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Modern human origins: progress and prospects

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The question of the mode of origin of modern humans (*Homo sapiens*) has dominated palaeoanthropological debate over the last decade. This review discusses the main models proposed to explain modern human origins, and examines relevant fossil evidence from Eurasia, Africa and Australasia. Archaeological and genetic data are also discussed, as well as problems with the concept of 'modernity' itself. It is concluded that a recent African origin can be supported for *H. sapiens*, morphologically, behaviourally and genetically, but that more evidence will be needed, both from Africa and elsewhere, before an absolute African origin for our species and its behavioural characteristics can be established and explained.

Keywords: *Homo sapiens*; evolution; Pleistocene; modern human; Neanderthal; DNA; Palaeolithic

1. INTRODUCTION

Over the past ten years, one topic has dominated palaeoanthropological debate—the origin of 'modern' humans. While it is generally agreed that Africa was the evolutionary homeland of Pliocene hominins (such as *Australopithecus*) and the earliest humans (members of the genus *Homo*), was it also the sole place of origin of our own species, *Homo sapiens*, during the Pleistocene (1.8–0.012 Myr ago) (see figure 1)? Originally centred on the fossil record, the debate has more recently drawn on archaeological and genetic data. The latter have become increasingly significant, and now even include DNA from Neanderthal fossils. Yet, despite the growth of such data, and the availability of increasingly sophisticated methods of analysis, there is still a perception in some quarters that the debate about modern human origins is sterile and as far from resolution as ever. In this review, I wish to discuss the impact of recent discoveries and analyses, and give my own perspective on the current debate, as well as discussing possible future progress. I hope to show that there are rich and stimulating differences of opinion and approach, even within the polarized factions that have grown up during the current vigorous debate, and that further exciting developments are imminent.

As discussed later, there is no agreement about the number of human species that have existed during the Pleistocene. For some workers there may have been only one—*H. sapiens* (e.g. Hawks *et al.* 2000*a*)—while for others, there may have been at least eight (e.g. Tattersall & Schwartz 2000). My preference lies between these extremes, and for the rest of this paper I will recognize and use four species names: *H. erectus*, its probable descendant *H. heidelbergensis*, and two probable descendant species of *H. heidelbergensis*: *H. neanderthalensis* and *H. sapiens*.

First, I will concentrate on the fossil records of Africa and western Eurasia. In order to discuss these in a consistent fashion, I am going to use the following morphologically based terms: '*Recent H. sapiens*' are members of the clade containing all living *H. sapiens* and their closest past relatives, inclusive of the last morphological common ancestor of the whole group. '*Archaic H. sapiens*' are members of the stem group (Smith 1994) of *H. sapiens*, more closely related to recent *H. sapiens* than are any members of the sister clade to *H. sapiens*, *H. neanderthalensis*, or the last common ancestor of *H. sapiens* and *H. neanderthalensis* which, in my view, is represented by the species *H. heidelbergensis*. *Homo sapiens* thus consists of the combination of the crown group of recent *H. sapiens* and the stem group of archaic *H. sapiens*. It should be noted that my usage of 'archaic *H. sapiens*' is distinct from, and more restricted than, others that may include Neanderthal or early Middle Pleistocene fossils from Europe and Africa. *Homo neanderthalensis* forms the sister clade to *H. sapiens*, and may be divided in a comparable fashion into 'late *H. neanderthalensis*' and 'archaic *H. neanderthalensis*'. The more primitive *H. heidelbergensis* represents the putative Middle Pleistocene ancestral species for the *H. sapiens* and *H. neanderthalensis* clades, and is used here for both Eurasian and African fossils.

The growing body of archaeological, morphological and genetic evidence concerning modern human origins is still generally assessed against two contrasting models known as 'Recent African Origin' (also called 'Out of Africa', 'African Replacement', or simply 'Replacement' model) and 'Multiregional Evolution' (also sometimes called 'Regional Continuity'). However, as Aiello (1993) discussed, there are two other models of modern human evolution that also merit consideration (figure 2). One ('Hybridization and Replacement') can be viewed as a variant of Recent African Origin, while the other ('Assimilation') combines elements of Recent African Origin and Multiregional Evolution. Aiello summarized them as follows (my editing [ ]):

1. [*Recent African Origin*] argues that modern humans first arose in Africa about 100 000 years ago and spread from there throughout the world.... Indigenous premodern populations in other areas of the world were replaced by the migrating populations with little, if any, hybridization between the groups [figure 2*a*].
2. *The* (*African*) *Hybridization and Replacement Model* is

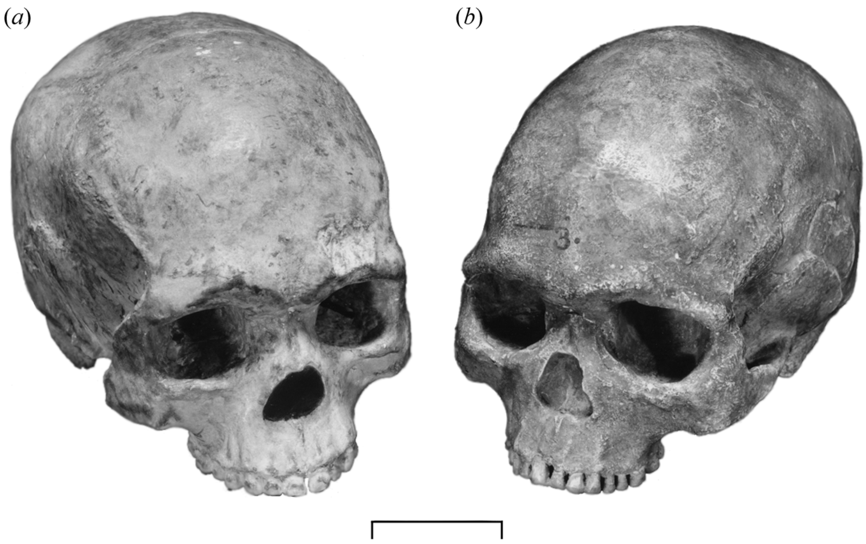

Figure 1. This comparison of late Pleistocene crania from Liujiang, China (*a*) and Fish Hoek, South Africa (*b*) highlights a central issue in modern human origins research. The cranium from Liujiang is seen by some workers as a link between archaic and recent Chinese populations, yet this visual comparison conforms with metrical analyses in showing its close resemblance to an African fossil from over 10 000 km away. Does such a resemblance reflect the late Pleistocene dispersal of a shared 'modern' morphology, or gene flow between different regions? Scale bar, 50 mm.

similar to the above, but allows for a greater or lesser extent of hybridization between the migrating population and the indigenous premodern populations… [figure 2*b*; Bräuer 1992].

(3) *The Assimilation Model* also accepts an African origin for modern humans. However, it differs from the previous models in denying replacement, or population migration, as a major factor in the appearance of modern human…. Rather, this model emphasizes the importance of gene flow, admixture, changing selection pressures, and resulting directional morphological change [figure 2*c*].

(4) [*Multiregional Evolution*] differs from the previous three in denying a recent African origin for modern humans…. It emphasizes the role of both genetic continuity over time and gene flow between contemporaneous populations in arguing that modern humans arose not only in Africa but also in Europe and Asia from their Middle Pleistocene forebears [figure 2*d*].

I discussed the development of Recent African Origin models in Stringer (1994). From 1980 to 1986, early Recent African Origin proposals argued that modern humans evolved in Africa about 100 thousand years (kyr) ago, spread to Western Asia by about 45 kyr, and to Europe by about 35 kyr. However, uncertainties about the records from the Far East and Australasia led to greater caution about events there, and a reluctance to propose a global model. Some early Recent African Origin formulations were implicitly punctuational, with the assumption of a relatively late evolution of a package of 'modern' morphological and behavioural features, and their subsequent rapid spread from Africa. This package included, morphologically, a high and mid-sagittally rounded cranial vault, a mental eminence and a lightly built skeleton, and behaviourally, the presence of blade tools, symbolism and (inferred) complex language. At this stage total replacement models, in which it was argued that archaic populations living outside Africa had become completely extinct, were rarely articulated due to the lack of relevant fossil evidence from many regions and time periods. Thus, the distinction between models 1 and 2 was not made in early presentations of Recent African Origin models.

From 1986 two significant developments began to force modification of the original models. The first was the development and application of new dating techniques that could reach beyond the range of conventional radiocarbon dating (*ca.* 40 kyr), in particular, luminescence applied to burnt stone tools, and electron spin resonance applied to fossil mammal tooth enamel (Taylor & Aitken 1997). These applications made their greatest impact on the dating of Neanderthal and early modern human burial sites in Israel, although they have also affected reconstructions of events elsewhere (Grün & Stringer 1991; Stringer 2001*a*). The second development was the increasing impact of genetic data on the debate, leading to greater polarization and a hardening of some Recent African Origin proposals in the direction of complete replacement (model 1, above). Pioneering genetic work on the reconstruction of early human evolution had been conducted by researchers such as Cavalli-Sforza & Bodmer (1971) and Nei & Roychoudhury (1982), but it was not until the late 1980s that clearer resolution started to become possible using genetic systems such as beta-globins (e.g. Wainscoat *et al.* 1986) and, in particular, mitochondrial DNA (mtDNA; e.g. Cann *et al.* 1987).

