

Mode 3 Technologies and the Evolution of Modern Humans

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The origins and evolution of modern humans has been the dominant interest in palaeoanthropology for the last decade, and much archaeological interpretation has been structured around the various issues associated with whether humans have a recent African origin or a more ancient one. While the archaeological record has been used to support or refute various aspects of the theories, and to provide a behavioural framework for different biological models, there has been little attempt to employ the evidence of stone tool technology to unravel phylogenetic relationships. Here we examine the evidence that the evolution of modern humans is integrally related to the development of the Upper Palaeolithic and similar technologies, and conclude that there is only a weak relationship. In contrast there is a strong association between the evolution and spread of modern humans and Grahame Clark's Mode 3 technologies (the Middle Stone Age/Palaeolithic). The implications of this for the evolution of Neanderthals, the multiple pattern of human dispersals, and the nature of cognitive evolution, are considered.

The last fifteen years have seen an intense debate over the origins and evolution of anatomically and behaviourally modern humans. This debate has largely been framed in terms of two contrasting hypotheses — the multiregional and single origin models. The Multiregional Model (MM) interprets the palaeontological evidence as indicating the gradual evolution of modern humans over a period of one to two million years. There would be no sharp chronological breaks in this evolutionary process, and most importantly, regional traits found in living populations would have been established in the deep past, modern features superimposed on them. In other words, the evolution of modern humans would have occurred across a broad geographical area from a number of regionally adapted archaic populations. The key mechanism in this model is continuous gene flow across the world throughout the Pleistocene, holding the hominid population together. This homogenizing gene flow would have taken place in a balanced equilibrium with regional selective pressures that allowed the establishment and maintenance of distinct morphologies. The Single Origin Model (SOM), on the other hand, proposes that modern

humans evolved in a restricted geographical area and dispersed in the relatively recent past across the world, displacing, for the most part, existing archaic hominid populations such as the Neanderthals. This model suggests that living humans are descended from an African population that lived about 150 thousand years ago (Kyr) (see Box for a brief description of the key issues and recent developments).

Archaeology has played a significant, if less central, role in this debate, and the archaeological record has been used as empirical support for both the MM or the SOM. Archaeological consistencies and anomalies brought into focus by the models have been used to support or refute them. But it is the archaeological record, with its potential for obtaining a far more diverse range of information than fossils or genes (cognition, tradition, technology, ecology, networks and social organization), that represents the richest record of the past. The problem lies in how to read the evidence in the same terms as the biologists read theirs. In effect this means putting phylogenetic issues back into archaeological methodology. What follows is a phylogenetic reading of late Pleistocene global patterns in stone tool

The modern human origins debate — the story so far

The debate over modern human origins continues a long-standing dispute among palaeoanthropologists about the relative contribution of archaic hominid diversity to the morphological diversity in present populations (Vallois 1954; Weidenreich 1943), about the relative antiquity and significance of human races (Wallace 1875), and about the differences between *Homo sapiens* and other types of hominid. The current phase of the debate took shape from Wolpoff and co-workers' establishment of the multiregional hypothesis as the most explicit formulation of a long-term anagenetic model, involving prolonged regional stability, gradual change and persistent gene flow (Frayser *et al.* 1993; Wolpoff 1989; Wolpoff *et al.* 1984), and from morphological (Howells 1976; Stringer & Andrews 1988; Stringer *et al.* 1984) and genetic proposals (Cann *et al.* 1987) for a recent and African origin for modern humans, involving human dispersal and replacement of archaic populations.

The basis for the Multiregional Model (MM)

Multiregional evolution has been based on morphological evidence from both fossils and extant populations. The two main empirical premises are: 1) regionally specific similarities between archaic and modern populations in Africa, Asia and Europe, indicating continuity of lines of descent within each region over long periods of the Pleistocene and across the archaic/modern transition (Weidenreich 1943; Wolpoff *et al.* 1984; Frayer *et al.* 1993); 2) the presence of signs of admixture between archaic forms and anatomically modern humans in eastern and central Europe (Smith 1992; Smith *et al.* 1989). Theoretically, the MM requires continuous global gene flow between regional populations.

The basis for a Single Origin Model (SOM)

Single origin views have been supported by evidence from a number of fields in biology and palaeoanthropology: 1) the earlier appearance of anatomically modern humans in Africa and the Levant in comparison with other regions (Deacon 1989; Grün & Stringer 1991; Singer & Wymer 1982; Stringer *et al.* 1989; Valladas *et al.* 1987; 1988); 2) the fossil evidence for the transition of hominid cranial morphology from archaic to modern forms in Africa, where clearly transitional forms are found (Florisbad, Ngaloba, Omo 2, Eliye Springs: Bräuer 1989; 1992; Rightmire 1989; Stringer 1992); 3) the absence of such transitional forms in Europe and Asia (Groves & Lahr 1994; Lahr 1996; Stringer 1989); 4) the relative lack of mtDNA diversity in humans compared to other hominoids (Ferris *et al.* 1981; Horai & Hayasaka 1990; Jorde *et al.* 1994; Kocher & Wilson 1991; Li & Sadler 1991; Morin *et al.* 1993; Wilson *et al.* 1985), indicating relatively little time for the accumulation of genetic variation; 5) an African rooting to the cladograms and trees built from human mtDNA and nuclear genetic variation (Cann *et al.* 1987; Bowcock *et al.* 1991; Vigilant *et al.* 1989; 1991), showing that Africans have greater diversity than any other continental population.

Critical developments

Both models have been criticized, but most of the evidence that has emerged over the last few years has been supportive of the SOM, with virtually no new data brought forward to support the MM.

1. Improved chronology has confirmed the pattern of an early transition from archaic to modern humans in Africa and the Levant, and a much later one in other parts of the world. Furthermore, in both Europe and in southeast Asia there is now evidence that archaic hominids survived as recently as 30 Kyr with no sign of admixture between them and modern humans (Hublin *et al.* 1995; Swisher *et al.* 1996).
2. Although the African rooting for the cladograms showing an early African split in the mitochondrial data was questioned (Maddison *et al.* 1992; Templeton 1993), more recent analyses, including trees built from a number of nuclear genes, have confirmed the early findings (Cavalli-Sforza *et al.* 1994; Nei & Takezaki 1996; Penny *et al.* 1995).
3. Criticisms that the African rooting of the mtDNA could reflect the dispersals out of Africa over a million years ago have themselves been refuted. Coalescence in a number of gene systems all indicate a most likely estimate for the last common ancestor for particular genetic systems in the later Middle Pleistocene (Bowcock *et al.* 1994; Cavalli-Sforza *et al.* 1994; Hasegawa *et al.* 1993; Horai *et al.* 1995; Jorde *et al.* 1994; Stoneking 1993; Tamura & Nei 1993; Vigilant *et al.* 1989).
4. A significantly greater diversity of African populations in relation to the rest of the world was confirmed in a variety of genetic systems (Bowcock *et al.* 1994; Harpending *et al.* 1993; Horai *et al.* 1993), as well as cranial morphology (Lahr 1996; Relethford 1995) and global patterns of genetic linkage disequilibrium (Armour *et al.* 1996; Tishkoff *et al.* 1996). These results are supported by data on the Y-chromosome (Hammer 1995; Paabo 1995; Santos *et al.* in press; Whitfield *et al.* 1995).
5. Genetically derived estimates of prehistoric population sizes indicate a recent genetic bottleneck in human evolution (Brown 1980; Haigh & Maynard Smith 1972; Horai *et al.* 1995; Jones & Rouhani 1986; Maynard Smith 1990; Rogers & Harpending 1992; Rogers & Jorde 1995; Takahata *et al.* 1995; Wills 1990). Mismatch pair analyses of differences within and between human populations in mtDNA variation show that such a bottleneck was followed by a number of marked demographic expansions, of which the African is the most ancient (Harpending *et al.* 1993; Sherry *et al.* 1994).

In addition, much of the theoretical and empirical basis of the MM has been questioned. Empirically, the MM is based on the evidence for regional continuity from archaic to modern outside of Africa. It has been shown, however, that the so-called East Asian and Australian regional continuity traits are not geographically discrete either in the past (Habgood 1989; Groves 1989; Groves & Lahr 1994) or the present (Lahr 1994), and are thus neither stable nor reliable as markers of populations. Statistical comparisons of possible ancestral morphologies between Neanderthals and early modern fossils show that the evidence conforms best with the expectations of the SOM (Waddle 1994). Overall, the fossil record has failed to show empirical support for what would be key transformational links in the MM — between Ngan'dong and modern Australians, between Neanderthals and modern Europeans, and between early modern Chinese populations and archaic Chinese fossils (Lahr 1996; Stringer 1995). Theoretically, the MM depends on continuous gene flow between regional populations over the Pleistocene in order to maintain species cohesion. The theoretical models on which evolutionary history is inferred from genes make assumptions about population size and stability. Recent work has shown that for the MM to have occurred the global population would have had to have been both remarkably small, subdivided and demographically stable (Manderscheid & Rogers 1996; Rogers 1995). These assumptions are not consistent with either the estimates of past population size or with the nature of human genetic variation.

Although the MM is a remarkably flexible model and can incorporate virtually all possibilities and still survive (Wolpoff 1996), the overwhelming trend in recent work has been to increase the empirical evidence in favour of a SOM, to undercut the theoretical and empirical basis for the MM, and to show that modern humans are derived from a relatively recent African source population. This is not to say that there are no issues unresolved or no development in the SOM. The extended chronology, the high levels of subsequent gene flow, the evidence for multiple dispersals, the changes in hominid populations in the later Pleistocene, all argue against a single revolutionary origin-dispersal-replacement event (Lahr & Foley 1994). Nonetheless, a recent African origin of modern humans is the best basis for examining later Pleistocene hominid prehistory.

technology, compared with hominid palaeontology and genetics. The central aim is to explore the extent to which archaeological data can throw light not just on the behaviour of early modern humans and the archaics, but also on their evolutionary relationships.

Behaviour and population history

Although the archaeological evidence has been an element in the reconstruction of modern human origins and dispersals, by and large, it has not been fundamental to arguments drawn from palaeobiology and genetics. With some notable exceptions (Klein 1992; 1995; Mellars 1989), archaeology has recently been used either as supplementary support for one particular model, or as a spoiler against another, but not systematically to build one. Where archaeology has been central is in adding a behavioural dimension to a debate about population history.

Archaeologically, the key issue is the degree and significance of differences between archaic and modern humans. To some extent this is the extension of an older and broader debate, harnessed to the modern human origins problem. Since the 1970s, there has been a tendency to emphasize the distinctiveness and recency of modern human behaviour (Binford 1981; Mellars 1991). Initially, this concerned the significance of hunting, but rapidly became extended to other aspects of behaviour — from food sharing, settlement patterns, technological complexity, technological flexibility, resource utilization and dispersing behaviour, to the presence or absence of art and other types of symbolic thought (Bahn & Vertut 1988; Binford 1981; 1984; Gamble 1993; Klein 1992; Mellars 1989; 1991; White 1989). Contrasts have also been drawn in terms of patterns of robusticity (Churchill 1996; Ruff *et al.* 1994), locomotor behaviour (Trinkaus 1992; 1993), language (Binford 1989; Lieberman 1989), and mortality profiles (Berger & Trinkaus 1995; Trinkaus & Shipman 1993).

Although disputed (e.g. Arensburg 1990 *et al.*; Clark & Lindly 1989), this was a major departure from the previous orthodoxy, which stressed the essentially human nature of archaic hominids (Isaac 1978). The link with the modern human origins debate is the expectation that an ancient divergence between modern humans and Neanderthals will be correlated with major behavioural differences, a low probability of inter-breeding, and a higher probability of replacement. The MM, proposing high levels of gene flow, has thus become associated with archaeological interpretations that stress the similarities between Neanderthals and modern humans, while the SOM,

proposing replacement, has required substantial differences as a mechanism for explaining modern human success. In effect this means that the archaeological record will support the SOM when it shows discontinuities in behaviour between archaics, especially Neanderthals, and modern humans for it is inferred that the greater the differences, the less likely gene flow will have occurred. The inferred cognitive and behavioural differences then become the explanatory basis for the success of modern humans relative to Neanderthals — more efficient use of technology and resources, or else more secure social and psychological adaptations. Cognition has perhaps been the crux of the archaeological debate, for it may be differences in neurobiology that will link inferred behavioural capacities to some sort of biological and evolutionary basis. The role of archaeology has thus been to emphasize questions of function, behaviour and cognition. In contrast, biologists have focused largely on phylogenetic reconstruction — the history of population relationships. The contrast between the functional and adaptive interests of most archaeologists and the genealogical concerns of most biologists is striking. The question we would pose here is: What happens if the approaches are reversed, archaeological data are treated as a primary source of phylogenetic information about recent human evolution?

