Human evolutionary history in Eastern Eurasia using insights from ancient DNA

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Advances in ancient genomics are providing unprecedented insight into modern human history. Here, we review recent progress uncovering prehistoric populations in Eastern Eurasia based on ancient DNA studies from the Upper Pleistocene to the Holocene. Many ancient populations existed during the Upper Pleistocene of Eastern Eurasia—some with no substantial ancestry related to present-day populations, some with an affinity to East Asians, and some who contributed to Native Americans. By the Holocene, the genetic composition across East Asia greatly shifted, with several substantial migrations. Three are southward: an increase in northern East Asian-related ancestry in southern East Asia; movement of East Asian-related ancestry into Southeast Asia, mixing with Basal Asian ancestry; and movement of southern East Asian ancestry to islands of Southeast Asia and the Southwest Pacific through the expansion of Austronesians. We anticipate that additional ancient DNA will magnify our understanding of the genetic history in Eastern Eurasia.

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The analysis of ancient DNA (aDNA) has increased our knowledge of human population history and evolution. Studies carried out in Western Eurasia have enabled us to compare and assess previously existing hypotheses on human population movement and mixture, as well as develop new models not previously considered [1,2,3•]. Ancient DNA studies are still in their infancy, with only a few studies from Eastern Eurasia [4–8], with most large-scale surveys focused on the Eurasian Steppe. Though many questions remain, a small but growing number of aDNA studies are providing us with more insight on human population history in Eastern Eurasia [5–11,12••,13••,14,15••,16,17••,18•]. In this article, we review these recent aDNA studies on Eastern Eurasian populations, discuss the different ancestries and migrations studied, and highlight the implications for modern human genetic history.

Modern human groups in Eastern Eurasia during the Upper Pleistocene

Before the Last Glacial Maximum, anatomically modern humans (AMH) dispersed across Eurasia, extending to the northern edge of Siberia [15••,19•,20,21], the western edge of continental Europe [22–24], and the eastern edge of continental Asia [18•,25,26]. To date, there is little genome-wide aDNA from the Upper Pleistocene of Eastern Eurasia, with none recovered from southern Eastern Eurasia (southern East Asia and Southeast Asia). Here, we summarize how available genome-wide aDNA sampled from Upper Pleistocene humans of northern Eastern Eurasia (mainly northern East Asia and Siberia) have clarified different ancestries found in AMH from Eastern Eurasia (Table 1 and Figure 1).

Three major groups have been documented from the Upper Pleistocene in Eastern Eurasia. One group did not contribute substantial ancestry to present-day populations and is represented by the oldest genomic data from an AMH, the Ust'-Ishim individual (∼45 000 years ago (ka)) from Western Siberia. Even though Ust'-Ishim's Y chromosome haplogroup is NO, a typical haplogroup in Eastern Eurasians [27], genome-wide data from him shows that he is equally related to ancient hunter-gatherers from Western Eurasia and ancient and present-day East Asians. This indicates that the Ust'-Ishim individual was from a population that diverged before or simultaneously with the ancestors of present-day Western and Eastern Eurasians [18•,19•] (Figure 1).

Another AMH group is related to East Asians, represented by an individual found in Tianyuan Cave outside Beijing, China (∼40 ka). This individual is genetically closer to ancient and present-day East Asians, most Southeast Asians, and Native Americans than to either ancient or present-day Europeans [18•] (Figure 1), revealing that separate Asian and European populations existed by at least 40 ka (Figure 1). Interestingly, the Tianyuan individual exhibits connections to a ∼35 000-year-old European individual, Goyet Q116-1 [23], indicating that

