Human palaeontology and prehistory

Environment, preferred habitats and potential refugia for Pleistocene *Homo* in Southeast Asia

Environnements, habitats préférés, et refuge potentiel pour les représentants pléistocènes du genre Homo en Asie du Sud-Est

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A B S T R A C T

Multiple lines of evidence suggest that Southeast Asia was dominated by a mix of savannah, open woodlands, and evergreen forests throughout much of the Pleistocene. These conditions are ideal for early hominin subsistence; however, they would have been rare for much of the rest of Asia during glacial periods. We explore the possibility that Southeast Asia would have served as a refugium for hominins during these periods. In particular, we draw parallels with the population source and sink model proposed for northern Europe (Dennell et al., 2010), with Southeast Asia acting as a population source and northern China acting as a population sink.

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R É S U M É

Plusieurs données suggèrent que l'Asie du Sud-Est a été dominée par un milieu naturel de savanes, de clairières et de forêts de résineux pendant la plupart de la période du Pléistocène. Ces conditions sont idéales pour la subsistance des premiers homininés ; cependant, elles furent rares pour le reste de l'Asie pendant les périodes glaciaires. Nous explorons la possibilité que l'Asie du Sud-Est ait eu une fonction de refuge pour les homininés pendant ces périodes. En particulier, nous établissons des parallèles avec le modèle « sources et puits » des populations, proposé pour l'Europe du Nord (Dennell et al., 2010), avec l'Asie du Sud-Est comme source de population et le Nord de la Chine comme puits.

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1. Introduction

In a recent detailed review of prehistoric human occupation of Asia, Dennell (2009) (p. 474) concluded that perhaps the most important driving force behind the patterning of hominin settlement during the Early and Middle Pleistocene was climatic, and in particular rainfall variation. Regional discontinuity and local extinction were therefore, in his view, largely the norm, implying that long-term refugia must have existed to enable populations to survive during critical periods. Among the possible areas that he identified in Southeast Asia as potential refugia were

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Java, Sumatra and Borneo, with the co-incident availability of food, water and flakeable stone as major constraints. However, one aspect of the discussion of refugia that may deserve further consideration is the effect of lowered sea levels on the Southeast Asian landscape during the glacial periods of the Pleistocene, conditions that existed for close to 90% of the time (Lambeck et al., 2002). In particular, we note the potentially large area that would become available southwards from the Gulf of Thailand down the Malaysian Peninsula to Sumatra and Java and then north-eastwards via Borneo and fingering out towards the Philippines (Voris, 2000), generally known as Sundaland.

Dennell (2009) (p. 145, Fig 5.9, Fig 7.12) acknowledged the presence of this area, but made little detailed mention of its potential as a refugium and showed it as containing mainly tropical lowland forest during the Last Glacial Maximum (LGM). This interpretation was based in large part on work by Sun et al. (2000) on pollen from deep-sea sediments in the region. However, we believe that a case can be made for a substantial savannah component to the vegetation based on the likely degree of aridity during glacial periods, resulting in a central corridor of more open landscape running through Sundaland (albeit one flanked on both sides by tropical rainforest) based on previous work by Heaney (1991) and more recent detailed studies by Bird et al. (2005) and Louys and Meijaard (2010). These discussions have proposed this corridor as a route by which dispersals may have taken place (Antón, 2002; Keates, 2004). Clearly, such a route has important implications for understanding the modern and past biogeography of the region during the LGM, but in this article, we explore the likelihood of Sundaland, Indochina and other exposed areas of the eastern coastline of China providing a significant refugium for much of the large-mammal fauna and for hominins throughout the Pleistocene, when climate changes that induced lowered sea level made conditions for occupation difficult or unattractive elsewhere in Asia. Such a review is in our view timely. Dennell et al. (2010) have recently undertaken a detailed assessment of the patterning of hominin demography during the Middle Pleistocene in Europe, and concluded that a model of populations occupying sources and sinks makes more sense of the variability seen in Middle Pleistocene hominins than the more conventional notion of ebb and flow movements in concert with the glacial and interglacial cycles. In so doing, they pointed to the likely parallels to be seen in Asian populations, specifically those from China. Against this background, recent efforts to characterise the habitats in the Nihewan Basin as relatively benign, and occupation by hominin populations therefore quasi-continuous (Ao et al., 2010; Pei et al., 2009), appear to us misplaced.