Function and phylogeny in the archaeological record

Quantitatively, the archaeological record is immensely richer than that of fossil hominids, and so could be the basis for building hypotheses about human evolutionary history. There is certainly historical precedence for this. Many archaeologists have made the straightforward assumption that similarities in artefact type represent shared culture — the 'culture-people hypothesis' (Childe 1956). Shared traits in artefacts were traditionally used to identify archaeological units. The basis of such archaeological units were either particular type fossils or artefacts, or overall assemblage structure, using techniques such as those developed by Bordes (1950; 1961a). Shared cultural traditions thus formed the basis for unity of form. Much of the archaeology of the first half of this century was based on this simple model, and prehistory was largely interpreted in terms of the movements and diffusion of people and their ideas. A reaction to these views came with the introduction of chronometric dating techniques and a greater interest in the mechanisms of cultural change and adaptation. Dating developments, such as the

radiocarbon method, were important as they showed that the appearance of similar artefacts in different parts of the world was not consistent with diffusionist models (Renfrew 1973). With ideas drawn from both ecology and cultural anthropology which suggested that material culture and economic systems reflected functional demands, archaeologists preferred to explain similarities in form in terms of local convergence, adaptation to local raw material availability and autochthonous developments, and more generally as complex systems (Clarke 1968). A consequence of this has been a view that the archaeological record does not possess 'phylogenetic' information, but is interpretable primarily in terms of adaptation. Similarities in form reflect similar environmental demands and constraints. The controversy over functional versus phylogenetic interpretations of the archaeological record is well-exemplified by the 'Mousterian debate'. On the one hand, Bordes accounted for the variability in Mousterian artefact assemblages in terms of alternating tribes or social groups occupying the caves of southwestern France in alternating sequence (Bordes 1961b). Binford (1973), on the other hand, saw the same pattern of variation in terms of function — different frequencies of scrapers and points reflected different activities and environments.

Essentially, the approach of archaeologists in the first half of this century accepted that the archaeological record had a high phylogenetic signal. In contrast, recent assumptions have played down the extent to which population history can be inferred from artefact typology and assemblage structure. Three factors, however, have led to a renewed interest in the extent to which population history — cultural, ethnic and genetic relatedness — may be inferred from the archaeological record.

First, the greater use of genetics to investigate historical aspects (Cann *et al.* 1987; Cavalli-Sforza *et al.* 1994; Takahata *et al.* 1995), has prompted the question of who, biologically speaking, the people of prehistory were. Access to this type of information has renewed archaeological interest in the mechanisms of cultural change — local adaptation, diffusion, replacement, migration and assimilation, as shown by growing research on genes, language and archaeology (Barbujani 1996; Renfrew 1991).

Second, both primatologists and archaeologists have become centrally concerned with cognition, especially differences between humans and other animals (Gibson & Ingold 1993). Ironically, a common interest in the social basis of cognition among both social and biological scientists has brought the issue of species differences and their markers to the fore.

Finally, the modern human origins debate has in fact led to a greater use of archaeological data to show the geographical aspects of evolutionary events, such as population ranges, dispersing patterns and routes (Mellars 1991; Gamble 1993). Archaeological data and ideas have thus been a constant part of the current debate.

Current phylogenetic interpretations of archaeology: the 'Upper Palaeolithic hypothesis'

The Upper Palaeolithic has been used as a shorthand for technological complexity, blade production (Mode 4 technology in Clark's 1977 classification), bone and composite tools, more extensive raw material utilization, intensive and efficient hunting, as well as the development of art and symbolism (Fig. 1). These traits show human behaviour that is fully compatible with modern human capacities and abilities as observed ethnographically. In the current debate this behavioural 'package' has been taken to be closely associated with the evolution of modern humans. The Upper Palaeolithic has been interpreted as a behavioural revolution (Mellars 1991; 1996), as a symbolic explosion (Knight *et al.* 1995; White 1989; Mithen 1996), and as the adaptive basis for global dispersal (Klein 1992; 1995). This human revolution has been ascribed to human capacity for language (Davidson & Noble 1989), symbolic thought, and theory of mind (Mithen 1996), or a shift in general neural competence (Klein 1992; 1995). This Upper Palaeolithic or 'Mode 4 hypothesis' takes two forms. In its stronger form, the anatomical evolution of modern humans would be expected to coincide with the development of Upper Palaeolithic technologies. Chronological discrepancies between the two events has led to weaker formulations, in which linkage between behavioural and anatomical change is not total.

It is clear, however, that the associations between the traits composing the behavioural 'package' and the Upper Palaeolithic, and between the Upper Palaeolithic and modern humans, are complex. Both Neanderthals and early moderns can be found associated with the same technology, modern humans may be associated with simpler technologies, and archaic hominids may also display parts of the Upper Palaeolithic package. These anomalies have been cited as evidence for a single behaviourally homogenous early Upper Pleistocene hominid population, and hence consistent with the MM (Clark, G.A. 1992; Clark & Lindly 1991). This is a functional hypothesis, with technologies converging for adaptive reasons, and thus providing no phylogenetic

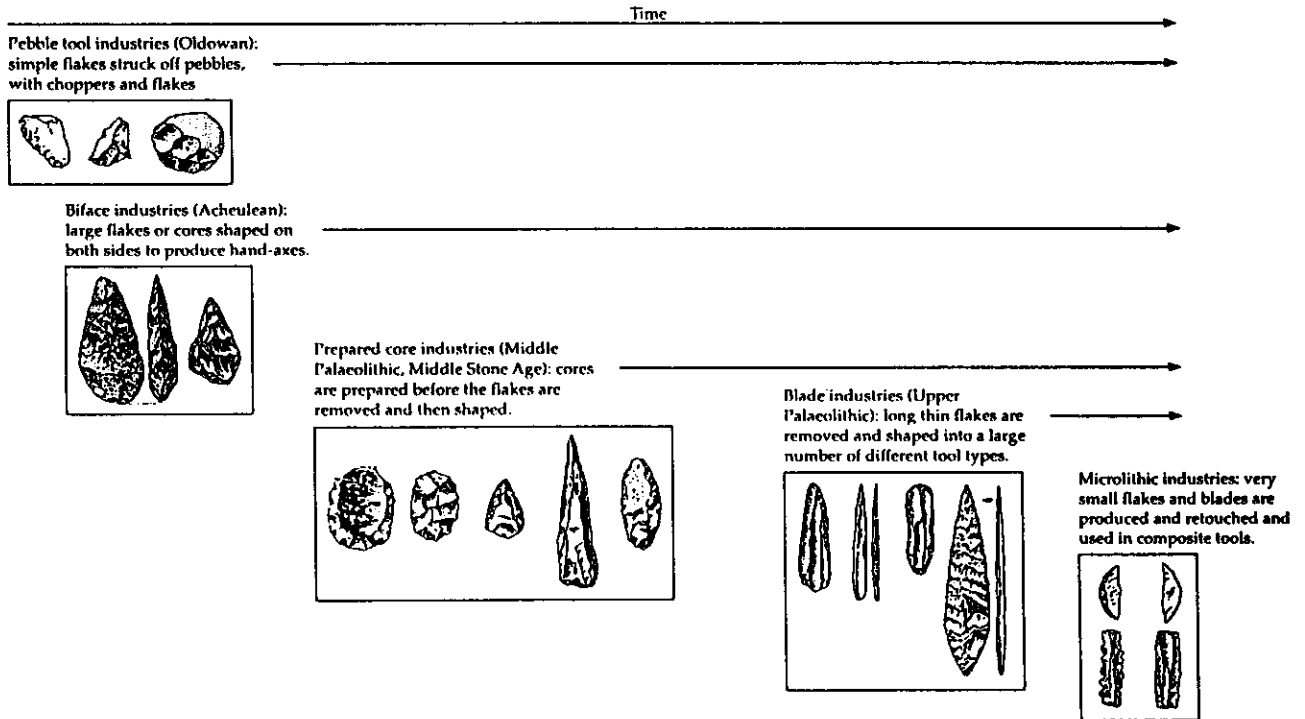


Figure 1. Clark's (1969) classification of technological modes recognized that the development of stone tools involved the addition of new traits. The principal technological characteristics of the modes are shown here. These are presented in a relative chronological order. A key element of the mode classification is that the development of a more derived mode does not necessarily mean the disappearance of more ancient ones, and characteristics are cumulative (see also Fig. 3).

information for or against the various models.

The suitability of a 'Mode 4 hypothesis' is dependent upon the extent to which Upper Palaeolithic elements occur as a package, and in turn whether these elements provide a signal for the dispersal of modern humans from an ancestral source. However, a number of discrepancies are found.

In the first place, Upper Palaeolithic elements occur within the context of Mode 3 or Middle Stone Age industries: blades in the Howieson's Poort in South Africa (90–60 Kyr) (Deacon 1989; Klein 1994; Singer & Wymer 1982); barbed points and fishing implements at the Katanda sites in the Semliki Valley in Zaire (Brooks *et al.* 1995; Yellen *et al.* 1995); blades in the pre-Aurignacian of Cyrenaica (McBurney 1960; 1967), and stemmed and tanged points in the Aterian of the Maghreb (Clark 1993; McBurney 1960; Wendorf *et al.* 1990). In the case of the southern African Howieson's Poort and the Aterian, the association between these 'advanced' assemblages and modern humans has been confirmed by fossil data (Bräuer 1992; Hublin 1993; Rightmire 1989; Stringer *et al.* 1984). While these associations have been taken to support the SOM (Deacon 1989; Stringer 1989) and

to show early 'modern' behaviour in Africa, they also pose problems. In the case of both the Howieson's Poort (Deacon 1989; Klein 1994) and the pre-Aurignacian (McBurney 1967), they are replaced by typical Mode 3 industries, and the Semliki finds appear to be an isolated occurrence. This might indicate the transitional nature of modern humans at this stage, but it is nonetheless unexpected.

A similar anomaly of Upper Palaeolithic elements within Mode 3 assemblages has been identified in some very late European Middle Palaeolithic (Mousterian) levels. The Châtelperronian of south-west France contains burins and endscrapers (Harrold 1989), as well as, at Arcy-sur-Cure, bone artefacts and beads (Hublin 1996). The Szeletian of Central Europe includes bifacially pressure-flaked leaf points (Allsworth-Jones 1986), and the Uluzzian backed points (Mellars 1996). Historically, these assemblages have been interpreted as the local transition of Neanderthals into modern Europeans (Bordes 1961a). The combination of chronological proximity and morphological distance between Neanderthals and early modern Europeans, however, is not consistent with indigenous evolutionary

change. Furthermore, recent discoveries have shown that these 'advanced' Middle Palaeolithic industries are associated with hominids with Neanderthal features at St Césaire (Lévêque & Vandermeersch 1981; Lévêque *et al.* 1993) and Arcy-sur-Cure (Hublin 1996). That their development was not universal among terminal Neanderthals is shown by the association of the very late Neanderthal at Zafarraya with a fully Mousterian assemblage (Hublin *et al.* 1995).

An alternative explanation is that the changes observed in the Châtelperronian, Szeletian and Uluzzian were the result of acculturation of the indigenous Neanderthals under the influence of the incoming modern humans who were associated with the first Upper Palaeolithic tradition, the Aurignacian (Mellars 1992; 1993). This may have occurred with (Bräuer 1992; Smith 1992) or without (Mellars 1992; 1993) interbreeding, and it may have been stimulated either by direct interaction and observation, or more indirectly as the Neanderthals adapted to the new elements in their environment. Such an interpretation is consistent with the basic structure of the SOM, and could involve admixture (Bräuer 1992; Smith 1992) or replacement (Harrold 1989; Hublin & Tillier 1992; Klein 1992; Mellars 1989; 1992; Stringer *et al.* 1984) between Neanderthals and moderns. In Europe, especially western Europe, the absence of evidence for transitional morphologies, the apparently prolonged period of overlap (between 10 and 15 Kyr), and the technological changes associated with the terminal Neanderthals, all indicate a complex process of competitive displacement, not a drastic and instantaneous replacement event. The European case shows no simple correlation between biology and technology, but there is nonetheless an evolutionarily meaningful pattern.

Another discordant pattern for the Mode 4 hypothesis is the co-occurrence of modern humans and less developed technological systems. The actual associations between modern humans and Mode 4 industries are either relatively young (50 Kyr), ephemeral (e.g. Pre-Aurignacian) or partial, such as the fact that the Howieson's Poort is very much a Middle Stone Age industry with some blades. The earliest fossils recognized morphologically as modern (Omo 1, Klasies River Mouth and Border Cave in Africa, and the Skhul and Qafzeh series in Israel) are all associated with Middle Palaeolithic or Middle Stone Age industries (Mode 3) (Allsworth-Jones 1993; Bar-Yosef 1993). The case of Skhul and Qafzeh, and their apparent association with local Levalluois-Mousterian artefacts is perhaps the most cited example of a mismatch between technology and biology

(Foley 1987). All the caves for the period 120–50 Kyr in Israel show a Mousterian technology, and it is only after this date that the Upper Palaeolithic makes its appearance (Bar-Yosef 1992; Marks 1990). The fossil evidence, though, is not so simple. Both early modern humans (110–90 Kyr) at Skhul and Qafzeh, and later Neanderthals at Tabun, Kebara and Amud, are associated with Levalluois-Mousterian assemblages. In Israel at least, modern humans and Neanderthals may not have shared genes, but they do seem to have shared stone tools. This mismatch is a major problem for the SOM as generally formulated, although it does not necessarily follow that it provides support for the MM, since the alternating morphologies do not imply continuous gene flow (Foley 1987).

A number of explanations have been proposed for the Levantine anomaly. Lieberman & Shea (1994) showed that there are seasonal differences in resource utilization strategies, with modern humans pursuing a more seasonally specific hunting strategy. Bar Yosef (1992) has suggested that there are detailed typological differences within the Tabun sequence, and that modern humans and Neanderthals in the Levant are not associated with exactly the same archaeological assemblages. These results show that in terms of both detailed assemblage structure and ecology, there is patterned variation in relation to biological differences. Nonetheless, the fact that two distinct groups of hominids with apparently different ancestry share the same broad technological system remains a major problem for modern human origins and for the Mode 4 hypothesis.

