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Ice Ages and the mitochondrial DNA chronology of human dispersals: a review

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Modern DNA, in particular maternally inherited mitochondrial DNA (mtDNA), is now routinely used to trace ancient human migration routes and to obtain absolute dates for genetic prehistory. The errors on absolute genetic dates are often large (50% or more) and depend partly on the inherent evolutionary signal in the DNA data, and partly on our imperfect knowledge of the DNA mutation rate. Despite their imprecision, the genetic dates do provide an independent, consistent and global chronology linking living humans with their ancestors. Combining this chronology with archaeological and climatological data, most of our own mtDNA studies during the past decade strongly imply a major role for palaeoclimate in determining conditions for prehistoric migrations and demographic expansions. This paper summarizes our interpretation of the genetic findings, covering the initial and modest spread of humans within Africa more than 100 ka, the striking re-expansion within Africa 60–80 ka, leading ultimately to the out-of-Africa migration of a single, small group which settled in Australia, Eurasia and America during windows of opportunity at least partly dictated by fluctuations in sea-levels and climatic conditions.

Keywords: female; migration; prehistory; genetics; palaeoclimate; demography

1. INTRODUCTION

Human mtDNA is the female equivalent of a surname: it passes down from mother to offspring in every generation, and the more offspring a mother and her female descendants produce, the more common her mtDNA type will become. Surnames are not immutable across the centuries (e.g. Forester has changed to Forster and can mutate to Foster even in the timespan of a conference), nor are mtDNA types. A natural mutation modifying the mtDNA in the oocytes of one woman will henceforth characterize her filial descendants. These simple fundamentals, unilineal inheritance and occasional mutation, are sufficient to allow geneticists to reconstruct *ancient* genetic prehistory from *extant* mtDNA types. How is this achieved? To visualize the link between prehistoric events and current DNA variation, the reader may consider a woman living for example 30 ka. This woman, located in space and time, would have had a particular mtDNA type, which is indicated by a small circle in figure 1.

(a) *Demographic expansion analysis*

Let us also imagine that this woman enjoyed favourable reproductive conditions (for example, a beneficial climate phase, colonization of new and unexploited territory, discovery of food production, high social status, an advantageous mutation, etc.), in which case her mtDNA type would have increased in frequency compared with that of most of her contemporaries elsewhere in the world. The frequency of her type (symbolized by the enlarged circle in figure 1) would increase especially if the favourable conditions persisted across several generations of her female descendants. After thousands of years, some descendants carrying this successful mtDNA would inevitably acquire a mutation (indicated by the starlike branches in the figure), and the original type would become less and less common, much like radiocarbon decay. At this stage it is no longer the original type, but the whole starlike cluster that testifies to the favourable conditions thousands of years earlier. After tens of thousands of years of mutation, the branches become longer and the original type can become extinct, or at least so infrequent that it is not likely to be sampled (see final cluster in figure 1). Also, mutations may occur at the same DNA position in different individuals, making it difficult to decide from which particular ancestral type a descendant type is derived. If unresolvable, these ambiguities need to be identified and displayed as reticulations, which can be simple squares or parallelograms as in the final phase in figure 1, or rectangles, cubes and higher-dimensional structures in more complex data. Our phylogenetic algorithms were developed to assist in reconstructing extinct DNA sequences and tracing the true tree among the network of reticulations (Bandelt *et al.* 1995). Turning to the quantification of the prehistoric expansion, the success of the initial increase ideally can be estimated by the relative frequency of the entire descendant cluster today. However, a descendant type might become exposed to favourable breeding conditions and become a successful type in its own right, (cf. the large peripheral circle in figure 1, final cluster) without any causal connection to the original expansion success of the cluster. A phylogenetic star contraction algorithm can be used as an *ad hoc* method to take this factor into account (Forster *et al.* 2001).

One contribution of 14 to a Discussion Meeting Issue 'The evolutionary legacy of the Ice Ages'.