The Assimilation Model (3, above) arose through integration of the emerging evidence for an important African role in modern human origins with multiregional views. It was developed by Smith (1992), who was originally a multiregionalist. Other multiregionalists also modified their position, although less explicitly. Aspects of the original Multiregional Model (4, above) can be found in Thorne & Wolpoff (1992, p. 83), where it is summarized as follows: 'Human evolution happened everywhere

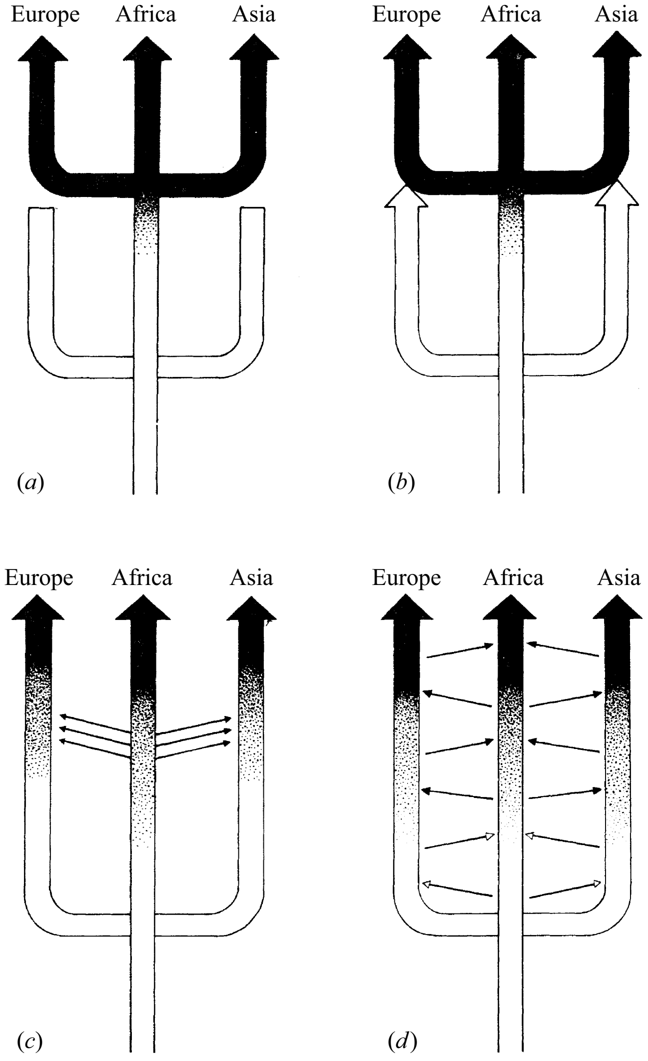

Figure 2. Evolutionary models of modern human origins (modified from Aiello 1993). (*a*) Recent African Origin; (*b*) (African) Hybridization and Replacement Model; (*c*) Assimilation Model; (*d*) Multiregional Evolution.

because every area was always part of the whole'. It was argued that each inhabited area showed a continuous anatomic sequence leading to modern humans, and those outside Africa showed no special African influence.

By 1997, Wolpoff and some colleagues had in many respects shifted to a position close to that of the Assimilation Model (Wolpoff & Caspari 1997). Because this shift was not explicit, I have distinguished it from the original Multiregional Model by the designation 'Multiregional 2' (Stringer 2001*b*). Multiregional 2 argues that an African influence predominated throughout Pleistocene human evolution because of larger population size, while populations outside Africa were more vulnerable to bottlenecking and extinctions. Thus, modern populations would mainly have African-derived genes and African-derived morphological characters, although these were predominantly acquired through gene flow, rather than via rapid replacement. It is argued that modern genes and characters accumulated over the entire Pleistocene within a genetic exchange network dominated by Africa (Hawks *et al.* 2000*a*).

There is now more than enough fossil evidence to demonstrate that most of the characters claimed to link archaic and recent populations in the same areas under multiregional evolution are either retained plesiomorphies or are not homologous (e.g. Stringer 1992; Lahr 1996). Neither the distinctive characteristics of the species *H. sapiens*, nor those of its modern regional variants, were present in the earlier Pleistocene, and this is supported by the absence of such characters even in Middle Pleistocene fossil samples that, on morphological grounds, may represent ancestors of Neanderthals and recent humans (see below). As is also discussed below, the estimated date for the mitochondrial last common ancestor of Neanderthals and recent humans is between 317 and 741 kyr, and this range of dates would appear to set another maximum age for the appearance of recent characters that were not already present in the common ancestor with Neanderthals. The original version of Multiregional Evolution thus appears no longer tenable, even to its previous adherents, while the data just discussed appear sufficient to falsify the aspects of Multiregional 2 that really distinguish it from the Assimilation Model (i.e. stipulation of the entire Pleistocene time-scale for the establishment of novel *H. sapiens* characters rather than a later Pleistocene one). Moreover, despite the careful arguments of Relethford (1999), the level of gene flow required to spread the ubiquitous modern morphology under Multiregional 2 would appear incompatible with the claimed parallel long-term maintenance of regional features in small peripheral populations.

All of the remaining models focus on the central importance of Africa in modern human origins during the later Pleistocene, while differing over the mechanisms by which modern characters spread from the continent and the relative importance of any extra-African genetic input. Therefore, in the rest of this article I will concentrate on the following aspects of the Middle–Upper Pleistocene fossil evidence: the origin of *H. neanderthalensis* and *H. sapiens*; the early African record of *H. sapiens*; the western Eurasian record of *H. neanderthalensis* and *H. sapiens*; and the later Pleistocene records of eastern Asia and Australasia (see figure 3). I will then discuss the relevance of recent genetic data and, finally, review recent and possible future developments in this research area, including a discussion of the concept of modernity.

2. THE ORIGIN OF *H. NEANDERTHALENSIS* AND *H. SAPIENS*

The European fossil human record of the Middle to Late Pleistocene has grown appreciably during the past decade, especially with the discovery of large skeletal samples from the Sierra de Atapuerca (Spain). This locality has produced important earlier (Gran Dolina—GD) and later (Sima de los Huesos—SH) fossil samples. The early component, dated at *ca.* 800 kyr, has been claimed to represent a new species ('*H. antecessor*'; Bermúdez de Castro *et al.* 1997) that was the last common ancestor of *H. neanderthalensis* and *H. sapiens*. It is argued that this species gave rise to *H. heidelbergensis* in Europe, which in turn evolved into *H. neanderthalensis*. A parallel African descendant lineage of '*H. antecessor*' gave rise to *H. sapiens*. However, while I recognize the distinctiveness of the '*H. antecessor*' material, I am cautious about its taxonomic

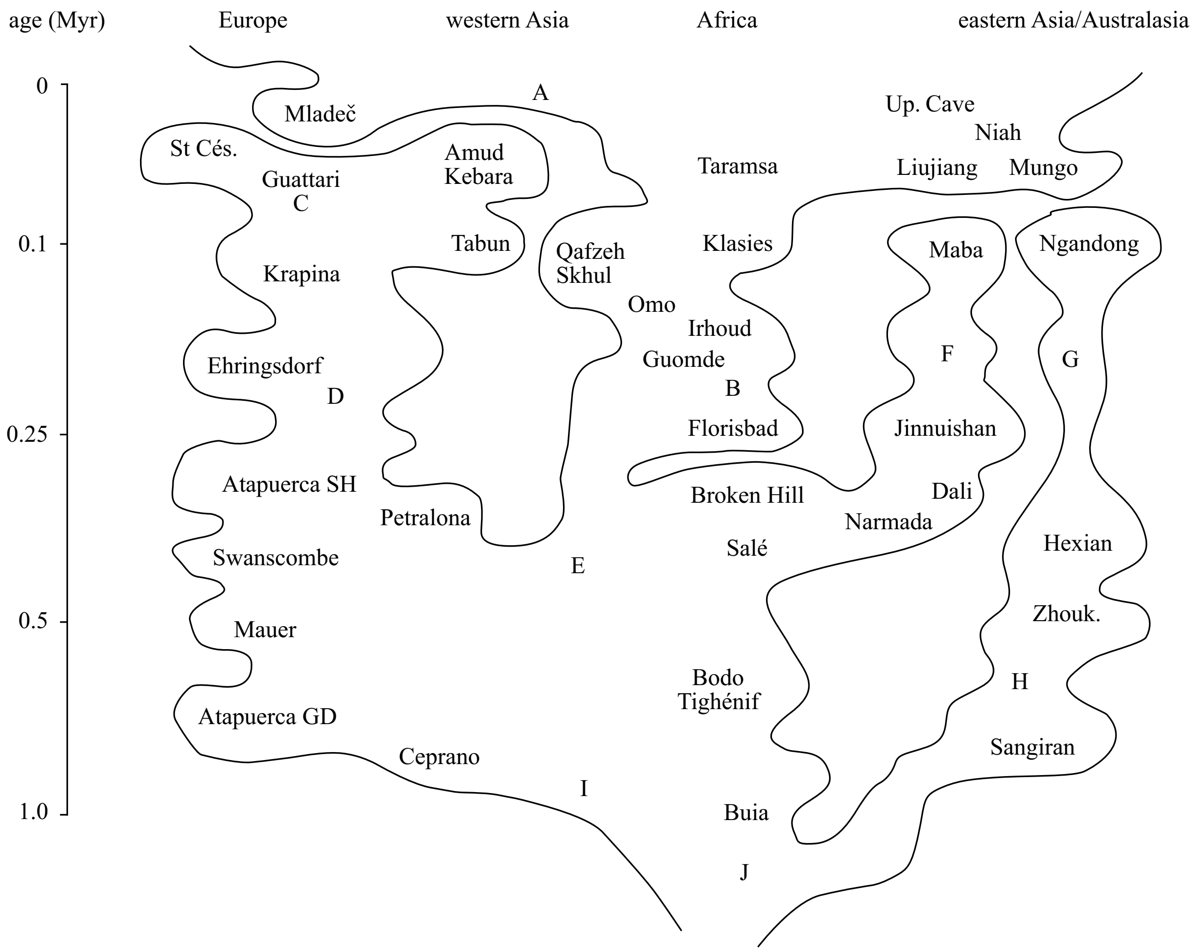

Figure 3. Distribution of selected Pleistocene fossil hominins in time and space, showing possible taxonomic groupings and relationships. (A) Recent *H. sapiens*; (B) archaic *H. sapiens*; (C) late *H. neanderthalensis*; (D) archaic *H. neanderthalensis*; (E) *H. heidelbergensis*; (F) possible Asian *H. heidelbergensis*/*H. neanderthalensis*; (G) late *H. erectus*; (H) early *H. erectus*; (I,J) *H. ergaster*/early *H. erectus*. It is uncertain whether group (F) represents evidence of homoplasy, or affinities, with populations in western Eurasia. Abbreviations: St Cés., St Césaire; Up. Cave, Upper Cave; Zhouk., Zhoukoudian.

