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A demographic history of late Pleistocene China

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Abstract

This paper proposes a demographic history of China in the last glacial cycle. This history is complex because China lies in both the Palearctic and Oriental biogeographic realms, and experienced several immigration events before *H. sapiens*. Immigration by our species into the Oriental Realm of south China from southeast Asia probably began as early as 80,000 years ago. North China has a different history: here, humans immigrated from Mongolia and southern Siberia ca. 45,000 years ago as part of a cold-adapted Palearctic fauna. These populations were largely independent of one another, and each needs to be seen as part of their respective biogeographic realms. The subsequent demographic history of China is one of mixing and inter-breeding of populations from both north and south China. In the LGM, north China (and Mongolia) were largely depopulated, and subsequent recolonization of north China occurred from both the north and the south. Explanations of the demographic history of China have to include developments beyond its borders, immigration, assimilation of new populations, and continuity of local groups.

Introduction

Although there has been considerable interest in establishing when our species first appeared in China, there has been much less interest in developing this information into a demographic history of our species in late Pleistocene China. This is complicated because the appearance of our species in China resulted from two different dispersal processes. One was a dispersal

of our species across southern Asia from Arabia into India and then into southeast Asia and south China (Dennell and Petraglia 2012; Boivin et al. 2013; Dennell and Porr, 2014) as well as Wallacea and ultimately Australia (see O'Connell et al. 2018). The other was a northern dispersal across continental Asia through central Asia, Siberia, Mongolia and north China (see Goebel, 2015), and ultimately to the Japanese islands and North America. China is unique in Asia because it was colonised from both north and south.

Here, we attempt to formulate a demographic history of late Pleistocene China by considering the biogeographical contexts in which human colonisation took place. We argue that human dispersal into the Oriental Biogeographic Realm of southeast and south China required fundamentally different responses from human dispersal into the Palearctic Biogeographic Realm of north China, Mongolia and southern Siberia (see Table 1). We also suggest that human (and other animal) populations in each realm remained largely separate, with only a small overlap in central China. Late Pleistocene China was in effect inhabited by two separate populations. First, the biogeographical background.

INSERT NEAR HERE: TABLE 1

The Palearctic and Oriental Realms

Biogeographical realms were first proposed by Alfred Wallace (the “father of biogeography”) in 1876, and continue to provide a useful framework for studying continental-scale ecosystems. Figure 1 shows a simplified version. The Palearctic Realm covers the whole of continental Eurasia. China north of the Qinling Mountains lies in the Palearctic Realm and includes the Loess Plateau, Xinjiang, Inner Mongolia, and the Northern Arid Area of China (NAAC) as well as Chinese Siberia and the Tibetan Plateau (see Figure 2). Annual rainfall is low (usually <500 mm, and <50mm in northwest China), and winters are usually sub-freezing, often for several months, with January temperatures averaging -20°C . near the Mongolian border and in -30°C . in Chinese Siberia. In cold, dry periods of the Late Pleistocene, precipitation decreased by ca. 40–75%, with levels as low as 100–200 mm over the central part of the Loess Plateau during the last glacial maximum and previous stadial (Liu et al., 1995). Conversely, during warm, moist periods such as MIS 5e, MIS 5a and MIS 3, the boundary of the summer monsoon moved northwards, rainfall increased by up to 20% (Liu et al., 1995) or even 80% (Maher and Thompson, 1995) in the last interglacial, and the desert margin would have contracted. As in Arabia, there were numerous palaeolakes in areas

of north China (see Yu et al., 2001); those in the Tengger Desert were largest in MIS 5a (80-90 ka) (Long et al., 2012), and not between 42-40 ka during MIS 3, as previously thought (Zhang et al., 2004). The vegetation today is temperate in the south to xerophyllic in the desert regions, and coniferous in Chinese Siberia and Manchuria. Today, wheat and millet are the main cereal crops. In the last glacial cycle, the Loess Plateau was predominantly *Artemisia* steppe (Sun et al., 1997) and further north in Inner Mongolia, conditions deteriorated from forest steppe and open forest steppe in MIS 5, to desert steppe in MIS 4, steppe in MIS 3, and desert steppe in MIS 2 (Cai et al., 2019).

INSERT FIG. 1 NEAR HERE: BIOGEOGRAPHIC REALMS

INSERT FIG. 2 NEAR HERE: MAP OF CHINA WITH REALMS AND SITES

During cold, dry periods of the Late Pleistocene, the fauna of north China was characterized by horse (*Equus przewalskyi* and *E. hemionus*), gazelle (*Gazella przewalskyi* (= *Procapra przewalskyi*)) woolly rhinoceros (*Coelodonta antiquitatis*), *Bison*, and *Bos primigenius*. Horse and gazelle were particularly important prey animals in neighbouring Mongolia; both can also migrate several hundred kilometres between winter and summer grazing (Agadjanian and Shunkov, 2018; Olsen et al., 2010; Zwyns and Lbova, 2019). During cold and dry episodes in MIS 3, woolly mammoth (*Mammuthus primigenius*) grazed in Inner Mongolia and Shandong Province south of Beijing (Larramendi, 2014; Takahashi et al., 2007), and even as far south as the Qinling Mountains in the LGM. In warmer, moister periods, these mega-herbivores would have been replaced by herbivores such as *Bubalus* (buffalo), *Cervus nippon* (sika) and pig (Li Y.-X. et al., 2012).

South of the Qinling Mountains, China lies within the Oriental Realm, which also include south-east and most of south Asia. The main feature of the climate of the Oriental Realm is that it is monsoonal, with a dry period generally from October to March, a hot season into June and then the summer monsoon that delivers most of the annual rainfall that is typically between 1,000 and 2,000 mm. Winters are above freezing, and therefore, there was no need for the warm, insulated clothing made from hide or fur that was essential for the northern dispersal across continental Asia. Unlike life in northern latitudes, the provision of clothing did not require substantial amounts of time and labour. Regarding plant resources, the vegetation is largely sub-tropical or tropical. Plant foods are available year-round, whether as leaves, fruits, nuts, roots or tubers. Today, rice is the main cereal crop. The fauna includes

panda (*Ailuripoda melaneuca*), tapir, and in the Pleistocene, the giant ape *Gigantopithecus*, *Megatapirus*, *Stegodon orientalis*, and oriental rhinoceros (*Rhinoceros sinensis*). Herbivores could usually find sufficient browse or grazing year-round so did not need to migrate long distances between winter and summer pastures. They and their dependant human populations could therefore remain localised within small annual territories. The Oriental Realm was probably the main refugium in Asia for human populations during the last glacial maximum, and may have contained (as now) most of the total population of Asia in the Late Pleistocene (see e.g. Atkinson et al., 2008).