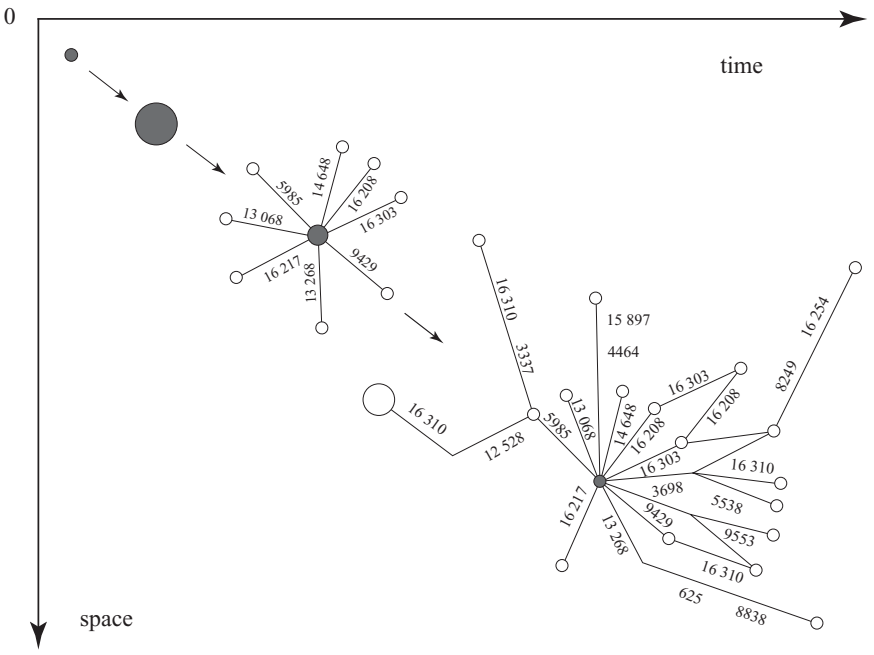

Figure 1. Starlike cluster of mtDNA types resulting from a successful prehistoric maternal lineage. The cluster at the bottom right is one of the major Papuan clusters today. The original phase of breeding success (top left) occurred *ca*. 30 ka, probably after the arrival in Papua New Guinea. Numbers refer to positions (1–16 569) on the mtDNA at which mutations have occurred.

Incidentally, the phylogenetic methods mentioned here are not restricted to DNA applications but have also been applied to the reconstruction of extinct amino acid sequences (Bandelt *et al.* 1999) and extinct languages (Forster *et al.* 1998; Forster & Toth 2003).

(b) *Geographical founder analysis*

Starlike clusters in the evolutionary tree are in themselves interesting for dating and geographically localizing prehistoric demographic increase of an mtDNA type (which may have increased relative to others because it lived at a time and place of climatic improvement, because it underwent an advantageous mutation, etc.), but they are not necessarily informative for counting and dating mtDNA types arriving in new territories. This is the task of founder analysis (e.g. Torroni *et al.* 1993*a*,*b*; Forster *et al.* 1996; Richards *et al.* 2000), where an ancestral node (whether living, or extinct and phylogenetically reconstructed) shared between a source continent (e.g. Asia) and a destination continent (America) is identified as a founder mtDNA type having entered the continent. The age of the founder mtDNA type would yield a time estimate for its arrival in the continent. In practice, several mtDNA founders (sometimes arriving at quite different times) are found in most continents. Often, founder types show the starlike signature of expansion (e.g. types A, B, C, and D in the Americas), which indicates that the discovery of a new continent led to noticeably increased survival of offspring. In other instances, such as with putative European U founder types, the starlike signal is much less evident (Richards *et al.* 2000). This may be due to the greater time-depths involved, during which much of the ancient lineage variation has been lost, or indeed there may have been no significant increase in the lineage at the time of entry into Europe, which was populated by Neanderthals until 30 ka.

(c) *Genetic dating*

Once the tree is reconstructed and an ancestral mtDNA type of interest (for example, an expansion type, a founder type or a disease type) is identified, the task of dating the ancestors can begin. The age of the cluster is obtained by equating the average length of the branches with elapsed time, measured in number of mutations (Morral *et al.* 1994). A standard error on each date can be calculated (Saillard *et al.* 2000); this error reflects the number of branches available for estimation (which in turn is dictated by the initial number of descendants generated, and by the extent of subsequent lineage extinction during the vagaries of evolution) and the branching structure (for example, five independent branches with one descendant each yield a more reliable time estimate than one branch with five descendants). 'Mutational' time can then be converted to absolute time by multiplying it with the mutation rate, if the DNA mutation rate is known (Forster *et al.* 1996). The mutation rate is the Achilles' heel for any DNA chronology. Whereas relative genetic dates and their relative standard errors (expressed in mutations) are straightforward to determine, their conversion to accurate absolute dates (expressed in years) depends entirely on the estimated mtDNA mutation rate. Some efforts, albeit unsystematic, have been undertaken to determine mtDNA mutation rates using three different methods.

(i) For fossil-based calibrations, species splits identified and physically dated in fossil phylogenies are compared with equivalent splits in the DNA tree of the living species, yielding a mutation rate for the DNA. The inherent drawback of any fossil calibration is the question of whether mutation rates have remained constant since the split.
(ii) Pedigree calibrations screen members of a family for new mutations. However, it is quite likely that DNA

mismatches are due to undisclosed adoptions, or unfaithful marriage partners. Without maternity testing in our own mtDNA pedigree study of 991 individuals (Forster *et al.* 2002), we would have 'found' 25 full mutations instead of none. Another problem in pedigree studies, specific to mtDNA, is the distinction between 'full' homoplasmic mutations and initial 'partial' or heteroplasmic mutations (Bendall *et al.* 1997). Such problems can lead to a considerable error, implying for example an implausible age of only 6 kyr for the mtDNA ancestor of all modern humans (Parsons *et al.* 1997). It is often thought that mutational hotspots explain this discrepancy, but that is an arithmetical faux-pas (Sigurðardóttir *et al.* 2000).