status, and in particular about the phylogenetic significance placed on the 'modern' morphology of the infraorbital region of the immature individual ATD6-69. The adult form of this fossil may be represented by the approximately contemporaneous Ceprano cranium (Manzi *et al.* 2001), and if so, this shows much less similarity to *H. sapiens*. In addition, there is enough variation in the infraorbital region of African and European hominins from the Middle Pleistocene to warrant caution about the taxonomic value of this character. In my view (cf. Manzi *et al.* 2001), the '*H. antecessor*' material and Ceprano may represent a transitional form between *H. erectus* and *H. heidelbergensis*. Thus, for the moment, I still prefer to group early Middle Pleistocene European (e.g. Arago, Petralona and Mauer) and African (e.g. Bodo, Broken Hill and Salé) material in *H. heidelbergensis* as representing the common ancestral species for *H. neanderthalensis* and *H. sapiens*. This usage is very comparable to that of Rightmire (1998).

The Middle Pleistocene European sequence shows an accretional (mosaic and gradual) appearance of Neanderthal characters (Hublin 1998; Stringer 1998*b*), but I would argue that this process only becomes marked towards the end of the Middle Pleistocene, making a clade origination with '*H. antecessor*' some 500 000 years earlier less probable. However, the apparent gradual nature of Neanderthal evolution does make recognition of the species/clade origin difficult. This is an important question, because if *H. neanderthalensis* is our sister group, then its origin also marks the origin of our own clade (Stringer & Hublin 1999). The inference of an early origin would imply that *H. sapiens* clade characters should be present in African fossils right through the Middle Pleistocene, but I would argue that these are not recognizable in fossils such as Bodo, Broken Hill and Salé, only appearing in the late Middle Pleistocene.

An alternative model of Neanderthal and recent human origins is that of Foley & Lahr (1997), who have hypothesized an even later divergence between Neanderthals and *H. sapiens*, *ca.* 250 kyr, linking this with the development of prepared core or levallois (Mode 3; Clark 1968, and table 1) technology in the 'Mode 3 Hypothesis'. In turn, they relate this archaeological innovation to the African species '*H. helmei*', based on the Florisbad cranium (now directly dated to *ca.* 260 kyr; Grün *et al.* 1996). In their view, '*H. helmei*' evolved from *H. heidelbergensis* in Africa and then dispersed to give rise to Neanderthals in Eurasia, and modern humans in Africa. '*H. helmei*' carried the

Table 1. Time relationships of technological categories in western Eurasia and sub-Saharan Africa.
(The earliest archaeological record extends beyond 1.8 Myr in Africa. The alternative 'Mode' nomenclature was introduced by Clark (1968).)

age (kyr)	stratigraphic	western Eurasia	Africa
12	—	—	
		Upper Palaeolithic	Later Stone Age
		(Mode 4)	
	Upper Pleistocene	—	—
		Middle Palaeolithic	Middle Stone Age
		(Mode 3)	
130	—		
	Middle Pleistocene	—	
790	—	Lower Palaeolithic	Early Stone Age
	Lower Pleistocene	(Modes 1–2)	
1800	—		

newly derived Mode 3 technology with it during its late Middle Pleistocene dispersal. For Lahr and Foley (Foley & Lahr 1997; Lahr & Foley 1998), '*H. helmei*' is represented by African fossils such as Florisbad and Jebel Irhoud, perhaps ultimately ancestral to *H. sapiens*, and European fossils such as Atapuerca SH and Ehringsdorf, ancestral to the Neanderthals. Their use of '*H. helmei*' hence differs from mine (e.g. Stringer 1996) when I argued that this species might lie within the modern clade, as an evolutionary intermediate between *H. heidelbergensis* and *H. sapiens*.

While I appreciate the rationale behind the Mode 3 hypothesis, I do not consider it provides a realistic model for the origins of *H neanderthalensis* and *H. sapiens*. First, Neanderthal characteristics were already evolving in Europe prior to the hypothesized appearance and dispersal of '*H. helmei*', e.g. in the Swanscombe specimen, dated to *ca.* 400 kyr (Stringer & Hublin 1999). Second, African specimens such as Florisbad and Jebel Irhoud make unparsimonious ancestors for the Neanderthals, since not only do they post-date the appearance of Neanderthal clade characters in Europe, but they appear to lack Neanderthal morphological characteristics that might be expected in a common ancestor. A large cranial capacity is cited by Lahr and Foley (Foley & Lahr 1997; Lahr & Foley 1998), but this is highly variable in Middle Pleistocene fossils and is more evident in the European fossils that might be assigned to '*H. helmei*', such as Atapuerca SH4 and Ehringsdorf calvaria 9, than in African examples.

Usage of Mode 3 technology as an ancestral 'taxonomic' characteristic is also problematic, in my opinion. This is partly because technologies might transfer between distinct populations or even different species, as has been hypothesized for the spread of Upper Palaeolithic elements in Europe (see below), but also because the time and place of origin of prepared core techniques are currently unknown. These apparently existed in Europe and Africa (Roebroeks & Gamble 1999; McBrearty & Brooks 2000) by Oxygen Isotope Stage 9 (OIS 9 *ca.* 325 kyr ago), but it is unclear in which area, or areas, they originated. Their origin may have been African, as Lahr and Foley (Foley & Lahr 1997; Lahr & Foley 1998) propose, European or Asian, or the concept might even have been developed independently in different regions. But if Mode 3 technology does identify the ancestor of *H. neanderthalensis*, this was already present in Europe during OIS 9.

Thus, I question the evidence not only for an early Middle Pleistocene origin for the Neanderthal and modern human clades, based on '*H. antecessor*' as the last common ancestor, but also for a late Middle Pleistocene divergence implied by the Mode 3 hypothesis. Instead, I believe that *H. heidelbergensis,* present in the Middle Pleistocene of both Europe and Africa, represents the probable common ancestral species for *H. neanderthalensis* and *H. sapiens* in the later Middle Pleistocene. In principle, recognizing the origin of either descendant species (*H. neanderthalensis* or *H. sapiens*) would indicate the time of origin of our own species. Neanderthal mitochondrial DNA has been used to estimate a Neanderthal/*H. sapiens* clade separation at *ca.* 600 kyr (see below), and this in turn has been used to support the view of a deep separation time for the Neanderthal–modern clades, as suggested by the '*H. antecessor*' material. However, using the analogy of recent human diversification, a rather different conclusion can be reached. This is because genetic differentiation inevitably precedes population and specific differentiation. It is probable that *H. sapiens* has been diverging genetically for some 150 kyr, and yet we are unquestionably still a single species. Thus, for a period of time, mtDNA differences must have been accumulating *within* a Middle Pleistocene species (?*H. heidelbergensis*) prior to cladogenesis. Hence, an estimated mtDNA coalescent date of *ca.* 600 kyr in fact provides a *maximum* age for any specific separation of *H. neanderthalensis* and *H. sapiens*.

This also raises the question of the evolution of morphological characteristics, and again analogy with recent *H. sapiens* is useful. If human evolution was continuing to take its Pleistocene course, present human populations in, say, Africa, Europe or Australia might eventually form new species. Looked at from a perspective half a million years in the future, it would be possible to detect genetic or morphological apomorphies characterizing the nascent species *within* present-day populations, i.e. recent geographic variants of *H. sapiens* would contain clade features of the future distinct species. This illustrates a fundamental point that apomorphies characterizing new species must necessarily originate within previously existing species. Therefore, the fact that some fossils attributed to

H. heidelbergensis (such as Mauer and Petralona) display apomorphies characteristic of *H. neanderthalensis* does not necessarily require their attribution to the Neanderthal clade, contrary to some arguments (e.g. those of Arsuaga *et al.* 1997; Bermúdez de Castro *et al.* 1997). As an example, metrical and morphological studies instead suggest that variation between the European Petralona cranium and the African Broken Hill cranium is comparable to the differences found today between geographically distinct populations of *H. sapiens* (Seidler *et al.* 1997). I would argue that *H. heidelbergensis* was a geographically widespread and diverse species that gave rise to *H. neanderthalensis* in Eurasia, and *H. sapiens* in Africa (cf. Rightmire 1998).

Finally, what might have driven the cladogenesis that culminated in *H. neanderthalensis* and *H. sapiens*? The ancestral, geographically dispersed populations would have been repeatedly bottlenecked as glacial–interglacial cycles intensified during the Middle Pleistocene. They would inevitably have diverged genetically and morphologically with the heightened effectiveness, during climatic changes, of biogeographic barriers such as an enlarged Caspian Sea and the cold, arid uplands of the Anatolian–Iranian plateaux. Possible gene exchange between eastern Europe and the Levant would thus have been regularly disrupted or prevented. Surviving populations in the, at times, arid Levant would also have been increasingly genetically isolated from those south of the Sahara. Thus, in my view, regional characters began to develop and accumulate in *H. heidelbergensis*, including idiosyncratic 'Neanderthal' cranial features found in European material from Arago, Petralona and Swanscombe, as well as those that might be related to climatic adaptation (e.g. comparing the tibia from Boxgrove with that from Broken Hill; Stringer *et al.* (1998)). While I would argue that the Atapuerca SH material represents archaic *H. neanderthalensis,* I recognize that it can equally be regarded as a late and derived form of the ancestral species *H. heidelbergensis*.