Table 1

Select ancient individuals from Eastern Eurasia

No.	Individuals	Group	Dating in average (ka)	Location	Latitude	Longitude	References
1	Ust'-Ishim	Ust'-Ishim	45 000	Western Siberia	57.68	71.15	[19•]
2	Tianyuan	Tianyuan	40 000	North East Asia	39.67	115.92	[18•,25]
3	Yana	Yana	31 600[a]	Northern Siberia	71.18	134.60	[15••]
4	Mal'ta 1	Mal'ta 1	24 000	Southern Siberia	51.94	103.77	[21]
5	Afontova Gora 3	Afontova Gora 3	17,000[a]	Southern Siberia	56.05	92.87	[23]
6	Kolyma1	Kolyma1	9800	Northern Siberia	69.08	161.39	[15••]
7	Bianbian	Shandong	9545–9480	Northern East Asia	36.10	118.50	[17••]
8	Xiaogao	Shandong	8771–8591	Northern East Asia	37.90	117.60	[17••]
9	Qihe	Qihe	8428–8359	Northern East Asia	25.40	117.60	[17••]
10	Boshan	Shandong	8320–8040	Northern East Asia	36.50	117.90	[17••]
11	Liangdao	Liangdao	8320–7560	Southern East Asia	26.30	120.20	[17••]
12	La368	G1	7950–7794	Mainland Southeast Asia	18.41	103.54	[13••]
13	Xiaojingshan	Shandong	7935–7721	Northern East Asia	36.50	117.90	[17••]
14	Devil's Gate	Devil's Gate	7658–7515	Northern East Asia	44.50	135.40	[15••,16]
15	Shamanka_EN	Baikal_EN	7123–6329	Southern Siberia	51.70	103.70	[5]
16	Lokomotiv_EN	Baikal_EN	6950–6130[a]	Southern Siberia	52.29	104.25	[5]
17	Xitoucun	Fujian	4644–4246	Southern East Asia	26.20	119.10	[17••]
18	Tanshishan	Fujian	4526–4225	Southern East Asia	26.10	119.20	[17••]
19	Ma911	G1	4415–4160	Mainland Southeast Asia	4.80	101.95	[13••]
20	Man_Bac	Man_Bac	4080–3600	Mainland Southeast Asia	20.95	105.74	[12••]
21	Funadomari	Jomon	3800–3500	East Asia	45.18	141.26	[10]
22	Oakaie	Oakaie	3200–2700	Mainland Southeast Asia	22.26	95.11	[12••]
23	Chokhopani	Tibetan	3150–2,400	East Asia	28.65	83.75	[9]
24	Vanuatu	Vanuatu	3100–2,740	Oceania	−15.55	167.09	[55,56]
25	Sanganji	Jomon	3000	East Asia	37.88	140.87	[11]
26	Ikawazu	Jomon	2720–2418	East Asia	35.19	136.90	[13••]
27	Mebrak	Tibetan	2400–1850	East Asia	28.67	83.99	[9]
28	In662	G5	2152	Mainland Southeast Asia	3.39	97.42	[13••]
29	Nui_Nap	Nui_Nap	2100–1900	Mainland Southeast Asia	20.50	105.30	[12••]
30	In661	G5	1917	Island Southeast Asia	3.53	97.23	[13••]
31	Phl534	G6	1877	Island Southeast Asia	18.18	121.37	[13••]
32	Samdzong	Tibetan	1750–1,250	East Asia	29.26	84.06	[9]

[a] These are indirect dates based on associated archaeological layers.

the separation between early Europeans and early Asians was not a single population split [18•,28•].

The third group is the ancient North Siberians [15••], which is composed of two individuals found at Yana River in Northeastern Siberia (∼31.6 ka) [20]. The ancient North Siberian population represents a distinct lineage with affinities primarily to European-related ancestry (∼71%) but also to East Asian-related ancestry (∼29%), and shows an early divergence of ∼39 ka [15••] (Figure 1). Later Upper Pleistocene Siberian individuals—represented by Mal'ta (∼24 ka) [21] and Afontova Gora 2 and 3 (∼17 ka) [23] from the Lake Baikal region—are more closely related to the Yana individuals than to other Western Eurasian hunter-gatherers and can be successfully modeled as descendants of the ancient North Siberian lineage [15••] (Figure 1). These studies indicate that ancient North Siberian related ancestry was once widespread among ancient Siberians. Around 25 ± 1.1 ka, a combination of ancient North Siberian-related ancestry and East Asian-related ancestry led to the origin of ancestral Native Americans (14–38% ancestry related to Mal'ta1)

[21,29•,30]. These distinct ancestries highlight the diversity of human populations that lived in Eastern Eurasia during the Upper Pleistocene.

Small amounts of archaic admixture have played a prominent role in shaping patterns of human genomic variation and adaptation [31–33]. In East Eurasia, evidence of two archaic humans, Neandertals and Denisovans, have been found [34–39]. In all Upper Paleolithic humans found to date, the proportions of Neandertal and Denisovan ancestry are consistent with that of present-day humans. The time of Neanderthal gene flow into the ancestors of these individuals likely occurred ∼50−60 ka [19•,23,24]. Evidence of Denisovans have been found in Siberia and the Tibetan Plateau, and small amounts of Denisovan-related gene flow has been found in present-day East Asians [34,36,37,40–42]. Future comparison of ancient DNA from other individuals dating to the Upper Paleolithic will help clarify the amount archaic admixture contributed to humans of different time periods to better understand the variation found today in Neanderthal and Denisovan ancestry of present-day humans.