Although the Mount Carmel anomaly is the best known, it is actually the Australian and southern Asian discrepancies that are more problematic for a 'Mode 4 hypothesis'. While the presence of early modern humans with Mode 3 industries has been explained by a later neural mutation within the context of already morphologically modern people (Klein 1995), the apparent absence of Mode 4 industries in certain parts of the world is difficult to accommodate within this model. According to a 'Mode 4 hypothesis', all modern populations of the world derive from the dispersal of the population that developed something like the European Upper Palaeolithic. In most parts of sub-Saharan Africa, however, and through southern Asia, across southeast Asia and southern China, and in Australia, there is no Upper Palaeolithic system as defined by the Mode 4 technological complex. The Upper Palaeolithic is a much more geographically restricted event, confined to Eurasia and north/northeast Africa.

The 'Mode 4 hypothesis' is the only current

model for the origin of modern humans derived from archaeological data, and it does so within the context of a SOM. The long-recognized association between the Upper Palaeolithic and anatomical modernity has been used as a base-line for interpreting cognitive differences between modern and archaic hominids (White 1989; Mellars 1989; 1991), thus stressing the biological significance of the evolution of modern humans. As can be seen from Figure 2, the empirical evidence for this association is real in certain parts of the world for the last 50–40 Kyr, but it cannot be extended to all regions and all modern populations, and it would be difficult to argue for a simple pattern of evolution and dispersal of Upper Palaeolithic populations over a relatively short period of time as the bearers of a uniform and adaptively superior technology.

Two responses to this complexity are possible. It could be concluded that archaeological data should not be used phylogenetically, and that the discordant morphological–technological associations are the real clue to the functional plasticity of archaeological assemblages. Such an attitude, however, would assume that all the concordant associations, which are the majority, are coincidental or without meaning. The second possibility is to search for different underlying patterns to the biological–technological relationship, and thus for alternative evolutionary hypotheses.

Concepts and methods in phylogenetic interpretations of archaeology

The archaeological record in general, and stone tools in particular, can provide phylogenetic information at two levels. The first is that the skills and capacities necessary to produce particular assemblages may be the hallmarks of levels of hominid cognition, and thus reflect significant evolutionary change, attributes that gave the holders such advantages that they came demographically to replace other groups. These changes would not *a priori* be species-specific, but could nevertheless be used to explore the behavioural transition from archaic to modern humans. It is this level that was employed in the Mode 4 hypothesis.

The second level of phylogenetic information does not reflect cognitive capacities, but group affinities. These may be reflected in overall assemblage structure and local innovations, and changes may appear and disappear, appear and be maintained, or appear and spread, depending on the survival, competitive and dispersal potential of populations in particular environmental circumstances. These, by definition, would be population-

specific, and could be explored to deal with the problem of modern human diversification.

The first level changes are behind Clark's mode classification (Clark 1977), as these may reflect respectively the appearance of intentional processes evidenced in the pattern and design in lithic artefacts (Mode 2), the appearance of abstract mental processes evidenced in the preparation of Levallois cores prior to the removal of intended flakes (Mode 3), and the appearance of systematic problem-solving processes and external expressions of self, aesthetic and socio-symbolic concepts (Modes 4 and 5). On the second level are typological aspects of assemblage structure. Similarity of certain artefact forms, it is assumed, reflects shared cultural knowledge, and by and large correlates with shared mating patterns and hence biological identity at the populational level. A concomitant assumption is that the spatial distribution of these artefact types will reflect the geographical range of specific populations. The scale of this will vary markedly, however, as it may represent the effective area of a population or the result of dispersing events of different temporal depth. Finally, a converse assumption is that differences in aspects of material culture will represent local adaptations in the absence of significant exchange with other groups, thus reflecting periods of cultural and biological barriers.

Applying these assumptions to the problem of modern human origins, it is possible to use the relative wealth of the archaeological record, compared to that of hominid fossils, to establish spatial and temporal patterns of diversity which *a priori* would cover but not necessarily correspond to two biological levels, hominid species and human populations. The archaeological record is used below to generate a model of the human evolutionary pattern in the later parts of the Pleistocene based on the working hypothesis that it is possible to track phylogeny in the archaeological record (Foley 1987).

A number of qualifying points should be made, as it is clear that the assumptions outlined above run counter to many that are currently employed in archaeology. First, they are exactly that, working assumptions that can be used to explore patterns in the data. We are not arguing that there is direct evidence that archaeological assemblages equate with biological populations, but rather that one possible working assumption is to look systematically for relationships. It will probably never be possible to test this assumption as a general assertion, although it could be possible in a number of specific cases. Rather than testing the assertion directly, we can

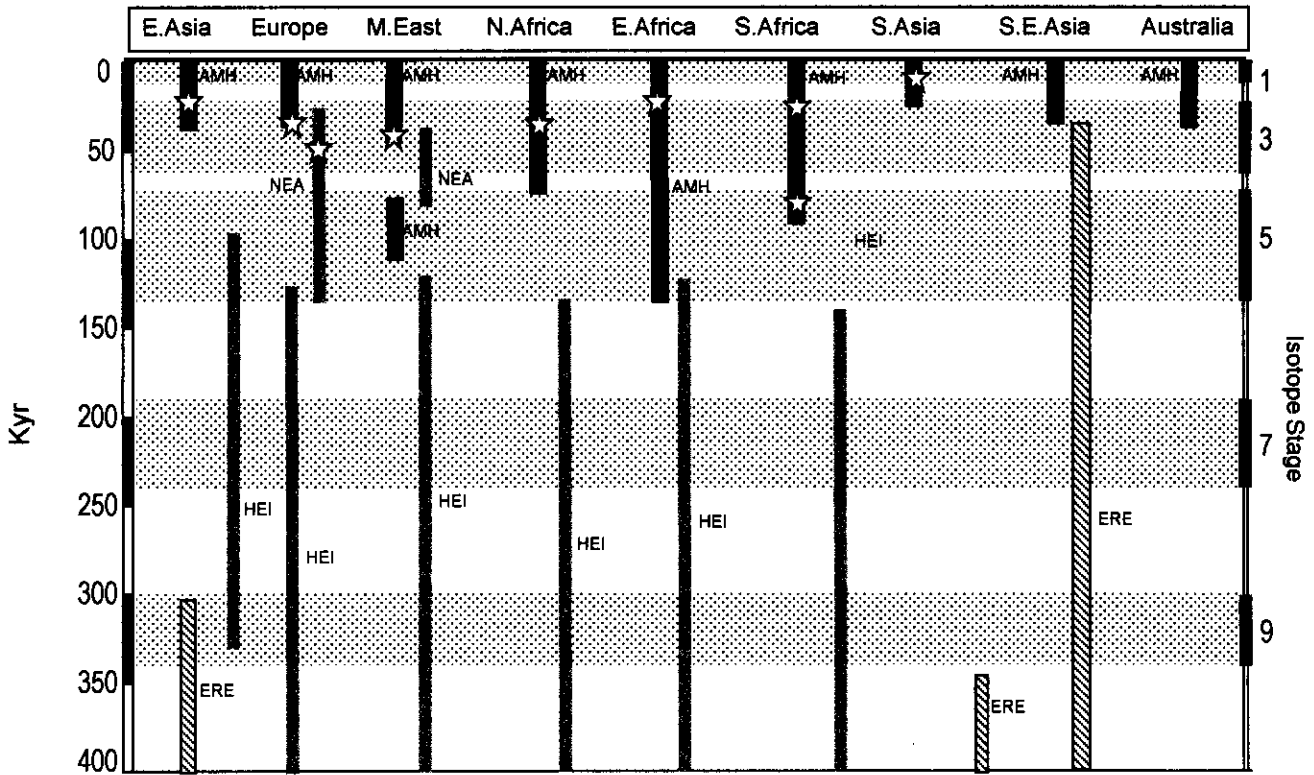


Figure 2. Association between hominid types and blade (Mode 4) technologies. The presence of blades is indicated by a star. As can be seen, blade technologies are found with both anatomically modern and archaic hominids, and modern humans occur with Mode 3 industries as well as Mode 4.

look for general correlations in patterns between fossils, archaeology and genetics. When such relationships are established, it will then be necessary to examine more closely their underlying basis.

Second, we are starting from the premise that it is extremely unlikely that there will be a universal relationship between cultural, technological and biological patterns. Enough is known about the complexities of the evolutionary, anthropological and ecological aspects of populations to be certain that a number of different relationships are likely to exist. In some circumstances, we may expect cultural and biological boundaries to coincide. In other cases, there may be no boundaries at all, merely clines of biology and culture that may or may not occur at the same rates. Or there may still be a complete disjunction between the two. The key point is not to presuppose the nature of the relationship, but to establish the pattern in order to consider what factors might affect whether there is a positive, neutral or negative relationship between biological and archaeologically-measured parameters. And third, while the term 'culture' is too deeply rooted into the archaeological literature for it ever to be replaced, we believe that it

is far too loaded a concept to be usefully employed in this case. Although what we will be examining have been referred to as cultures, and that has been the basis for definition in many cases, the assumptions that go along with it will probably neither be useful nor shared by all archaeologists. We are using the concept of operational taxonomic units (OTUs) that ultimately reflect generally perceived 'cultures' in that they can be identified on the basis of the material record, principally the style and technique of stone tool manufacture. In effect, these are 'archaeological taxonomic units' (ATUs) with patterns available for interpretation according to different assumptions or theoretical perspectives.

In order to use archaeological data systematically as the basis of an evolutionary hypothesis, the first task is to establish the pattern of archaeological variability over the relevant time period, from approximately half a million years ago to around the end of the Pleistocene.

One of the advantages of using Clark's classification of technological modes is that they can describe observed variation at a global level. They can also be applied across assemblages that have been

relatively unevenly described and studied, and have indeed been widely used.

The key to the technological mode classification is that it is normative and progressive; normative in the sense that it describes the predominant method of stone tool production and, in particular, of core reduction. Assignment to a particular mode does not preclude a minority occurrence of other techniques belonging to a more derived category. Of course, this can lead to some of the difficulties that have led to criticisms of the method, in particular that it is essentially qualitative. Nonetheless, at this categorical level, it remains a useful way of obtaining a broad view of the pattern of basic technological processes employed. The taxonomic system is progressive in the sense that adoption of a Mode 2 technology does not mean that Mode 1 elements are lost. Technological development is thus progressive in that, where the innovation is taking place, new elements are added to the existing assemblage. Even the most sophisticated Solutrean pressure flaker must occasionally have considered an Oldowan flake to be adequate for the task. A progressive system such as this is, in fact, concordant with the principles of cladistic methods for reconstructing evolutionary relationships (Foley 1987; Robson Brown 1995). Cladistics uses only derived features for classifying lineages; the presence of traits inherited from ancestors in the more distant past or from common ancestors are not useful for distinguishing separate lineages. In this context, the presence of a Mode 1 artefact in a Mode 4 industry may be interesting and important from an adaptive and functional point of view, but not in terms of phylogenetic systematics (Fig. 3).

There is little doubt that Clark's technological modes and specific typological categorization of assemblages do not serve the needs of many archaeological projects. They are far too coarse-grained for answering detailed questions about behaviour at a local level, or accounting for variation within relatively homogeneous technologies. They are useful, however, for tackling variation on a global scale over large time spans.

Archaeological assemblages 500–10 Kyr: broad patterns

The description of the archaeological assemblages of the last half million years which follows has two very specific purposes; first, to map in time and space the distribution of Clark's archaeological modes, and second, to summarize the history (first appearance, last appearance, and pattern of spread

and contraction) of specific elements with which modern human fossils are associated. These distributions will be employed as a proxy for hominid populations, to create an archaeologically-based evolutionary model for comparison with fossil and genetic data.

Distribution of Modes

All of Clark's five technological modes can be found in the last half million years, but they have distinct spatio-temporal distributions. The archaeological record begins with Mode 1 industries during the late Pliocene in eastern Africa (2.4–2.3 Myr). These are cores and flakes, the former without a standardized shape and the latter typically large, unprepared or retouched (Schick & Toth 1993). Mode 2 industries appear in East Africa at Konso-Gardula (Ethiopia) about 1.6–1.4 Myr (Asfaw *et al.* 1992), characterized by the standardized bifacial shaping of cores. In

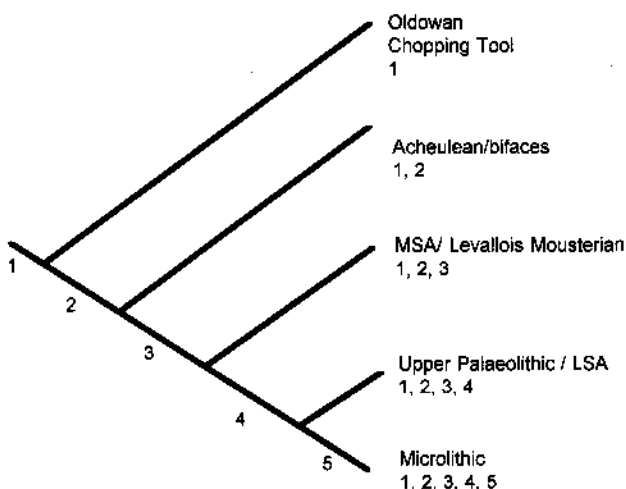


Figure 3. Clark's technological modes (1–5) can be treated in terms of phylogenetic systematics or cladistics. The cladogram shows the branching sequence involved in the development of modes. At each branching point in the cladogram a new trait is added, but at the same time the more ancient ones do not disappear. In cladistic terms they become plesiomorphies. Plesiomorphies do not provide phylogenetic information. The more derived traits (in this case, the most derived modes) are apomorphies and can give useful phylogenetic information. The particular branching sequence shown here follows that implied by Clark's original formulation, but as is discussed in the text, this may not accurately reflect the relationships between Modes 4 and 5. (See Foley 1987 and Robson Brown 1995 for a full discussion of the application of cladistic terminology to hominid technology.)