(iii) In archaeological calibrations, the archaeological record ideally is dense enough to provide benchmarks for initial settlement or resettlement of a defined area. If these settlers have left at least some surviving allele lineages until today, then the diversity of each of these founding lineages can be equated separately with the elapsed time since the archaeological benchmark. We have used this approach in Alaska and in the Cook Islands (Forster *et al.* 1996; Macaulay *et al.* 1997). It would fail if founding lineages were replaced completely by later immigrants. Another potential problem is the demographic history of the founding alleles: if a marked allele increase did not occur soon after the benchmark, then there is a paucity of lineages and thus of independent estimators to the founder type, generating a large standard error in the calibration, as we ruefully noted in Saillard *et al.* (2000). Nevertheless, the archaeologically based mutation rate we obtained (Forster *et al.* 1996, 2001) is similar to the value obtained from the independent calibration of Horai *et al.* (1995) using primate mtDNA, and serves as a reference value for this paper. Any future improved calibration for the mutation rate can directly be multiplied with the values presented throughout this paper to obtain improved absolute time estimates. For example, if the out-of-Africa founder date were doubled from 55 to 110 ka (e.g. to accommodate the Skhul/Qafzeh remains as the ancestors of today's Eurasians), then the mtDNA date for the migration into the Americas would correspondingly increase from 25 to 50 ka. Likewise, a new calibration (Mishmar *et al.* 2003) assuming a human–chimpanzee split 6.5 Ma yields mtDNA age estimates that are in general somewhat older than those proposed here.

(d) *Nomenclature*

When referring to branches (also known as 'clades' or 'haplogroups') in the mtDNA tree, the mtDNA phylogenetic nomenclature initiated by Torroni *et al.* (1993*b*) and updated by Macaulay *et al.* (1999) and Richards & Macaulay (2000) is used. Each branch consists of several mtDNA types, either extinct or living. The types discussed in this paper are named after the branches in which they lie. Only a selection of mtDNA types is shown on the maps of figure 2, for space reasons.

2. RESULTS: THE HUMAN MITOCHONDRIAL DNA CHRONOLOGY

(a) *Before modern humans: 2.5–0.2 Ma*

The rise of the genus *Homo* at *ca*. 2.5 Ma in Africa is characterized by the first significant increase in brain size since the split from the apes more than 5 Ma, and by the widespread use of stone tools. It may well be these advances that enabled *Homo* to spread out of Africa, unlike his Australopithecine predecessors, leaving a fossil trail in Dmanisi, Georgia (1.75 Myr old (Vekua *et al.* 2002)) and in Java (more than 1.5 Myr old (Larick *et al.* 2001)). Between this early migration and the migration of modern humans out of Africa less than 100 ka, lies the date of the human–Neanderthal split *ca*. 0.5 Ma calculated from ancient Neanderthal mtDNA (Krings *et al.* 1997). It should be noted that this date times the split between the modern human and Neanderthal *mtDNA lineages*. It would time the *species* split only if just one mtDNA type were present in the common ancestral population. Assuming such monomorphy as a rough approximation of the truth (indeed, modern human mtDNA as well as the few Neanderthal mtDNA sequences obtained so far have relatively limited mtDNA diversity), the 0.5 Ma date would place the Neanderthal–human split at the time of *Homo heidelbergensis* (Lahr & Foley 1998).

(b) *Rise of* Homo sapiens*: 200–80 ka*

The maternal lineages of all living humans coalesce in 'mitochondrial Eve', born in South or East Africa more than 130 ka. The earliest lineages, known as L1 types (Watson *et al.* 1997), are restricted to Africa and, at frequencies of less than 1%, immediately adjacent Arabian and Mediterranean areas. In the fossil record, this period also marks the transition to anatomically modern humans (Day & Stringer 1982; Bräuer 1989; White *et al.* 2003), in the remains of Herto and Omo (East Africa), Klasies River Mouth (South Africa) and Skhul/Qafzeh (Israel). The fact that today's mtDNA lineages ultimately coalesce in one woman is not remarkable; all genes necessarily coalesce at some point in the past. But it is interesting that rather few mtDNA lineages (probably between one and eight distinct mtDNA types, see for example fig. 2 of Salas *et al.* (2002)) have survived from the time of the fossil archaic–modern transition, possibly suggesting that the breeding female population size at the birth of our species was modest. The mtDNA tree for several of these earliest lineages shows strong geographical structure today: clades L1d and L1k occur only in southern Africa, particularly in the Khoisan (Bushmen), clade L1c is found only in central and western Africans, particularly in the Biaka (West Pygmies), and L1e and L1f are characteristic for a proportion of east Africans. This pattern has been interpreted (Watson *et al.* 1997) as the surviving footprints of an early spread across Africa, dated between the coalescent age of 130 ka or more, and the onset of the major African re-expansion 60–80 ka. This early wave across Africa coincides with the emergence of modern human behaviour: the first evidence for a marine diet is documented at *ca*. 125 ka in east Africa (reviewed by Stringer 2000) and geometric notches on bone (rudimentary art?) dated to 70 ka are found at Blombos Cave in South Africa (Henshilwood *et al.* 2002).