We begin with an outline of the larger patterning of Early and Middle Pleistocene hominin dispersal and the broader stone toolkit with which they appear to have been equipped in order to establish the likely timespan of concern. We follow this with a review of the Southeast Asian fauna and the palaeoenvironmental evidence for savannah-like conditions in the region, and a consideration of the suitability and attraction of the broader geographical region as a refugium for hominins. Finally, we consider the likely preferred environments in which dispersal is likely to have taken place.

2. Eurasian hominin dispersal

The earliest dispersal of Eurasian hominins is a matter of considerable debate in the literature, not least because relatively few fossil occurrences are available although archaeological sites add to the potential patterning. So far as fossil specimens are concerned, a Later Pliocene/Earliest Pleistocene origin in Africa is perhaps the most widely accepted model for the evolution of *Homo* (Dennell, 2009; O'Regan et al., 2010; Turner and O'Regan, 2007a,b), with the earliest known hominin material outside Africa coming from Dmanisi in Georgia (∼1.7 Ma). Specimens from there have been assigned to either a very primitive form of *Homo erectus* (Rightmire et al., 2006) or a new species *H. georgicus* (de Lumley et al., 2006), with the latter authors placing *H. georgicus* closer to the *Homo habilis-Homo rudolfensis* lineage than to *H. ergaster/H. erectus* and thus, implying a first Late Pliocene/Early Pleistocene dispersal of most primitive *Homo* from Africa to Dmanisi.

In Southeast Asia, a date of 1.8 Ma was claimed for *H. erectus* in Java (Swisher et al., 1994), but material from the top of the Sangiran Formation at close to 1.6 Ma is now considered to be the earliest (Bettis et al., 2009). *Homo* sp. has been identified at Yuanmou in southern China with a date of 1.7 Ma (Zhu et al., 2008), but this claim has been strongly questioned, most recently by Dennell (2009). Isolated teeth from 'Ubeidiya in Israel, dated to ∼1.5 Ma (Belmaker et al., 2002), have been attributed to *H. erectus* or *H. ergaster* and the record has recently been extended in Europe with the publication of a hominin mandible from the Sima del Elefante at Atapuerca, dated to between 1.2–1.1 Ma (Carbonell et al., 2008).

Earliest Eurasian archaeological remains, regarded as Oldowan (or Pre-Oldowan), also come from Dmanisi (de Lumley et al., 2005). Early Pleistocene sites outside Africa with Oldowan (Mode 1) technology are also found in Spain (Barranco-Leon 5 and Fuente-Nueva 3 and lowest levels of Atapuerca (Carbonell et al., 2008; Gibert et al., 1998; Martínez-Navarro et al., 1997; Oms et al., 2000), and are claimed at Pirro Nord in Italy at 1.6–1.3 Ma (Arzarello et al., 2007), the Pabbi Hills in Pakistan ∼1.9 Ma (Dennell, 2004), Yuanmou in southern China ∼1.7 Ma (Zhu et al., 2008) and Majuangou in north-eastern China dated to 1.66 Ma (Zhu et al., 2004). We shall return to the question of the success of human occupation in northern China in a later section.

