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Denisovans and *Homo sapiens* on the Tibetan Plateau: dispersals and adaptations

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Abstract

Recent archaeological discoveries suggest that both archaic Denisovans and *Homo sapiens* occupied the Tibetan Plateau earlier than expected. Genetic studies show that a pulse of Denisovan introgression was involved in the adaptation of Tibetan populations to high-altitude hypoxia. These findings challenge the traditional view that the plateau was one of the last places on earth colonized by *H. sapiens* and warrant a reappraisal of the population history of this highland. Here, we integrate archaeological and genomic evidence relevant to human dispersal, settlement, and adaptation in the region. We propose two testable models to address the peopling of the plateau in the broader context of *H. sapiens* dispersal and their encounters with Denisovans in Asia.

High-altitude settlement and selective pressures

Tibetans are the largest indigenous population living in high-altitude environments who have developed a suite of traits to cope with the harsh environment of the Qinghai–Tibetan Plateau (Tibetan Plateau, hereafter, TP) [1-3]. With an average elevation of 4000 m above

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sea level (masl), it is surrounded by natural barriers with a cold and arid environment and significant seasonal variations [4]. During the Late **Pleistocene** (see Glossary), the highly frequent millennial-scale oscillations of the **last glacial cycle** are additional obstacles for human expansions to the high-altitude ecosystem [5-7]. In addition, increased elevation causes a rapid reduction of oxygen concentration that leads to a physiological stress known as **hypoxia**. Usually experienced at elevations above 2500 masl, hypoxia results in severe and sometimes life-threatening symptoms, such as intrauterine growth restriction during pregnancy and low birth weight, that cannot be alleviated solely by behavioral adjustments and require physiological adaptation [2,8,9].

Yet, Tibetans have successfully settled in the TP for generations, but when, how, and by whom the highlands were permanently inhabited are still a matter of debate. Existing models addressing these questions are mostly based on archaeological evidence [10-12]. Archaeological studies are informative on subsistence practices, behaviors, and human distributions, while they do not provide direct insight for the biological adaptation to hypoxia. By contrast, genomic studies have identified several candidate adaptive genes in Tibetans [1,9,13], inferred the **population split** between Tibetans and lowland Chinese [14-17], and detected the Denisovan-like **introgression** that facilitated the genetic adaptation of Tibetans [18,19]. Therefore, archaeological and genetic studies are complementary to reconstruct the picture of the peopling process of the plateau. However, studies with a comparable emphasis on the two fields are absent so far. In the light of recent discoveries (such as Nwya Devu and Baishiya cave [20,21]), we evaluate relevant archaeological, genomic, fossil, and paleoenvironmental evidence under one framework to propose two parsimonious models and their predictions concerning the population history of this plateau.

The archaeology of human occupations and paleoclimates

Archaeological research on TP began in the 1960s but well-documented excavations and dated sites are limited so far [10,11,22] (Figure 1). The available archaeological data suggest that there were four major periods of human occupation on the TP.

Marine Isotope Stage 6–4

In the **Marine Isotope Stage** (MIS) 6, the Xiahe mandible (Baishiya Karst Cave) suggests that archaic hominins reached the marginal plateau (3200 masl) around 160 thousand years ago (hereafter ka) [21]. The fossil specimen has archaic mandibular and dental features that differ from those of Neanderthals, and the paleoproteomic analysis indicates a close affinity with 'Denisovans' [21,23]. In addition, Denisovan mitochondrial DNA (mtDNA) was extracted from the cave sediments dated to 100 ka, 60 ka, and possibly to 45 ka from reworked deposits [24]. Jiangjunfu 01 is a site dated to 120–90 ka that is identified by a small sample of lithics collected from exposed geological sections [25]. Recently, the Acheulean-like handaxes from the Piluo site were reported older than 130 ka, but are known only from press releases [26]. More surprising is the claim of early rock art at Chusang site that is said to be ca. 226–169 ka [27]. It raises concerns regarding the dating of the footprints and handprints, and their interpretation as evidence for art. There is an increasing number of findings challenging the view that *H. sapiens* was the first and only hominin species to

adapt in a hypoxic environment [28,29]. Overall, the evidence points toward a longer history of hominin activities on the TP. However, the Xiahe specimen lacks archaeological context, and the mtDNA retrieved from sediments is unable to identify genomic variants relevant to high-altitude adaptation. So, further evidence of ancient nuclear DNA, fossils, and full-scale excavations are needed to understand the morphology, biology, and behavior of the archaic hominins on the plateau.