The boundary between the Oriental and Palearctic faunas in China was not static but fluctuated frequently and often considerably during the Pleistocene, particularly north of the Qinling Mountains (Norton et al., 2010). However, because cold-adapted animals rarely moved south of the Qinling Mountains, there was greater faunal stability in south China. Several animal taxa did move north of the Qinling Mountains in warmer and moister periods. Tong (2007) notes that *Hystrix*, *Macaca*, *Palaeoloxodon*, *Dicerorhinus* and *Bubalus* are the most frequently recorded warm-adapted elements that appeared in north China. Because *Hystrix* has been found at 22 localities in north China, it is probably one of the best faunal indicators of a warm climate in this region (Tong, 2008).

The fossil skeletal evidence

Three conclusions can be drawn from the Chinese skeletal record: i) China contained a diverse population before the immigration of *H. sapiens*; ii) *H. sapiens* appeared in south China before it entered north China; and iii) the main affinities of the earliest *H. sapiens* populations in north China were with Upper Palaeolithic ones in west Eurasia and not with south China.

i) hominin populations in China before H. sapiens

Some Middle Pleistocene Chinese fossils indicate that immigration from western Eurasia may have occurred during warm periods. Rightmire (2001), for example, classified as *H. heidelbergensis* the specimens from Dali (ca. 240-280 ka-old, Sun et al., 2017) and Jinnuishan (ca. 280 ka-old, Lu et al., 2003). Others have commented on the overlap between *H. erectus* and non-erectus Middle Pleistocene *Homo*. Under the “continuity with hybridisation model” of hominin evolution in East Asia (see e.g. Liu et al., 2010a), “the suite

of traits exhibited by Dali could be indicative of a local transition between *H. erectus* and *H. sapiens* that included some influence from western Eurasian populations during the Middle Pleistocene” (Wu and Athreya, 2013: 154).

One of the most intriguing sets of specimens are from Xujiayao (=Hujiayao), in the western part of the Nihewan basin in north China (Xing Song et al., 2015; Wu and Trinkaus, 2014). The age of this material is uncertain. One study indicates an age older than 140 ka and likely between 160-220 ka (Tu et al., 2015), but another study implies an age range of ca. 260-370 ka (Ao et al., 2017). The hominin specimens are particularly interesting for their mosaic of primitive and derived dental features because these suggest a population of unclear taxonomic status with regard to other groups such as *H. sapiens* and *H. neanderthalensis*. The scarcity of fossil information available from Denisova prevents a detailed comparison with the Xujiayao specimens. However, Martín-Torres et al. (2017) pointed out intriguing parallels between the morphological and genetic mosaic of the Xujiayao and the Denisova samples, respectively, which point in both cases to a hominin lineage that is different from *H. sapiens*; shares features with *H. neanderthalensis*; and preserves the heritage of a “mysterious” and primitive hominin, which in the Xujiayao fossils could be reflected in the preservation of some typical Asian Early and Middle Pleistocene features. Overall, the morphology of the Xujiayao hominin specimens implies that their main similarities lie with hominin populations at Denisova in the Altai Mountains of Siberia and not with populations further south.

This assessment is consistent with their faunal context in a steppe or semi-arid environment. It is also consistent with a recent report of a Denisovan mandible from Xiahe on the edge of the Tibetan Plateau, ca. 3000 m above sea level (Chen et al., 2019). The Xiahe mandible is very robust, relatively low and thick, with a strongly receding symphysis, departing from the typical morphologies seen in Neandertals and modern humans and similar to other Middle Pleistocene hominins and at the limit of the *Homo erectus* distribution. The anteriorly broad and flattened dental arcade is reminiscent of Neandertals and looks like if it has a retromolar space, but this could be a side-effect of the agenesis of the M₃. What could really align Xiahe with Denisova is the large dentition. The large bucco-lingual diameters are typical of *H. erectus*, although they fall at the high end of the range of *H. erectus* specimens. However, we should not forget that dental size is a feature that is insufficiently specific to make taxonomic and phylogenetic assessments, and that the Denisova sample is too small indeed to

characterize the group. Protein molecules extracted from the Xiahe mandible are claimed to have closer affinities to Denisova than to *H. sapiens* and *H. neanderthalensis*, so it is possible that is a Denisovan but this is at present only a claim, and not an unambiguous demonstration. It might, however, hint at an emerging Denisovan population extending from Denisova to the edge of the Tibetan Plateau and across northern and central China. If confirmed, this emerging population would provide a source population for the presence of Denisovan DNA in Southeast Asia and Melanesia (Reich et al., 2011)

The Xiahe mandible is claimed to share features with a mandible recovered in fishing nets in the Penghu Channel between Taiwan and the mainland, and dated by the type of fauna occasionally found by fishermen to less than 450 ka but most likely 190 ka in age (Chang et al., 2015). The Penghu mandible resembles the claimed Denisovan mandible from Xiahe in being low and thicker than other coetaneous mandibles, with perhaps the exception of the Hexian mandible (Liu et al., 2017), and because of the agenesis of the third molar and a particular and rare conformation of its second molar root. This is an uncommon feature, present in both the Xiahe and Penghu specimens, and future studies should clarify its evolutionary meaning. However, Bailey and colleagues (2019) recently claimed that this type of three-rooted molar was a rare trait that was relatively common in modern Asian populations and was evidence of introgression in present-day Asian populations. This paper was contested by Scott et al. (2020) since the trait they discuss is not homologous to this one, as this is not a three-rooted molar in the classic sense that was posed by Turner et al., in the ASUDAS (Arizona State University Dental Anthropology System) system.

Another major recent discovery are two hominin crania from layer 11 of the site of Lingjing in Xuchang County in Central China that are dated by OSL to ca. 105-125 ka and are thus dated to MIS 5e or MIS 5d. The fauna is diverse and includes Palearctic grassland or steppe animals such as *Equus caballus* and *E. hemionus* (onager) and *Procapra* (gazelle), and open woodland or grassland such as *Cervus*, *Bos* and *Coelodonta*. The overall shape of the crania indicates continuity with earlier Middle Pleistocene hominins from East Asia, but they also show some Neandertal features. Together, these features “argue both for substantial regional continuity in eastern Eurasia into the early Late Pleistocene and for some level of east-west population interaction across Eurasia” (Li Zhanyang et al., 2017: 971). An intriguing possibility is that these crania have belonged to Denisovans, as suggested by Stringer and

Martinon-Torres: “something with an Asian flavor but closely related to Neandertals” (see Gibbons, 2017: 899). The Xiahe mandible strengthens this proposal.

ii) H. sapiens was in south China before it appeared in north China

It is surprisingly difficult to establish when *H. sapiens* first appeared in south China because of doubts over the stratigraphic context of skeletal evidence; its dating; and its identification as unambiguously that of *H. sapiens*. The earliest claimed evidence for our species in southeast Asia is a left upper third premolar (P³) (PU-198) from Punung, Java (Storm et al., 2005) but Polanski et al. (2016) recently suggested that the tooth could indicate *H. erectus*. The clearest evidence for the first recorded presence of *H. sapiens* in southeast Asia is probably that from Lida Ajer, Sumatra, where two teeth that can be confidently attributed to *H. sapiens* were found in a layer between two flowstones that are dated at 63 and 73 ka (Westaway et al., 2017), which places them in MIS 4 (58-74 ka). At Tam Pa Ling, Laos, the remains of five individual *H. sapiens* are present (Demeter et al., 2012, 2015, 2017; Shackelford et al. 2018), dated to a minimum of 46 ka and a maximum of 70 ka for the mandible TP3 (Demeter et al., 2017).