Such a technology, although simple, provides a range of sharp flakes and thus gives a significantly increased range of options for obtaining and processing both foods and other, non-lithic items of everyday use, and the vast numbers of such items found on sites testify to the extent of use and amount of time and effort that must have been put into locating suitable stone. However, the stone tools at 'Ubeidiya are Acheulean, a form that first appears ∼1.7 Ma at Konso Gardula in Ethiopia (Asfaw et al., 1992), so that its presence at 'Ubeidiya suggests that at least one hominin dispersal out of Africa occurred between 1.7 Ma and 1.5 Ma and that the populations concerned were equipped with an
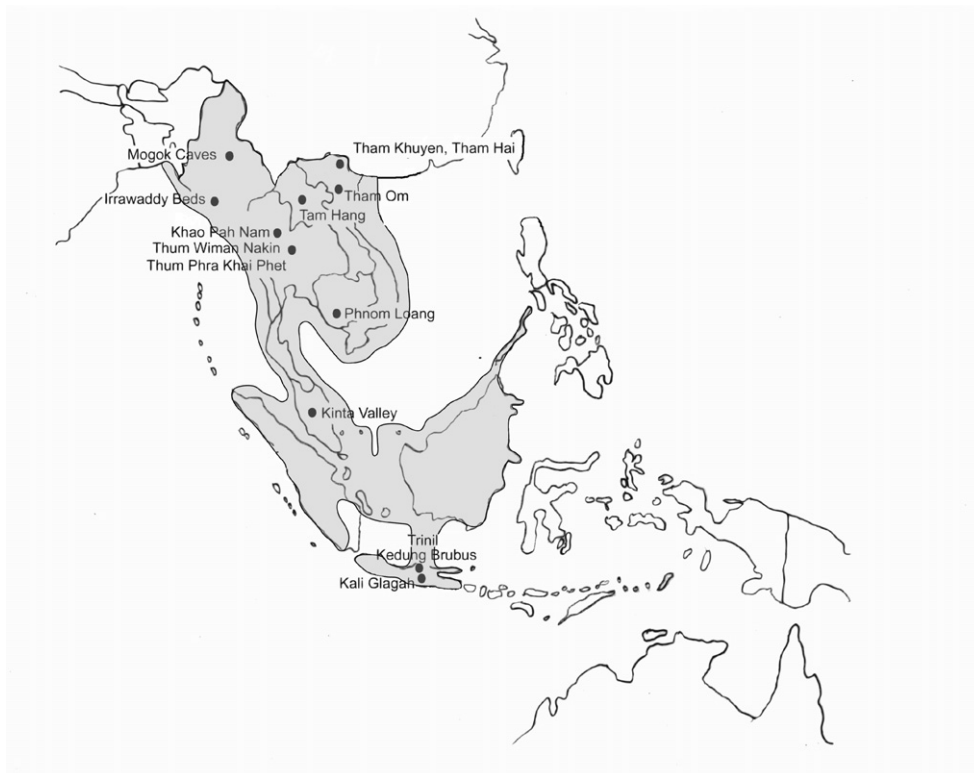
Fig. 1. Southeast Asia, showing the hypothetical extent of land exposure over Sundaland and Indochina during the Middle Pleistocene (based on reconstructions by Meijaard (2004) (Fig. 5.9). Southeast Asian sites and series discussed in the text are illustrated.
Fig. 1. Carte de l'Asie du Sud-Est montrant l'extension du territoire hypothétique sur le Sundaland et la Péninsule d'indochinoise pendant le Pléistocène moyen (à partir des reconstructions de Meijaard (2004) (Fig. 5,9). Les sites et série d'Asie du Sud-Est décrits dans le texte sont illustrés.

even more sophisticated technology. Directions and timing of early hominin dispersals into and around eastern Asia have been considered by Antón (2002) and Keates (2004), and clearly, there was no technological impediment to dispersal, although finding suitable sources of stone may have dictated the success of various movements.

3. Palaeogeography, palaeoenvironments and faunas of Southeast Asia

3.1. Palaeogeography

The shallow seas of the Sunda shelf around the Indonesian archipelago are an obvious site for increased landmass during falls in sea level (Voris, 2000). Indeed, as Bird et al. (2005) (p. 2229) remark "there is no other area in the tropics where the contrast between the modern distribution of land and sea with their distributions during the Last Glacial Period (LGP) and the LGM is so marked". The latter authors went on to contrast the main alternative interpretations of the resultant Sundland vegetation, from the "savannah corridor" idea of Heaney (1991) to the tropical rainforest interpretation of others such as Sun et al. (2000) (based on pollen) and Otto et al. (2002) and Crucifix et al. (2005) (based on vegetation models). Bird et al. (2005) reviewed these ideas and concluded that all the evidence from geomorphology, biogeography, palynology and vegetation modelling taken together offered strong support

for the notion of northward expansion of open vegetation from southern Sundaland during the LGM. They suggested a minimal savannah corridor occupying sand plains and ridges in a 50–150 km wide belt during such times, and acknowledged that a maximal belt similar to that proposed by Heaney (1991) may even have existed while pointing out that clear evidence for the latter is currently lacking. We find their arguments and interpretation compelling, and in previous studies based upon them Louys (Louys, 2007, 2008; Louys et al., 2007) has suggested that the periodic loss of savannah landscapes during the interglacial episodes of the Pleistocene may have been one of the triggers for extinctions of mammal species in the region adapted to grazing or reliant on freshwater. That argument is based on the idea that a sea level below the present-day one is in fact the norm for most of the Pleistocene based on calculations by Chappell and Shackleton (1986), so that sea level rise during the interglacial periods would interrupt that normal situation.