Figure 1
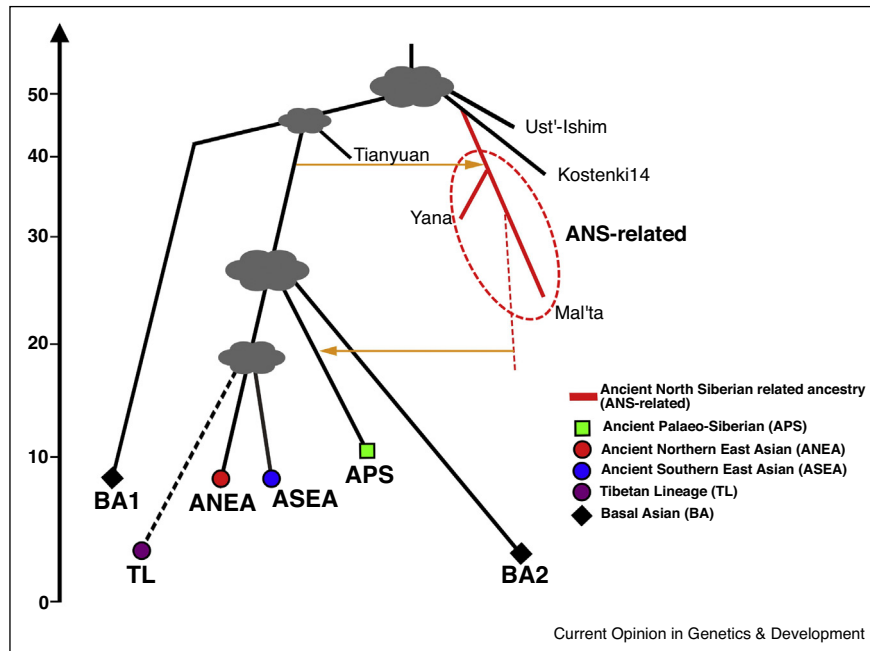
Schematic of peopling history in Eastern Eurasia. The yellow arrows indicate two major possible substantial gene flow events in Ref. [15••] during the Upper Pleistocene. Dark clouds represent events with uncertain dates or structures. The black dotted line to Ancient Tibetans means this branch is a tentative placement that needs more evidence. The ancient North Siberian lineage is represented by Yana (~31.6 ka) and Mal'ta (~24 ka); the ancient Palaeo-Siberian lineage is represented by Kolyma1 (~9.8 ka); the ancient Northern East Asians are represented by individuals from Devil's Gate (~7.7 ka), Shandong (~9.5–7.7 ka), and Lake Baikal (~7.1–6.3 ka); the ancient Southern East Asians are represented by Qihe (~8.4 ka) and Liangdao (~8.3–7.5 ka); the two Basal Asian lineages in Holocene are represented by the Hòabìnhian hunter-gatherers (La368 (~8 ka) and Ma911 (~4.3 ka)) (BA1) and individuals from the Late Jomon (~3.8–2.5 ka) (BA2); the Tibetan lineage is represented by ancient individuals found on the Tibetan Plateau (e.g. Chokhopani, ~3.1–2.4 ka) and present-day Tibetans.

Population structure of Early Neolithic populations in Eastern Eurasia

Early Neolithic populations in Eastern Eurasia exhibited different genetic populations. In this section, we discuss the major ancestries present in the Early Neolithic that contributed to later populations according to their geographic and genetic distribution, especially the ancient Palaeo-Siberians, ancient Northern East Asians, ancient Southern East Asians, and two different Basal Asians (Figure 1). Although not dating to the Early Neolithic, we also present information from ancient populations on the Tibetan Plateau.