Skeletal evidence from south China confuses rather than clarifies our understanding of when *H. sapiens* first entered this region. The clearest evidence is probably that from Fuyan, where 47 teeth that are unquestionably those of *H. sapiens* were found under a flowstone dated at 80 – 120 ka (Liu Wu et al., 2015; Martín-Torres et al., 2017); this age estimate is consistent with the associated fauna that includes five extinct species (Dennell, 2015). The flowstone is continuous throughout the whole cave and palaeomagnetic and rock-magnetic analyses proved it was in situ, the stratigraphy is relatively simple and consistent through the whole system. The ²³⁰Th dating was also more extensive than at many other sites in the region. Finally, radiocarbon dating was indeed attempted in one human tooth and three associated faunal remains. Only one faunal remain provided collagen and the radiocarbon age was estimated as 43,000 calibrated years bp, beyond the limits of the radiocarbon technique at the Peking University lab due to its organic material background. This, together with the biostratigraphic evidence of five extinct taxa, supports an early Late Pleistocene age rather than a late one.

As stated in the paper by Liu et al. (2015), the teeth are highly derived. We agree with Michel et al. (2016) that more dating work would be desirable – either directly on the teeth, or further dates from unit 2 that contained the teeth. Isotopic analysis of the teeth and other mammalian teeth in that unit would also be useful in establishing whether the unit 2 assemblage is homogenous. We would also welcome micro-sedimentological analysis of the unit 2 sediments to establish their taphonomic history. However, until this type of research has been undertaken, we feel that the dating should be accepted, at least provisionally, until otherwise disproven.

Regarding the presence of caries in the Fuyan teeth, it is interesting to note that the same type of cavities have been found in some of the teeth from Zhirendong and Tubo (Ganjian cave), both also claimed to be ca. 100 ka in age. The Zhiren 2 mandibular molar (see below) had a massive caries (Lacy et al. 2012), and two of the Tubo upper molars also had caries (Wu and Poirier 1995, 210-211). These could be potentially related to a change of diet in the first groups that arrived in East Asia, particularly in the light of recent studies that suggest that modern humans may have exploited rainforest resources in southern and southeast Asia earlier than usually assumed (e.g. Roberts and Petraglia, 2015; Roberts et al., 2016). The first dispersals outside Africa could be related to the exploitation of new resources and perhaps, greater susceptibility to suffer caries, although this needs further research. Along the same line, it is worth highlighting that some teeth from Daoxian and Huanglong Cave (Liu et al., 2010a) present activity-related wear marks such as elongated wear facets and the cement-enamel junction or pronouncedly oblique occlusal planes, that could be exemplifying some behavioural innovations in these groups related with the cultural use of their teeth.

One interpretation is that the teeth from Fuyan indicate an immigration event of *H. sapiens* from Southeast Asia during late MIS 5/early MIS 4, i.e. at a time when sea levels were lower than today (i.e. MIS 5d, MIS 5b, or MIS 4), thus providing a wide corridor for entry into China when the vegetation was more open.

It is also important to understand Fuyan within the context of a growing body of evidence in support of a pre-50 ka dispersal by *H. sapiens* into south China (see Martín-Torres et al., (2017) and Dennell (in press) for further discussion of the available fossil evidence). At Zhiren cave, a toothless mandible and two molars were recovered from the upper part of layer 2 of Unit B and associated with a late Middle or early Upper Pleistocene fauna (Jin et al.

2009; Liu Wu et al. 2010b). These were dated by reference to the lowest of a series of flowstones in the cave profile that was dated to 106.2 ± 6.7 ka. Cai and colleagues (2017) considered the faunal, palaeomagnetic and U-series dates and suggest that the human fossils are between 116 and 106 ka in age. In a recent re-dating of the layer containing the human fossils, Ge et al. (2020) argue that these were deposited during MIS 6, between 190 and 130 ka. Both studies are consistent in dating the human remains to >100 ka.

Luna Cave produced two teeth attributed to *H. sapiens* with a likely minimum age of 70 ka (Bae et al., 2014). Seven teeth of *H. sapiens* were recovered from layer 3 at Huanglong Cave (Liu et al., 2010b), but their age is unclear. U-series dating of two rhinoceros teeth gave an age range of 94.7 ± 12.5 ka and 79.4 ± 6.3 ka. Speleothem dating by U-series indicated ages of 103.7 ± 1.616 ka and 103.1 ± 1.348 ka, but ESR dating of a rhinoceros tooth produced an age of 44.18 ± 4.54 ka on a late uptake model and 34.78 ± 3.28 ka on an early uptake model. It is also unclear whether the speleothem sample from the section came from above or below the hominin teeth. This point highlights the difficulty of correlating speleothems exposed in a cave section with material found in the cave floor. Two teeth from the cave of Longtanshan, Yunnan Province, are identified as *H. sapiens* and dated to 60-83 ka, although further dating work may be required (Curnoe et al., 2016). There is also a partial skeleton from the cave at Liujiang that was found when local farmers were digging for fertiliser. The deposits in which it is thought to have been found are dated to between 68 ka and >153 ka, with a probable age of 111-139 ka (Shen et al., 2002), but there is no way of knowing how these dates relate to the skeleton. It could be much younger – for example, it might represent an individual who was buried in a grave cut into those deposits. Until the skeleton is dated directly, it cannot be used as evidence of an early presence of *H. sapiens* in south China. If one accepts the evidence from Fuyan, *H. sapiens* was present in south China at or possibly before 80 ka BP.