Fig. 1, adapted from Meijaard (2004) (Fig. 5.9), shows the extent of land present in Southeast Asia during the Middle Pleistocene. Fig. 2, from Louys (2008) (Fig. 3) shows a summary of inferred global sea levels for the past 1.2 Ma. The pattern of sea levels in Fig. 2 seems to reflect the effects of the Middle Pleistocene Transition (MPT) between ca 900 and 600 ka, when the global climate changed from one dominated by the 41 ka cycle to the 100 ka cycles that have characterised the past glacial-interglacial sequence
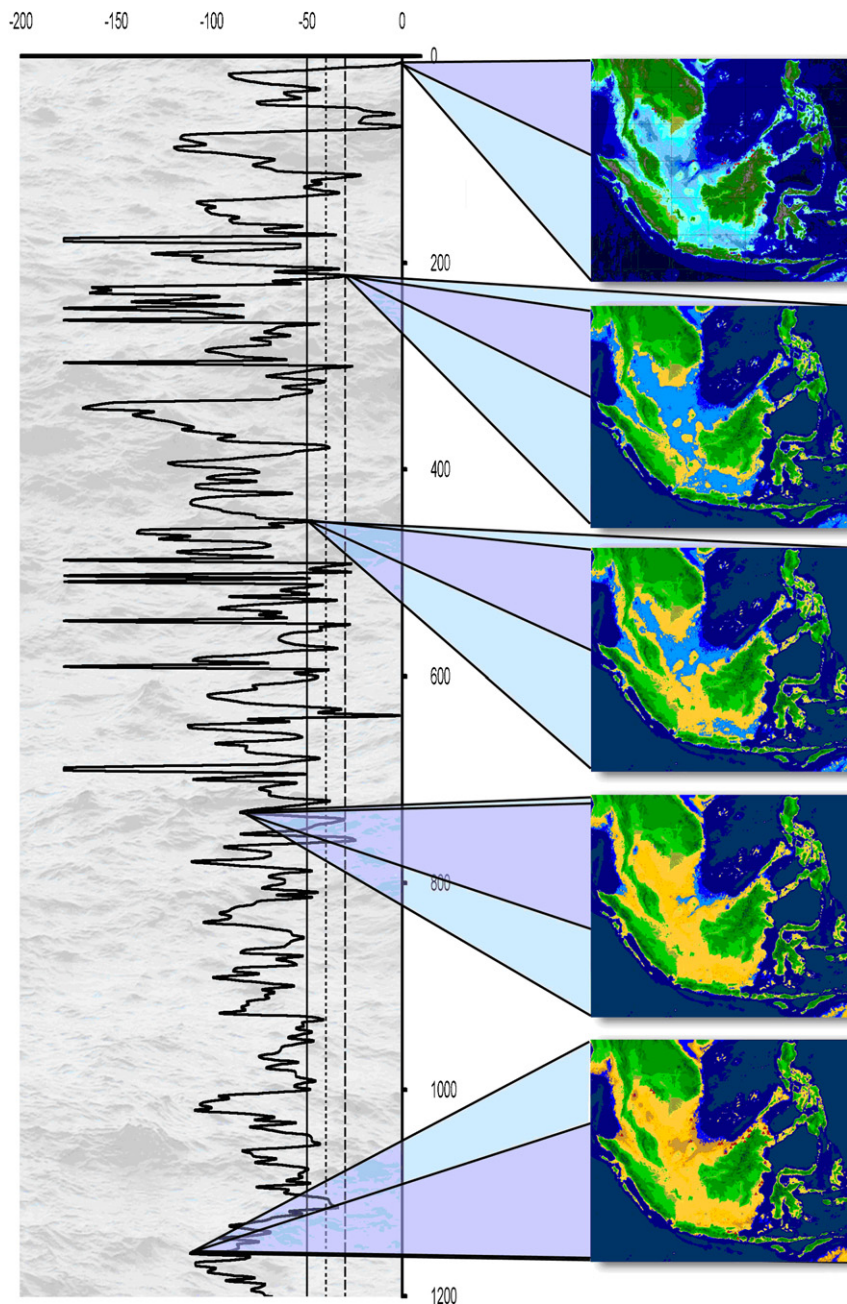
Fig. 2. Global sea level (*x*-axis) for the past 1.2 Ma (*y*-axis). The points at which the major Indonesian islands were connected are indicated by the vertical lines: Sumatra (dashed), Borneo (dotted) and Java (solid). Snapshots of Southeast Asia at selected relative sea levels are shown. Relative sea level calculated from Chappell and Shackleton (1986), relative ages calculated from Shackelton and Opdyke (1976), maps of Southeast Asia from the Field Museum of Natural History (Voris, 2000; Sathiamurthy and Voris, 2006) (from Louys, 2008: Fig. 3).