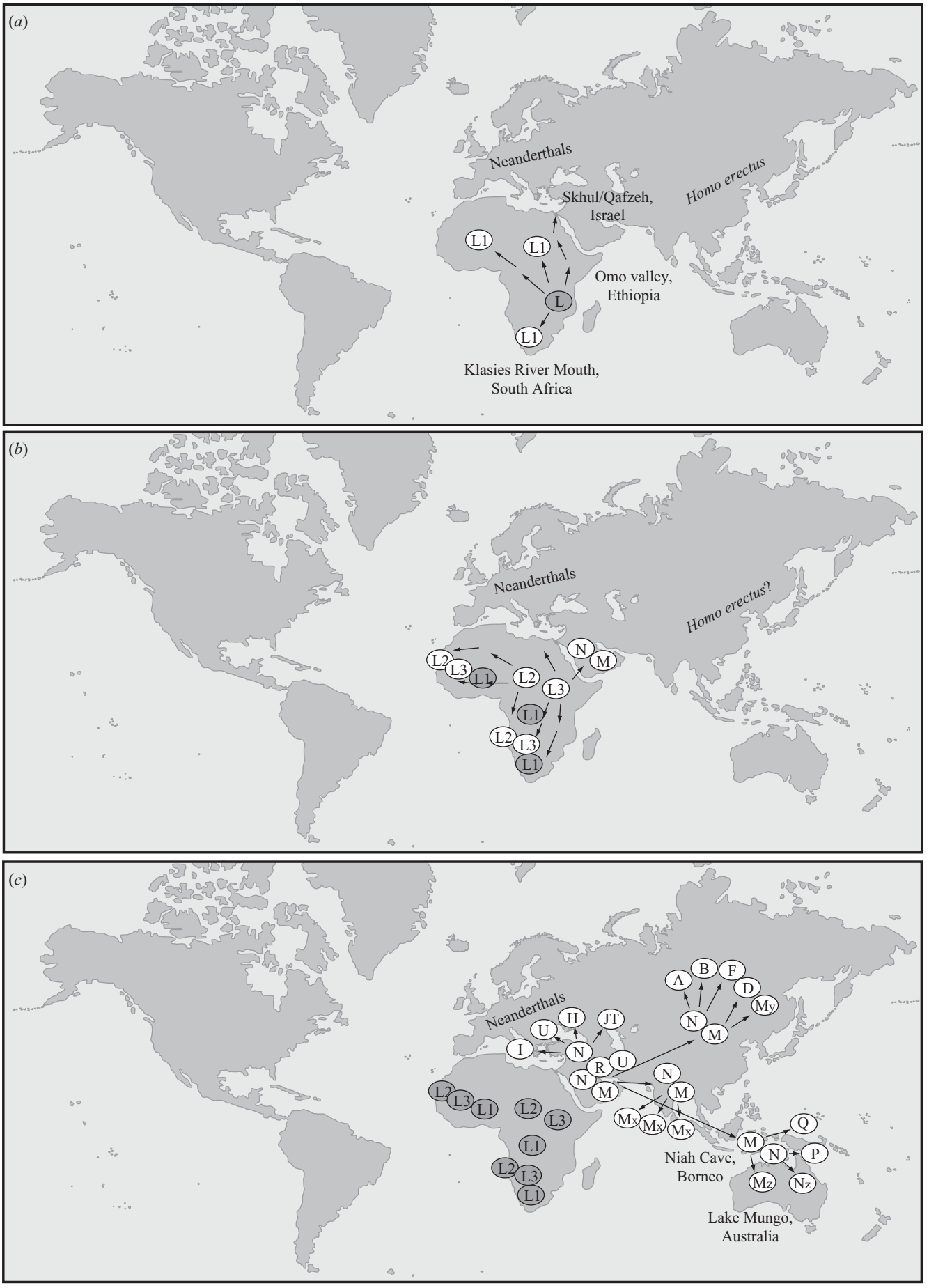

Figure 2 (*a–c*). Evolution, expansion and migration of human mtDNA types across the world: (*a*) 200–100 ka; (*b*) 80–60 ka; (*c*) 60–30 ka.