In north China, there is no evidence of *H. sapiens* before 42,000 years ago. The earliest skeletal evidence for our species is from Tianyuandong, near Beijing, where a human femur has been dated to $40,328 \pm 816$ yr. cal. BP (Shang et al., 2007), and Upper Cave, Zhoukoudian, where the layer containing human crania are now dated to 33,551-38,376 yr. cal. BP (Li Feng et al., 2018a). In neighbouring Mongolia, the Salkhit partial cranium has recently been dated to a calibrated age of 34,950–33,900 yr. BP (Tseveendorj et al., 2016; Devière et al., 2019).

iii) the affinities of early H. sapiens in north China

Dentally, the Tianyuan individual shared similarities with teeth from European Upper Palaeolithic humans from Arene Candide (Italy), Dolní Vestonice and Mladeč (Czech Republic) (Shang et al., 2007). Analysis of the nuclear DNA of this individual showed that it was derived from a population that was ancestral to many present-day Asians and Native Americans but had already diverged from the ancestors of present-day Europeans. The proportion of Neandertal or Denisovan DNA sequences in its genome was also no larger than in present-day people in the region (Fu Qiaomei et al., 2013). Another study showed that the Tianyuan individual was more related to Asians than to past and present Europeans, but the 35,000-year-old individual from Goyet, Belgium, shared more alleles with Tianyuan than any other west European. The similarity of the Tianyuan individual to this specimen and some South American populations implies the persistence of structured populations that lasted until the colonisation of the Americas (Yang et al., 2017).

The most significant aspect of the Upper Cave material from Zhoukoudian is that the Upper Cave crania 101 and 103 share more features with similar evidence from Siberia, Mongolia and western Eurasia than with south China and “may represent members of an as yet undifferentiated early modern human population that expanded across Eurasia in the Late Pleistocene” (Harvati, 2009: 761). Li Feng and colleagues (2018a: 170) conclude that the inhabitants of Upper Cave “were part of dispersal events across northern Eurasia toward Siberia and eventually reaching into northern China”.

Population dynamics of China

Two factors need considering when thinking about the population dynamics of China during the Pleistocene. The first is how humans (and other animals) responded to climatic change, particularly the repeated shifts in the respective strengths of the winter and summer monsoon that determined the severity or mildness of winter temperatures (particularly in the north of China) and the degree of aridity. The second factor is immigration into China – specifically, when, from where and under what climatic conditions.

Population dynamics in response to climate change in China

The response of warm-adapted faunas to the repeated climatic shifts in China between cold, dry climates and ones that were warmer and moister can be envisaged in a simple source-sink model (see Figure 3) similar to that proposed by the authors for Middle Pleistocene Europe (Dennell et al., 2011). Martínón-Torres et al. (2016) applied this type of model to China and showed how the Chinese hominin record could be modelled in terms of population contraction, expansion, coalescence and fragmentation.

INSERT FIG. 3 NEAR HERE: SOURCE-SINK MODEL

The basins along the Luohe and Hanjiang Rivers in the Qinling Mountains are potential areas of glacial refugia and source populations for those that expanded northwards in warm, moist periods (Sun et al., 2018). The Qinling Mountains provided some shelter from the winter monsoon, and although some loess was deposited in these basins, it was much less than on the Loess Plateau, and winters appear to have been milder. Basins such as the Luonan and Lushi have been systematically surveyed for several years by Chinese teams and contain ca. 270 palaeolithic sites that date from 1.2 Ma to the last glacial cycle (see e.g. Lu Huayu et al., 2011a, 2011b; Sun et al., 2018). What makes this area especially interesting is that these basins were occupied in cold periods of loess deposition (equivalent to glaciations in Europe) as well as in periods of palaeosol development (equivalent to European interglacials) – as one would expect for glacial refugia. The Yangtze Valley was also another likely glacial refugia for southern populations no longer able to inhabit northern China.

These models consider hominins as part of a warm-adapted, Oriental fauna that would have expanded northwards when conditions became warmer, and retreated southwards towards glacial refugia when conditions became colder. Cold-adapted animals such as lemmings or mammoth can also be modelled in terms of source-sink populations, but these would have expanded southward when conditions were cold, and retreated northwards into interglacial refugia when conditions were at their warmest. This point is especially relevant to Pleistocene China in that there were repeated opportunities in cold periods for immigration by cold-adapted faunas into north China from Siberia, Mongolia and Manchuria (Li Y.-X. et al., 2012). Elephants provide a clear example, with the expansion southwards of the cold-adapted woolly mammoth *Mammuthus primigenius* when the climate of north China was extremely cold, and its replacement by the warm-adapted *Palaeoloxodon* when the climate became milder.

The fascinating aspect of China's population dynamics in the Pleistocene is that humans belonged to both the cold-adapted Palaearctic and warm-adapted Oriental Realms (Dennell in press). A key factor here is the extent to which a hominin or human population was cold-adapted in terms of its ability to survive extremely cold winters. The most important adaptations would have been warm, insulated clothing and footwear as well as food storage techniques and effective control over fire. Neandertals (and probably Denisovans) most likely had effective winter clothing as one of their survival technologies in the Palaearctic Realm of continental Eurasia; indeed, Soressi et al. (2013) argues that lissoirs (bone polishers used in hide processing) were first developed by Neandertals. (As seen below, Neandertals may have colonised continental Asia as far east as Inner Mongolia). The colonisation by our species of regions such as northern Mongolia – where winter minima can fall below -45°C . (Zwyns et al. 2014b) and Inner Mongolia (where winter temperatures can fall below -40°C .) would have been impossible without effective winter clothing and effective over-wintering technologies. Current evidence strongly implies that these adaptations were part of the expansion of the Initial Upper Palaeolithic (IUP) in southern Siberia, Mongolia and north China. Indirect – and so far the earliest - evidence for the habitual use of footwear comes from the lack of wear on the toe bones of the Tianyuan individual, dated at ca. $40\,328 \pm 816$ ka BP calibrated (*Trinkaus and Shang 2008).

The IUP background of southern Siberia and Mongolia

At Denisova in the Altai Mountains of Siberia, four pendants that were made from red deer (*Cervus elaphus*) and elk (*Alces alces*) teeth were radiocarbon dated at $\sim 32,000$, $\sim 40,000$ and $\sim 45,000$ cal BP and two bone points were dated to 42,660–48,100 and 41,590–45,700 cal BP. These dates place the IUP at Denisova at ca. 43,000–48,000 cal BP (Douka et al., 2019). These dates match those for the *H. sapiens* femur from Ust'Ishim (Fu et al., 2014), and strongly imply that our species was the manufacturer of the IUP. This is not to dismiss the possibility that it might have interbred with Denisovans or even Neandertals at the time of contact and we might expect evidence of that when eventually an IUP skeletal part is found in Denisova or elsewhere in the Altai.