The Great Lakes Period (late MIS3)

The late MIS3 (40–30 ka) of the plateau, sometimes referred to as the 'Great Lakes Period', is characterized by increased temperature, precipitation, and lake levels due to an enhanced summer monsoon [6,30-32]. Dated between 40 and 30 ka, the systematically excavated open-air site of Nwya Devu indicates that hunter-gatherers reached the hinterland (4600 masl) during this temperate episode, much earlier than previously known [20]. This site documents the earliest **blade** production uncovered in the highland, a technology rare in China but typical for the early **Upper Paleolithic** in the Eurasian Steppe [33,34]. Other sites, such as Siling Co, Xiao Qaidam, and Lenghu Locality, have been indirectly dated to ca. 30 ka – for example, samples from neighboring geological sections [11,35,36]. But Siling Co is an example that warrants caution as it was recently argued to be much younger [37]. With only a single excavated site, what the settlement patterns and behavioral adaptation of the hunter-gatherers were during the Great Lakes Period remain unclear.

Last deglaciation

Starting from ca. 25 ka, the **last glacial maximum** (**LGM**) is marked by a significant cooling, with temperatures 4–7°C lower than they are today [38-40]. There is no site firmly dated to this period, suggesting an elusive human presence on the plateau in such an inhospitable environment before the milder climate of the **last deglaciation** – another period suitable for human occupation [41]. Madsen and colleagues referred to sites of this period as 'Late Upper Paleolithic short-term logistical camps' [42,43], primarily studied from surveys and test-pits [43,44]. A recent zooarchaeological study by excavation on site '151' in Qinghai has provided an example of high mobility and short occupation [45]. Stone tools are described as **microblades**, a technology that was widespread in lowland North China after the LGM [46]. For this period, we note that sites cluster in the northeast margin of the TP (Figure 1) but whether this pattern represents a behavioral, preservation, or visibility bias is unclear.

Holocene climate optimum

The abrupt cooling in the **Younger Dryas** (**YD**) [44,47] appears to correspond with a significant reduction in human activities. Then the fourth period coincides with the onset of the **Holocene climate optimum** [48,49]. Sites dated between 8 and 6 ka mainly document a technological continuity from previous traditions (e.g., microblade) [50-52], while after 6 ka, **Neolithic** cultural innovations, such as ground stone, painted pottery, and agriculture, gradually appeared and sometimes coexisted with microblade technology [53-57]. The distribution of various artifact forms illustrates contacts and exchange networks with different lowland groups. Additionally, some researchers argued that year-round settlements

were established by farming groups around 3.6 ka during this period [12,58], thereby opposing the claim that it was made by hunter-gatherers between 30 ka and 8 ka [22,59,60].

To summarize, we observe four distinct periods of human occupation, separated by apparent gaps in the archaeological and fossil records. Denisovans would be the first to visit TP long before late MIS3. Evidence for *H. sapiens*, indicated by cultural artifacts, is as early as 40 ka, and occupations appear roughly correlated with temperate episodes and technological changes along with gaps under cold/dry climates. However, the gaps between these occupations may reflect a low-resolution dataset, a behavioral pattern, or a combination of both. The connection between archaeological occupations and environmental records has not been fully established yet.

Genetic adaptations: archaic introgression and natural selection

Geographic isolation from lowlands and the selective pressure of hypoxia are essential factors for the shaping of fitness of Tibetan populations. Hence, genetic studies have focused on identifying the beneficial genes for high-altitude adaptations and inferring the Tibetan demographic history. Another key component in the high-altitude adaptation of Tibetans is the role of adaptive introgression from Denisovans [18], while the timing and geographical range of the introgressions remain controversial.

Archaic Denisovan introgression

Long-term exposure to a hypoxic environment has led to a suite of changes in the physiology of Tibetans [61,62]. As a result, multiple genes involved in regulating oxygen supply and cardiovascular functions have been identified as candidates contributing to high-altitude adaptation [62-66]. Among all the genes, the *Endothelial Pas1* (*EPAS1*) gene is the most studied one for its strong positive signal associated with an unelevated hemoglobin level in a hypoxic environment – which is considered beneficial and unique to Tibetan populations [13]. *EPAS1* shows a signature of adaptive introgression from Denisovan-like hominins [18,19,67], which is characterized by the adaptive haplotype of *EPAS1* exhibiting a strikingly high affinity to the Denisovan genome sequenced from a fossil at Denisova Cave in the Altai Mountains [23,68]. The haplotype is either absent or present at an extremely low frequency in neighboring populations [18,69], suggesting an adaptive introgression from Altai Denisovan hominins.