Africa, Mode 1 industries coexist alongside Mode 2 ones for a considerable length of time (Clark *et al.* 1994; Phillipson 1985). In Eurasia, with one exception, all the earliest archaeological sites contain only Mode 1 industries: Dmanisi in Georgia at 1.8–1.6 Myr (Bar-Yosef 1994; Gabunia & Vekua 1995), south-east Asian sites between 1.8 and 1.6 Myr (Swisher *et al.* 1994); Chinese sites from 1.0 Myr (Nihewan Basin: Schick & Dong 1993) and possibly 1.9 Myr (Longgupo: Huang *et al.* 1995); and in the case of Europe, a number of late Lower or earliest Middle Pleistocene sites like Gran Dolina at Atapuerca, Spain (Arsuaga *et al.* 1994; Carbonell *et al.* 1995; Pares & Perez-Gonzalez 1995), Cueva Victoria, Spain (Palmqvist *et al.* 1996), and possibly Isernia la Pineta, Italy (Coltori *et al.* 1981), Karlich, Germany (Bosinski 1986), and Solihac, France (Collins 1986). The exception is the Middle Eastern site of 'Ubeidiya (1.4–1.3 Myr), which contains two temporally close levels of occupation, the lower one with Mode 1 and the higher with Acheulian handaxes (Mode 2) (Bar-Yosef 1994; Tchernov 1994) (Fig. 4A).

Mode 1 industries continue beyond 500 Kyr in Eurasia (e.g. Clactonian), but after that date Mode 2 industries appear at several sites in the Levant and Europe: Gesher Benot Ya'acov, Giv'at Shaul (Bar-Yosef 1994; Goren Inbar *et al.* 1992), Boxgrove (M. Roberts *et al.* 1994), Hoxne (Singer *et al.* 1993), Cagny-la-Garenne (Bourdier 1976; Villa 1991), Fontana Ranuccio (Segre & Ascenzi 1984), Torralba and Ambrona (Howell 1966; Freeman 1994). Mode 2 industries are also found in the Middle Pleistocene of northern India (Narmada), although there are no more precise dates. Mode 1 industries persist in southeastern and eastern Asia, and the absence of Mode 2 in these areas creates the controversial Movius line (Fig. 4B).

The east-west differences persist until at least 350 Kyr. At this time, elements of a Mode 2 industry (bifaces, possible retouched cleavers) may be present at the site of Dingcun in northern China, but these never show the standardized form of the western Acheulian (Clark & Schick 1988). Mode 1 industries continue in southern China. In southeast Asia, associations between hominid occupation and stone tools can be documented only for the Kabuh levels, and these are simple Mode 1 flakes (Simanjuntak & Semah 1996). Between 350–250 Kyr, Mode 2 industries dominate in Europe (Gamble 1986). Regional fragmentation of Mode 2 industries also seems to occur: the Levantine Mode 2 differentiates into the Acheulo-Yabrudian (Bar-Yosef 1993); in sub-Saharan Africa into forms like the southern African Fauresmith, the

Dakla, Langoan, and Sangoan (Clark, J.D. 1992). Mode 3 is essentially a core preparation and reduction refinement. Early manifestations (>250 Kyr) are found in Africa and Europe. The African Victoria West perhaps represents the earliest diagnostically distinctive form of Levallois-style core preparation. In contrast, the European record shows a more complex process involving, on the one hand, reduction in handaxe size, to converge on Levallois cores, and on the other, a patchy appearance of Levallois technique with a continuing Acheulean tradition (Fig. 4C).

After 250 Kyr, typical Mode 3 industries, in which the emphasis is on comparatively small flakes obtained through previous core preparation, are observed in South, East and North Africa (at Florisbad: Grün *et al.* 1996; at Gademotta Formation: Wendorf & Schild 1974; and at Ngoloba: Hay 1987), and in Europe (at Ehringsdorf: Blackwell & Schwarcz 1986; and Pontnewydd: Green 1984). Although broadly contemporaneous, the relationship between Mode 2 and 3 industries in Africa and Europe is very different. In Africa, Mode 3 elements can be observed in Mode 2 contexts, but once Mode 3 industries get established, handaxes become rare or absent (McBurney 1960; Phillipson 1985). Distinct Mode 2 and 3 industries are not found alongside each other in Africa. Rather, Mode 3 becomes the norm except for the forested areas of western Africa, where the Sangoan (a Mode 2 ATU) persists (Clark, J.D. 1992). During the period 250–50 Kyr, regional variations in Mode 3 industries developed. In Africa, these include the variable appearance of elements of Modes 4 and 5 — blades (Howieson's Poort, Cyrenaican pre-Aurignacian, Sebilian at Kom Ombo), task-specific tools (Ishango harpoons) and tanged elements (Aterian), as well as diminutive Levallois flakes, small backed blades and geometric forms (Kom Ombo, Fayum) (Vignard 1923; McBurney 1960; Deacon 1989; Clark, J.D. 1992; Allsworth-Jones 1993). Overall, the African archaeological record shows the sporadic, transient and dispersed development of various forms of blade, microlithic or advanced bone technology. The European situation is different. Mode 3 or Middle Palaeolithic industries are maintained until these are permanently replaced by Mode 4. The only exception are those terminal assemblages, such as the Châtelperronian (see above, page 7). In India some Mode 3 assemblages have been interpreted as showing similarities to the East African Middle Stone Age (Allchin & Allchin 1982), but those in the Rajasthan Desert, dated by TL to 163 Kyr (Misra & Rajaguru 1987), appear closer to the Eurasian Middle Palaeolithic. In southeast Asia there are no

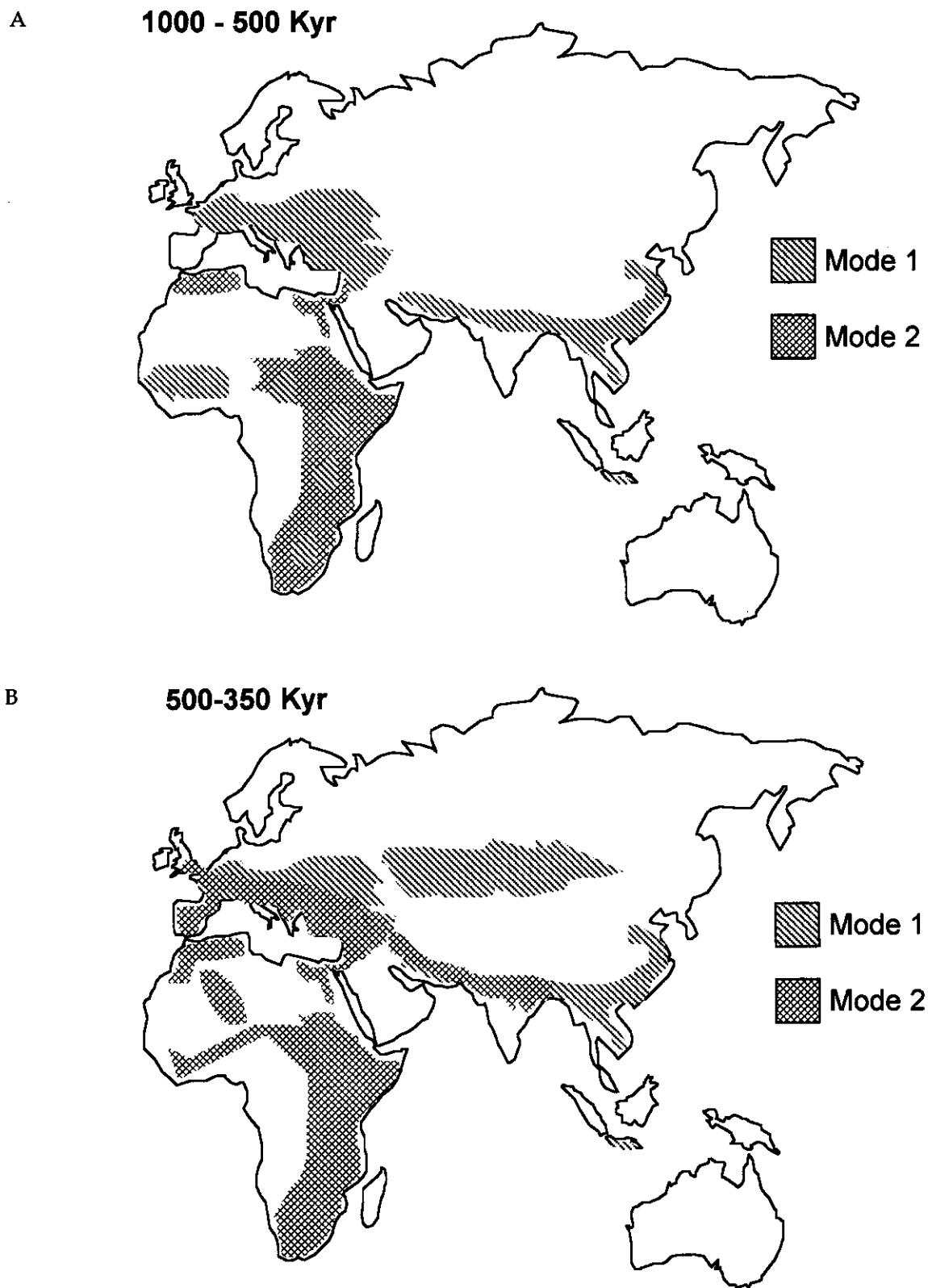
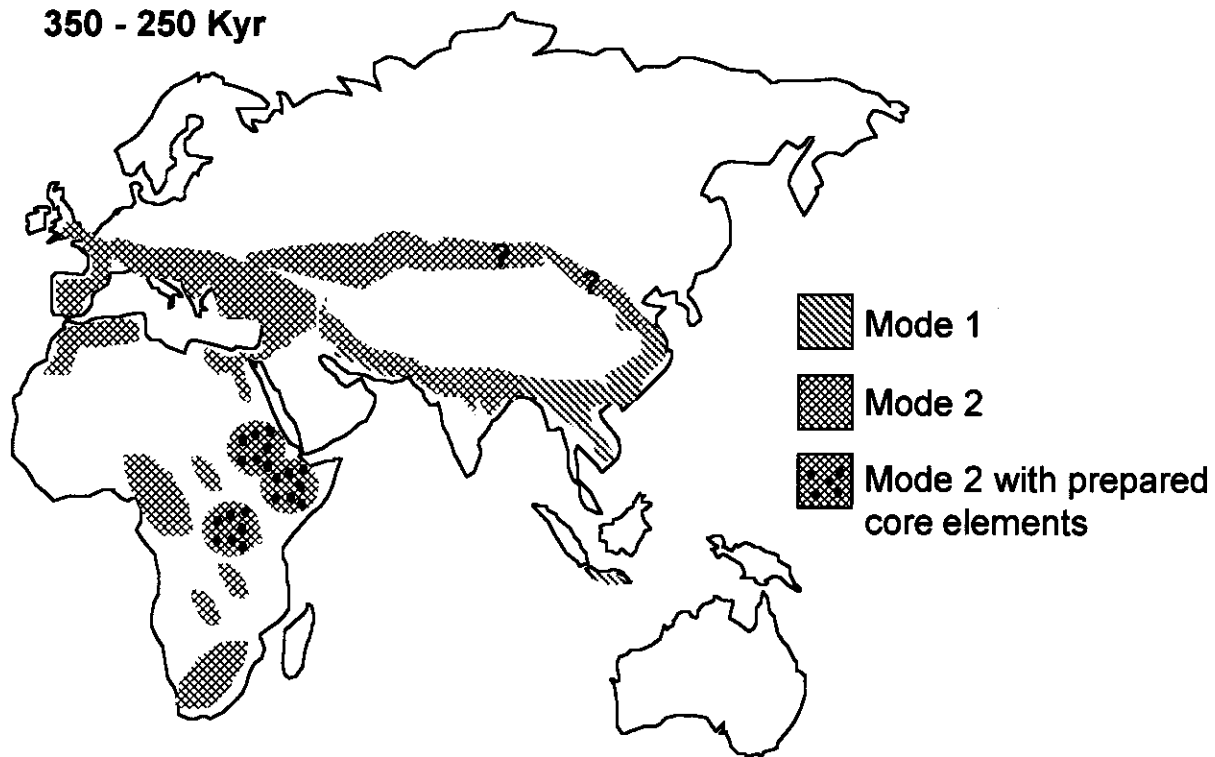
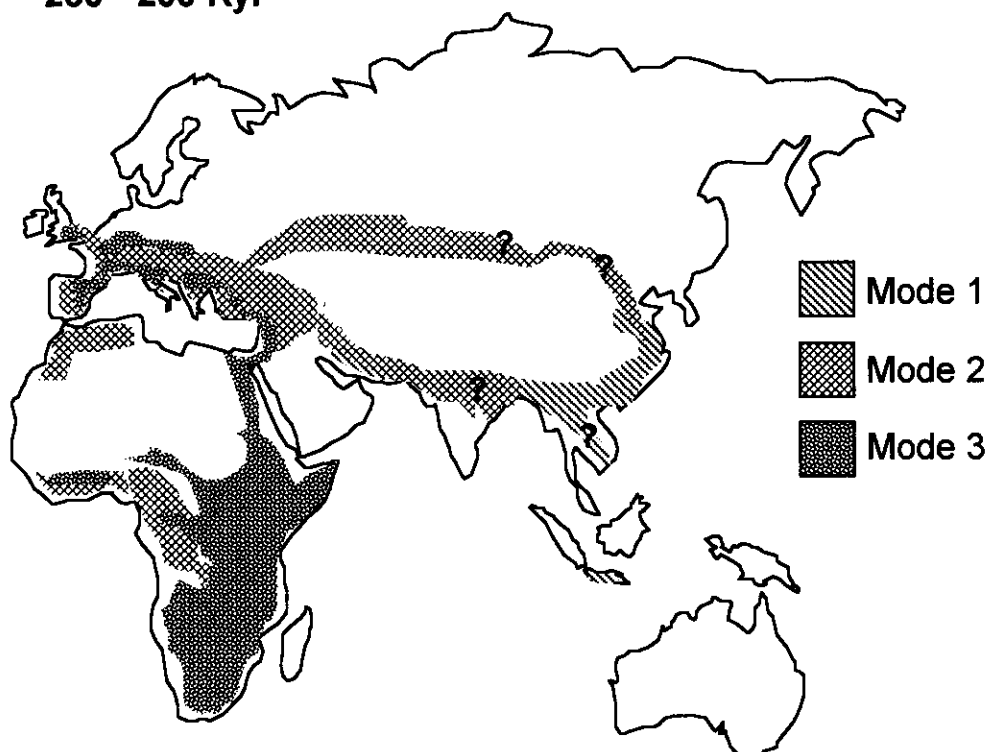