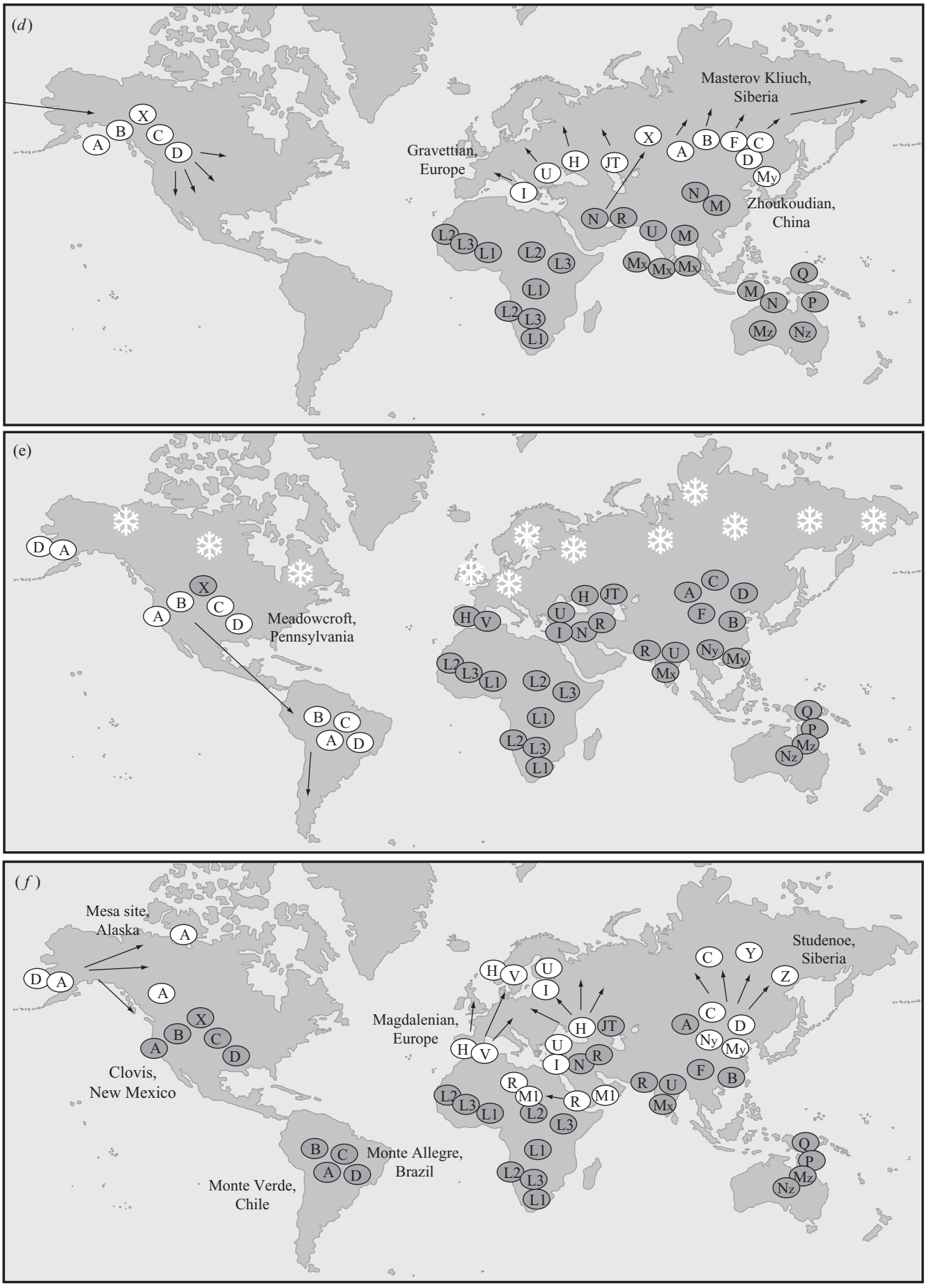

Figure 2 (*d–f*). (*d*) 30–20 ka; (*e*) 20–15 ka; (*f*) 15–2 ka.

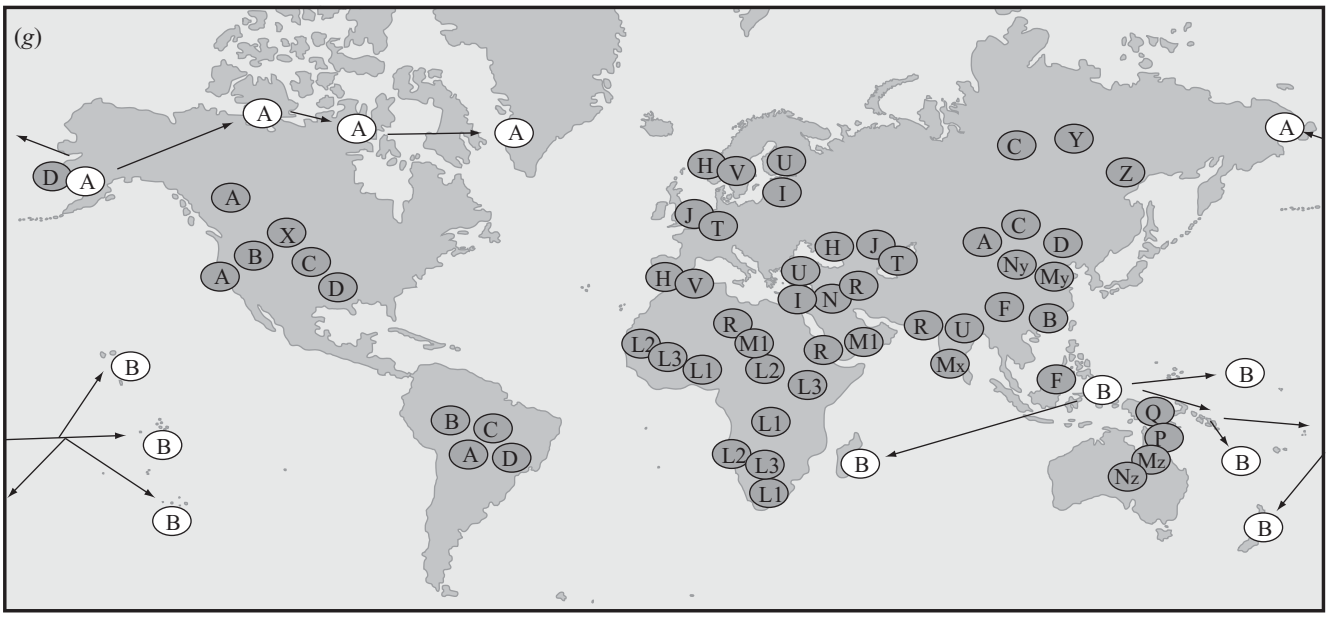

Figure 2 (*g*). Less than 2 ka.