The ancient Palaeo-Siberian lineage is represented by Kolyma1 (~9.8 ka) from the Duvanny Yar site in Far East Russia [15••]. The ancient Palaeo-Siberian population is predominantly of Asian ancestry and derives from a mixture of East Asian-related and ancient North Siberian-related ancestry (the latter contributing ~16.6% ancestry to ancient Palaeo-Siberians ~20.2 ka) (Figure 1), similar to Native Americans. In Siberia, the Early Neolithic marks the entry of Asian-related ancestry that becomes a major component of the genetic variation found in Siberia by ~9.8 ka [15••,29•] (Figures 1 and 2).

The ancient Northern East Asian lineage is represented by Early Neolithic samples from northern East Asia, including six individuals (~7.7 ka) from Devil's Gate, Far East Russia [15••,16]; six individuals (~9.5–7.7 ka) from Shandong province, Northern China, along the lower reaches of the Yellow River [17••]; and 15 individuals (~7.1–6.3 ka) from Lake Baikal, Southern Siberia [15••]. Additional information on these individuals are provided in Table 1. These Early Neolithic individuals form a clade and are more related to present-day populations in northern East Asia than all other humans, including ancient and present-day populations from southern East Asia [17••] (Figure 1). However, ancient Palaeo-Siberian-related ancestry was also found in individuals from Boshan in Shandong province (~8.1 ka), Devil's Gate, and Lake Baikal (Baikal_EN, ~7.1–6.3 ka), indicating that a population related to ancient Palaeo-Siberians had a connection with ancient Northern East Asians by at least 8 ka [17••] (Figure 2). Interestingly, a high level of genetic continuity is observed in the Devil's Gate region during the Holocene with no major population replacement [15••,16]. In contrast, there was a population replacement in the Lake Baikal region, Southern Siberia, in which Upper Paleolithic hunter-gatherers with ancient Palaeo-Siberian-related

Figure 2
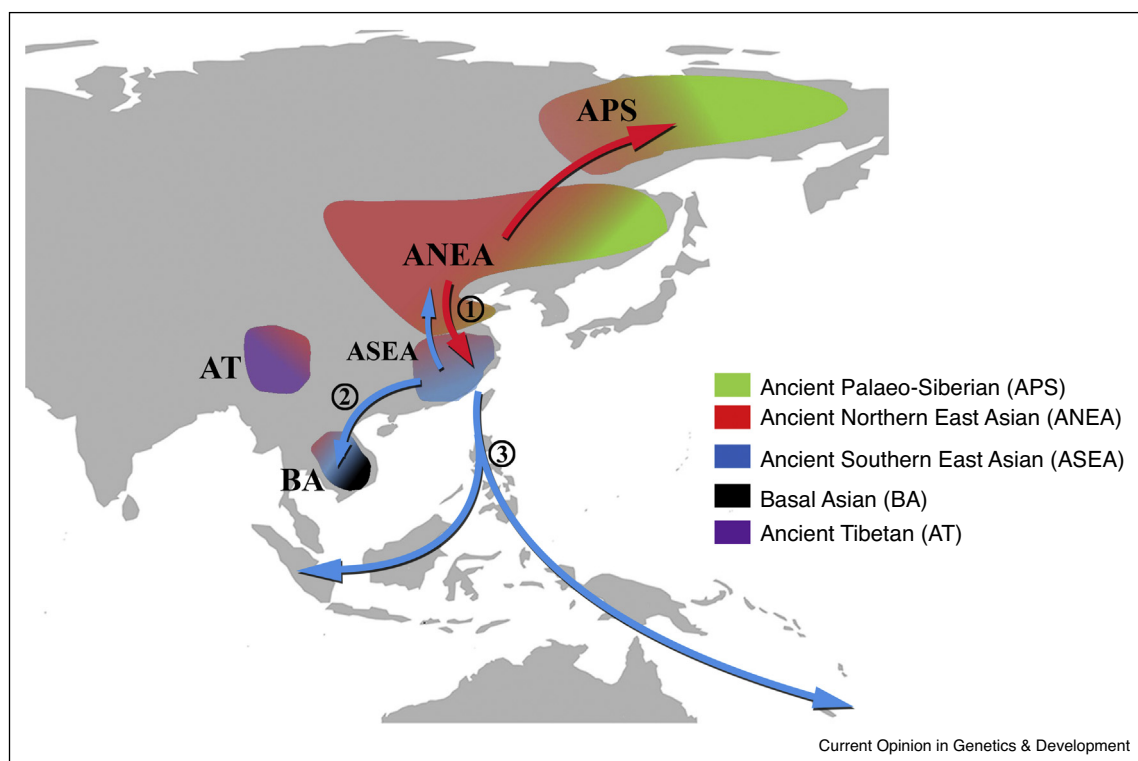
Depictions of the main migratory events associated with the genomic history of Eastern Eurasians during the Holocene. The different colors represent the five Early Neolithic ancestries who contributed to later populations in Eastern Eurasia. Colors loosely indicate genetic groupings between or within a region, with color gradients showing the connections that may have existed between different ancient populations. Three major southward migration events (might include several minor migration events over a long period) are marked with the circled numbers 1–3. (1) Ancient Northern East Asian ancestry contributed to ancient Southern East Asians; (2) gene flow from ancient East Asians into Southeast Asians; and (3) the dispersal of Austronesians with mainland ancient Southern East Asian-related ancestry. The red arrows indicate possible migration events of ancient Northern East Asian-related populations; one red arrow shows the northward migration of ancient Northern East Asian-related populations to Siberia (described in Section 'Population structure of Early Neolithic populations in Eastern Eurasia' Northern East Asian part); the blue arrows indicate the possible migration events of ancient Southern East Asian-related populations. There are likely to have been other migrations (e.g. the spread of agricultural populations into Japan and Qinghai-Tibetan Plateau), but the details of other population movements will be investigated in future studies.