Figure 4. Maps showing schematically the distribution of the technological modes during the Middle and Later Pleistocene (A–G).

C 350 - 250 Kyr

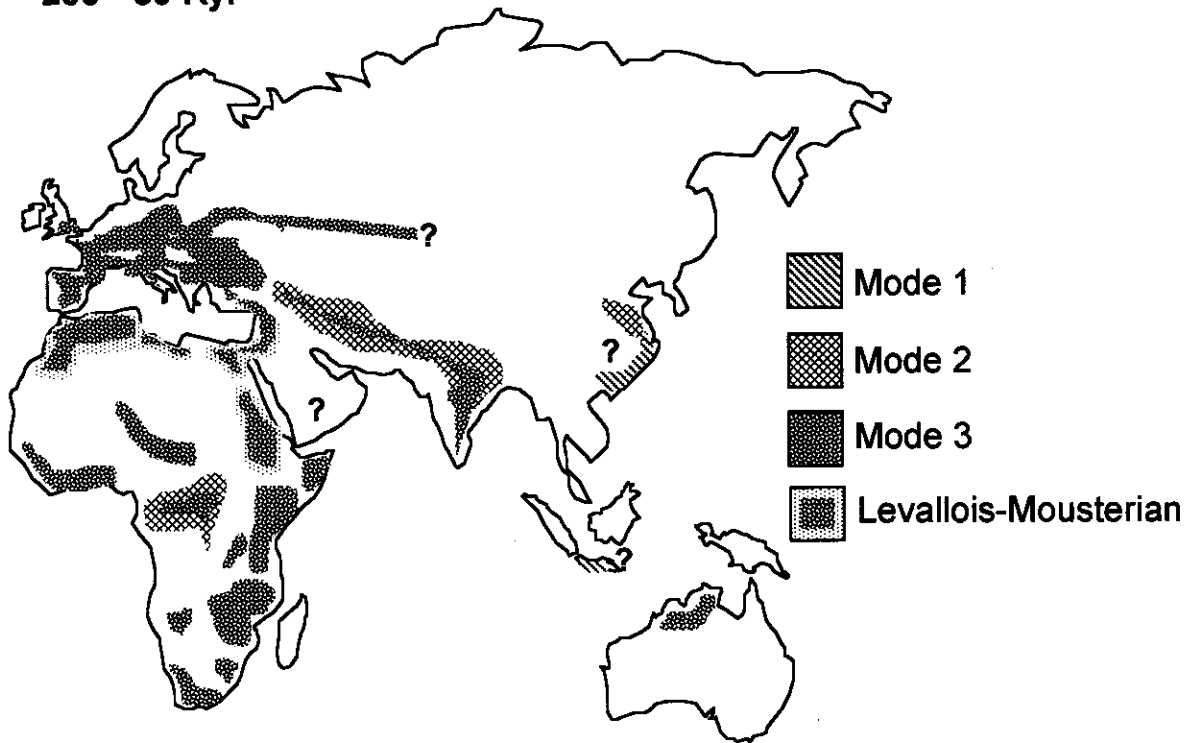


D 250 - 200 Kyr



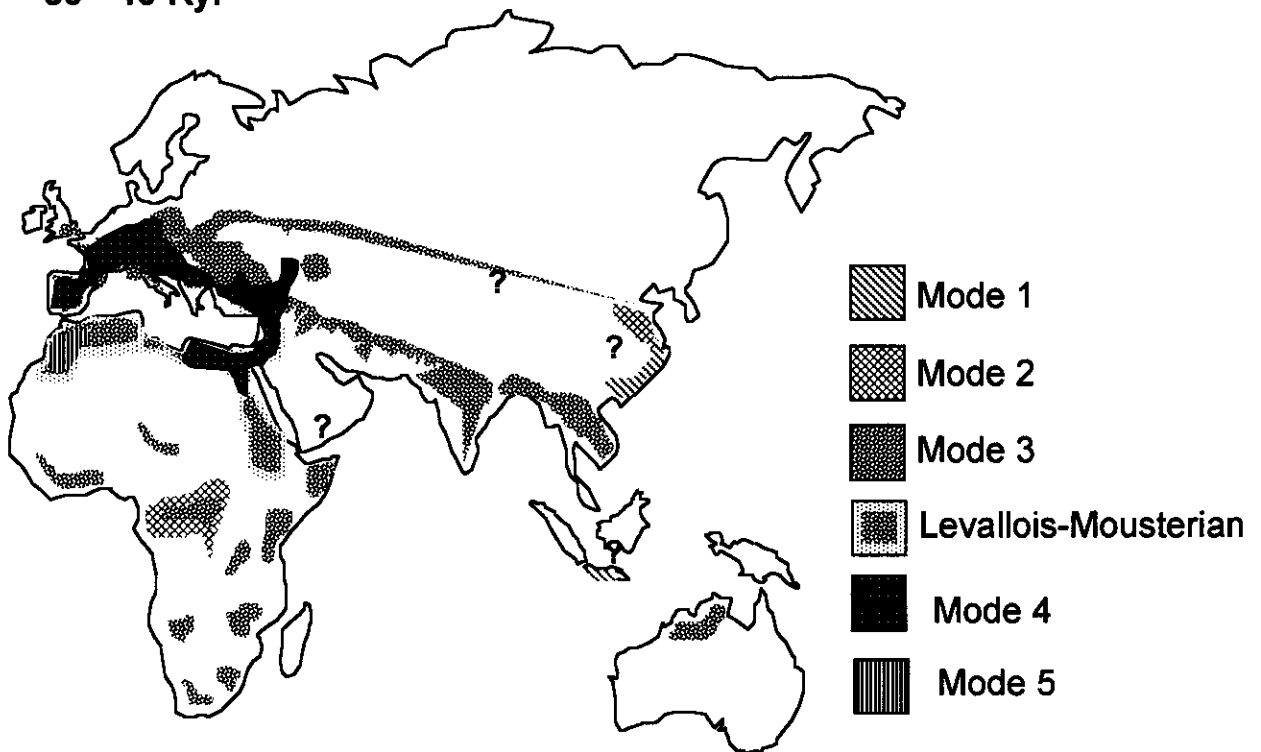
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200 - 50 Kyr



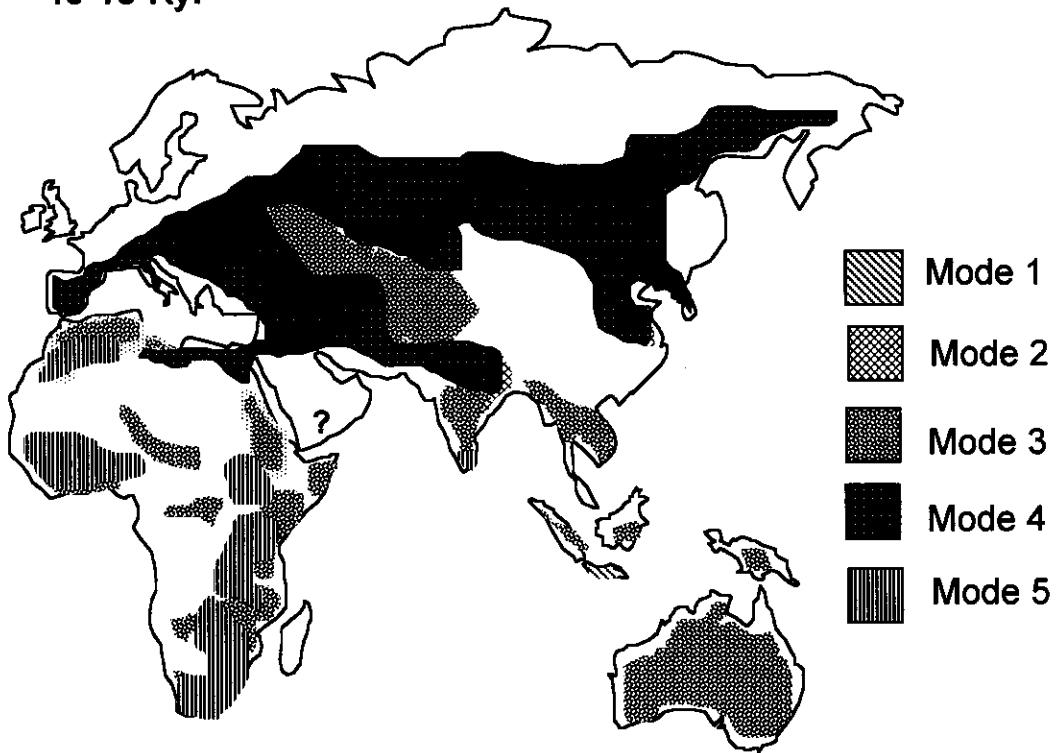
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50 - 40 Kyr



G

40-15 Kyr



certain archaeological sites for the period in question. The fossil hominids of Ngandong from Java do not have associated stone tools, and the earliest archaeological sites (as opposed to surface finds) are Niah in Sarawak, where a human skull was found in association with 'Middle Soan-Indian' Middle Stone Age artefacts (Harrison 1959; Zuraina 1982), and Long Rongrien in Thailand (Anderson 1987), both dated to ~40 Kyr. In northeastern Asia, the absence of absolute dates and the non-primary context of many sites precludes the establishment of spatio-temporal patterns. As indicated by those sites that can be attributed a late Middle–early Upper Pleistocene age, like Xujiayao, Mode 1 industries continued to be made. Mode 3 and soft hammer techniques are not documented (Clark & Schick 1988). The closest to a Mode 3 industry would be that of Zhoukoudian Locality 15 (Clark & Schick 1988) (Figs. 4D & 4E).

After 50 Kyr, Mode 4 industries appear in the Middle East (at Boker Tachtit: Marks 1990; and Ksar Akil: Bergman & Stringer 1989), and before 40 Kyr they are found relatively widely distributed throughout Europe (at Istallosko, Hungary: Vogel & Waterbolk 1972; Bacho Kiro, Bulgaria: Strauss 1993–4; El Castillo and L'Abreda, Spain: Bischoff *et al.* 1989; Cabrera & Bischoff 1989; and Trou Magrite, Belgium: Strauss 1993–4). The point of origin of European and Mediterranean Mode 4 industries is still

debated, one possibility being northeastern or northern Africa. Mode 4 industries or Mode 4 elements are later found across northern Eurasia, including Korea and Northern China, possibly northern India, and in the Maghreb and northeastern Africa. Although less well dated — possibly as early as 50 Kyr, but more likely after 30 Kyr — Mode 5 industries (the Late Stone Age) appear throughout large parts of sub-Saharan Africa. At less than 30 Kyr they are also found in Sri Lanka (at Batadomba Lena: Kennedy & Deraniyagala 1989) and later still (<10 Kyr) in Australia. Microlithic industries have also been reported in other parts of Asia but the dating of most of these remains unclear. In parts of Europe, Mode 5 industries occur at the end of the Pleistocene. There is no consensus about the age of the first occupation of Australia, with proposed dates ranging from 170 Kyr to less than 50 Kyr (Fullagar *et al.* 1996; R. Roberts *et al.* 1994). Archaeological sites only become frequent after 40 Kyr (Smith & Sharp 1993). The non-lithic elements of the Pleistocene archaeological record in Australia are unequivocally derived — extensive trade of exotic materials, elaborate art and ochre. The lithics are generally recognized as a flake-based industry similar to the overall structure of Mode 3, but they lack the formal secondary shaping found elsewhere, resulting in a strong retention of Mode 1 elements.