In Transbaikalia, dates from Kamenka, Tolbaga, and Varvarina Gora suggest that occupation of what was then tundra-steppe (Bezrukova et al., 2010) began ca. 45,000 – 44,500 cal. BP

and continues to ca. 35,000 cal BP (Buvit et al., 2015; Graf and Buvit, 2017). The earliest Upper Palaeolithic in the Transbaikal - most likely by *H. sapiens* - appears to be an intrusive development that “indicates migrations within a limited territory and restricted home ranges” (Rybin 2015: 481). In northern Mongolia, several Upper Palaeolithic sites indicate systematic occupation of what were then taiga and steppe grasslands (Kolomiets et al. 2009; Ma et al. 2013) after 40,000 cal years ago. The earliest sites are in the valley of the river Tolbor which flows into the Selenga, which in turn flows into Lake Baikal and thus provides a corridor into northern Mongolia from Transbaikalia. Today, the average temperature is between -0.9°C . and -1.6°C . (with minima below -45°C .): settlement in this region would clearly be impossible without warm, wind-proof clothing and footwear, and the ability to survive brutally cold winters. The earliest IUP site so far identified may be Tolbor 21, at which two radiocarbon dates on bone are 42,878-44,033 and 46,196-49,457 cal BP. Tolbor 15 (horizons 6 and 7) and Tolbor 16 have calibrated radiocarbon ages greater than 38,000 years (Zwyns et al. 2014a). North China marks the southward expansion from Mongolia of human groups using an IUP technology after 42 ka.

Immigration into China

Figures 4 and 5 present two simple models of the climatic and environmental conditions that would facilitate or impede immigration. The first assumes conditions were similar to those in the equivalent of an interglacial, when it was warm and the summer monsoon could penetrate much of northern China and stronger westerly winds could bring some rain into Xinjiang in northwest China. These conditions would be the most optimal for immigration into south China from the Oriental Realm of southeast Asia. They would also have enabled immigration into north China from the west and north from Siberia and Mongolia: the desert and steppe margins would have retreated northwards; there would have been numerous lakes in the Gobi and neighbouring deserts; and winters would have been less severe. Li Feng and others (2019a) have recently suggested that there may have been a desert corridor through a “green Gobi” at times of higher rainfall.

<INSERT FIGURE 4 NEAR HERE – IMMIGRATION IN A WARM PERIOD>

Figure 5 summarises conditions at the height of a glacial maximum. In north China, desert and steppe would have been at their greatest extent. With the fall in sea levels, the emergence

of the East China coastal shelf would have moved the coastline several hundred kilometres eastwards, and this would further have reduced the amount of precipitation inland. Winters would also have been much more severe. As an extreme example, the average annual temperature on the Loess Plateau during the deposition of loess (L)15 1.2 Ma-ago may have been as low as 1.3 – 3.0° C., similar to that of a polar desert (Guo et al., 1998). Under these conditions, immigration into China by a warm-adapted mammal from the north or west would have been difficult, if not impossible. In contrast, conditions that were cooler and drier in southern China would have facilitated immigration because corridors of savannah grassland and open woodland would have provided corridors for immigration.

<INSERT FIGURE 5 NEAR HERE – IMMIGRATION IN A COLD PERIOD BY A WARM-ADAPTED FAUNA>

The Palaeolithic record

In south China, the early Palaeolithic continues throughout the last glacial cycle with little change, and consisting of simple, non-standardised flakes and cores, but it would be uncritical to dismiss them as simple and monotonous (Qu et al., 2013; Wang, 2017). Ma'an Shan, for example, in Guizhou Province, has the earliest formal bone tools in China that date back to ca. 35 ka, and these include barbed bone points, dated at 23-28 ka (Zhang et al. 2016). Xiaodong in Yunnan Province in southwest China has the earliest Hoabinhian assemblage that is dated to 45 ka (Ji et al., 2015) and indicates links with southeast Asia. Because Xiaodong lies in rainforest, this site may also indicate the earliest colonisation of rain forest in mainland southeast Asia. There is probably far greater complexity and variety in the palaeolithic of southern China than we currently recognise.

The late Palaeolithic record of north China shows four immigration events from Mongolia and south Siberia. The first is a recent indication that Neandertals may have expanded eastwards into Inner Mongolia, ca. 2000 km east of the previously recorded easternmost location in the Altai region of Siberia. At the cave of Jinsitai in Inner Mongolia, levels 7 and 8 contained assemblages classified as Mousterian that date from at least 47-42 ka and persisted until around 40-37 ka. It was thus a substantial occupation episode. Although the correspondence of Mousterian with Neandertals is not automatic – as in the Levant – most Mousterian sites are associated with them, and in Central Asia, Neandertals are the only

hominin associated with Mousterian assemblages, so the same is likely at Jinsitai (Li Feng et al., 2018b). However, we cannot discount the possibility that the occupants of Jinsitai were partly or even wholly Denisovan, given the evidence for inter-breeding between Denisovans, Neandertals and our own species.

The second immigration event is evident in the Shuidonggou (SDG) site cluster. The lower cultural layer of SDG 1 contains an IUP blade-based technology produced by Levallois and prismatic methods of core reduction (Peng Fei et al., 2014). Similar assemblages are known from South Temple Canyon (Madsen et al., 2014), SDG 2 cultural layers 5a and 7 (Li Feng et al., 2014), SDG 7 and SDG 9 (Niu Dongwei et al., 2016). Ostrich egg shell beads are also present, similar to those seen in Siberia and Mongolia (Peng Fei et al., 2018), and an engraved limestone core was also found (Peng et al., 2012). OSL dating indicates that the SDG 1 assemblage dates from ca. 43 ka (Nian et al. 2014). Overall, the SDG 1 assemblage is similar in age and composition to the IUP assemblages that are seen in Mongolia and the Altai Mountains (Peng Fei et al., 2018; Li Feng et al., 2019b).

To take a wider perspective, the IUP in northern China should be seen as part of a cultural realm that included Mongolia, Cis- and Transbaikalia (Rybin, 2014). An important unifying characteristic of this region is the use of ostrich egg shell beads and pendants made from animal teeth, as well as the occasional use of ochre. These first appear in Transbaikalia ca. 42-45 ka (Buvit et al. 2015; Graf and Buvit 2017; Lbova 2019), and ca. 40-42 ka in the Tolbor Valley of northern Mongolia (Gladyshev et al. 2010, 2012; Zwyns et al. 2014a, 2014b). The ornaments from Upper Cave are most like those from Denisova, and both assemblages include perforated canine teeth of various types of deer and small carnivores, round beads, bone pendants, and perforated shells, none of which are found in south China but are widespread across Mongolia and southern Siberia (see Rybin, 2014; Lbova, 2019).

Because of the similarities of the lithic assemblages from Shuidonggou, Mongolia and southern Siberia, and the common element of ostrich eggshell beads, the SDG 1 and SDG 2 occupants were presumably part of an extensive network of groups that operated over an enormous territory in pursuit of highly mobile migratory prey such as horse and gazelle. A high degree of mobility would also involve a high degree of risk and uncertainty, thereby increasing the need to sustain long-distance social networks. As a long-term strategy, the risk may have been too great, and this may be why the initial blade-based tradition was short in

north China compared with the succeeding flake-based occupations. It may be worth noting that there is no middle Upper Palaeolithic in the Tolbor Valley in Mongolia. On current evidence it is possible that the IUP and EUP (early Upper Palaeolithic) groups in Mongolia went locally extinct, and those in north China were absorbed into groups using a flake-based lithic tool-kit.