Fig. 2. Niveau général de la mer (axe *x*) pour les derniers 1,2 Ma (axe *y*). Les points où les îles majeures d'Indonésie étaient connectées sont indiqués par les lignes verticales : Sumatra (tirés), Bornéo (pointillés) et Java (trait plein). À droite, sont présentées des images de l'Asie du Sud-Est pour différents niveaux marins. Le niveau de la mer a été calculé à partir de Chappell et Shackleton (1986), les âges relatifs ont été estimés à partir de Shackelton et Opdyke (1976), et les cartes de l'Asie du Sud-Est ont été dessinées à partir des données du Field Museum of Natural History (Voris, 2000 ; Sathiamurthy et Voris, 2006) (extrait de Louys, 2008 : Fig. 3).

(Mudelsee and Schulz, 1997). The change increased the amplitude of cold and arid periods but reduced their frequency, and that increased amplitude locked up more ice and increased the fall in ocean levels compared with those of the Early Pleistocene. However, Fig. 2 also shows that even the lesser sea-level falls of the Early Pleistocene averaged around 70 m below the present, still more than sufficient to connect the islands of Sumatra, Java and Borneo and produce a considerable area of low-lying land (Bird et al., 2005: Fig. 4); (Voris, 2000).

3.2. Fauna of Southeast Asia during the Early and Middle Pleistocene

Early Pleistocene faunas from Sundaland are known almost exclusively from Java. The earliest recorded fossils from the island may date back to 3 Ma (Kramer et al., 2001), or even earlier, although dates between 2.0 and 2.7 Ma may be more realistic (see Meijaard, 2004 for a discussion on this). The Early Pleistocene faunas of Java, such as those recovered from the upper and lower Kali Glagah series, are characterised by proboscideans, hippopotamus, cervids and bovids. Chronological control of these faunas is often difficult to establish and the palaeobiology of the extinct species remains largely unstudied, although synecological (community-based) analyses of medium- and large-bodied mammals indicate the presence of savannahs and open woodland during this period (Louys and Meijaard, 2010).

As we have pointed out, the earliest evidence of *H. erectus* in Java is from Sangiran at ca. 1.6–1.02 Ma (Bettis et al., 2009). Thirteen mammal taxa can be identified from the deposits, and they include two species of proboscidean, rhino, hippo, bovids, cervids, suids and the giant hyaena, *Pachycrocuta* (Bouteaux et al., 2007). Dennell (2009) has pointed out that while the deposits of the Sangiran Formation and those of the overlying Bapang Formation represent respectively swampy estuarine and fluvial conditions, the hominin remains and perhaps those of several other species are likely to derive from upstream, based in large part on the discussion by Turner et al. (2002) on the taphonomic history of corpses in fluvial contexts. It is thus clear that environmental conditions during the deposition at Sangiran remains largely unchanged from earlier periods (Bettis et al., 2009; Bouteaux, 2005), that is characterised by riparian forests, savannahs and open woodlands. While some authors (Bettis et al., 2009; Sémah et al., 2010) contend that early hominins in the region would have become adapted, and perhaps restricted, to areas of denser forest during the Early Pleistocene, we suggest that the mosaic, savannah-like environments which predominated during the Early Pleistocene would have been ideal for early hominin subsistence.