*Patterns of ATUs within Modes 3, 4 and 5**Mode 3*

While the distribution of Clark's modes provides one level of population marker, variation within modes can provide more fine-grained information. Local innovations in artefact type or technique lead to regional differences in assemblage structure, and local industries, facies, or in our terminology, ATUs. In Africa, variations in Mode 3 technology can be found in ATUs such as the Pietersburg and Howieson's Poort in southern Africa, the Lupemban in western Africa, the Mumba in East Africa, and Bambatan in eastern Central Africa. In Europe, variants of the Mousterian have been recognized based on both type-fossils (small bifaces, Quina points, Szeletian points) and assemblage frequencies (Bordes 1961b). There is both geographical and chronological patterning to these variants (Mellars 1996), and they may represent both functional and populational differences. The situation in Europe is complicated by the occurrence of certain Mode 2 elements within the Mode 3 (the Mousterian of Acheulian Tradition or MTA). While Europe (classic Mousterian) and Africa (the African Middle Stone Age) represent to some extent two different trajectories within the Mode 3 technology, North Africa, the Levant and north-eastern Africa provide a mixed pattern. Gademotta in the Ethiopian Rift has characteristic Mousterian side scrapers, unifacial, and bifacial points, K-Ar dated to 180–140 Kyr (Wendorf *et al.* 1975). The Levant and North Africa also have affinities with the European Mousterian, but are nonetheless distinctive (Bar-Yosef 1992). More generalized African elements can also be found in these regions. These regional variants in stone tool technology suggest that there were regional populations and traditions in Africa and Europe between 200 and 30 Kyr, at both a continental and sub-continental scale.

Mode 4

Mode 4 industries appear as a 'package' in the Levant between 50–45 Kyr (Bar-Yosef *et al.* 1996); some elements of this package seem to be registered early in eastern North African sites (Marks 1990). The Aurignacian is the first typical Mode 4 ATU, with formal stone artefacts, blades and burins, objects used in ornamentation and artistic elements (Mellars 1993; White 1989). It is found throughout Europe from about 45 Kyr (Strauss 1993–4). The Gravettian, which appears after 28 Kyr, is found across an immense area from Russia to the Iberian peninsula (Svoboda

1990), and overlaps with the Aurignacian. In Europe, the succeeding development and range of ATUs reflects fragmentation leading up to the glacial maximum, followed by later expansion and relative homogenization as populations came into contact again (Kozłowski 1990; Otte 1990). Mode 4 industries are found along southern Siberia after 35 Kyr (Klein 1992; Morlan 1987), in the area of Lake Baikal (Turner 1985) and in northern China, Korea and Japan (Bellwood 1990; Chen & Olsen 1990; Clark & Schick 1988; Jia & Huang 1985; Olsen 1987; Reynolds & Kaner 1990). In central Asia, the local Mode 3 industries are not followed by Mode 4 but by a later Mode 5 or Epi-Palaeolithic (Davis 1990). In the Levant, the Mode 4 ATUs are succeeded by the Natufian, with major changes occurring at the development of agriculture.

North Africa shows a different pattern in its eastern and western areas. As before, the east is under the influence of both the Levant and East Africa, while the Maghreb undergoes periods of isolation and local differentiation. Mode 4 industries appear in the area of the Gebel Akhdar Hills, Cyrenaica (McBurney 1960; 1967) and along the Nile Valley (Vermeersch *et al.* 1984; Wendorf *et al.* 1976). On the eastern edge of the Gulf of Sidra, Mode 4 industries are found at sites like Hagfet et Tera, Haua Fteah and Hagfet ed Dabba, but these are not uniform in character. Mode 4 at Hagfet et Tera differs from the typical Eurasian Upper Palaeolithic, while at ed Dabba, Levantine influences are observed (McBurney 1960). Mode 4–5 industries reach the Maghreb towards the end of the period in the form of two ATUs — the Iberomaurusian and the Capsian — which replace the long standing local Mode 3 ATU, the Aterian. The Iberomaurusian is documented from 22 Kyr (early levels at Taforalt, Morocco; and Tamar Hat, Algeria: Camps *et al.* 1973; Roche 1976). Mode 3 directly overlain by Iberomaurusian levels is documented in several sites (Sidi Mansur, Tunisia; La Mouillah, Algeria; Kifan bel Ghomari: McBurney 1960). South of the Sahara, Mode 4 is restricted to the northeast, found in sites like Hargeisan in Somalia or the Gobedra rockshelter in Ethiopia, and in the ATU called Eburran or Kenyan Capsian, restricted to a small area near Lake Nakuru (Phillipson 1985).

Mode 5

Mode 5 industries succeed both Mode 3 and Mode 4, and show considerable geographical and chronological variation. Mode 5 elements (large number of very small blades, often trimmed by steep backing

into crescents and trapezoidal forms) can occur very early, as they do in the Howieson's Poort. Southern Africa in general shows the first widespread evidence of backed-microlithic production (Phillipson 1985). The site of Enkapune Ya Muto, Kenya, with a date of 46 Kyr using obsidian hydration methods, has standardized artefacts, as well as ostrich egg-shell beads (Ambrose 1996) and is possibly the earliest evidence of the African Late Stone Age. In Asia, microlithic industries occur in the later Pleistocene in China (sites like Xueguan (13.5 Kyr) and Xiachuan (21.7–19.6 Kyr)), associated with Mode 3 elements (Clark & Schick 1988). During the early Holocene microlithic industries are widespread, occurring in Europe, southern Asia, Australia and across Africa.

The geography of the Pleistocene archaeological record

Despite major gaps in the record, especially in Asia and central and western Africa, a geographical pattern can be discerned.

- 1) During the second half of the Middle Pleistocene the main differences in archaeology are between the east and west — the Movius line. These differences seem to be attenuated later in northern China, but there is no information to assess south-east Asia.
- 2) The innovations behind Mode 3 industries appear most clearly in Africa within terminal Mode 2 industries.
- 3) Mode 3 industries appear around 250 Kyr in both Africa and Europe. In Africa they largely replace the local Mode 2, while in Europe the latter is maintained; at a later date they are found in southern Asia and ultimately Australia.
- 4) Mode 3 industries are replaced by Mode 4 or 5 in some areas by 50 Kyr, but in others may persist through to the Holocene.
- 5) Mode 3 may be replaced by either Mode 4 or Mode 5 industries, and these appear to be alternative technological trajectories that occur regionally.
- 6) Mode 4 technology represents a regional variant of Mode 3 that is ultimately found over most of Europe, northern, western and central Asia, and restrictively in the most northerly part of eastern Africa.
- 7) Mode 5 industries appear as a variant of Mode 3 in Africa, and are later found over southern Asia and over most of the Mode 4 range.

An archaeological phylogeny: population history and environmental context

Stage 13 and older

Hominids developed both Mode 1 and Mode 2 industries in Africa, and carried them with them as they dispersed into Eurasia. All Eurasian dispersals prior to 0.5 Myr are characterized by Mode 1 industries. The exception is the presence of older Mode 2 industries at Ubeidiya (1.4 Myr) in Israel. Although the main corridor to dispersals out of Africa is the Levant, this region cannot be treated as a permanent part of Eurasia throughout different periods. The Levant behaves, in biogeographic terms, as the northernmost limit of African faunas during wet climatic phases, and as the southernmost limit of Eurasian biotas during cold/dry periods (Tchernov 1992). Ubeidiya at 1.4 Myr does not represent a true dispersal into Eurasia, but northern extensions of the African hominid population. The second documented dispersal out of Africa occurs around 500 Kyr, when Mode 2 industries become the norm throughout the Middle East and Europe (Klein 1995). That the origins of this dispersal lie in Africa rather than elsewhere in Eurasia is supported by patterns of animal movement during the different phases of glacial cycles. African taxa regularly reached the Levant during the beginning of interglacials, other factors influencing further dispersals into Eurasia. Eurasian faunal expansions into Africa during cold/dry periods would be limited by the maximum extent of the Saharan barrier during glacial climates. During these glacial episodes, however, Eurasian faunas exploited an east-west corridor along southern Siberia. Thus a pattern of African dispersals northwards during the beginning of warm phases and east-west Eurasian exchange during cold periods would have been the norm during the Middle and Upper Pleistocene (Lahr & Foley in prep.). Lack of chronometric control precludes determining the exact dates for this Mode 2 dispersal. Nevertheless, using the environmental context, a northward expansion of African hominids could have occurred at the onset of interglacial conditions at the beginning of Stage 13 (~500 Kyr) or Stage 11 (~430 Kyr).

This is consistent with the appearance of Mode 2 industries in the Middle East, documented at the sites of Gesher Benot Ya'acov and Giv'at Shaul (Bar-Yosef 1994; Goren-Inbar *et al.* 1992; Tchernov 1992). The 'Movius line' would thus be the product of a geographically limited dispersal of the first Eurasian Mode 2 populations. An alternative explanation is the so-called 'bamboo barrier' (Pope 1988); according to this, handaxe manufacture was abandoned for

ecological and functional reasons as a single original hominid Eurasian dispersal reached eastern Asia. However, all evidence of hominid occupation outside Africa (except Ubeidiya) prior to 500 Kyr is in the form of Mode 1 industries, and the appearance of Mode 2 in western Eurasia after this date seems to represent a separate and more restricted dispersal. In particular, these Mode 2 hominids did not reach southeast Asia. That may have been the result of ecological or competitive factors (Larick & Ciochon 1996), but, whatever the cause, from 500 Kyr ago the eastern and western hominids pursued somewhat different trajectories, as the latter became directly influenced by African events.

Stages 11–9

The period 430–300 Kyr corresponds to the long Holsteinian interglacial (Stages 11 to 9), interrupted by a short cold phase around 350 Kyr. (This long interglacial is now divided in two by many researchers, only the earliest of which would correspond to the Holsteinian.) Approximately 300 Kyr ago (Stage 8), the severe Saale glaciation began. During this time, when the Sahara was a barrier, Eurasian and sub-Saharan patterns diverged. At this time southern Siberia may also have been a diffusion corridor linking Europe and northern Asia. The possible appearance of bifacial artefacts in northern China at this time may be the result of this process. In sub-Saharan Africa, a reduction of the range and density of populations caused by arid conditions is reflected in the fragmentation and regionalization of Mode 2 industries within the continent.

Hominid populations in Africa around 300 Kyr were sparse and scattered, promoting local adaptation and diversification. It is during this time of isolated hominid populations that Mode 3 elements in the form of clear 'proto-Levallois' techniques appear in terminal African Mode 2 assemblages. The setting for the appearance of the radiations represented by Mode 3 is therefore one of moderately diverse and locally isolated populations. Where among these populations the Mode 3 technology developed is not clear. A case can be made for eastern or northeastern Africa. In central Kenya the Victoria West industry contains clear proto-Levallois forms (Gowlett 1980; Leakey *et al.* 1969; van Noten 1982), and Mode 3 also develops out of Mode 2 at Melka Kunture in Ethiopia, at the Kinangop Plateau in central Kenya (Clark 1989; Phillipson 1985) and in the Horn (Clark 1951). Beyond eastern Africa, some form of 'proto-Levallois' is known possibly in Europe, in North Africa (El Mael Abid, Algeria, Sidi Abderrahman and stages VII

and VIII of the Moroccan sequence, Wadi Saoura and in the Kharga depression: Balout 1955; Biberson 1961; Clark 1989; McBurney 1960; Phillipson 1985), and in the southern African Fauresmith (Goodwin & van Riet Lowe 1919; van Riet Lowe 1945). Other sites in Africa (e.g. Cave of Hearths and Montagu Cave), however, show a break in the sequence between Mode 2 and Mode 3 industries. It appears that the development of Mode 3 technology occurred over a certain period of time, during which climatic fluctuations led to intra-African and even European dispersals, and thus to a broader distribution of the 'proto' forms, leading to geographical blurring of the ancestral source.

Stage 7

After full Mode 3 industries appear in Africa, there is a rapid dispersal into Eurasia between 250–200 Kyr. A northward dispersal around 250 Kyr would be consistent with palaeoclimatic events, as it corresponds to the onset of interglacial conditions during Stages 7a and 7b. An interesting aspect of this expansion is the subsequent relationship between Mode 2 and Mode 3 industries in either continent. The Levallois technique represents a shift of key artefacts from core to flake, so that any one core can be made to produce a number of tools, thus representing a far more efficient and task-specific technology. In Africa this technological innovation appears in relatively discrete populations during the stringent arid conditions of glacial Stage 8. The rapid expansion and associated disappearance of Mode 2 industries in eastern and southern Africa suggests a clear demographic and competitive advantage. Populations with Mode 3 industries were clearly also successful in Europe, for they rapidly became established. Nevertheless, Mode 2 industries did persist, suggesting that any competitive advantage provided by Mode 3 industries was not sufficient to replace the local populations. It is possible that more than one hominid population was present in Europe during Stage 7. If so, any biological or behavioural interactions that may have occurred between them are important for interpreting subsequent evolutionary patterns in Europe. The absence of archaeological assemblages from this period in southeast Asia precludes the reconstruction of events there. Eastern Asia clearly remained predominantly an area with Mode 1 populations, but there is some evidence in the northeast for the spread of Mode 2 technology.