(c) *The African re-expansion: 80–60 ka*

About 60–80 ka, a renewed expansion repopulated Africa with L2 and L3 mtDNA types (Watson *et al.* 1997), whereas the original L1 types eventually became a minority almost everywhere, except in the ancestors of Khoisan (Bushmen) and Biaka (West Pygmies). The African re-expansion led to the first (and only) successful modern human migration out of Africa by 54 ± 8 ka (Forster *et al.* 2001). All non-Africans today are descended from an L3 type, which gave rise to two founder types outside Africa, M and N. The group leaving Africa must have been very small, given that only that L3 type survived. By comparison, no modern African tribe contains only one mtDNA type, and the same is true of non-African tribes, with the arguable exception of some Polynesian islanders. Two possible routes out of Africa have been proposed: down the Nile and then by land across the Sinai Peninsula, or by sea across the Bab el Mandab Strait to Yemen. The Red Sea crossing may have been easier 55–80 ka than today and has received some attention by anthropologists (Lahr & Foley 1994), and indeed has recently been argued as the sole exit route (Oppenheimer 2003). A minor factor in assessing the likelihood of an exodus through the Red Sea is the tectonic movement of the Arabian plate away from Africa at the rate of *ca*. 18 mm per year (Sella *et al.* 2002), which means that the distance across the mouth of the Red Sea would have been 17 km rather than the 18 km of today. A more important factor influencing the width at the time would have been the sea-level (the Bab el Mandab Strait is only 137 m deep), which reached a local minimum at 60–65 ka (Siddall *et al.* 2003). It is not yet clear whether M and N arose in Africa just before the exodus (M and N are found in parts of Africa), or just after it (as indicated by the close relationship and similar ages for M and N (Forster *et al.* 2001)) or even further east in India (as indicated by the high diversity of M there (Kivisild *et al.* 2003)). An ancient presence of the current M types in Africa is debatable because they are similar to an Indian M type (Maca-Meyer *et al.* 2001) and because M in Africa is mostly restricted to Afro-Asiatic-speaking areas, which may indicate a reverse migration in the past 20 kyr or so.

(d) *Coexistence with Neanderthals: 60–30 ka*

The out-of-Africa migrants soon split along different routes, the tropical coastal route to Australia and Papua New Guinea being the fastest. Modern human remains at Niah Cave (Barker *et al.* 2002) and at Lake Mungo (Bowler *et al.* 2003) are dated to *ca*. 40 ka, in agreement with mtDNA dates (Forster *et al.* 2001). The northern Eurasian migrants would have encountered harsher conditions, including perhaps the terrain, Neanderthals, seasons, and a sharply fluctuating climate during the earlier stages of the last Ice Age. In the period 60–30 ka, pioneering Eurasians gained tenuous footholds in the continents of the Old World, and their M and N types mutated into descendant founder types, the mtDNA 'haplogroups', which are still continent- or region-specific today. It is notable that Europeans today do not have M types, possibly owing to early loss in the initial founder conditions. Although the detailed dates and geographical routes were not known at the time, the stalled spread out of Africa and the formation of regional founder populations had already been anticipated and dubbed the 'Weak Garden of Eden' hypothesis (Harpending *et al.* 1993), as opposed to the 'Strong Garden of Eden' hypothesis, the nickname for an uninterrupted expansion process out of Africa.

The genetic date of 54 ± 8 ka, at the latest, for the human migration out of Africa implies that *Homo sapiens* must have encountered Neanderthals in the Near East and/or Europe, because the most recent Neanderthal fossils are dated at *ca*. 30 radiocarbon kyr ago in Europe. Even a combined sample of a thousand modern European mtDNAs (Torroni *et al.* 1994; Richards *et al.* 1996) did not contain a single mtDNA type which is sufficiently divergent to derive plausibly from a Neanderthal or from other pre-modern species, and this conclusion has not changed using the current database containing over 10 000 European samples (Röhl *et al.* 2001). So the interesting question arises as to whether these encounters were

brief and incompatible with life for Neanderthals, or whether there was coexistence, possibly for many millennia. Much has been made of the proximity of Middle Eastern 'modern' crania in Skhul/Qafzeh dated at *ca*. 100 ka, to neighbouring Neanderthal fossils in Tabun dated at *ca*. 50 ka (reviewed in Jordan 1999). But the Skhul/Qafzeh fossils may not be relevant to the question of Neanderthal/modern human coexistence, because the genetic out-of-Africa date indicates that the Skhul/Qafzeh individuals were an evolutionary dead-end, in agreement with their rugged morphology, which includes pronounced brow-ridges. Likewise in Europe, the raw archaeological dates suggest coexistence between moderns and Neanderthals during the initial period (45–30 ka) of the Aurignacian culture, whereas the mtDNA record finds only some evidence for human presence before the appearance of the Gravettian culture at 30 ka (Richards *et al.* 2000). The mtDNA may suggest therefore that archaic humans such as Neanderthals survived contemporaneously with modern humans for a few thousand years at best, and only because the population density of moderns was initially low.