3. THE AFRICAN RECORD

The pattern of human evolution in Africa remains less well understood than that of Europe, but the developing picture suggests that there are parallels between the two continents. Twenty-five years ago the prevailing view, based mainly on radiocarbon dating, was that although the earliest humans may have originated in Africa, subsequent human development lagged behind that of Europe. Thus, the earliest technological stage, the Lower Palaeolithic, was believed to have continued in Africa until *ca.* 50 kyr, whereas the subsequent Middle Stone Age may have only given way to the Later Stone Age at *ca.* 12 kyr, some 25 kyr later than the equivalent Middle–Upper Palaeolithic transition in Europe. The hominin sequence was thought to be comparably retarded, with the archaic Broken Hill cranium (Zambia) perhaps dated to 130 kyr, and the somewhat less archaic Florisbad (South Africa) specimen dated to *ca.* 40 kyr (Stringer 2001*a*).

The situation now is dramatically different. Argon–argon dating has shown that stone tool making began in Africa by at least 2.3 Myr, and the whole time-scale of the African Palaeolithic has been stretched back in time (Klein 1999). The Middle Stone Age is now believed to have begun by at least 250 kyr and the transition to the Later Stone Age began prior to 45 kyr (table 1). Thus, the African record can now be seen to be in concert with, or even in advance of, the record from Eurasia. The hominin record has been similarly reassessed. Biostratigraphic correlation suggests that the Broken Hill cranium (*H. heidelbergensis*) probably dates from at least 300 kyr (Klein 1999), while a combination of electron spin resonance dating on human tooth enamel and luminescence dating of sediments suggests that the Florisbad cranium—an archaic *H. sapiens*—actually dates from *ca.* 260 kyr rather than the former estimate of *ca.* 40 kyr (Grün *et al.* 1996).

Fossil specimens showing mosaic archaic–modern *H. sapiens* characters from Guomde (Kenya) and Singa (Sudan) are now dated by gamma rays, and a combination of electron spin resonance and uranium series, to at least 150 kyr (Bräuer *et al.* 1997) and 133 kyr (McDermott *et al.* 1996). *Homo sapiens* fossils such as Omo Kibish 1 (Ethiopia), Border Cave 1 (South Africa) and those from the Middle Stone Age levels of the Klasies River Mouth Caves (South Africa) are of comparable, or somewhat younger, age, although much of this material is fragmentary and difficult to date more precisely (Klein 1999). Overall, the picture of human evolution in Africa over the last 300 kyr can now be seen to parallel that of Europe. Both regions appear to show a mosaic and perhaps gradual transition from *H. heidelbergensis* to a more derived species: in Europe *H. neanderthalensis*, and in Africa *H. sapiens* (Bräuer *et al.* 1997; Rightmire 1998; Stringer 1998*b*).

If this model of gradual, regional, evolution can be applied to the African fossil record, an accretional mode of *H. sapiens* evolution would consequently be expected (Stringer 1998*b*). In which case, how can we recognize when identifiably 'modern' humans appear? So far, I have avoided further discussion of the term 'modern', but it will be necessary to discuss the use of this important but complex concept in detail later. However, the term is generally used to contrast the shared characteristics of recent humans (whether morphological, behavioural or cultural) with those of earlier (non-modern or archaic) humans. Unfortunately, there are no generally agreed definitions or diagnoses of the term as applied to the fossil or archaeological record. Moreover, acceptance of a gradualistic scenario for the origin of modernity means that diagnosing 'modernity' will be dependent on the particular criteria selected. In addition, in the case of morphology, while individual anatomical characters may be used to recognize which fossils belong to the *H. sapiens* clade, membership of this clade will not necessarily be synonymous with modernity as an assemblage, since this may have evolved long after the cladistic origin of *H. sapiens* (which, in my view, was at the *H. neanderthalensis–H. sapiens* cladogenetic event). Thus, fossils such as Florisbad, Singa, and even those from Skhul and Qafzeh, probably belong to *H. sapiens* cladistically, but do not necessarily represent 'modern' humans.

4. THE WESTERN EURASIAN RECORD

The Levant occupies a unique geographical position linking Africa and Eurasia, but its Middle Pleistocene hominin record is much poorer than that of adjoining regions. Only fragmentary specimens from sites such as

Zuttiyeh and the lower levels of Tabun provide physical evidence of the Levantine human populations before *ca.* 130 kyr, but they are insufficient to provide much information about the nature of those populations (Klein 1999). Interpretations of the regional fossil record after this period have undergone some remarkable upheavals brought about by the application of new dating techniques. As late as 1985, it was believed by most workers that the pattern of population change in this area paralleled that of Europe, or rather preceded it by a small amount of time. Thus, Neanderthals at Israeli sites such as Tabun and Amud evolved into, or gave way to, early modern humans such as those known from Skhul and Qafzeh by *ca.* 40 kyr ago (e.g. Trinkaus 1984). For some workers technological and biological changes were interlinked, leading to an evolution of modern humans in the region, and it was postulated that these early moderns could then have migrated into Europe, giving rise to the Cro-Magnons (the term used for Upper Palaeolithic-associated *H. sapiens* in Europe). One of the first applications of the newer chronometric techniques (thermoluminescence applied to burnt flint) seemed to reinforce this pattern, dating a recently discovered Neanderthal burial at Kebara in the anticipated time-range of *ca.* 60 kyr ago (Valladas *et al.* 1987).

Shortly afterwards, the first application was made to the site of the Qafzeh early modern material, giving a surprisingly old age estimate of *ca.* 90 kyr, more than twice the generally expected figure. Further applications of non-radiocarbon dating methods have amplified the pattern suggested by the age estimates for Qafzeh and Kebara (see reviews in Grün & Stringer 1991; Klein 1999). It seems probable that the early modern burials at Qafzeh and Skhul date from more than 90 kyr, and some may be as old as 130 kyr. The Neanderthal burials at Kebara and Amud date younger than this figure, in the range 50–60 kyr ago. As the intervening period approximates the transition from the supposedly predominantly interglacial stage 5 to predominantly glacial stage 4, this has led to a proposed scenario where Neanderthals only appeared in the Levant after the onset of glaciation further North (Akazawa *et al.* 1998).

In this context, it has been difficult to establish the age of the Tabun Neanderthal burial, for two different reasons. First, while age estimates for the stratigraphy at Tabun based on electron spin resonance and luminescence both considerably stretch the late Pleistocene time-scale previously proposed for the site into the Middle Pleistocene, the methods do not give compatible results. Luminescence estimates from burnt flint excavated from the rear of the cave are much older than electron spin resonance estimates from mammal teeth from correlated levels nearer the mouth of the cave (compare Grün *et al.* (1991) with Mercier *et al.* 1995). Second, the stratigraphic position of the Tabun burial cannot be established with certainty over 60 years after its excavation, giving further doubt about its actual age (Garrod & Bate 1937; Bar-Yosef & Callander 1999). Direct non-destructive gamma ray (uranium series) dating of the mandible and leg bones from this skeleton had suggested a surprisingly young age of less than 40 kyr (Schwarcz *et al.* 1998). However, the accuracy of this estimate was questioned (Millard & Pike 1999; Alperson *et al.* 2000) and direct electron spin resonance dating of a tooth enamel fragment from a molar on the mandible has now given a much older age estimate of *ca.* 120 kyr (Grün & Stringer 2000). Thus, the extent of Neanderthal–early modern contemporaneity in the Levant over the period 90–130 kyr ago is still an open question, but given that the region lies in the potential overlap zone of range expansions of either the evolving African *H. sapiens* lineage or that of Eurasian Neanderthals, this was certainly probable (Stringer 1998*b*). Yet, after this time, the Neanderthals appear to have predominated in the region until *ca.* 45 kyr ago, when the development of new technology and behaviour by early modern humans may have fuelled major range expansions, heralding the eventual extinction of the Neanderthals.

Having discussed the beginning of the Neanderthal and modern human lineages and their presence in western Asia, I will now examine the fate of the Neanderthals. New luminescence and electron spin resonance dating, in concert with the accelerator radiocarbon technique (which requires much smaller samples of organic material than conventional methods), has generally confirmed previous views of the Middle/Upper Palaeolithic sequence, but with some additional complexity, especially in Europe. Upper Palaeolithic industries such as the Aurignacian, by inference associated with early modern humans, have been dated in parts of Eurasia (e.g. northern Spain and Hungary) by luminescence, electron spin resonance, uranium series or radiocarbon accelerator methods to *ca.* 40 kyr. Middle Palaeolithic (Mousterian) industries, actually or presumably associated with Neanderthals, start to disappear from some areas of Europe from about this time. However, both the old favoured models of rapid *in situ* evolution of Neanderthals into Cro-Magnons or a rapid replacement of Neanderthals by them can now be shown to be invalid. Late Neanderthal levels at French sites such as Le Moustier and Saint-Césaire have been dated in the range 35–40 kyr ago, while those at Arcy have been radiocarbon dated at *ca.* 32 kyr ago (Mellars 1999). These dates may well be compatible, given that radiocarbon dates at this period could underestimate calendar ages by several millennia (Stringer & Davies 2001). Moreover, Neanderthal fossils have now been dated at *ca.* 30 000 radiocarbon years in areas such as Southern Spain, Croatia and the Caucasus, and regions such as southern Iberia and the Crimea show a parallel persistence of Middle Palaeolithic industries (e.g. Hublin *et al.* 1995; Smith *et al.* 1999; Ovchinnikov *et al.* 2000). If these dates and associations are accurate, it appears that Neanderthals survived quite late in some regions, and had a potential coexistence with the Cro-Magnons of at least ten millennia.