Middle Pleistocene sites in Sundaland are again almost exclusively restricted to Java. Trinil, deposited during the beginning of the Middle Pleistocene, is perhaps the most well known of these. The fauna from Trinil includes a number of carnivores, bovids, cervids, a proboscidean and primates, and Louys and Meijaard (2010) suggested that it represents a habitat with significant open areas, but did not preclude the existence of some trees. This type of habitat would be congruent with glacial conditions, and thus lowered sea levels, and indeed Meijaard (2004) strongly argues for a connection between Java and the rest of Sundaland during this time. Van den Bergh et al. (2001) have argued for only very brief periods of connection between Java and the mainland prior to 800 ka, and clearly the timing and duration of connections remains to be established. The Kedung Brubus fauna, deposited after Trinil, demonstrates the invasion of a large number of mammalian species into Java, and includes mammals such as *Elephas* (elephant), *Rhinoceros unicornis* (Indian rhinoceros), *Manis palaeojavanica* (giant pangolin), *Tapirus indicus* (tapir), *Pachycrocuta brevirostris* (giant hyaena) and *Lutrogale palaeoleptonix* (otter) (Aimi and Aziz, 1985; Bandet et al., 1989; Van den Bergh et al., 2001). Environmental conditions during the deposition of the Kedung Brubus fauna indicate more closed (i.e. more forested) habitats than Trinil, although these are likely to be more representative of open woodlands and evergreen forests than rainforests (Louys and Meijaard, 2010).

Other potential Middle Pleistocene palaeontological collections from Sundaland include fauna from a site in the Kinta Valley, on the Malaysian peninsula. The age of this site is unresolved, and it could in fact date from the Late Pleistocene (Louys and Meijaard, 2010). Taxa recovered from this locality include proboscideans, cervids, bovids and suids (Medway, 1972). Unstratified proboscidean finds from Borneo could also date back to the Middle Pleistocene (Medway, 1972).

The Irrawaddy beds of Myanmar in the Indochinese subregion are most likely to be Early Pleistocene in age. The faunas found in these beds include several species of proboscidean, bovids, including a species of gazelle and antelope, two species of equid and a hippo, and a species of suid and rhinoceros (Colbert, 1943). These taxa indicate open environments; however they also represent both reworked and in situ finds. We also note the absence of any carnivores in this list. Middle Pleistocene sites are more abundant in Southeast Asia, and include the Mogok Caves in Myanmar (Colbert, 1943), Tam Hang in Laos (Bacon et al., 2008), Tham Khuyen, Tham Om and Tham Hai from Vietnam (Olsen and Ciochon, 1990), Phnom Loang in Cambodia (Beden and Guérin, 1973) and Tham Wiman Nakin, Thum Phra Khai Phet, and Kao Pah Nam in Thailand (Pope et al., 1981; Tougard, 2001). Fauna found at these sites include bovids, cervids, primates, carnivores including the giant panda and giant hyena, proboscideans, tapirs and rhinoceroses.

Louys and Meijaard (2010) have recently reviewed the palaeoenvironments of both the Sundaic and Indochinese subregions as indicated by the large-bodied mammals found in palaeontological sites. They suggest that Sundaland was dominated by a heterogeneous vegetation complex throughout the Early to Middle Pleistocene, and argue that their palaeoenvironmental reconstructions together with other palaeoecological evidence reviewed in the paper suggest that the fluctuation of glacial and interglacial cycles paralleled vegetation changes throughout the Pleistocene. They therefore conclude that habitats with evergreen forests, open woodland and extensive shrub and grasslands were the norm for much of the Pleistocene, and thus not restricted to the LGM, and that the dominance of rainforests in Southeast Asia has been a relatively rare and infrequent phenomenon. They also propose that heterogeneous environmental conditions present in Sundaland during the Early and Middle Pleistocene extended well into the Indochinese subregion, implying that occupation and dispersal in Southeast Asia during the Pleistocene would only have been restricted during interglacial periods when higher sea levels would have fragmented landmasses and habitats would have become more dominated by rainforest. Note that, the "mixed" vegetation category reconstructed for most Mid-

dle Pleistocene sites in Southeast Asia encompasses the definition of savannah (see below), albeit not exclusively.