Moreover, recent studies identify at least four pulses of Denisovan-like **admixture** in populations of Asia and Oceania: one shared within Asians and Oceanians [70-72], one unique to Papuans [71-73], one unique to East Asians [70,72,74], and one to Ayta Magbukon in the Philippines [75]. The genetic estimations of these introgressions yielded a broad range from as early as 55 ka to as recently as 12 ka (Table 1). This age discrepancy may reflect a difference in estimating methods, type and sample of analysis data, or the assumption of single pulse of Denisovan introgression in studies prior to 2018. Consequently, it raises the questions of when, where, and from which Denisovan population the beneficial *EPAS1* haplotype was passed to Tibetans. A recent study identified an East Asian-specific introgression around 48 ka being the event that introduced the beneficial *EPAS1* haplotype [74]. Two other studies also revealed the introgression at ca. 46 ka, including East

Asians [71,72]. Generally, the encounters between *H. sapiens* ancestors of East Asians and Denisovans around 48–46 ka are possibly instrumental in the high-altitude adaptation of present-day Tibetan populations.

The onset of positive selection and the Tibetan–Han population split

The genes with exclusively high frequency in Tibetans, compared with neighboring lowland populations, are considered targets of positive selection for high-altitude adaptation. Therefore, the timing of selection of these genes is often used as a proxy for the onset of adaptation and permanent settlement. Age estimates for the selection of the *EPAS1* gene show a relatively wide range (18.3–2.8 ka) (Table 1). Despite the large interval, the majority of studies indicate that selection occurred after the LGM, much later than the Denisovan introgression. Findings of human remains with ancient (nuclear) DNA from this plateau can provide additional context and finer resolution for the timeline of high-altitude adaptations. However, ancient nuclear DNA is rare on the TP, and so far, only one study has reported limited samples on the Nepalese side of the Himalayas, from 1.75 to 1.25 ka, that contain the adaptive *EPAS1* allele [76].

Considering the geographic isolation of the TP, the timing of the population split between Tibetans and lowland Chinese is another reference to the adaptation, but it bears similar problems of chronological resolution that varies from 60 ka to nearly 2.7 ka (Table 1). In addition to the difference in samples and methods, the inconsistency in the age of the population split can be partially explained by the continuous gene flow between Tibetans and Han Chinese [17,77], which has increased substantially in recent history and may conflate the coalescence between Tibetans and lowlanders.

In sum, genetic studies have elucidated the age of the Denisovan introgression into East Asians, suggesting that contacts between Denisovans and the ancestors of East Asians took place somewhere between the Siberian Altai and the TP no sooner than 48–46 ka [71,72,74]. The separation between Tibetans and Han Chinese likely occurred after the Denisovan introgression. The age estimates can be confounded by multiple aforementioned factors that range from 60 ka to 3 ka. Lastly, most results on the positive selection on introgressed *EPAS1* cluster around the boundary of Pleistocene/**Holocene** (ca. 13–7 ka). On this account, the positive selection would have happened before the introduction of agriculture in the region and favors a scenario of permanent settlements by hunter-gatherers. While the genetic estimated times of archaic introgression, selection, and population split currently share the same issue of bearing large intervals, this is caused by multiple factors including the stochasticity during long-term evolution, the complex mechanisms contributing to the observed genomic patterns, as well as the assumptions of genetic models. Until more ancient DNA becomes available to refine the demographic models, the genetic age estimates should be used with caution and supplemented with archaeological and paleoanthropological data.

Human occupations of the TP: discontinuity or continuity?

The earliest occupation of the TP is likely by the Denisovans, as is indicated by data from Baishiya Cave; the Denisovans visited the northeast margin several times between 160 ka and 60 ka, possibly earlier or later [21,24]. Nevertheless, we still do not know if these

Denisovans were biologically adapted to high altitudes as no Denisovan nuclear DNA that includes the *EPAS1* locus is known from the highland. Future discoveries are critical to examine whether they had direct contacts with *H. sapiens* on the plateau.

For occupations of *H. sapiens*, three major issues stand out. First, despite multiple occupation episodes identified in the archaeological record, the beginning of permanent settlements is unclear. Second, whether there was a direct link between occupation gaps and climate change requires confirmation from high-resolution research data. Third, the wide range of estimated times regarding the key events related to adaptive introgression provides a rough outline for the emergence of adaptations in Tibetans. Consequently, two hypothetical peopling models posit a discontinuous occupation and a continuous occupation and are both consistent with existing evidence (Figure 2). Currently the low-resolution data does not allow a complete validation/rejection of either hypothesis. However, the models could establish an interpretative framework with clearly archaeological and genetic predictions for further studies.

Model A: discontinuous occupation

This model postulates a discontinuous human occupation with multiple visits/attempts at settlement by Denisovans and Pleistocene *H. sapiens*, but the plateau was not permanently occupied until the Holocene. The failure of settlement attempts during the Pleistocene could be explained by local extinctions or retreats to lowlands due to external factors such as hypoxia and extreme climate.