The previous relatively clear picture of the Middle Palaeolithic/Neanderthal and Upper Palaeolithic/*H. sapiens* interface in Europe has also become cloudier since the identification of Neanderthal remains in Châtelperronian (early Upper Palaeolithic) levels at the French sites of Saint-Césaire and Arcy (Hublin *et al.* 1996). Moreover, there is an apparent association of Neanderthals with symbolic artefacts such as pendants at Arcy. Furthermore, it has been suggested that other industries with supposed Upper Palaeolithic affinities in central Europe (Szeletian) and Italy (Uluzzian) may also have been the handiwork of late Neanderthals (see reviews in d'Errico *et al.* 1998;

Klein 1999). Thus, the Neanderthals appear to show some of the same technological and behavioural innovations as the Cro-Magnons. For some researchers (e.g. Klein 1999; Mellars 1999), this late pattern of regionalization in the Neanderthals reflects the final fragmentation of their formerly continent-wide range, while in contrast the wide distribution of the Aurignacian reflects the dispersal of early modern humans across much of Europe. Present dating evidence no longer clearly demonstrates a wave of advance of the Aurignacian, since its oldest manifestations may be as ancient in northern Spain as in the east of the continent. The assumed external source for the Aurignacian and its manufacturers is also now unclear, and it remains possible that *H. sapiens* first arrived in the region with a pre-Aurignacian, even Middle Palaeolithic, technology. Such a precursor industry that might mark the appearance of early modern pioneers, although currently without diagnostic fossil material, is the Bohunician of eastern Europe, dated beyond 40 000 radiocarbon years (Stringer & Davies 2001).

Workers such as Zilhão and Trinkaus have proposed still greater complexity in the European picture (e.g. d'Errico *et al.* 1998; Duarte *et al.* 1999). To them, Middle–Upper Palaeolithic transitions are indicative of complex and changing population dynamics as incoming Cro-Magnons mixed and merged with native Neanderthals over many millennia. In this scenario, the Neanderthals were arguably as culturally advanced as the Cro-Magnons, and were simply absorbed into a growing Cro-Magnon gene pool. It is even claimed that a hybrid child has been discovered at Lagar Velho in Portugal, dated to *ca.* 25 000 radiocarbon years (Duarte *et al.* 1999), but this claim remains unresolved until more detailed studies have been published. Whatever the outcome of that particular proposal (and I still consider that this may represent an unusually stocky modern human child), the impact of new dates and discoveries in Europe shows that the whole gamut of population interactions between the last Neanderthals and the first Cro-Magnons could, and perhaps did, occur, ranging from conflict to possible interbreeding. Nevertheless, the outcome of these processes was the extinction of the Neanderthals after a long period of survival in the challenging and unstable climates of Pleistocene Europe. MtDNA studies, discussed later, suggest that the genes of the earliest Cro-Magnons are not necessarily well represented in recent Europeans, because of intervening replacement or bottlenecking (Richards & Macaulay 2000). Therefore, any small Neanderthal genetic component 30 kyr ago could easily have been subsequently lost.

5. THE LATER PLEISTOCENE RECORDS OF EAST ASIA AND AUSTRALASIA

Homo erectus was present in both China and Indonesia prior to 1 Myr ago (Culotta 1995; Klein 1999). The largest sample of Chinese material of this species, from the Zhoukoudian Lower Cave, is now dated at *ca.* 400–500 kyr by uranium series and electron spin resonance, and comparable southern Chinese material from Hexian is of similar, or somewhat younger, age (Grün *et al.* 1997, 1998). Other Middle Pleistocene fossils are indicative of morphological and perhaps, specific diversity, but limited knowledge of them has prevented their integration into the wider fossil record. Relatively complete, but heavily distorted, cranial material from the site of Yunxian (Etler 1996) may exhibit variation away from the standard *H. erectus* pattern towards that of *H. heidelbergensis*, while a partial cranium from Nanjing, still not described in detail, even appears reminiscent of Neanderthals in nasal, although not maxillary, morphology (C. Stringer, personal observation). These populations were apparently succeeded by more derived humans formerly attributed to 'archaic *H. sapiens*', represented by fossils from sites such as Jinniushan and Dali, and dated to *ca.* 250–300 kyr ago (Etler 1996; Yin *et al.* 2001). Their affinities are still unclear, with some workers (e.g. Etler 1996) seeing them as descended from local *H. erectus* antecedents, others (e.g. C. Stringer; Lahr 1996; Rightmire 1998) regarding them as possible eastern representatives of *H. heidelbergensis*. The isolated Narmada calvaria from India (Klein 1999) may also represent such a population (figure 3). Fragmentary early late Pleistocene fossils (*ca.* 100 kyr) from Chinese sites such as Xujiayo and Maba may record further local evolution, with Maba showing possible affinity to western Eurasian Neanderthals. However, the arrival of *H. sapiens* in the region is still poorly dated and poorly understood. That arrival must precede the modern human fossils known from the Upper Cave (Shandingdong) at Zhoukoudian, dated by radiocarbon on associated fauna to between 12 and 30 kyr ago, and might even extend back beyond 70 kyr if the Liujiang skeleton (figure 1) is of that age (Shen & Wang 2001). On the basis of cranial data, neither these specimens nor the late Pleistocene Minatogawa material from Japan seem very closely related to recent populations in the region (Brown 1999; Stringer 1999), and may provide evidence of early diversity that is either now lost or survives in the form of aboriginal isolates such as the Ainu of Hokkaido and the Andamanese Islanders.

In Indonesia, several *H. erectus* fossils have been indirectly dated to *ca.* 1.7 Myr ago using argon–argon dating on volcanic sediments (Klein 1999), although some workers doubt that the fossils have been correctly associated with the dated rocks (Culotta 1995). Other *H. erectus* fossils are dated by combinations of argon–argon, palaeomagnetics and biostratigraphy to between 500 kyr and 1.2 Myr ago (Klein 1999). The Ngandong and Sambungmacan fossils have been even more controversially dated to less than 50 kyr by electron spin resonance and uranium series on associated fauna, implying a survival of *H. erectus* in Indonesia as late as Neanderthals survived in Eurasia (Swisher *et al.* 1996). Other workers have argued that these dates must be underestimates (Grün & Thorne 1997), but further uranium series determinations, including direct measurements on the fossils, do support these dates (Falguères *et al.* 2001). The date of arrival of modern humans in the region is still uncertain, but given the evidence from Australia discussed below it must lie before 60 kyr. Known fossils such as Wajak (Java) and Niah (Sarawak) remain poorly dated, but may derive from the late Pleistocene.

Exactly when humans first arrived in Australia has been unclear until recently. Sites such as Malakunanja II, Nawalabila and Devil's Lair appear to contain artefacts or evidence of human–faunal interaction dating from at least 50 kyr, based on luminescence or minimum-age radiocarbon dates (Roberts *et al.* 1990, 1994; Turney *et al.* 2001). However, in none of these sites were associated human remains preserved, thus leaving the nature of the first Australians uncertain. Two different views have predominated in recent debate about the peopling of Australia. For some workers, there were two original colonizations of the continent (Thorne & Wolpoff 1992; Frayer *et al.* 1993). An early colonization, originating from the archaic people of Java (here regarded as *H. erectus*, although regarded as early *H. sapiens* by some of the last group of authors) introduced a robust population at, perhaps, 50 kyr ago. This colonization event was supposedly represented by the Willandra Lakes human fossil known as WLH-50 (Willandra Lakes Human-50), and by subsequent populations sampled at sites such as Kow Swamp, Cohuna and Coobol Creek. A second colonization, purportedly derived from China, arrived via an eastern route and brought the more gracile people known from the Mungo fossils at *ca.* 30 kyr ago and sampled at later sites such as Keilor and King Island. Under this dual origin hypothesis, present day Australian Aboriginal variation is the result of Holocene hybridization between these robust and gracile peoples. A second, contrasting, view saw the robust and gracile peoples as parts of a single morphologically variable population. Their differences probably developed within Australia following a single colonization event, with recent Aborigines representing the end product of this process (Pardoe 1991; Brown 1992).

Recently, the Mungo 3 burial has been redated using a combination of the techniques of gamma ray uranium series dating on skull fragments, electron spin resonance on a piece of tooth enamel, uranium series on attached sediment, and optically stimulated luminescence applied to the sands containing the burial (Thorne *et al.* 1999). The dates obtained are 62 ± 6 kyr, approximately double the ages originally estimated from radiocarbon (Bowler & Thorne 1976). By correlation, these new age estimates may also apply to the Mungo 1 cremated individual found nearby. There has been critical debate about the accuracy of these new determinations (Grün *et al.* 2000), although even critics appear to accept that Mungo 1 and 3 are older than previously thought.

If these new dates for Mungo 1 and 3 are indeed accurate, they imply that gracile people were the first inhabitants of Australia. This is because, in a related study, skull fragments of the supposedly more archaic fossil WLH-50 were dated by the gamma ray method, giving a preliminary age estimate of only *ca.* 14 kyr (Simpson & Grün 1998). Thus this specimen, and the other robust fossils so far dated (Brown 1992), all apparently post-dated the last glacial maximum *ca.* 20 kyr ago. The sequence of morphologies supports a model of diversification within Australia, not derivation from separate ancestors. Otherwise, one would have to postulate the movement of 'gracile' people through Indonesia into Australia by 60 kyr ago, without replacement or interaction with existing 'robust' people, and then the arrival of surviving 'robust' people from Indonesia, who managed to disperse through Australia without significant intermixture with existing 'gracile' inhabitants.