(e) *Consolidation outside Africa: 30–20 ka*

The climatic oscillations of the last Ice Age stabilized at 30 ka (the transition from glacial stage 3 to stage 2), local *Homo sapiens* populations grew strongly, evidenced by starlike mtDNA clusters (Forster *et al.* 2001), expanded into Europe and northern Asia, and drove *Homo neanderthalensis* to extinction. Our ancestors appear to have replaced all pre-existing Eurasian *Homo erectus* or *Homo neanderthalensis* mtDNA types, given that no divergent (i.e. Neanderthal) mtDNA types have been found in any survey of modern humans (see above). The demographic expansion signal in the mtDNA, dated to 30 ka, may incidentally coincide with archaeological evidence for modern human presence increasing at this time (Gravettian culture in Europe, Zhoukoudian fossils in China). Another major result of this expansion was the settlement of the Americas. About 25 ka the sea-level was 120 m lower than it is today, and America and Asia were connected by the wide land bridge of Beringia, now submerged. Beringia is known to have supported large mammals (Zazula *et al.* 2003). According to mtDNA founder analysis (Forster *et al.* 1996), a small group of Asians from northern Siberia moved into the Americas, whose characteristic mtDNA types A, B, C and D are found today in tribes across the Americas (Merriwether *et al.* 1994): all of them speakers of an ancestral Amerind language according to the late Joseph Greenberg and colleagues (1986). In other words, linguists are capable, in principle, of reconstructing Ice Age language relationships.

(f) *Retreat during the glacial maximum: 20–15 ka*

About 20 ka the glacial maximum was attained, forcing humans to retreat southwards. Based on mtDNA star analysis, we have proposed glacial refuges in Beringia and Iberia, where survivors were narrowed to A/D and H/V types respectively. The migrant group that entered America just before the glacial maximum was subsequently split into two areas by the glacial conditions. One group survived in Beringia (losing the original B, C and X types) and their descendants would later become the Eskimo-Aleut and Dene-speaking peoples. The other, larger group were the Amerinds who proceeded to colonize the Americas, arriving in Meadowcroft (Pennsylvania) by *ca*. 18 000 calendar years ago (Adovasio 1993), and in Monte Verde (Chile) by 14 000 calendar years ago (Dillehay & Collins 1988). If we accept our 20–25 ka mtDNA date for the entry into Alaska, then the minimal southward migration speed of Amerinds from Beringia to Chile would amount to *ca*. 1000 m per year. This rate seems plausible as it is the same order of magnitude as the minimal eastward migration speed of 300 m per year from Africa to east Asia, assuming a mean value of 31 ka as a lower limit for the arrival in east Asia of the African founders (a distance of *ca*. 8000 km) and 54 ka as the starting date. Similarly, the arrival of the east African L2/L3 expansion (60 kyr old) in west Africa by 30 ka (Watson *et al.* 1997) implies a westward migration speed of at least 200 m per year. An entry into America 20–25 ka, and the subsequent arrival date in South America, is therefore consistent with migration rates determined for other continents.

(g) *Postglacial recolonization: 15–20 ka*

The Bølling/Allerød warm phases (15–13 ka) caused a partial glacial retreat and a resettlement of northern latitudes by humans. The resulting reduced diversity in the north is evidenced today by the striking predominance of A (nearly 100%) in Eskimo-Aleut and Na Dene speakers, by the very high percentages (50–60%) of H and V in northwestern Europeans, which appears to have arisen from a founder effect from the Iberian peninsula or southern France (Torroni *et al.* 1998, 2001) and by the complete loss of the minor type X and even the major type B in northern Asia (Shields *et al.* 1993). Distinctive archaeological cultures testifying to the re-expansion after the LGM include the Magdalenian culture in Europe and the Clovis culture in North America. Furthermore, linguistic signals for the post-LGM expansion have been proposed for Europe (reviewed by Hamel *et al.* 2002).

The last phase (the Younger Dryas phase) of the Ice Age ended suddenly 11.4 ka (Björck *et al.* 1996), within just a decade (Alley *et al.* 1993). The ensuing climatic stability, unprecedented in the last 100 kyr, allowed the development of agriculture, with which major proto-languages may have spread, e.g. proto-Indo-European in Europe (Renfrew 1987; Forster & Toth 2003). Whether the spread of farming was also accompanied by a measurable immigration of mtDNA types is the subject of current research (Richards *et al.* 1996, 2000; Caramelli *et al.* 2003).

(h) *The final Holocene dispersals: less than 2 ka*

Remarkable settlement stories in the recent Holocene include the peopling of Madagascar after *ca*. 2 ka (Dewar & Wright 1993) and the Pacific (by 1 ka (Green 1991; Spriggs & Anderson 1993)) by seafaring Austronesians (Richards *et al.* 1998), and the re-colonization of Greenland by neo-Eskimos setting out from Alaska 2 ka. The neo-Eskimo migration is perhaps the most recent example of glacial cycles significantly shaping human mtDNA variation: palaeoclimatological research on Greenland ice cores has uncovered a 2600 year cooling cycle active throughout the Holocene (O'Brien *et al.*

1995). The last cooling event was the Little Ice Age from AD 1350–AD 1850, which extinguished the Viking colonies in Greenland after five centuries of flourishing existence (Lynnerup 1998). In contrast to the Vikings, the contemporary Greenlandic Eskimo inhabitants survived this latest cycle relatively unscathed, but their palaeo-Eskimo predecessors had been less fortunate in the previous cooling event. According to a founder analysis of Siberian, Alaskan and Greenlandic Eskimo mtDNA, all current Eskimos, whether Yupik or Inuit speakers, derive from an Alaskan homeland as recently as 2 ka (Saillard *et al.* 2000). This genetic date implies that the first Greenlandic palaeo-Eskimo culture, radiocarbon-dated to 4.5 ka, succumbed to the subsequent cooling event 2.9 ka, in agreement with the archaeological record (Fitzhugh 1984).