The third immigration event is shown by the colonisation of the Tibetan Plateau at 4600 m asl, where a blade assemblage at Nwya Devu has recently been dated to ca. 30-40 ka BP (Zhang et al., 2018; Zhang and Dennell, 2018). An interesting perspective on the colonisation of the Tibetan Plateau is that the adaptation that may have enabled humans to live at such a high altitude may have come from the Denisovans because they may have contributed our adaptation to high-altitude hypoxia through a gene region known as EPAS1. (If the Xiahe mandible is indeed Denisovan and the dating is correct, hominins were already living at 3000 m above sea level 160,000 years ago). The unusual haplotype structure of this gene is found only in Tibetans and Denisovans (Huerta-Sánchez et al., 2014). We know that Denisovans interbred with Neandertals, and Neandertals interbred with humans, and therefore it is likely that the Tibetan Plateau was colonised by humans that had interbred with Denisovans.

The fourth immigration event into north China is evidenced by the late glacial microblade industry which probably originated in Siberia (Yi Mingjie et al., 2014, 2016) and appeared in north China at sites such as Longwangshan ca. 27-25 ka cal. BP (Yi Mingjie et al., 2016). This industry produced a superb lightweight toolkit by pressure-flaking minute blades that could be slotted into arrow shafts or handles, and is widely distributed across Siberia, Japan, the Korean Peninsula, and in China as far south as Linjing in Central China (Li and Ma, 2016). Post-LGM, southern Siberia, Mongolia and north China were re-colonised by groups using a microblade technology (Dennell, 2018). Shuidonggou 12 is an excellent end-Pleistocene example of a microblade hunting camp focussed on trapping fur animals (Yi Mingjie et al., 2014). As Yi Mingjie and colleagues (2016: 138) point out, “microblade technology was a perfect solution to problems of provisioning through long, harsh winters when resources were less abundant and more difficult to access, and when failure to procure sufficient resources had fatal consequences”. The diffusion of a microblade technology across Central Asia, Mongolia, and southern Siberia provides a clear demonstration of how successful humans had become at surviving some of the most hostile environments of the Pleistocene.

Was north China depopulated in the LGM?

During the LGM, ca. 21-18 ka, north China was a cold, arid desert and steppe, with permafrost extensive above 1000-1300 m (1000m lower than today), and annual temperatures 8-12° C. colder than now (Cui et al., 2004). Mongolia may also have been largely depopulated as there is no record of occupation in the Tolbor or Kharganyn Gol valleys between 30,000 and 19,000 years ago (Khatsenovich et al., 2017). In southern Siberia, regions such as Transbaikalia were either abandoned or made archaeologically invisible for at least 2–3 kyr between about 24.8 ka and 22.7 ka (Graf and Buvit, 2017). It is unclear whether north China was occupied during the LGM. Sites such as Xiachuan (28 – 19 ka) in the Yellow River Valley and Shizitan locality 14 (23 – 19,500 cal BP) may pre-date the LGM; Ma'anshan in the Nihewan Basin is dated at 18 ka but few details are available (Yang et al. 2018). We suggest that north China was largely, but probably not totally, depopulated during the LGM between 21 and 18 ka BP.

Discussion

There are four main features of the demographic history of Pleistocene China. The first is that it was never a closed system and has to be studied in a much wider context that includes mainland southeast Asia, Mongolia and southern Siberia. The second is that the dominant pattern of immigration into China before 50 ka would have been from the Oriental Biogeographic Realm into south China from neighbouring southeast Asia and perhaps South Asia. As proposed here, successive influxes of immigrants would have inter-mixed with indigenous populations. Those that dispersed in warm, moist periods north of the Qinling Mountains into the Palearctic Realm of north China would have faced local extinction in cold, dry periods unless they were able to retreat into refugia in the basins of the Qinling Mountains or the Yangtze Valley. In warm, moist periods, there would also have been some immigration into north China from Central Asia and southern Siberia, although this was probably minor before 50 ka. The third feature is that major changes in the population dynamics of Pleistocene China occurred after 50 ka, when at least four immigration events from Mongolia and southern Siberia. The first of these, as evidenced by the presence of Mousterian assemblages at Jinnsitai, may have been by Neandertals, and the colonisation of the Tibetan Plateau may have involved Denisovans, or human-Denisovan hybrids. The fourth feature of China's demographic history is that or substantial parts of north China were

probably depopulated in the LGM. China's demographic history is therefore one of continuity in the south, and repeated colonisation and abandonment in the north. In both cases, the skeletal and Palaeolithic evidence for *H. sapiens* and its predecessors in China needs to be studied in its biogeographic context.

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Table 1: Summary of differences between the Palearctic and Oriental Realms of China and neighbouring regions.

	Altai-Baikalia-Mongolia-N. China	South China and mainland SE Asia
Biogeographic realm	Palearctic	Oriental
Climate	cool/cold, dry; sub-freezing winters	warm, wet; warm winters
Precipitation	largely winter	monsoonal; summer
Plant foods	scarce and seasonal	abundant year round
Animal foods	herd and migratory (horse, gazelle)	small groups or solitary; localised
Subsistence	highly mobile; large annual territories	largely sedentary; small annual territories
Population size and density	small, dispersed	larger, less dispersed
Level of risk	high	low
Type of clothing	clothing – hide/fur	optional, or plant based
Occupation records	discontinuous	continuous
Raw materials	sometimes over large distances	usually local
1 st appearance of <i>H. sapiens in China</i>	45-40 ka BP	possibly as early as 80-100 ka BP

Figures

Figure 1: Biogeographic realms of Asia during MIS 3 and MIS 4.

The Oriental Realm covers most of south and southeast Asia, and China south of the Qinling Mountains. North China and Mongolia lie within the Palearctic Realm. Sea-levels are shown at 40-60m below present levels for the Arabian-Persian Gulf, Sunda and Sahul. Redrawn and modified from Holt et al. 2013, Figure 1.