Additionally, the description of the robust crania as archaic and *H. erectus*-like (e.g. Thorne & Wolpoff 1992; Frayer *et al.* 1993) has been challenged by several workers who instead argue that their distinctive features can be related to large size, artificial deformation, or pathology (Brown 1992; Lahr 1996; Stringer 1998*a*; Antón & Weinstein 1999). Nevertheless, continued attempts have been made to demonstrate regional continuity between the WLH-50 calvaria and archaic Indonesian predecessors (Hawks *et al.* 2000*b*), but these have been idiosyncratic in the scoring of morphological characters (cf. Lahr 1996) and failed to control for the confounding effect of size in metrical comparisons (cf. Stringer 1998*a*).

Overall, it seems probable that a modern human dispersal had reached Australia, via boats, by *ca.* 65 kyr ago. This may have been the endpoint of a long-term coastal expansion from Africa (Stringer 2000), but until more is known of the late Pleistocene populations of southern Asia, this will remain unclear. The relationship of the first Australians to later inhabitants of the continent is still uncertain. Late Pleistocene morphological diversity may well have been accentuated by the severity of the last glacial maximum, leading to isolation and the forcing of morphological change in some Australian populations. If archaic populations such as those known from Ngandong *did* survive into the late Pleistocene, an analogous situation to that in Europe might have obtained, raising the possibility of gene flow with dispersing *H. sapiens* (cf. Hawks *et al.* 2000*b*). Given previously discussed data from Europe and China, it is also possible that the genes of the first human colonizers are poorly represented in the aboriginal people of today because of extinctions, bottlenecking, or because later population expansions have largely overprinted their traces, physically, genetically and linguistically.

6. GENETIC DATA

Genetic data have assumed an increasing importance in reconstructions of recent human evolution over the past 15 years. Earlier studies had to work with population frequencies of genetic markers, the products of the genetic code (e.g. blood groups, proteins). By combining data from populations, attempts were made to reconstruct the genetic history of humans (Cavalli-Sforza & Bodmer 1971; Nei & Roychoudhury 1982). The advent of techniques that revealed individual molecular sequence data allowed phylogenetic trees or genealogies of specific genes or DNA segments to also be constructed. Two pioneering papers published in *Nature* in 1986 and 1987 illustrate, respectively, population-based and phylogenetic approaches using DNA markers called RFLPs (Restriction Fragmentation Length Polymorphisms). Using the former approach, Wainscoat *et al.* (1986) studied polymorphisms close to the beta-globin gene, and showed by genetic distance analyses that African populations were quite distinct from non-African ones. The following year, Cann *et al.* (1987) published their paper giving a genealogy of 134 mitochondrial DNA 'types' constructed from restriction maps of 148 people from different regions. The genealogy was used to reconstruct increasingly ancient hypothetical ancestors, culminating in one female, most parsimoniously located in Africa. Moreover, using a mtDNA divergence rate calculated from studies of other organisms, it was estimated that this hypothetical female ancestor lived *ca.* 200 kyr ago. These

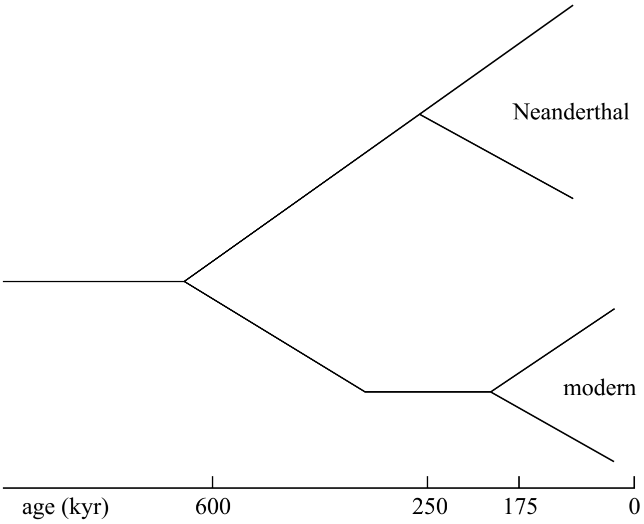

Figure 4. Schematic depiction of Neanderthal–modern human mtDNA relationships, with approximate coalescence dates (from data in Ovchinnikov *et al.* (2000) and Krings *et al.* (2000)). The small sample of Neanderthal sequences is sufficient to suggest comparable diversity to, but clear distinctiveness from, recent humans.

conclusions were extremely controversial, and were subjected to critical scrutiny concerning the samples, methods and calibration used (Templeton 1993). Although it is now evident that Cann *et al.* (1987) were premature in the confidence with which they presented their results, much more extensive analyses (e.g. Ingman *et al.* 2000) have shown that they were fundamentally correct in their conclusions.

In the past ten years, with the development and application of PCR techniques, a wealth of sequenced data has been made available from autosomal (biparentally inherited) DNA, Y-chromosome DNA (inherited through males) and mitochondrial DNA (inherited through females).These data have been used to compare the DNA of human populations in ever greater detail (Tishkoff *et al.* 2000; Kayser *et al.* 2001), to estimate coalescent (last common ancestral) dates for various gene systems (Ingman *et al.* 2000), to reconstruct ancient demographic patterns (e.g. Rogers 2001), and to develop phylogeographic studies to map ancient dispersal events (e.g. Richards & Macaulay 2000; Underhill *et al.* 2001). While most of these data support a recent African origin for recent humans and their genetic diversity (e.g. Jorde *et al.* 2000; Ke *et al.* 2001), others may not (Zhao *et al.* 2000). Although the data are growing in power and resolution, analyses cannot yet resolve the precise time and place of our origins, nor establish whether there was only one or perhaps several significant dispersals of *H. sapiens* from Africa during the later Pleistocene.

Some genetic data, in the form of mtDNA, are now available from Neanderthal fossils (Krings *et al.* 2000) and these suggest a separation time of their lineage from that leading to recent humans of *ca.* 600 kyr (Krings *et al.* 2000; Ovchinnikov *et al.* 2000; figure 4). As explained earlier, such estimates necessarily provide *maximum* ages for evolutionary separation, since any population and species separations would inevitably post-date the first mitochondrial divergence by an unknown amount of time. But they are consistent with fossil evidence of an effective separation date of the *H. neanderthalensis* and *H. sapiens* lineages at *ca.* 300 kyr and also with subsequent genetic divergence among recent humans beginning less than 200 kyr ago (Stringer 1998*b*). Both the morphological data and the limited amount of fossil DNA available suggest that Neanderthal–recent human differences were of the order of two or three times that found within recent humans. But even in this case, where genetic and morphological differences are clear, the data can be used to support a placing of Neanderthals and recent humans in either the same or different species, given the recency of common ancestry.

There have also been recent claims for the recovery of ancient DNA from Australian fossils. Adcock *et al.* (2001) reported that 10 out of 12 specimens tested from Willandra Lakes and Kow Swamp had yielded mitochondrial sequences. One of these, from Mungo 3, was claimed to form an outgroup with a previously reported mitochondrial nuclear insert, distinct from the other fossils and from recent human sequences. Adcock *et al.* (2001) claimed, moreover, that the distinctiveness of the Mungo 3 sequence undermined genetic support for a recent African origin. In an accompanying commentary, Relethford (2001) used the results to support alternative multiregional interpretations, and to question previous interpretations of Neanderthal DNA. However, Cooper *et al.* (2001) in turn criticized various aspects of the work. First, they observed that the claimed recovery rate for the Australian ancient DNA was exceptional compared with results from elsewhere, and that standard experimental protocols had not been employed, suggesting the possibility of contamination. Second, they reanalysed the data, using a larger number of recent Australian and African sequences, and demonstrated that the Mungo 3 sequence did not now form an outgroup to recent human mtDNA in the most parsimonious phylogeny. Third, they observed that even the original published phylogeny presented no serious challenge to Recent African Origin. Australian fossils classed by multiregionalists as 'robust' and 'gracile', purportedly derived from archaic Indonesian and Chinese ancestors respectively, grouped with the recent human sequences from regions such as Europe and Africa, while Mungo 3 was more closely related to all these than it was to the Neanderthal sequences used as an outgroup.

7. NEW APPROACHES TO MODERN HUMAN ORIGINS RESEARCH

In these concluding sections, I would like to draw together aspects of this review and also look at new approaches to some remaining problems. In my opinion, variants of one of the polar extremes in the debate about modern human origins discussed at the beginning of this paper—Multiregional Evolution—have been falsified, and the fundamental mode of modern human origins can be assumed to be that of a recent African origin. But until we have better records of late Pleistocene events in human history from regions such as China and Australia, we will continue to depend on genetic data to inform us whether a strict Recent African Origin model is likely to be adequate, rather than a variant incorporating a greater and more gradual (assimilation) or a lesser and more rapid (hybridization) degree of gene flow with contemporary populations outside Africa. However, even the strict Recent African Origin model has undergone considerable recent development in the Multiple Dispersals model of Lahr and Foley (1994, 1998), and this will be discussed next.

The Multiple Dispersals model proposes that significant recent human population subdivisions developed within Africa, and that there may then have been multiple dispersals of already differentiated populations from there, perhaps using different routes. This model has concentrated attention on the African fossil record of the late Middle Pleistocene. Other researchers recognized the high variation in these samples, but accepted that ancestors of recent humans were probably represented amongst them (Hublin 1993; Bräuer *et al.* 1997; Rightmire 1998; Stringer 1998*b*). Lahr & Foley (1994, 1998) have taken this further in arguing that they might represent subdivided and distinct populations, with some or many not representing ancestors for recent *H. sapiens*. Following a bottleneck during OIS 6 (*ca.* 150 kyr), one African population recovered and spread into the Levant during OIS 5 (*ca.* 125 kyr), as represented by the Skhul-Qafzeh fossils. However, in the Multiple Dispersals model, these Levantine pioneers went extinct around the onset of OIS 4 (*ca.* 70 kyr). Surviving Africans, meanwhile, became divided into subgroups that were to form the ancestors of both African and non-African populations. A subsequent Middle Palaeolithic-associated dispersal occurred via Arabia and southern Asia, eventually reaching Australia, while later dispersals took the ancestors of recent European, Asian and Oriental people out of Africa following the development of Later Stone Age–Upper Palaeolithic technologies. Other workers have raised the possibility of separate early dispersals to Australia, but Lahr & Foley (1994, 1998) proposed a specific coastal route for this via the Straits of Hormuz (Bab el Mandeb). Subsequently, Stringer (2000), using new evidence of Middle Stone Age littoral adaptations, argued that coastal expansion around the Red Sea basin could have facilitated a range expansion of modern humans towards Australasia without necessarily using the Straits of Hormuz. By focusing attention on the development of diversity within Africa, the Multiple Dispersals model has provided fruitful hypotheses for testing from fossil, behavioural and genetic data.