4. Sundaland as a hominin refugium

Suggesting that Sundaland may have acted as refugium during the LGP, and by implication during previous episodes of lowered sea level, raises the obvious question of a refugium from what? What were the general conditions in Asia during glacial periods? Dennell (2009) has usefully summarised much of the evidence for changes in the climate of the region as a whole during the Pleistocene, and laid stress on the changes in the cyclical fluctuations of the glacial-interglacial cycle that occurred with the MPT, and in particular the increased length and intensity of cold and arid periods and the growth of deserts. Indeed, the increase in these conditions has led him to term the area from northeastern Africa across Asia and into North China during the latter part of the Middle Pleistocene through until the Last Interglacial "Aridistan" (Dennell, 2009: Fig. 7.20), in contrast with an earlier "Savannahstan" (next section). This shift in conditions would suggest that during the cold periods of the Middle and Late Pleistocene much of the area of central and western Asia was a rather inhospitable place for hominins, while the steppe-like conditions of China north of the barrier produced by the Qinling Mountains (Ferguson, 1993) would have been equally unattractive. This latter point is reinforced by the results reported for the Nihewan Basin by Ao et al. (2010) and Pei et al. (2009) to which we shall return in the next section. We suggest that only Southeast Asia would have provided an area of suitable conditions for the maintenance of long-term populations in Asia during the Middle Pleistocene. Clearly the increase in the size of that area afforded by the sea-level falls in Sundaland adds considerably to the extent of the likely refugium.

But what of conditions during the colder periods prior to the MPT in "Savannahstan"? Dennell (2009) argues that aridity occurred on a much smaller scale at this earlier time, with the differences between glacial and interglacial climates much more muted. In consequence, a larger area of Asia would have remained hospitable during the colder periods, while the area of increased land in Sundaland exposed by the lower amplitude falls in sea levels would have been much less. However, we should also bear in mind that technological developments and abilities of hominins were presumably less the further back in time we go, so that even less extreme conditions might have been rather taxing. There is also the point, well made by Dennell in his concluding remarks (Dennell, 2009: p. 476), that hominin settlement of Asia is always likely to have been constrained and rendered patchy by the need for what he terms the "fortunate coincidence" of stone, water and food prior to the development of long-distance exchange networks that only become obvious in the later stages of prehistory.

5. Preferred hominin palaeoenvironments during the Early and Middle Pleistocene?

Against this background can we offer any general inferences – or hazard a guess – about likely habitats preferred by early hominins, something that we could use as a baseline to assess how attractive or otherwise an area may have been? Dennell (2009) (Table 2.2) has pointed out that hominin localities in Africa prior to 2.5 Ma might be taken to indicate a preference for woodland, although this clearly reflects the history of discovery as much as anything else and finds in Chad (Brunet et al., 1996; Zazzo et al., 2000) and Bouri (Asfaw et al., 1999; de Heinzelin et al., 1999) now show an ability to survive in open savannah grasslands.

After 2.5 Ma, it is broadly clear that the development of the global cooling trend that led to the glacial-interglacial cycles produced essentially more arid and seasonal conditions, exemplified in Africa but also seen across continents (Fernández and Vrba, 2006; Turner, 1995, 1999; Vrba, 1995, 1999). Dennell (2009) (pp. 33–4) has pointed out that the development of more open landscapes has been generally seen as a factor behind the appearance of *H. erectus* in eastern Africa as a species able to exploit grasslands, and although he mentions a number of caveats to that interpretation Dennell and Roebroeks (2005) had already suggested the term "Savannahstan" as a way of stressing the significant geographic spread of such Late Pliocene and Early Pleistocene habitats from North Africa across into central Asia. However it is worth stressing that savannahs are really tropical grasslands and the term should not be confused with that of grasslands. Savannahs can be defined as landscapes with a continuous grass layer and some trees providing an unclosed canopy cover, with strong alternating wet and dry seasons in tropical and subtropical systems (Scholes and Archer, 1997). Outside of the warmth of the tropics the temperate grasslands may mimic features of savannahs, with grazing ungulates, but the grasses are shorter and the variety of trees – especially drought-resistant forms – reduced (Cox and Moore, 1993); indeed the map of Asian grasslands at 3.0 Ma reproduced by Dennell (2009) (Fig. 3.25) clearly shows an area of "savannah, grassland, steppe". Thus, although earliest hominin dispersals outside of Africa can hardly have avoided crossing and therefore surviving in grassland areas, a preference for savannahs does not automatically translate into a preference for all grasslands, especially in terms of ability to sustain a population in the face of harsher conditions outside the tropics.