Stages 6 and 5

The glacial climate of Stage 6 again created the conditions for relative isolation of Europe and Africa, and

it coincides with the fragmentation of Mode 3 into distinct regional groups. Eurasian Mode 3 populations could also have reached northern China at this time, in the same way as Mode 2 ones may have done during the previous glacial stage, but there is no clear indication that they did. At the onset of the last interglacial, African hominids were again divided into a number of populations. The Maghreb had been separated from both the Levant and sub-Saharan Africa, and the Levant from Europe. Habitat expansion throughout the phases of the last interglacial (Stages 5a to 5e) was accompanied again by population expansion and, in some cases, dispersal. In southern Africa, the Howieson's Poort industry becomes a regional phenomenon lasting until ~60 Kyr, when contraction occurs again. At this time, a northeast African fauna which included early modern humans dispersed northwards into the Levant. The archaeological record does not show this dispersal, possibly because at this time the area covered by the Levant, eastern North Africa and parts of northernmost central Africa cannot be divided into distinct ATUs, but rather comprised a single industry, the Levallois-Mousterian. The presence of a Mousterian assemblage in northern Ethiopia during Stage 6 (180–140 Kyr), however, and the large number of Mode 3 sites across the Saharan desert during the last interglacial (at Adrar Bous: Clark 1993; Bilma: Maley *et al.* 1971; Bir Tarfawi: Close 1993; Wendorf *et al.* 1991; 1993; Bouko in the Tchad Basin: Tillet 1983; Erg Tihodaine: Arambourg & Balout 1955; and Lake Ounanga: Arkell 1964) could be evidence for these movements. The Maghreb is again in contact with both the Levant and sub-Saharan Africa, with consequences for hominid diversity since there are at least two very different routes that reach into western North Africa. The first runs from either Tripoli to the Fezzan or from the southern Atlas to the Hoggar, across the Hoggar massif to the Niger or along the Tummo ridge to Chad. This route brings central African influence into the area. The second route is from Abyssinia along the Nile to eastern North Africa and the Levant, followed by coastal communication from Cyrenaica along the Gulf of Sidra. This brings both East African and Levantine influences into the Maghreb. However, the periods of such contact were relatively discrete. In Europe, the last interglacial sees the establishment of the Mousterian as the main local Mode 3 ATU; Mode 2 assemblages have by then disappeared.

Stage 4

The onset of the last glaciation induces again a process of fragmentation. In Europe, this fragmentation

is relatively small, with just the development of Mousterian facies. In the Levant, local Mousterian industries become separated from north and sub-Saharan African ones. In north Africa, aridity again settled along the Gulf of Sidra in the Libyan desert, the most arid part of the Sahara, and also dried the wadis that connect the Atlas to the Hoggar, creating allopatric conditions in the Maghreb. Local Mode 3 industries differentiate into a relatively derived ATU that has been called a 'desert' culture — the Aterian, which lasts until around 22 Kyr. Stage 4 fragmentation in sub-Saharan Africa is not well documented for the lack of chronometric control. In southern Africa, where chronological control is best, the disappearance of the Howieson's Poort industry is followed by a period of very low density occupation and abandonment of large areas (Klein 1992; 1994), indicating that again, arid glacial conditions in Africa were accompanied by a process of reduction in population range and size. Out of this fragmentation emerges the African Late Stone Age, a primarily Mode 5 industry.

Before the onset of glacial climates, hominids with a Mode 3 technology reached Australia. This dispersal is not documented archaeologically along southern Asia, and its source is unclear. Two possibilities exist: one would derive it from the Eurasian Mode 3 ATUs (Mousterian and Levallois-Mousterian), but they are not found in southeastern Asia. The other possible source would be the East African Mode 3 industries, which would require a dispersal route across the Strait of Bab el Mandeb, from the Horn of Africa into Yemen. This southern coastal route, which may have been used during the earliest hominid dispersals into tropical southern Asia (Larick & Ciochon 1996), would be consistent with populations able to use water-craft (needed to reach Australia) and with the timing of Australian colonization (as at 60 Kyr, or even >100 Kyr, the Sahara represented a barrier to northward movement). Towards the end of the Pleistocene, Mode 5 industries appear across southern Asia. This may imply another southern dispersal, independent from Eurasian-Levantine events, or convergent developments from the local Mode 3.

As part of the process of population fragmentation and differentiation during the last glaciation, Mode 4 technology appears in northeastern Africa. This technological development is associated with population expansion occurring not just as preferred habitats expand, but across habitat and biota boundaries. There were still environmental or competitive constraints, however, since this Mode 4 population

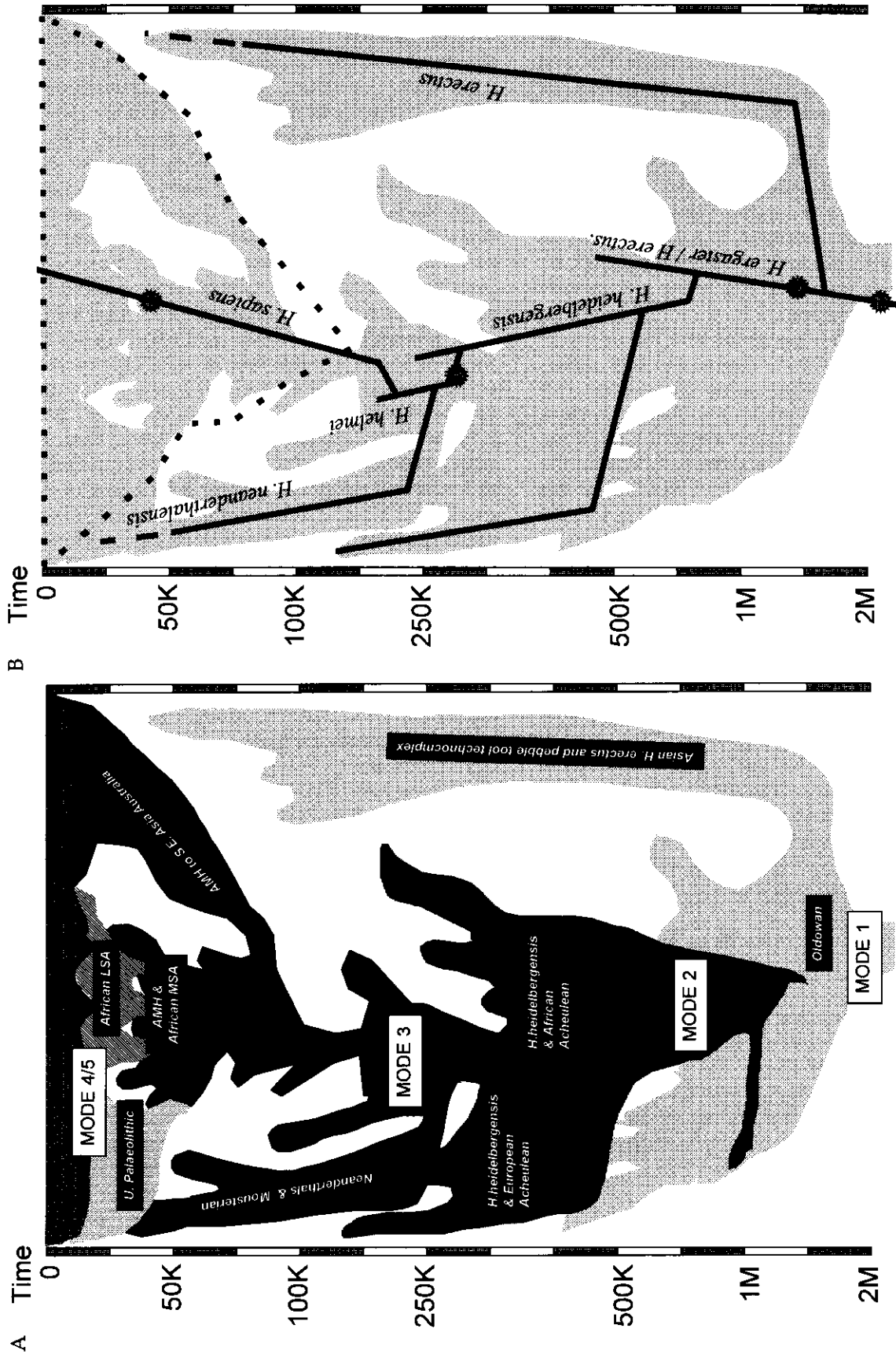


Figure 5. A) Summary of the distribution in time and space of the radiations of the technological modes; B) superimposition of hominid taxa on to the modes, showing major cladogenic events (stars), and the major changes in technological modes.

did not cross the desert barrier into the Maghreb where the Aterian tradition continued. It did disperse into the Middle East between 50–45 Kyr, and from the Middle East into Europe and possibly the Caucasus. As discussed above, archaeological evidence suggests that a process of competitive displacement of the local Mode 3 populations followed, until only Mode 4 industries are found after 30 Kyr. Mode 4 technologies expanded along the southern Siberian corridor, and reached, in a diffuse form (as was the case with Mode 2) northern China, Korea and Japan, where they met with Mode 1–2 towards the end of the Pleistocene.

It is probably at this point that the utility of technological modes breaks down, and now differences between ATUs reflect cultural traditions with far less certain implications for population barriers, and far greater levels of inter-regional gene flow. One example of this is the widespread distribution of Mode 5 industries from the end of the Pleistocene, in both Eurasia and sub-Saharan Africa. Its ubiquitous occurrence is likely to be the product of both larger social and economic networks, and convergent adaptations and technological development of composite tools.

The character of most of the world population during the late Middle Pleistocene reflects the demographic success of populations using a Mode 3 technology, as these dispersed first within and then out of Africa into Eurasia and southern Asia. These dispersals were then followed by regional differentiation of technological traditions within Mode 3. In this sense, Mode 4 and 5 industries both represent the mastering of a number of techniques derived from the Mode 3 repertoire. None of these later industries, including the Upper Palaeolithic, was a global event.

The Mode 3 hypothesis: towards an integrated approach

How does this archaeological phylogeny compare with the biological evidence for the same period, both fossil and genetic? Figure 5 is a summary diagram that attempts to show how the distribution of technological modes in time and space can be used to map the dispersals of hominids, and to infer phylogenetic relationships.

Archaeological phylogeny and the fossil record

Early *Homo* and Mode 2

The broad pattern of later hominid evolution consists of a dispersal out of Africa and into Eurasia

from an African lineage between 2.0 and 1.5 Myr. The archaeological evidence would thus imply that the eastern Asian hominids were derived from an early *Homo* population prior to the development of bifaces (Mode 2) in Africa, most probably the very early *Homo erectus* lineage (*Homo ergaster*). This dispersal would have given rise to Eurasian *Homo erectus*. This form is thought by many to be a uniquely Asian taxon (Andrews 1984; Tattersall 1986), but very few contemporaneous African and European fossils are available for study. The latter show that absolute morphological distinctions between the two groups are difficult to make (Bräuer 1994; Bräuer & Mbua 1992; Kennedy 1991; Rightmire 1990). The development of Mode 2 industries in sub-Saharan Africa occurs around 1.4 Myr, and this industry acquires a very broad all-African distribution. At about 1.2 Myr, a *Homo erectus* specimen (OH9) is found associated with a Mode 2 industry at Upper Bed II of Olduvai in Tanzania (Leakey 1961). Other associations of *Homo erectus* and Mode 2 industries in Africa are found in the early Middle Pleistocene of North Africa (Tighenif) and at Upper Bed IV at Olduvai (OH12 and OH 28) (Rightmire 1996). The latter have a similar age to the findings at Bodo in the Middle Awash of Ethiopia (~600 Kyr) (Clark *et al.* 1994), and indicate the complexity of hominid evolution within Africa.

The population represented by Bodo, which was also found associated with Mode 2 technologies, had already differentiated from a *Homo erectus* morphology. It represents a new species, *Homo heidelbergensis* (Rightmire 1996; Stringer & Gamble 1993), to which the possibly slightly younger remains of Kabwe, Ndutu and Elandsfontein also belong (Bräuer 1989; 1992; Rightmire 1996). This is the population that would have introduced Mode 2 technologies into Europe around 500 Kyr as shown by the morphological similarities between this group of fossils and European ones of similar age or possibly younger (Arago, Bilzingsleben, Boxgrove, Ceprano, Mauer, Petralona, Vertesszöllös) (Rightmire 1988; 1990; 1996; Stringer 1993; 1996). The somewhat later Steinheim and Swanscombe fossils, dating from the interglacial following the Holsteinian (Stage 9) and associated with Acheulian artefacts (Stringer 1996) would be part of this *Homo heidelbergensis* population.