A number of taxonomic issues in modern human origins remain unresolved. However, new ways of comparing past human taxic diversity with that of recent primates are being developed, and new techniques of investigation are adding further data from the expanding fossil record. One of the most serious remaining areas of uncertainty and confusion in studies of modern human origins is the question of species recognition. Some workers (e.g. Tattersall & Schwartz 2000) argue that many distinct morphological groups in the fossil record warrant specific recognition, with the existence of at least eight such species of the genus *Homo* supported during the last two million years. Others (e.g. Thorne & Wolpoff 1992) argue that only one species warrants recognition over that period—*H. sapiens*. An additional complication is that different species concepts may become confused—for example, some multiregionalists have applied biological species concepts to the fossil record in an attempt to show that *H. neanderthalensis* and *H. sapiens* must have been conspecific. However, even if we accept controversial claims for the existence of supposed Neanderthal–modern hybrids (e.g. Duarte *et al.* 1999), it is well known that many closely related mammal species (including primates) can hybridize, and may even produce fertile offspring. However, if this is not a widespread or reproductively successful behaviour, it may have little or no impact on the populations that constitute the core of the different species or on future generations. The limited genetic data on Neanderthal–recent relationships show that Neanderthals and recent *H. sapiens* represent distinct but nevertheless closely related lineages, but are ambiguous about whether these samples represent different species. Thus, in fossils, morphological criteria necessarily remain the mode of species recognition, but recent research is providing better testing of the assumptions involved.

Harvati (2001) used differences in temporal bone morphology between common chimpanzees and specifically distinct bonobos to compare the level of difference between Neanderthals and recent *H. sapiens*. She concluded that Neanderthal–recent differences in the temporal bone were at least as great as those between the two chimpanzee species. As she recognized, this result was based on only one cranial area, and further tests were required before reaching more definitive conclusions. In a similar study based on cranial measurements, Schillaci & Froehlich (2001) compared the level of differentiation of fossil (Upper Palaeolithic) *H. sapiens* and Neanderthals with that calculated between species of macaques that are known to hybridize, or not to hybridize. Again, the degree of difference between the fossil human cranial samples exceeded that found between the recent primate species. Thus, both these studies supported the distinctiveness of *H. neanderthalensis*. Apart from more cranial studies, it would be valuable to extend this approach to comparisons of mandibular morphology and metrics (e.g. extending the data of Humphrey *et al.* (1999)) and of dental morphology (see discussion of the work of Bailey (2000) below).

In recent years, traditional osteometric methods of recording the size and shape of fossil bones and teeth have been complemented and increasingly superseded by techniques that capture such information digitally through digitizing or scanning (Harvati 2001). The medical technology of Computed Tomography (CT) has been particularly successful in extending such work into anatomical structures that are either difficult to measure through traditional techniques (e.g. external and internal frontal bone shape: Bookstein *et al.* (1999)) or are otherwise inaccessible (e.g. inner ear bone shape: Hublin *et al.* (1996)). The techniques of geometric morphometrics are now being used to investigate both ontogeny and phylogeny (e.g. Ponce de León & Zollikofer 2001). Much wider and more detailed comparisons of fossil and recent samples will undoubtedly have major impacts on future taxonomic and phylogenetic research on modern human origins.

Dental morphological variation provides an alternative and still rather neglected approach to reconstructing human population histories, despite the pioneering work of researchers such as Turner (1992) and K. and T. Hanihara (Hanihara 1992). Turner's 'Out of Asia' scenario for recent human evolution was based on phenetic distance

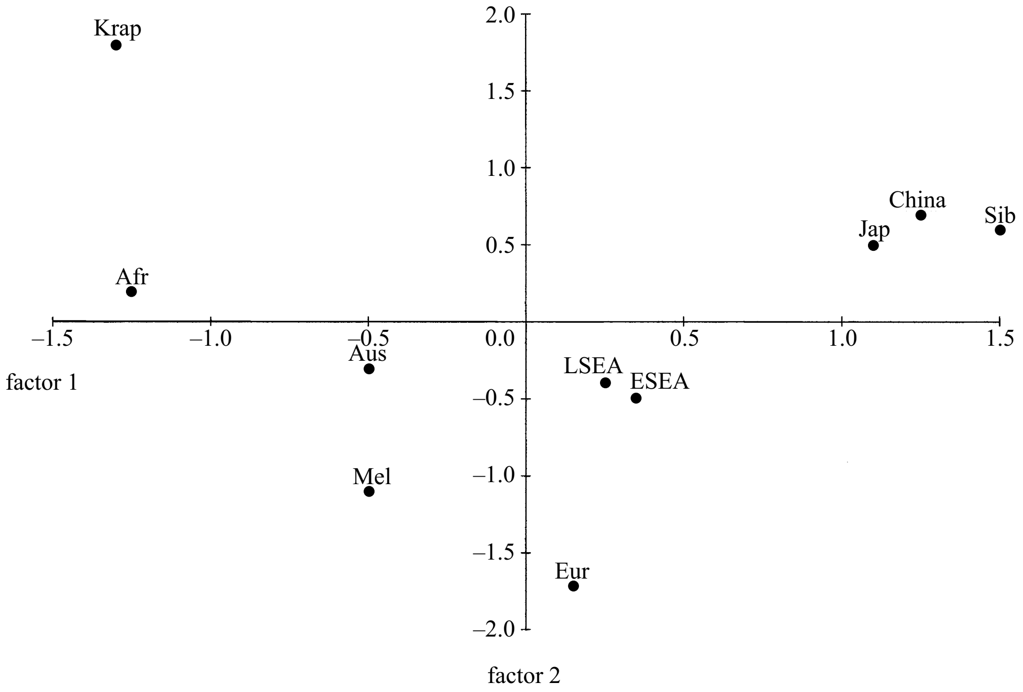

Figure 5. Plot of first and second principal components using dental morphological data from Stringer *et al.* 1997 (redrawn from Stringer (1999), principal components analysis by L. Humphrey). The use of comparative data from the Krapina Neanderthals as a guide to polarity suggests that recent African and Australian populations may be closer to the ancestral modern human dental pattern than those of Southeast Asia (*contra* Turner 1992). Abbreviations: Krap, Krapina; Afr, recent sub-Saharan African; Aus, recent Australian; Mel, recent Melanesian; Eur, Holocene European; LSEA, recent Southeast Asian; ESEA, Holocene Southeast Asian; Jap, recent Japanese; China, recent Chinese; Sib, recent Siberian.

analyses and assumptions of relatively constant rates of dental evolution. It postulated that the 'Sundadont' aboriginal peoples of Southeast Asia were closest to the original modern human dental pattern and that this indicated the original source area for *H. sapiens*. However, this approach was unable to account for the relatively close phenetic distance between Australian and African dental patterns, and no attempt was made to test the hypothesis by the use of fossil data as an outgroup. These limitations were remedied in the work of Stringer *et al.* (1997), Irish (1998) and Tyrell & Chamberlain (1998), who found that the use of either a Neanderthal or archaic African outgroup supported a sub-Saharan, not Asian, root for recent human dental dendrograms or cladograms. Figure 5 shows the first two factors of a principal components analysis from the data of Stringer *et al.* (1997), with the inclusion of the Krapina Neanderthal sample as an outgroup. It is evident that if the Krapina dental sample is a representative outgroup, then European and East Asian ('Sinodont') samples appear derived, 'Sundadont' samples are rather average for recent humans (as Turner and the Haniharas have reported), while Australian and sub-Saharan African samples are relatively plesiomorphous. The dental ancestor for recent humans thus probably combined characters most commonly found today in sub-Saharan Africans and Australians. Shields (1998), using a different dataset derived from digitized dental radiographs, also concluded that Australians displayed the most plesiomorphous morphology of non-African populations, while 'Mongoloid' and Native American samples were more derived. Thus, it appears that in both dental and morphological/metrical characters the 'Mongoloid' cranial form is very derived. Bailey (2000) has extended dental morphological studies to a wider range of fossils, including those of the western Eurasian Upper and Middle Palaeolithic. She concluded that Eurasian Neanderthals were similar to each other but quite distinct from other fossil, and recent, human samples. Both the Skhul–Qafzeh and Upper Palaeolithic groups showed recent affinities, with the former closer to sub-Saharan Africans, the latter to Europeans and North Africans.