ancestry were largely replaced by Early Neolithic communities with ancient Northern East Asian ancestry [15[••]]. These patterns indicate a shared northern East Asian ancestry across northern East Asia and extending northward into Siberia (Figure 2).

The ancient Southern East Asian lineage is represented by Qihe from the southern Chinese province of Fujian in mainland East Asia (∼8.4 ka) and Liangdao from an island in the Taiwan Strait (∼8.3–7.5 ka) [17[••],43] (Table 1). Ancient Southern East Asian ancestry differs greatly from that found in ancient Northern East Asians and persists into more recent individuals from Fujian (∼4.6−4.2 ka); Qihe and Liangdao cluster with these later individuals (Figure 1). The ancient Southern East Asians contributed ancestry to Austronesian speakers and some Southeast Asians [17[••]]. The spread of ancestry related to ancient Southern East Asians is discussed in greater detail in Section 'Substantial southward migrations in Holocene of Eastern Eurasia'.

One of the two known Basal Asian lineages is mainly represented by the Hòabìnhian hunter-gatherers (individuals La368 (∼8 ka) and Ma911 (∼4.3 ka), Table 1) (BA1 in Figure 1) [13[••]]. They cluster with present-day Onge from the Andaman Islands [13[••]], who together belong to the 'first layer' of ancestry in Southeast Asian populations. Basal Asian ancestry has a deep divergence from other Eastern Eurasian populations (likely as deep as the Tianyuan individual), and is an outgroup to most present-day East Asians [13[••]] (Figure 1). A second Basal Asian lineage, associated with the Late Jomon culture in Japan (∼3.8−2.5 ka, Table 1) (BA2 in Figure 1) [10,11,13[••]], also separated very early from the ancestors of present-day and ancient East Asians (Figure 1). These Jomon individuals share a closer relationship to Northern and Southern East Asians than to Tianyuan and the Hòabìnhian hunter-gatherers, but likely separated from Northern and Southern East Asians earlier than Native Americans separated from them [10,17[••],44].

The Tibetan lineage is represented by ancient individuals found on the Tibetan Plateau (e.g. Chokhopani, ~3.1–2.4 ka, Table 1) and present-day Tibetans. Amongst present-day populations, Tibetans are closely related to East Asians [9,45] (Figure 1). However, comparison amongst ancient East Eurasians show that the Tibetan lineage shares more connections with Northern East Asians [17••,46]. In a recent mitochondrial DNA study, 5000–3000-year-old humans from on and near the Qinghai-Tibetan Plateau were shown to have partially contributed to present-day Tibetans, indicating there are older ancestries on the Tibetan Plateau not yet detected. The available evidence imply that ancient Tibetans were more complex and diverse than previously thought. Ancient DNA from Tibet is still considerably lacking and requires much more research.

Substantial southward migrations in Holocene of Eastern Eurasia

Past migrations also played a major role in the development of current Eastern Eurasian population structure. There were at least three major southward migrations during the Holocene, evidenced by an increase in Northern East Asian-related ancestry in southern East Asia, admixture between Basal Asians from Southeast Asia and East Asians from China, and the close association of Austronesian ancestry with ancient samples from southern China (Figure 2).