Under this model, the observed gaps in LGM and YD are sterile layers between occupation periods that should be confirmed by well-established geoarchaeological records leading to the fact of 'evidence of absence'. Another prediction is that well-documented archaeological and environmental sequences will demonstrate the association between population discontinuity and the climate deteriorations. Besides, substantial changes in material culture of the TP would be synchronous with those cultural changes in the near lowlands, following a similar pathway as hunter-gatherer behaviors change over time. More importantly, it means that, in the discontinuous model, permanent occupation or year-round settlement at high altitudes would emerge only in the Holocene. Namely, the Pleistocene sites of the TP would be mere incursions, or seasonal occupations, in contrast to residential base camps at low altitudes. Their geographic distribution would therefore illustrate distinct settlement patterns between high and low elevations.

Genetically, the Denisovan introgression likely occurred to ancestral East Asians as early as 48–46 ka [71,72,74], prior to the population split between Tibetans and Han Chinese in the lowlands. If ancient nuclear DNAs were to be yielded from Denisovan remains on the TP, it is unlikely that they would harbor the adaptive *EPAS1* haplotype and would show little genetic contribution to the modern Tibetan gene pool. Likewise, Pleistocene *H. sapiens* in the region would be unlikely to have adaptive genes and would not be direct ancestors to present-day Tibetans. As a result, the onset of positive selection on all high-altitude adaptive genes, including *EPAS1*, should be around the Holocene at a similar time to the Tibetans' isolation from the lowland Chinese.

Model B: continuous occupation

This model posits a greater time-depth for permanent settlements by *H. sapiens* from the Great Lake Period to the Holocene (Figure 2), with limited population fluctuations caused by genetic bottlenecks in highland populations or migrations from lowlands. In this context, hunter-gatherers of the late MIS3 successfully settled in the high-altitude environment and were among the direct ancestors of the present-day Tibetans.

In terms of archaeology, this model predicts that the gaps are due to small sample size and/or preservation bias. Thus, we expect new findings with secure dates from the LGM and YD to fill these gaps. Behaviorally, we may anticipate a divergent pace of cultural changes between lowlands and highlands. Cultures at high altitudes would be found with local innovations, transmitted over time, that are adaptations to the environmental pressures rather than lowland incursions. Early year-round settlements before the Holocene should be established by studies on site functions and fauna analysis relevant to seasonality and mobility. Ecological models may be supplementary to predict refugia or movement patterns during climate degradations [78,79]. In this case, hunter-gatherers continually occupy high elevations despite extreme climates in LGM and YD, and agriculture is not the prerequisite for year-round settlement.

In genetics, the Denisovan introgression could have occurred in lowlands around 48–46 ka, as in Model A. If more Denisovan fossils were found on the plateau, especially if they contained the adaptive *EPAS1* haplotype, it would open the possibility of additional adaptive introgression(s) into *H. sapiens* at high altitudes. For high-altitude adaptation we would expect that selection of major adaptive genes, including *EPAS1*, would predate the LGM. However, other mechanisms (e.g., recent admixture, the presence of deleterious mutations) may impact the inference of positive selection and the identification of adaptive introgression [80]. For example, Deedu Mongolians adapted to high altitudes only recently, after their initial migration to the TP, 500 years ago [81], and it remains unclear whether such adaptation represents an independent process – or was facilitated by recent migrations or by shared ancestry with Tibetans. Lastly, a deep divergence between Tibetans and Han Chinese prior to the LGM is expected due to their early isolation from the lowlands.

Concluding remarks

New discoveries accumulate rapidly and continue to improve our understanding of the population history of the TP, while the few existing syntheses relied heavily on archaeological findings [10,11,22]. Using a cross-disciplinary approach, we propose two parsimonious but distinct models for the population history of the high-altitude TP. The models are constructed to reach the consistency between archaeology and genetics, but the challenges specific to each field remain. For example, archaeological data seemingly illustrate multiple discrete occupation episodes, but this may reflect the fragmentary nature of the record. Genomic studies provide chronological estimates for the split between Tibetans and lowland Chinese and for the selection of adaptive genes; nonetheless, the results are consistent with both continuity and discontinuity (Table 1). So, a high-resolution dataset is required to overcome such challenges in order to test the model predictions presented above.

As data resolution improves, it might open another possibility of less parsimonious scenarios (e.g., more than one adaptation in different groups), but for now, even the two simple models cannot be fully validated or rejected. Current evidence suggests that Denisovans may have visited the highland repeatedly between (or beyond) the MIS6–MIS4. Nevertheless, without ancient nuclear DNA, directly associated fossil and cultural remains, and explicitly geographic distribution, it is unknown whether or not they adapted to high altitudes. Among the identified Denisovan introgressions, the specific pulse from Altai Denisovan-related populations to East Asians likely introduced the *EPAS1* haplotype around 48–46 ka in lowlands [18,71,72,74]. Many results suggested the haplotype being positively selected between terminal Pleistocene and early Holocene (Table 1), nearly 40 000–30 000 years after the initial introgression. Yet, it seems too early to conclude which human species – *H. sapiens*, Denisovans, or other unknown archaic hominins [82] – was the first to physiologically achieve adaptation in the high-altitude environment. The presence of the high-altitude-adaptive *EPAS1* haplotype in a single Denisovan reference genome does not inform on its frequency in Denisovan populations, nor does it speak to its biological function at the species level.