8. PROBLEMS WITH THE CONCEPT OF 'MODERNITY'

The fundamental problem of diagnosing ancient examples of 'modern' humans, morphologically and behaviourally, nevertheless persists because there is no agreement on how this should be carried out. In the past, I favoured the use of recent skeletal variation to diagnose whether a fossil could be termed 'modern' (Stringer 1994). It is now apparent that recent skeletal variation is smaller than that recognized for *H. sapiens* in even the late Pleistocene, and members of the *H. sapiens* clade in the African late Middle to early Late Pleistocene were much more distinct and diverse (Howells 1989; Stringer 1992; Lahr 1996). While there seems little doubt that Aurignacian and Gravettian-associated humans from 25–35 kyr ago in Europe share enough morphological and behavioural features with recent populations to warrant the application of the term 'modern', problems arise as we move further back in time. The samples from Skhul and

Qafzeh in Israel appear to represent a primitive form of *H. sapiens* (Trinkaus 1984; Vandermeersch 1989; Stringer 1992; Lahr 1996) but reassessments of their morphology, and that of samples from sites such as Klasies River Mouth, Omo Kibish, Singa, Ngaloba, Jebel Irhoud and Guomde (e.g. Lahr 1996; Trinkaus 1997; Pearson 2000) show mosaic evolutionary patterns. This means that a morphological definition of modernity based on recent samples will be problematic when applied further back in time.

A further problem with the use of recent samples to assess fossils is that current 'regionality' appears to have evolved quite recently. In both China and Europe it may only really have developed during the last 20 kyr (e.g. Stringer 1992; Lahr 1996; Brown 1999). Is this a reflection of a relatively late colonization of these regions by modern humans compared with Africa and Australia, or is it reflecting the impact of the last glacial maximum *ca.* 20 kyr ago, purging the earliest colonizers and followed by recolonization with the actual ancestors of today's inhabitants? While the combination of a morphological and metrical approach by Lahr (1996) undermined classic multiregional claims for the long-term persistence of regional characters, her studies did confirm the individuality of Australians in some respects. She argued that concepts of *H. sapiens* should not just be based on recent representatives, as in several aspects such as reduced size and robusticity we represent a restricted and atypical sample of the species as it was even in the late Pleistocene.

If, as suggested earlier, the characteristic morphology of modern humans evolved in a gradual, mosaic fashion, what of modern human behaviour? The concept of a 'Human Revolution', demarcating a punctuational origin of a package of recent human behaviours, such as complex language, symbolism and specialized technologies, has been central to much archaeological debate over the past ten years (Klein 2000). Originally focused on apparent contrasts between the Middle and Upper Palaeolithic records in Europe, this concept has now been extended to the Middle to Later Stone Age transition in Africa (table 1). It is argued that the major changes in human behavioural evolution occurred there by *ca.* 50 kyr (possibly related to mutations that enhanced brain function, leading to changes in cognition or language; Klein 2000). In turn, this led to the successful expansion of modern humans and now-modern behaviour beyond Africa, and the replacement of the remaining archaic populations. Thus morphological and behavioural evolution were decoupled, since 'morphological modernity' may have evolved before 'behavioural modernity'. This pattern is counterintuitive for those who argue that behavioural change lay behind the transformation of the archaic skeletal pattern into that of modern humans. However, it is based on the fact that, despite their morphological 'modernity', fossil samples from sites such as Klasies River Mouth and Skhul or Qafzeh are associated with Middle Palaeolithic artefacts, comparable with those made by Neanderthals, and apparently lack other aspects of 'modern' behaviour. The contrast between their morphology and their inferred behaviour is sufficient for Klein (2000) to employ the term 'near-modern' for them, implying that they represent an evolutionary stage where modern anatomy was evolving *prior* to truly modern behaviour.

Workers such as Lahr & Foley (1998) and McBrearty & Brooks (2000) have instead argued that previous views of modern behavioural origins display a Eurocentric bias and a failure to appreciate the depth and breadth of an African Middle Stone Age record that precedes the supposed 'Human Revolution' by at least 100 kyr. In this view, 'modern' features, such as advanced technologies, increased geographic range, specialized hunting, aquatic resource exploitation, long distance trade and the symbolic use of pigments, occur across a broad spectrum of Middle Stone Age industries. This suggests a gradual assembly of the package of modern human behaviours in Africa during the late Middle–early Late Pleistocene, and its later export to the rest of the World. Thus the origin of our species, behaviourally and morphologically, was linked with the appearance of Middle Stone Age technology, dated in many parts of Africa to more than 250 kyr ago.

It is thus debatable whether African Middle Stone Age humans really lacked 'modern' behaviour. Moreover, the Middle Palaeolithic associated Skhul–Qafzeh samples display morphological signs of behavioural change (Churchill 2001) as well as burials that apparently display evidence of 'modern' symbolic behaviour in the form of grave goods. There are also more remote indications that the dispersal of modern humans was not dependent on the appearance of the Later Stone Age/Upper Palaeolithic, and that symbolic behaviour existed before their development. As discussed earlier, there is growing evidence that Australia was colonized prior to 50 kyr ago and prior to the technological changes characterizing Mode 4 industries. Not only would this have required the development of maritime adaptations, but if the earliest Mungo fossils are representative of the first colonizers, these people were also engaging in complex behaviours such as burial with red ochre, and cremation.

In my opinion it is still too early to definitively determine when and where 'modern' morphology and behaviour developed, especially when these concepts are apparently so fluid. In my view, Africa was the ultimate source of the basic elements of both our anatomy and our behaviour. But it has also become evident that some claimed unique attributes of recent human behaviours were present even during the Middle Pleistocene outside Africa, for example, the evidence for systematic hunting of large mammals from sites such as Boxgrove and Schöningen, and the carefully crafted wooden javelins from the latter site (Dennell 1997; Stringer *et al.* 1998). Additionally, the debate about Neanderthal, and specifically Châtelperronian, capabilities highlights the issue of potential versus performance. d'Errico *et al.* (1998) have argued that Neanderthals were developing 'modern' symbolic behaviour independently of a *H. sapiens* morphology, thus producing a contrasting decoupling of modern anatomy and behaviour from that envisaged by Klein (2000). Others (e.g. Mellars 1999) argue that Neanderthals were developing complex behaviours only through contact with dispersing modern humans, not independently of them. The question of whether behavioural innovations arose regularly and independently in different populations in human prehistory (but were often lost during population crises or extinctions), or they spread widely by diffusion or dispersals, even between distinct populations and even species, remains unresolved.

While the temperate–cold climates of western Eurasia may well have influenced the evolution of the Neanderthals (e.g. Holliday 1997), it is still unclear what drove the evolution of *H. sapiens* in Africa. The large habitable area of that continent, combined with dramatic changes in precipitation and vegetation, might have forced evolutionary change through isolation and adaptation. As discussed earlier, there is also growing evidence for the precocious appearance during the Middle Stone Age of aspects of modern human behaviour such as symbolism. It may well be that the predominance of Africa was fundamentally a question of its larger geographical and human population size (Relethford & Jorde 1999), giving greater opportunities for innovations to both develop and be conserved (Shennan 2001), rather than the result of a unique evolutionary pathway, perhaps based on mutations affecting cognition (Klein 2000). The rapidity and repetition of late Pleistocene climatic oscillations outside Africa may well have continually disrupted long-term adaptation by its human populations, while Africa perhaps had shallower resource gradients (Foley 1989), greater chances of isolation and endemism (Lahr & Foley 1998), or encouragement of 'variability selection' responses to its environmental fluctuations (Potts 1998). While the admittedly limited evidence does seem to point to a gradual assembly of recent human morphology and behaviour in Africa during the period from 300 to 100 kyr ago, rather than major punctuational events, genetic data are ambivalent on this question. Several genetic datasets suggest that there was at least one major population bottleneck during this time-period (Jorde *et al.* 2000; Ingman *et al.* 2000; Takahata *et al.* 2001), with effective population size reduced to only a few thousand individuals. Such population crashes might indeed have produced saltational changes in morphology and behaviour within what must have been a diverse early *H. sapiens* clade. However, other evidence of the conservation of older (?African) population subdivisions suggests that there cannot have been severe, localized bottlenecks, as these could not have conserved earlier geographical substructuring (e.g. Tishkoff *et al.* 2000; Watkins *et al.* 2001).

9. CONCLUDING REMARKS ON MODERN HUMAN ORIGINS

It seems to me that the ideas discussed, whether ultimately supported or falsified, are important for the way that they highlight difficulties inherent in any absolute concept of 'modernity', behavioural or morphological. Yet, such concepts are critical to the reconstruction of our origins. Was 'modernity' a package that had a unique African origin in one time, place and population or was it a composite whose elements appeared at different times and places, and were then gradually assembled to assume the form we recognize today? While I argue that variants of the Multiregional Model have lost their validity when applied globally, could there have been an African-based multiregional model where 'modern' behaviours, morphologies and genes coalesced from different parts of that continent during the Middle Pleistocene? If so, we will need, yet again, to account for the unique importance of Africa in human evolution. Foley & Lahr (1997) argued that the contrasting geographies of Eurasia and Africa would have favoured latitudinal expansions and contractions in Eurasia but longitudinal ones in Africa. Consequently, both a larger population size and geography would have facilitated dispersal from Africa, but not in the reverse direction. However, much more evidence from the African late Middle Pleistocene archaeological, palaeontological and palaeoenvironmental records will be required to test such ideas. The burgeoning genetic data from present and, to a lesser extent, past populations will continue to illuminate events in human prehistory. These will feed into new models of modern human origins and dispersal. It also seems likely that many questions concerning the origins of the peoples of eastern Asia, Australasia, the Americas and even Europe will only be fully answerable when Asia yields up a later Pleistocene record to compare with that already recovered from Europe and beginning to be recovered from parts of Africa. Only then will we be in a position to finally establish whether all the most significant events in the early history of *H. sapiens* occurred in Africa and whether, as evidence is now suggesting, the main morphological and behavioural components that characterize our species had already developed there by 100 kyr ago.

Note added in proof. Several relevant publications have appeared since the completion of this paper. These include:

Balter, M. 2002 What made humans modern? *Science* **295**, 1219–1225.

Barham, L. & Robson-Brown, K. (eds) 2001 *Human roots: Africa and Asia in the Middle Pleistocene*. Bristol: Western Academic and Specialist Press.

Templeton, A. 2002 Out of Africa again and again. *Nature* **416**, 45–50.

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