3. CONCLUSIONS

This synthesis argues that Ice Age conditions in the past 100 kyr have substantially determined times and routes for prehistoric humans settling the world. An early exodus out of Africa evidenced by the remains at Skhul and Qafzeh 100 ka has not left any descendants in today's Eurasian mtDNA pool. By contrast, the successful exodus of women carrying M and N mtDNA at *ca*. 60 ka, ancestral to all non-African mtDNA today, may coincide with the unprecedented low sea-levels at that time, probably opening a route across the Red Sea to Yemen. Whereas proto-Australian and proto-Papuan mtDNA may have taken advantage of the southern dispersal route along the borders of the Indian Ocean to arrive at their destinations relatively rapidly (i.e. by 46 ka), more difficult conditions in northern latitudes would have inhibited colonization there by the newcomers, giving Neanderthals a few millennia of respite before becoming extinct. At about the time of the transition between glacial stages 2 and 3, significant expansions take place in Europe (witnessed by the Gravettian culture 30 ka and the disappearance of Neanderthals) and northern Asia (witnessed by the Zhoukoudian finds), the latter ultimately leading to the settlement of the Americas just before the LGM 20 ka, when the crossing to North America was facilitated by the lowered sea-level, turning Beringia into a land bridge. This glacial maximum would have subsequently isolated most of America from its Beringian and Asian source area, and depopulated northern latitudes across the world. The end of the Ice Age enabled repopulation of northern Europe, Asia and America from continental glacial refugia, leaving a geographical signature in mtDNA and nuclear genes which is evident today. This overall account diminishes the genetic role of Holocene movements, such as the spread of Neolithic farmers, and historical or mythological migrations by Phoenicians, Greeks and others. In terms of genetic impact, only movements in much more recent colonial and postcolonial times can compare with the Ice-Age movements of people 60–11 ka.

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APPENDIX A

(a) *Notes arising from the conference discussion*

The mtDNA history recounted here was reconstructed since 1992 with teams of collaborators, and is only one view among several in the field. This is because a consensus on methodological questions has not yet been reached. In particular, the lineage approach described in § 1 is equated by some with the conceptually different population approach (the differing aims of the two are discussed in Forster *et al.* 2001) and the role of data errors in undermining meaningful analyses of mtDNA in the past decade is only gradually becoming apparent (Röhl *et al.* 2001; Forster 2003). The strategy adopted in this paper is to integrate those modules of colleagues' results that are relevant to the lineage analytical perspective. Inevitably, future genetic research and archaeological discoveries will change many of the conclusions presented here, and some details have been omitted intentionally for space reasons. To remedy the latter shortcoming, the reader may wish to consult the literature below and our website for updates: http://www.mcdonald.cam.ac.uk/genetics/research.html.

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Discussion

S. J. Oppenheimer (*Green College, University of Oxford, Oxford, UK*). You are suggesting that the permafrost line defines human absence during the LGM but there is evidence for human persistence in the steppe–tundra of Siberia.

P. Forster. In fact I used the (unfortunately ambiguous) term 'depopulation', by which I mean reduction in population rather than extinction. Indeed, the survival of mitochondrial A and D types in the Beringian glacial refuge demonstrates that survival was possible north of the permafrost line, in agreement with the archaeological record.

G. Rowe (*School of Biological Sciences, University of Sussex, Sussex , UK*). You show mitochondrial haplogroup X entering North America from the west. There have been some suggestions that it entered from the east, via Europe. Would you comment on this, please?

P. Forster. This recent idea is motivated by the presence of X in Europe and America, and its rarity or absence in Siberia. By contrast, we suggested in 1996 that the American mtDNA X entered Alaska via northeastern Siberia as did all the other American mtDNA types. In this hypothesis, X would have undergone the same fate as mtDNA type B in northern Asian and American latitudes during the LGM, namely extinction. Given that the very frequent mtDNA type B went extinct in the north, it is not surprising that a minor type such as X (generally less than 5% in Americans and Europeans) is likewise absent in northern Siberia and northern America today.

C. Tyler-Smith (*Department of Biochemistry, University of Oxford, Oxford, UK*). Archaeological evidence suggests that the people who reached Australia *ca*. 50 ka were using Middle Palaeolithic technology, whereas those who reached western Asia slightly later were using Upper Palaeolithic technology. Can you reconcile this with a single migration out of Africa?

P. Forster. Australians have the same two founder types M and N as do all other non-Africans. It seems to me unlikely that a hypothetical second migration out of the diverse African mtDNA pool would yield the same two M and N founder types, and no other types.

GLOSSARY

LGM: last glacial maximum