After the period of Denisovans, acknowledging current data limitations, it is worth noting that the archaeological and genetic evidence converge on a scenario of human dispersal. The sudden occurrence of blade technology at Nwya Devu (40–30 ka) points toward a potential connection with the Initial Upper Paleolithic (IUP) dated to 48–40 ka in the eastern Steppe zone (including Central Asia, Siberian Altai, and North Mongolia) [34,83], which is contemporaneous with *H. sapiens* fossils in Siberia (45 ka) [84] and the Denisovan *EPAS1* introgression into East Asians (48–46 ka). IUP assemblages as the earliest systematic blade production widely found in the Siberian Altai and North Mongolia are usually perceived as evidence of early *H. sapiens* dispersal [28,34,85] (Box 1). In addition, the human remains from Bacho-Kiro cave indicates that the *H. sapiens* inviduals produced the IUP stone tools and had genetic connections to present-day East Asians [86,87]. In lowland East Asia, blade assemblages are rare but a clear example of IUP assemblage is dated to 41–34 ka at the Shuiddongou site in North China [33,88,89]. Collectively, the blade assemblages and the *H. sapiens* fossils, with the adaptive introgression from Denisovans, suggest a hypothetical but compelling scenario: *H. sapiens* arrived in the Siberian Altai near 48 ka, reached North Mongolia around 45 ka, and finally expanded to North China and the TP as early as 40 ka. Hunter-gatherers might have brought a form of blade technology along with the introgressed *EPAS1* haplotype into East Asia. Connections between Steppe belt and East Asia might also be frequent in a later period, as Neolithic Tibetans are genetically closer to northern Neolithic East Asians and Siberians than to southern Neolithic groups [90].

Finally, our two models should help with refining the population history of the plateau and addressing specific issues (see Outstanding questions), such as early contacts between the plateau and the Steppe belt, or the geographic and chronological overlap between *H. sapiens* and Denisovans. We emphasize the value of integrating archaeology and genetics into the population history and evolutionary process of the high-altitude adaptation in the TP. We hope that this study will encourage further collaborations across disciplines in and beyond this region.

Acknowledgments

Glossary

Admixture

the exchange of genetic materials between two previously isolated populations, often facilitated by migrations.

Blade

a type of stone flake whose length is at least twice the width. It often shows two parallel edges, and the negatives of previous blade removals on its upper face show the systematic character of the production.

Holocene climate optimum

a period of temperate climate usually dated from 8 ka to 4 ka years ago.

Hypoxia

a condition that occurs when there is insufficient oxygen supply to tissues. Hypobaric hypoxia is caused by decreased oxygen concentration in the air at high altitudes leading to altitude sickness that could be fatal for human beings.

Introgression

a form of admixture, the introduction of genetic information from one species to another as a result of hybridization, such as genetic materials originally carried by extinct archaic hominins (Neanderthals or Denisovans) into *Homo sapiens*.

Last deglaciation

a period of deglacial process that occurs around 17–11.7 ka with melting glacial ice sheets and a rising sea level after LGM.

Last glacial cycle

the glacial period from 115 ka to 11.7 ka between the penultimate and current interglacial.

Last glacial maximum (LGM)

an extremely cold and dry period (25–19 ka) when global ice sheets reach the maximum and the sea level is about 110–125 m lower than it is today.

Marine Isotope Stage (MIS)

a global climatic sequence established from the marine record based on the isotopic composition of ice cores; it refers to glacial/interglacial cycles with an assigned number for each stage: even numbers for glacial and odd numbers for interglacial. MIS6 is a glacial

episode of 190–130 ka. MIS5 is between 130 ka and 71 ka. MIS4 is from 71 ka to 60 ka. MIS3 is a relatively warm phase around 60–30 ka.

Microblade
like blades, microblade is smaller in size and produced by pressure flaking instead of direct percussion.

Neolithic
regional changes around the boundary of Pleistocene and Holocene when some human cultures shifted to an economy characterized by agriculture, animal husbandry, and technologies like ground stone tools and pottery.

Pleistocene and Holocene
the Pleistocene, ranging from 2.6 million years ago to 11.7 ka, is divided into the Early, Middle, and Late Pleistocene by 770 ka and 126 ka respectively. After 11.7 ka, it enters the Holocene.

Population split (divergence)
refers to the forming of isolated subpopulations from ancestral populations without gene flow; it usually predates genetic divergence, the coalescence time from last common ancestors.