The definition of grassland versus the more restricted term savannah lies at the heart of the argument in the paper by Ao et al. (2010), who suggest that palaeoenvironmental evidence from the Nihewan Basin of northern China indicates intensified aridification and cooling leading to reduced tree cover and an increase in what they term open, savannah grasslands. They go on to suggest that the archaeological record from the area can thus be taken to indicate Early Pleistocene dispersal of savannah-adapted hominins into that region. However, the grasslands developed there would seem better characterised as temperate grasslands or indeed steppe rather than savannahs, and it is not clear to us that the archaeological and hominin fossil record from the region supports the inference of a sustained and flourishing population there as some authors propose. We note that the fauna from the Nihewan basin also suggests a grassland or steppe environment (Keates, 2010). Although they avoid use of the term savannah, we

argue that the same point can be made in response to the interpretation offered by Pei et al. (2009) for hominin habitats at Donggutuo in the Nihewan Basin during the Early Pleistocene. The latter authors do not argue for continuous occupation, but do conclude that conditions were more benign than we would interpret them to be, with reconstructed average annual temperatures often below, and rarely above, the 7.5 °C of the present day. By way of comparison, we may note that average present-day annual temperatures for the United Kingdom range between 7.0 and 11.0 (Metoffice, 2010), with the highest being in England and in coastal areas, and the averages conceal some often savage winter temperatures that have to be survivable if continuous occupation is to be achieved. Unfortunately, the figures for annual temperature in the Nihewan Basin include no indications of associated errors or temperature ranges, but at the very least it seems to us questionable whether hominins at that time could sustain long-term populations in northern China in such circumstances, since nothing in any savannah-adapted background would seem to have equipped them to survive the cold conditions that would be found in such regions during the colder parts of the year. One might characterise occupation of the Nihewan Basin as a steppe too far for long-term success.

6. Discussion and conclusion

What we have attempted to show here is the potential of Southeast Asia, and in particular the increased land area represented by Sundaland, to act as a refugium for savannah-adapted species, and particularly hominins, during the periods of lowered sea level and environmental changes that characterised so much of the Pleistocene. As Bird et al. (2005) stressed, while precise details of vegetation cover are difficult to reconstruct in the area now covered by seas the presence of open vegetation on sandy areas of exposed land seems very likely, based on the differing lines of evidence that can be brought to bear for the LGM. Louys and Meijaard (2010) have extended this argument to suggest that habitats with open woodlands and grasslands were present during much of the Pleistocene.

For hominins occupying such areas, elements of the fauna such as cervids, bovids and probably suids would seem to have offered an attractive range of resources, as discussed in some detail by Louys et al. (2007). The detailed archaeological evidence for subsistence activities – and the lithic and possible non-lithic tool kit involved – we leave for others to decipher and interpret, but it seems clear that the known range of Southeast Asian stone tools alone would have more than equipped them to deal with medium-sized ungulates, smaller animals and the likely (although unknown) range of other non-animal resources available to them (Dennell, 2009). We therefore believe that the area of Sundaland can be added to the list of likely Asian refugia summarised by Dennell (2009) (pp. 475–6), although further work will be needed to decide whether sufficient quantities of stone were locally available to satisfy the trio of co-incident requirements suggested by him. In particular, we stress the favourable conditions for hominins in Southeast Asia during Middle Pleistocene glacials, condi-

tions otherwise largely absent from much of Asia during this period.

Although the current consensus view is that northern China experienced a continuous level of occupation during the Early and Middle Pleistocene (Ciochon and Bettis, 2009; Keates, 2010), the result of supposedly benign conditions such as those inferred by Pei et al. (2009) and Ao et al. (2010), we propose that a different scenario may be more plausible for this region. Following on from the "source and sink" population model for Middle Pleistocene Europe put forward by Dennell et al. (2010), we agree that such a model may indeed have the parallels in eastern and southeastern Asia that they suggested. In particular, during the extreme environmental conditions present during the Middle Pleistocene glacials, we propose that northern China may have acted as a population "sink", in much the same way as northern Europe did. Certainly southern, more warm-adapted mammals, such as *Hystrix*, *Palaeoloxodon* and *Bubalus,* show repeated incursions and excursions into and out of northern China during the Pleistocene, as they did in northern Europe, most likely in response to shifting climatic conditions (Tong, 2006, 2007). In much the same way, we propose local hominin population extinctions or contractions would have been counterbalanced by northern re-incursions from Southeast Asia, where environmental conditions, even during the LGM continued to be favourable for hominin populations to flourish.

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