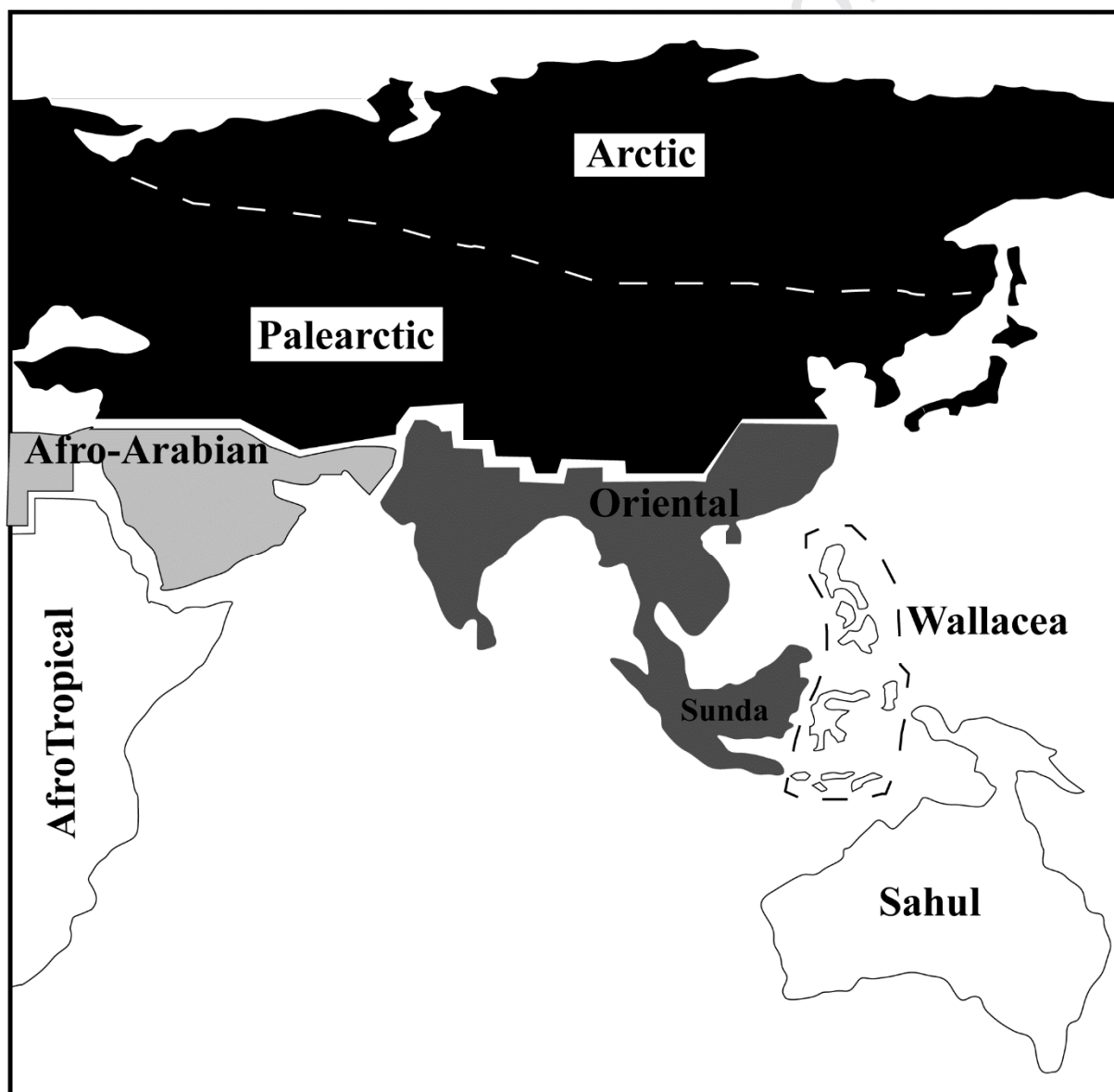
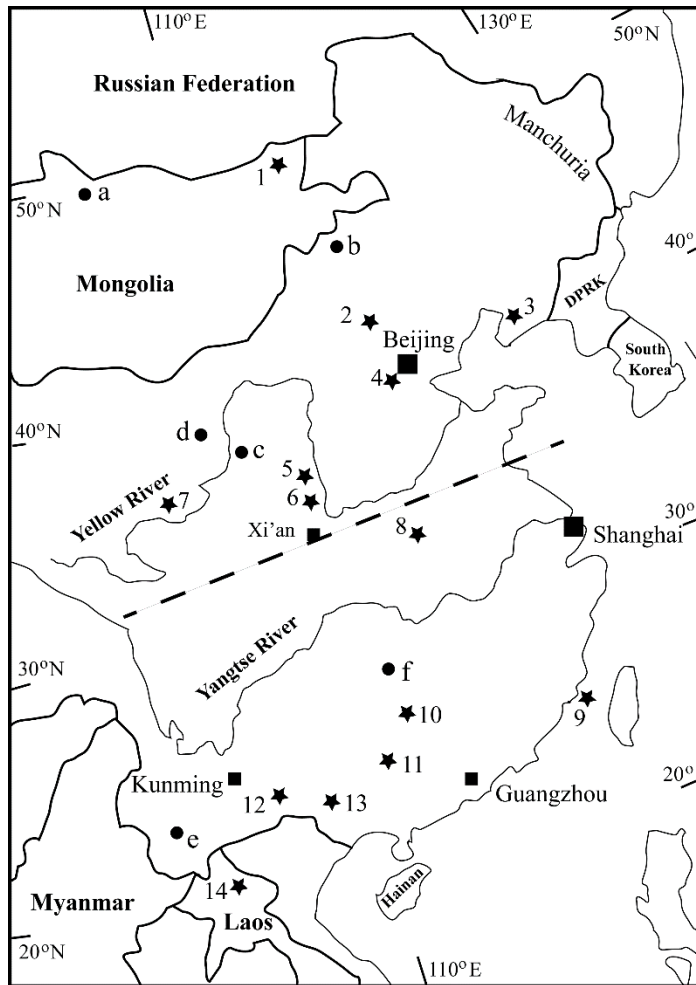


Figure 2. Fossil hominin and early Upper Palaeolithic sites in China and neighbouring countries. Source: Dennell.

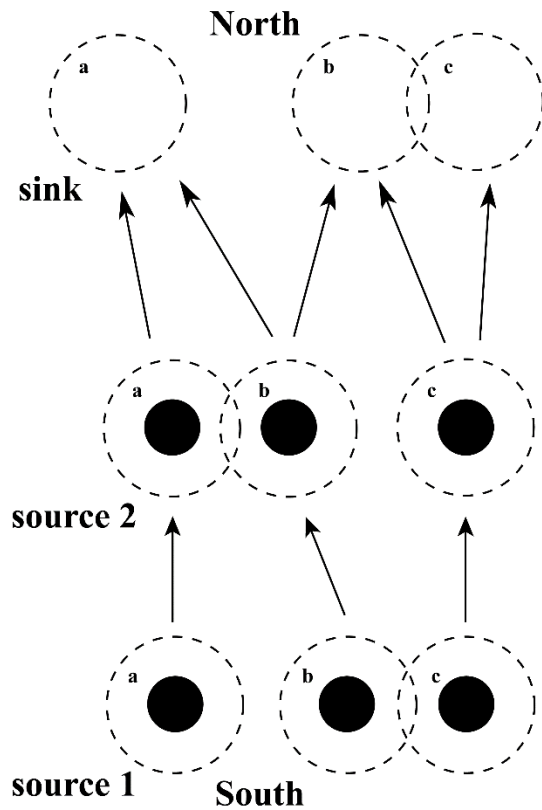


The dashed line indicates the present boundary between the Palearctic Realm of north China and the Oriental Realm of south China. This boundary shifted considerably during the Pleistocene, depending upon the relative strengths of the winter and summer monsoons. The Qinling Mountains that divide north from south China lie south of Xian and the Yellow River, and approximately along the modern boundary between the Palearctic and Oriental biogeographic realms.