Upper Paleolithic
part of a periodization system, used in Eurasia, based on major changes observed in the archaeological record. Dependeing on the region, it usually startsfrom 50 ka to 30 ka and is defined by technological changes in lithic production (such as blade and bladelet), formal tools made of bone, antler or ivory, personal ornaments, and cave arts, as well as a general shift toward diversified subsistence practices.

Younger Dryas (YD)
an abrupt cooling in 12.8–11.7 ka; it is named after a cold-adapted Arctic wildflower expanding into Europe during this period.

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Highlights

The peopling of the Tibetan Plateau is a spectacular example of human adaptation to high altitudes as Tibetan populations have thrived for generations under strong selective pressures of the hypoxic environment.

Recent discoveries are leading to paradigmatic changes in our understanding of the population history of the Tibetan Plateau, involving *H. sapiens* and the archaic hominin known as Denisovan.

Archaeological and genetic studies provide essential insights into behavioral and biological human adaptations to high elevations but there is a lack of models integrating data from the two fields. Here, we propose two testable models for the peopling process on the plateau leveraging evidence from archaeology and genetics.

Box 1.

The dispersal of *H. sapiens* and the Initial Upper Paleolithic

Following the 'Out of Africa II' model, two expansion routes into eastern Asia are proposed: the southern route and the northern route. The southern route favors a dispersal from East Africa, following coastlines of South Asia and arriving in Australia as early as 60–50 ka [95,96]. The northern route refers to a dispersal through the Levant and then across Central and North Asia into East Asia around 50 ka [97,98]. The two dispersal routes may imply different adaptive pathways. The northern route has a mostly middle and relatively high-latitude continental climate. It is supported by the fossil of Ust'-Isinhim in Western Siberia and Tianyuan Man in North China dated to 45 ka and 42–39 ka respectively [84,99,100], as well as by the spread of an archaeological technocomplex known as the Initial Upper Paleolithic industry (IUP). The latter is a type of specific stone tool technology that appeared at the age of transition between the Middle Paleolithic and the classic Upper Paleolithic [101]. It is widely found and known in West Asia (Levant), Eastern Europe, and Central and North Asia. IUP sites of the eastern Eurasian Steppe (including Central Asia, Siberian Altai, and North Mongolia) are mostly dated to 48–40 ka [28,34,83,102] and are contemporary with the *H. sapiens* fossils mentioned above. The IUP assemblages are chiefly dominated by systematic blade productions following specific methods (such as asymmetric cores and burin-core reductions) [34,103]. They are sometimes also uncovered with the formal bone, antler, or ivory tools, and the use of personal ornaments [104]. The dispersal of the IUP is viewed as an early step toward the generalization of behaviors that characterize the early *H. sapiens* hunter-gatherer populations, along with the shift in subsistence practices and social organization, and/or spectacular developments in mobile and cave art [28,105,106]. The new discovery at the Bacho-Kiro cave (Bulgaria) in Eastern Europe indicates that *H. sapiens* is the maker of IUP based on the human remains that were found directly associated with the stone tool assemblage dated to ca. 45 ka, and the fossil individuals had a closer genetic affinity with present-day East Asians than with modern Europeans. [86,87].

Outstanding questions

The identification of Denisovan remains on the TP raises fundamental questions on how and when this population expanded up to the high-elevation plateau. Were the archaic hominins adapted to high-elevation environments? Did they adopt a specific behavior at high altitudes? What was the demography and geographic distribution of archaic Denisovans in Asia?

A haplotype of the *EPAS1* gene transmitted from Denisovans as early as 48 000 years ago benefits the high-altitude adaptation of Tibetan populations, but the positive selection of the haplotype is much younger. With multiple admixture events between Denisovans and *H. sapiens* now documented, in which region did *H. sapiens* get the *EPAS1* introgression? How frequent was the *EPAS1* haplotype within the Denisovan regional populations?

Specific behaviors, such as the production of blades, suddenly appeared on the TP as early as 40 000 years ago, probably coming from the Eurasian Steppe. How did the hunter-gatherers adapt their technology to the extreme environment? What mechanisms led to the diffusion of technology: cultural diffusion or population movements?