There was an increase in Northern East Asian-related ancestry in southern East Asia [17••]. Late Neolithic Southern East Asians (4.6−4.2 ka) already show some ancient Northern East Asian-related ancestry, as they tend to share greater affinities to Early Neolithic Northern East Asians than Early Neolithic Southern East Asians do. Furthermore, all present-day mainland East Asians show more affinity to ancient Northern East Asian ancestry than to ancient Southern East Asian ancestry. Mixture models show that ancient Northern East Asian ancestry highly influenced present-day populations in mainland southern East Asia, though ancient Southern East Asian ancestry still exists to some extent (Figure 2). Among the Early Neolithic populations in northern East Asia, the ancient Shandong populations along the lower reaches of the Yellow River are the most related to the Northern East Asian ancestry found in all present-day mainland East Asians [17••]. Ancient Southern East Asian ancestry is also slightly detected in some northern East Asian populations [17••] (Figure 2).

The expansion of East Asian ancestry into Southeast Asia ~4 ka demonstrates that gene flow from southern China had a profound influence on the genetic makeup of Southeast Asians [12••,13••]. However, traces of the Basal Asian ancestry (BA1 in Figure 1) represented by Southeast Asian hunter-gatherers are still found in Southeast Asians today, suggesting a complex transition characterized by multiple waves of East Asian-related migrations that mixed with indigenous Southeast Asians [12••,13••,47] (Figure 2). Ultimately, both Basal Asian ancestry ('first layer') and later East Asian ancestry associated with farmers ('second layer') contributed to the current diversity of Southeast Asians, which is consistent with previous hypotheses [48–51] (Figure 2).

The ancient Southern East Asians show the greatest connection with present-day Austronesians [17••], which is consistent with a proto-Austronesian origin from the Southeast coast of mainland China [52–54]. The descendants of proto-Austronesians may have dispersed to Taiwan, with the initial divergence between Taiwan aboriginals and Han Chinese being around 8–10 ka [43]. Interestingly, an ancient Austronesian population from Oceania (Vanuatu, ~3 ka) [55,56] is more closely related to Late Neolithic (4.6−4.2 ka) than Early Neolithic (8.4−7.5 ka) ancient Southern East Asians (Figure 2). In addition, individuals (<1.9 ka) from the Philippines cluster with present-day and ancient individuals from Indonesia (~2.3−1.8 ka) and can be modeled as a mixture of Austronesian-like and Austroasiatic-like ancestry, indicating that expansion of Austronesians into Southeast Asia reached Indonesia by at least ~2.1 ka and the Philippines by ~1.8 ka [13••] (Table 1 and Figure 2). Overall, the aDNA data from Southern China and Oceania indicate a southward wave from Southern East Asia down into the islands of Southeast Asia and the Southwest Pacific.

Migration southward played a major role in the formation of current Eastern Eurasian populations, highlighting that gene flow has had a major impact on Eastern Eurasian population history.

Perspectives

The increasing availability of ancient Eastern Eurasian genomes has significantly increased our understanding of the genetic and evolutionary history of Eastern Eurasia [6,8,10,12••,13••,15••,17••,18•]. However, aDNA studies are still lacking, especially those focusing on mainland East Asia. Recently, more aDNA studies based on remains found in Southern China and Southeast Asia have been published [12••,13••,17••,57], indicating that techniques for retrieving aDNA in hot and humid regions are developing rapidly, allowing us to directly access more ancient genetic material than possible before.

Future research will address many unresolved questions, and denser sampling in East Asia will allow us to detail population changes and interactions at a finer scale. For example, how did populations make the transition from being hunter-gatherers to agriculturalists? Data from understudied regions will provide new insights into past population expansions and help us develop a more complete history of modern humans. For instance, more ancient data from the Tibetan Plateau will provide evidence to help explain how and when populations with agricultural practices expanded into high-altitude areas. Ancient data can also help us to determine how natural

selection and adaptive introgression from archaic hominin affected our species, such as how modern humans adapted to high-latitude and high-altitude areas [32,58,59]. Additional aDNA studies will help clarify the complex history of Eastern Eurasian populations, and with increased focus on ancient samples from Eastern Eurasia, we can expect a greater understanding of the interactions affecting Eastern Eurasian human prehistory.

Conflict of interest statement
Nothing declared.

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- •• of outstanding interest

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