Key: Sites with hominin remains: 1 Salkhit; 2 Xujiayao; 3 Jinnuishan; 4 Zhoukoudian Upper Cave and Tianyuandong; 5 Huanglong; 6 Dali; 7 Xiahe; 8 Xuchung (Linjing); 9 Penghu; 10 Fuyan; 11 Liujiang; 12 Longtanshan; 13 Luna; 14 Tam Pa Ling (Laos).

Archaeological sites: a Tolbor; b Jinsitai; c Shuidonggou; d South Temple Canyon; e Xiaodong; f Ma'anshan

Figure 3: Sink and source populations.



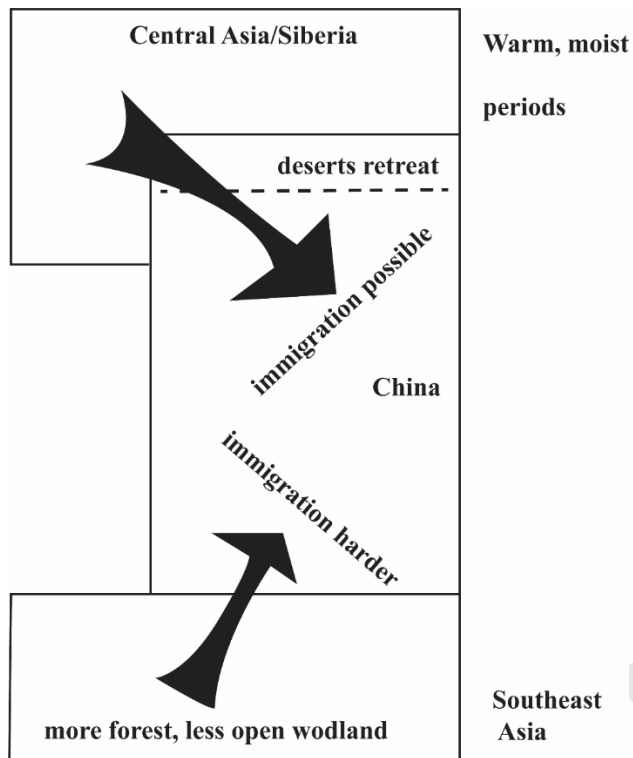
Source and sink populations: Here, the bottom row indicates three metapopulations, or palaeodemes, in glacial refugia at the southern limit of the species' range. These are source populations that provide the basis for later expansion. The solid circles denote metapopulations during cold periods when populations contract into refugia; the dashed circles indicate interglacial or interstadial conditions when expansion from them is possible. Each is separated in glacial conditions, but in interglacial conditions, metapopulations b and c overlap. The middle row indicates how each expands in interglacial times and becomes a source population: here, metapopulations 2a and 2b overlap, but 2c (derived originally from demes b and c) remains isolated. The top row indicates the maximum expansion during an interglacial; here, deme 3a (derived from demes 2a and 2b) is isolated, but demes 3b and 3c overlap, although each has a different ancestry. At the northern edge of the species range, the metapopulations are sink populations in that they require recruitment from source populations to remain viable.

In this scenario, the process of expansion results in inter-demic mixing, and this schematic representation of population fragmentation, dispersal and recombination could lead to the type of demic variability exhibited by the Chinese fossil record during the late Middle and early Upper Pleistocene.

Source: Dennell.

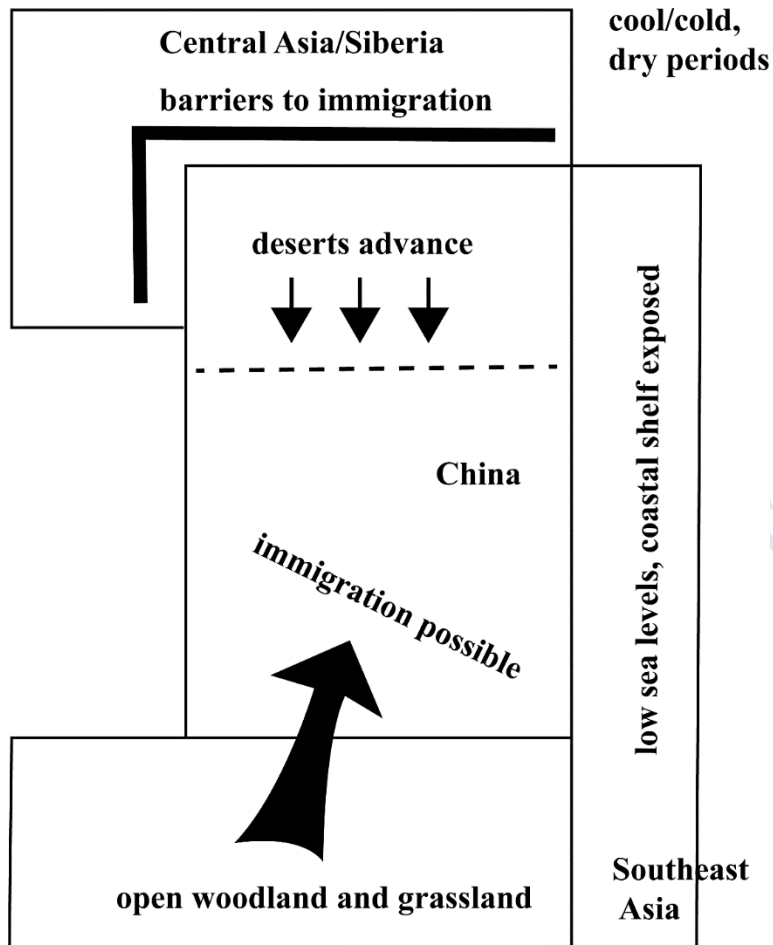
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Figure 4: Model of immigration into China in warm periods



In warm, moist periods, the desert boundary retreated and immigration into north China was possible from regions to the north and west. In south China, immigration from southeast Asia might have been more difficult because of the expansion of rain forest. Source: Dennell.

Figure 5: Model of immigration into China by warm-adapted mammals in cold periods



In cold, dry periods, the desert boundary shifted southwards in north China, and immigration from regions to the north and west would have become more difficult. Lower sea levels resulted in a greatly expanded coastal shelf along the east coast of China. On the other hand, the contraction of rain forest and expansion of open woodland and grassland in south China would have facilitated immigration from southwest Asia. Source: Dennell.

Conflict of interest

There are no conflicts of interest in the ideas and data presented in this paper.

Regards

A handwritten signature in black ink, appearing to read "Robin Dennell". The signature is written in a cursive style with a period at the end.

Robin Dennell

Corresponding author

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