Kaufman 1983; Boëda and Bonilauri 2006; Kuhn et al. 2009; Leder 2017; Kadowaki et al. 2021), East Europe (Richter et al. 2008; Fewlass et al. 2020; Hublin et al. 2020), Siberia-Mongolia (Zwyns et al. 2012; Derevianko et al. 2013; Kuhn 2019; Zwyns and Lbova 2019; Zwyns et al. 2019; Rybin et al. 2020), and East Asia (Boëda et al. 2013; Morgan et al. 2014; Peng et al. 2020) in <5 kyr, reaching as far South as Papua New Guinea before 38 ka, and which eventually died out in Europe after repeated admixtures with Neanderthals (Bacho Kiro and Oase1 being two notable examples) (fig. 2B). In Western Europe, in the same time-frame, this interaction has been suggested as a trigger for the development of Chatelperronian material culture (Roussel et al. 2016), whereas the Uluzzian techno-complex in Mediterranean Europe may tentatively be better explained by an additional, yet uncharacterized expansion from the Hub (Benazzi et al. 2011; Marciani et al. 2020) although genomic data from Uluzzian strata are still lacking. The Uluzzian techno-complex is indeed characterized by unprecedented versatility and efficient management of production costs, considerably lower standardization in design compared with Mousterian industries, lower time, and energy expenditure for initialization and management of volumes, and a much shorter response time to change in raw material or environmental conditions (Riel-Salvatore 2007, 2009, 2010; Moroni et al. 2013; Moroni et al. 2018; Peresani et al. 2019; Arrighi, Marciani et al. 2020; Collina 2020; Marciani et al. 2020; Silvestrini et al. 2021). In addition, this technological change is linked to the appearance of complementary tools (sensu [Haidle et al. 2015]; e.g., [Sano et al. 2019]), innovations in hunting strategies (Boscato and Crezzini 2012; Romandini et al. 2020), and a shared package of symbolic artifacts (Arrighi, Bortolini et al. 2020; Arrighi, Moroni et al. 2020). All these almost unique and distinctive elements make it very difficult to infer heritable continuity with local Mousterian material culture, or preferential technological proximity with any other IUP/UP Eurasian technology, and support the hypothesis of an independent population expansion. The last major expansion needed to explain the observed data (UP) took place later than 45 ka and before 38 ka and repopulated (Kostenki, Sunghir), or interacted with, preexisting human groups (GoyetQ116-1, BK1653, Supplementary fig. S6, Supplementary Material online) in Europe, and admixed with members of the previous IUP wave in Siberia (Yana, Mal'ta and perhaps Salkhit) as it moved East in the subsequent 5–10 ka (fig. 2C). The split time between East and West Eurasians estimated at ~40 ka (Malaspinas et al. 2016) from modern genomes and the differentiation of these two macropopulations can therefore be explained by the inferred timing of the IUP exit from the Hub, followed by subsequent diversification within the Hub of the ancestors of West Eurasians, later mitigated by ongoing cross-Eurasian gene flow. Importantly, the qpGraph results that form the basis for this emerging picture describe only one of the many possible arrangements of the genetic data we explored and, by itself, it should not be interpreted as the only possible outcome. Nonetheless, the results of qpGraph have also been confirmed by an unsupervised method (OrientAGraph/Treemix) and, remarkably, the arrangement described here matches and simplifies scenarios inferred from material culture evidence, and provides a framework for placing genetic and cultural data onto a coherent landscape.

In this paper, we used extensive cultural categories that are in agreement with the demic movements at the present, coarse scale of analysis. The general trends observed here emerge from a broad perspective, and further work is needed to test specific hypotheses concerning actual processes of branching, local adaptation, cultural transmission, and convergence (Kuhn 2019; Groucutt 2020). Similarly, we remain oblivious about the precise location of the inferred population Hub, although North Africa or West Asia seems the most plausible candidates. More ancient genomes are needed, as well as a better understanding of the role of South and SouthEast Asia, for which currently known material culture suggests complex trajectories (Petraglia et al. 2010; Dennell and Petraglia 2012; Allen and O'Connell 2014; Michel et al. 2016; Clarkson et al. 2017; Westaway et al. 2017; O'Connell et al. 2018; Shackelford et al. 2018; Bird et al. 2019; Bradshaw et al. 2021).

Materials and Methods

We downloaded the aligned sequences for the Bacho Kiro individuals from the European Nucleotide Archive (accession number PRJEB39134), and merged files from the same individual. We clipped three bases off the ends of each read to avoid excess of aDNA damage using trimBam (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam) and then generated pseudohaploid calls with the genotype caller pileupCaller (https://github.com/stschiff/sequenceTools/tree/master/src-pileupCaller) randomly picking one allele when more than one was present. Only positions with base quality and read quality higher than 30 were considered. The processed Eigenstrat files (random haploid calling on capture data) of the Zlatý Kůň individual were kindly provided by Prof Cosimo Posth and Dr He Yu.

We merged the files with the 1240K "Allen Ancient DNA Resource" v44.3 database (https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data), then kept only

autosomal SNPs (1,150,639) using Plink 1.9 (Chang et al. 2015) and then converted back to Eigenstrat format using Admixtools convertf (Patterson et al. 2012). Detailed information on the samples we used is reported in Supplementary table S3, Supplementary Material online.

To mask out the majority of the recently introgressed Neanderthal segments in Oase1, we obtained their coordinates from the original publication (table S5.1 of Fu et al. 2015) and removed them completely from the dataset using plink –exclude range.

We ran Admixtools qpGraph (Patterson et al. 2012, https://github.com/DReichLab/AdmixTools, qpGraph version: 7365) with the following parameters: outpop: NULL, blgsize: 0.05, lsqmode: YES, diag: 0.0001, useallsnps: NO, bigiter: 6, forcezmode: YES, initmix: 10000, precision: .0001, zthresh: 3.0, terse: NO, hires: YES.

To run OrientAGraph/Treemix (Pickrell and Pritchard 2012; Molloy et al. 2021), we computed allele frequencies for each population using plink –freq –family excluding SNPs with missing data with –geno 0, then converted the data with the script plink2treemix.py (available at https://bitbucket.org/nygcresearch/treemix/wiki/Home), then run OrientAGraph/Treemix with the following parameters: -k 1000, -climb, -mlno, -allmigs.

Supplementary Material

Supplementary data are available at *Genome Biology and Evolution* online.

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Author Contributions

Conceptualization: L.V., L.P.; Data analyses: L.V., G.M., E.B., S.A.; Drafting of the manuscript: L.V., G.M., E.B., L.P.; Interpretation of results: T.P., S.B., L.P.; Revision of the manuscript: all authors.

Data Availability

No new data or software was generated for this study. All software, lithic information, and genomes are publicly available from the published sources. Allen ancient DNA resource data repository: https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data. European Nucleotide Archive (accession numbers *PRJEB39134*; *PRJEB39040*). Paleoenvironmental data: https://www.ncei.noaa.gov/. Software: https://github.com/DReichLab/AdmixTools, qpGraph version: 7365 https://github.com/sriramlab/OrientAGraph OrientAGraph version 1.0.

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