Living hunter-gatherers often adapt the frequency of their movement to the landscape, depending on seasons and natural resources. How did Pleistocene hunter-gatherers adjust their mobility and settlement patterns to the harsh highland environments?
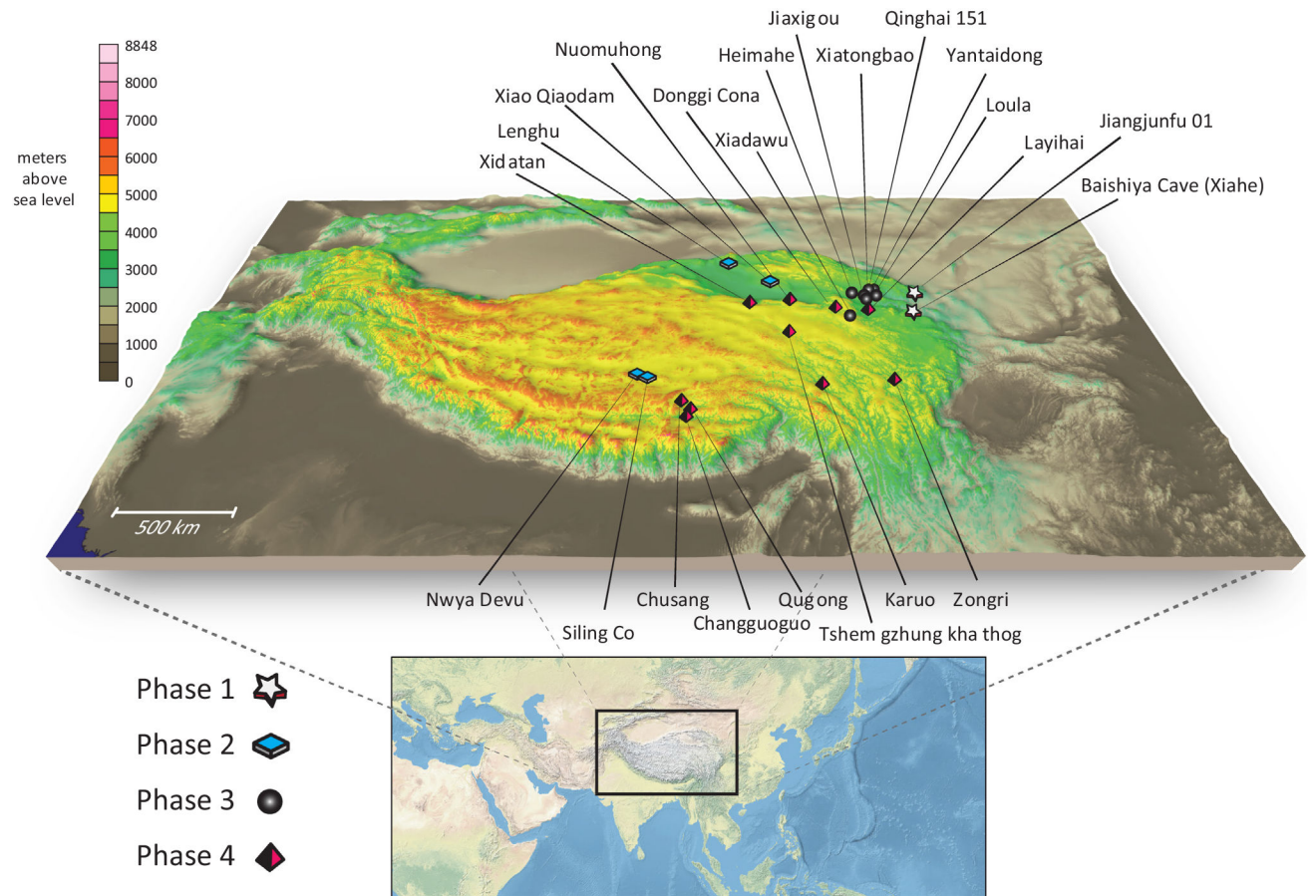
Figure 1. The distribution of archaeological sites on the Tibetan Plateau (TP).

Sites were either dated directly through excavations or the age of sites and survey materials was estimated. Four major occupation periods are included: (i) MIS 6–4 (Phase 1): Baishiya Cave (Xiahe), Jiangjunfu 01; (ii) Late MIS3 (Phase 2): Nwya Devu, Siling Co, Xiao Qiaodam, Lenghu; (iii) Last deglaciation (Phase 3): Jiangxigou, Qinghai 151, Xiadawu, Heimahe, Yantaidong, Koula, Xiatongbao; and (iv) Holocene climate optimum (Phase 4): Tshem gzhung kha thog, Donggi Cona, Xidatan, Layihai, Chusang, Karou, Zongri, Nuomuhong, Changguogou, Qugong. (Geographic map[i] and GMTED2010 digital elevation data[ii] [91].)
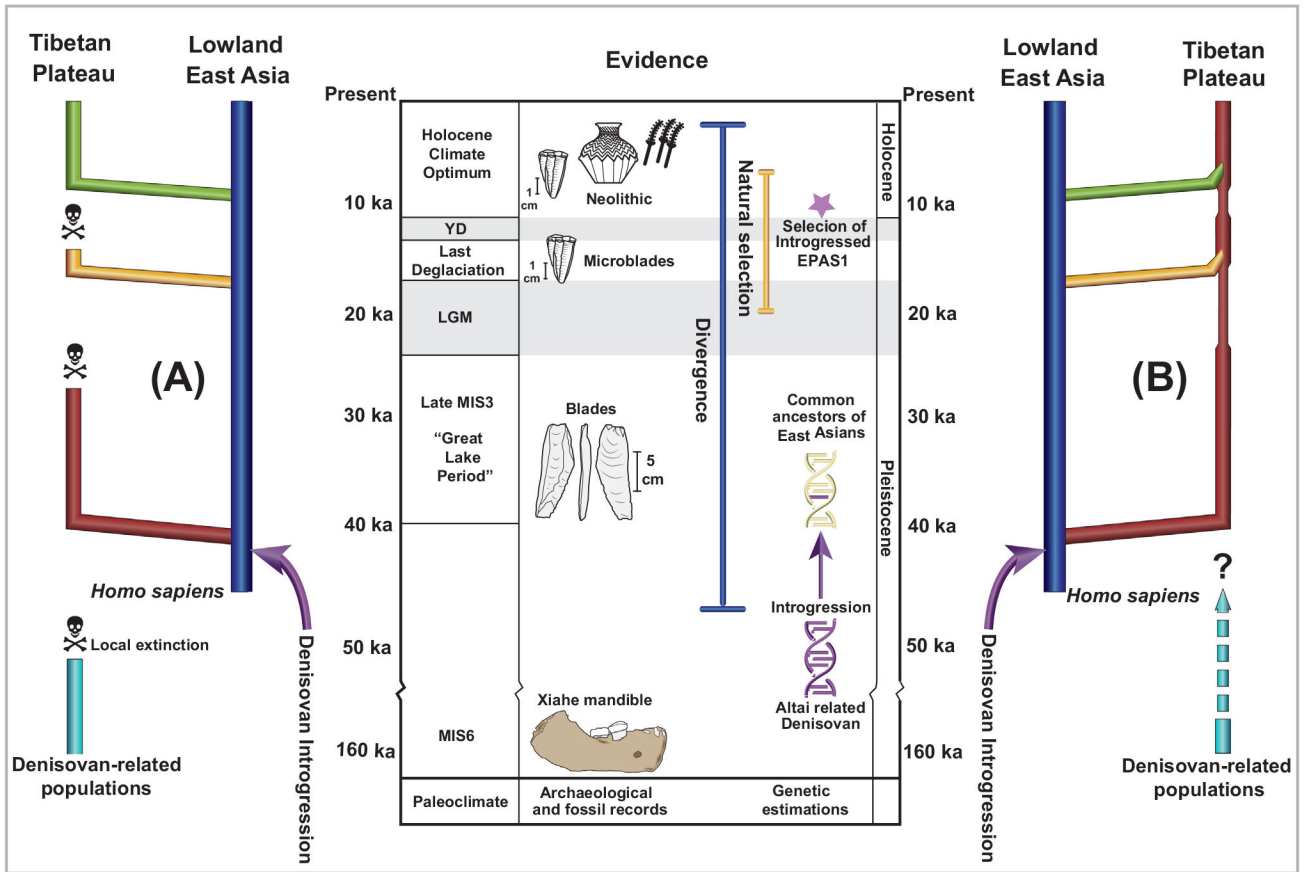
Figure 2. Current evidence and two models for the population history of the Tibetan Plateau (TP).

The middle of the figure shows existing evidence from archaeology and genetics of a timeline, with four periods of occupation: (i) represented by Baishiya Cave since late MIS6 to the MIS4; (ii) a blade assemblage, excavated from the Nwya Devu site in late MIS3, also known as the Great Lake Period; (iii) microblade assemblages of the Late Upper Paleolithic; and (iv) the Holocene Neolithic expansion. The genomic studies provide molecular chronological estimates for the Denisovan introgression, natural selection, and population divergence. Model A (left) displays discontinuous occupations before permanent settlement occurred during the Holocene. It means local extinctions for Pleistocene groups due to hypoxia, extreme climate events, and/or other factors. Model B (right) illustrates a continuous occupation from the Great Lake Period to the Holocene, with permanent settlements as early as 40–30 ka, possibly with population inputs from lowlands. Abbreviations: ka, thousand years ago.

Table 1.

The date of genetic estimations of the three events related to high-altitude adaptations

Date of estimation (ka)			Refs
Denisovan admixture	**Han–Tibetan divergence**	***EPAS1* selection**	
–	2.7 ka	–	[14]
–	–	18.3 ka	[63]
–	30 ka	–	[15]
–	–	12.8 ka	[92]
–	–	10–2.8 ka	[69]
54–44 ka	–	–	[93]
62–38 ka	15–9 ka	9–7 ka	[16]
–	4.7 ka	–	[94]
32–12 ka	58–44 ka	12 ka	[17]
46 ka (Asia and Oceania); 30 ka (Papua)	–	–	[72]
46 ka (East/Southeast Asia); 25 ka (Papua)	–	–	[71]
48 ka (East Asia)	–	9 ka	[74]
53 ka (Philippine Ayta)	–	–	[75]