In Asia, where Mode 1 industries persist from the first establishment of hominids in the area, the fossils around 500 Kyr are *Homo erectus*. This difference in relation to contemporary Afro-European hominids is another indication of the allopatric conditions of world hominid populations at the beginning of the Middle Pleistocene. The possible

appearance of bifacial tools in northern China later in the Middle Pleistocene, however, could indicate a period of contact between Eurasian and northeasternmost populations in China. The evidence for this east-west contact along southern Siberia, in the form of bifacial tools, is nevertheless, scant. The fossil data, on the other hand, clearly show the appearance of a different hominid population in China at this time. This population, represented by fossils like Jinni Shan, Maba and Dali, differs in a number of traits from the local *Homo erectus* (Groves & Lahr 1994; Pope 1992), which co-exists for at least part of this period (Hexian at ~300 Kyr: Grün *et al.* in press; levels 3-4 at Zoukhoulian at 230 Kyr: Chen & Zhang 1991; Zhou & Ho 1990). Proponents of multiregional evolution have considered this population the result of processes of local differentiation (Etler 1994; Li & Etler 1992; Wolpoff *et al.* 1984), but these fossils show a number of features that relate them to Eurasian *Homo heidelbergensis* (Stringer 1988; 1995; Groves 1989; 1992; Groves & Lahr 1994). These shared characteristics would be consistent with a westward dispersal of Mode 2 industries at this time, although if this was the case, the diffuse character of Mode 2 influence on the typically Mode 1 Chinese archaeological record has to be explained. In palaeoclimatic terms, it could have taken place along a southern Siberian corridor during a short glacial corresponding to Stage 10 (~350 Kyr) following the Holsteinian Interglacial.

Mode 3

The onset of cold Stage 8 (~300 Kyr) would have caused new regionalization and fragmentation of Afro-European populations. The fossil data in Africa are insufficient to assess morphologically the effects of this process. Archaeologically it is reflected in the formation of regional Mode 2 ATUs and the appearance of Mode 3 elements within this context. The archaeological phylogeny implies that the Mode 3 African population dispersed throughout Africa and into the Levant and Europe, and was the main source of the subsequent hominid populations in these areas. Three facts make the fossil interpretation of this point difficult. First and foremost, the poor chronological control of Middle Pleistocene material precludes a detailed examination of which fossils are particularly close to the possible date of introduction of Mode 3 industries in Europe. (They should, under this model, show closer affinities towards contemporary African material than to either earlier or later European specimens.) Second, there is the evolutionary proximity of the populations under consideration, which would in any case share a

common ancestor around 500 Kyr. And third, the co-existence of Mode 2 and Mode 3 industries in Europe after 250 Kyr raises questions about admixture between indigenous Mode 2 *Homo heidelbergensis* and incoming Mode 3 populations. There are traits shared between fossils like Swanscombe and the later Neanderthals (Stringer 1996), but these could be the result of convergent climatic adaptation, *Homo heidelbergensis* plesiomorphies or admixture. Atapuerca may be a key site here, but the 300 Kyr age of the important fossils of Sima de los Huesos, with their apparent Neanderthal affinities (Arsuaga *et al.* 1993) is under revision, and a later Stage 7 date is likely (Stringer 1996). Furthermore, the fossils were not found in association with stone tools.

The earliest fossils associated with Mode 3 industries in Europe, dating to Stage 7, are those of Ehringsdorf in Germany (Blackwell & Schwarcz 1986) and Pontnewydd Cave in Wales (Green 1984). These already show some morphological features (e.g. the occipital region of Ehringsdorf 9: Stringer *et al.* 1984; Stringer 1996) that will become fixed in the Neanderthal population. However, the extent to which these features are uniquely European at this stage is unknown, for they could reflect the morphological pattern of the dispersing Mode 3 population at 250 Kyr, for which African fossils are rare (the closest in known age would be the cranium of Florisbad: Grün *et al.* 1996). If this was the generalized morphology of the ancestral Mode 3 population, it could explain the complex combination of traits in the Jebel Irhoud remains of Morocco, with a date of 100-200 Kyr (Grün & Stringer 1991). This pattern would disappear in sub-Saharan Africa during Stage 6, as hominids differentiated towards a modern anatomy (see Stringer & McKie 1996, 100). The African taxon that developed Levallois techniques would thus be the source population for both the evolution of modern humans in Africa around 150-100 Kyr, and of Neanderthals in Europe over approximately the same period of time. The model would further suggest that this differentiation occurred during a glacial period (Stage 6) in which African populations were again fragmented, and contact between sub-Saharan Africa, the Maghreb and Europe was interrupted.

This is consistent with the evidence of the relevant fossils. They show a strong trend towards local adaptation in Europe, where the Neanderthal morphological complex appears in mosaic form in fossils of this period (Biache, La Chaise-Suard, and the later group of La Chaise-Bourgeois Delauney, Krapina and Saccopastore). Neanderthals proper appear in the European record around 100 Kyr, and

their diagnostic traits have been interpreted as cold-dry adaptations to a mode of life that required large levels of robusticity (Franciscus & Trinkaus 1988; Rak 1986; Ruff 1991; Trinkaus 1992). Neanderthals are consistently associated with Mousterian tools, and both biology and technology last until approximately 30 Kyr, when they are replaced by modern humans associated with Mode 4 industries.

Anatomically modern humans in Africa

In contrast, the African fossils during Stages 7 and 6 show high levels of diversity (Eliye Springs, Florisbad, Laetoli 18, Omo 2, Singa), that persist through to the earliest modern forms. These are found from 130 Kyr in Ethiopia (Omo 1), northern Kenya (Guomde, KNM-ER 999, KNM-ER 3884) and southern Africa (Klasies River Mouth, 16424, 16425, 41815; Border Cave 3, 5, ?1 and ?2). African Stage 6 hominids may have had divergent evolutionary trajectories which were homogenized in the following short warm-wet phase. The subsequent period (from Stage 5d) is one of renewed fragmentation of populations, during which different archaeological traditions, like the Howieson's Poort appear. The only dated remains are those associated with the Howieson's Poort in southern Africa, which show a particularly gracile and sexually dimorphic population (Bräuer 1989; Caspari & Wolpoff 1990; Deacon & Schuurman 1992; Rightmire 1989; Smith 1992). Some authors relate this to the present Khoisan (Rightmire 1981; 1984) while others fail to see a relationship to any particular recent group (Ambergen & Schaafsma 1984; Campbell 1984; De Villiers 1973; De Villiers & Fatti 1982; Morris 1992; van Vark 1986).

The fossil data from Skhul and Qafzeh clearly show that an African early modern population made an incursion into the Levant around 100 Kyr. These modern populations possessed the Mode 3 technology that by then was widespread in Africa and Europe. Subdivision of these technologies into geographically local ATUs may provide information about biological affinities: in Europe, the Mousterian with its various facies; in the Levant along the Nile, Abyssinia and northernmost central Africa, the Levallois-Mousterian; in the East African Rift, the Mumba Site; in southern Africa, the Howieson's Poort; in western Africa (somewhat later) the Lupemban. The faunal affinities imply that the early modern population that reached the Levant 100 Kyr may have originated in East Africa, but technologically it was part of a larger northeast African-Levantine Levallois-Mousterian population. In the Maghreb, the onset of the last glaciation brought isolation again, reflected

in the differentiation of the Aterian. This elaborate Mode 3 ATU may be much earlier, as suggested by the findings at Bir Tarfawi dated to 140–120 Kyr (Aitken & Valladas 1992; Schwarcz 1992; Wendorf *et al.* 1990), but as Aterian tanged points are absent, this assemblage has been reclassified as Denticulate Aterian or Denticulate Middle Palaeolithic. The fossils associated with the Aterian (Dar es-Soltan, Temara), which lasts until almost the last glacial maximum, are fully modern (Hublin 1993). The first fossils associated with Mode 4 industries are in the Levant (Ksar Akil), but significantly later. These are fully modern in morphology (Bergman & Stringer 1989).

Dispersals into Asia

In southeast Asia, the absence of an archaeological record for the period 250–50 Kyr precludes the inclusion of this area in the archaeological phylogeny. But there are fossils in Java. All the archaic Javanese remains, which may be as late as 25 Kyr (Swisher *et al.* 1996), are *Homo erectus* (Santa-Luca 1980; Rightmire 1994), consistent with the long-standing persistence of Mode 1 industries in eastern Asia generally. The only artefacts found with the first modern fossils in the area (Wadjak, Java) are two blades or flake-blades, which is consistent with the appearance of people with at least Mode 3 technological abilities during the later Pleistocene (Simanjuntak & Semah 1996).

In China, the long surviving Mode 1 industries are associated with *Homo erectus*. A distinct hominid form in the late Middle Pleistocene, similar to *Homo heidelbergensis*, may correspond to the introduction of Mode 2 elements in the region, but these associations remain obscure. The first modern fossils are those of the Upper Cave at Zoukhouidian, which show a variable and distinctly non-Mongoloid morphology (Weidenreich 1938–9; Kamminga & Wright 1988; Lahr 1996). These fossils were associated with an Upper Palaeolithic bone tool assemblage, including a bone needle and ornamental objects (Pei 1938–9; Weidenreich 1938–9). All subsequent remains are also fully modern in character (Liujiang, Minatogawa). The presence of Mode 4 and 5 elements in northern and southern China respectively may reflect the easternmost point of convergence of southern and northern east–west dispersal routes. In Australia, the technology is broadly Mode 3, although there is little by way of formal tool types. All fossils are modern, and show a robust morphology more consistent with the early modern African forms than that of the modern humans associated with Mode 4 industries. This would be consistent with a separate route of dispersal from Africa across southern Asia.

The archaeological phylogeny and genetic data

The genetic variation of living humans has been used extensively in the last few years to provide information about recent human evolution. Much of what has been discussed above is consistent with current interpretations of the genetic evidence — that is, that *Homo sapiens* evolved in Africa and dispersed out over the course of the later Pleistocene. There are, however, a number of points that might be worth highlighting. The first of these is that the date that recurs in discussions of human evolutionary genetics is the period between 150–300 Kyr. This is the broad range over which the genealogy of a number of human genes coalesce (Cavalli-Sforza *et al.* 1994; Horai *et al.* 1995; Nei & Takezaki 1996; Stoneking 1993; Takahata 1993, among others). Different genes have different genealogical histories, but used in combination they can portray the true evolutionary history of a taxon (Avise & Wollenberg in press), and give very consistent results (Cavalli-Sforza *et al.* 1994; Nei & Takezaki 1996). This temporal range pre-dates the appearance of a modern morphology and the Mode 4 'package', but is consistent with the period when Mode 3 industries appear.

Second is the question of interbreeding and re-placements. The genetic evidence has been used to determine over what areas and times gene flow occurred and had a significant effect on human evolution. This is extremely difficult to integrate with either archaeological or fossil data, which seldom provide unambiguous evidence. If both the modern human and Neanderthal lineages derive from a common Mode 3 population around 250 Kyr, it may mean that their last common ancestor was sufficiently recent in time for Neanderthal genetic variation to lie within that of modern humans. However, the fossil and archaeological evidence in Europe, perhaps more so than anywhere else, do seem to indicate a discontinuous pattern of change in the late Pleistocene.

Third, the chronology of colonization around the globe following the development of Mode 3, with greater antiquity in Africa, Australia and south-east Asia than in Europe and northern Asia, is compatible with the relative amounts of genetic diversity found within continents, and with a model of multiple dispersals. The longer chronology for the diversification of humans proposed here, and the idea of multiple dispersals, help to account for the genetic structure of human populations that shows a combination of some deep patterns of variation with some much more superficial ones.

Archaeological phylogeny and implications for behaviour

Implications for behavioural evolution also flow from these discussions. Conventionally, the appearance of Mode 4 technologies and associated cultural attributes have been interpreted as a sign of symbolic thought, language or some generally greater capacity for complex behaviour (Mellars 1989; Klein 1995; Mithen 1996). There has also been a tendency to emphasize the behavioural differences between modern humans and Neanderthals, to lump Neanderthals with all other archaic hominids, and to elevate the Upper Palaeolithic nature of the African Middle Stone Age. Critics have focused on the many disjunctions between biology and technology discussed above. If Mode 3 is a critical change, then one implication is that any descendant of these founding populations will share certain derived characteristics. Neanderthals and modern humans both show larger cranial capacities than other hominids, and the Middle Stone Age and Middle Palaeolithic are also more complex than preceding assemblages. A number of lines of evidence would also indicate that both the modern and Neanderthal lineages possessed relatively similar capacities for language (Aiello & Dunbar 1993; McLarnon 1993) and life history parameters (Foley 1996). There is also evidence that Neanderthals developed complex strategies of food procurement (Stiner 1994) and lithic production (Kuhn 1996), and that these changed during the middle of the last glaciation (Allsworth-Jones 1993; Kuhn 1996; Mellars 1996; Stiner 1994). Furthermore, it is probable that Neanderthals buried their dead and, in the later stages at least, worked bone (Arcy-sur-Cure: Hublin 1996). In other words, while there are significant differences between modern humans and Neanderthals, the latter can, nonetheless, be differentiated from other archaic populations.

In a sense, this is consistent with the working assumptions made here, that technological mode differences would reflect basic biological cognitive attributes. A population ancestral to Neanderthals and modern humans evolved a level of cognitive development reflected in the appearance of Mode 3 industries that was later shared by both its descendant groups. On the other hand, important cognitive differences between Neanderthals and modern humans in the ability to invent material and behavioural solutions to immediate problems clearly had consequences for the potential of each lineage for survival and dispersal. This potential may be reflected in the relatively high number of innovative elements in the

African Middle Stone Age. It could be argued that during Stage 6, the African branch of Mode 3 populations evolved new cognitive skills, leading to better utilization of raw material and new ecological attributes like larger home ranges, day ranges, group size and dietary selectivity (Foley 1989). The evolution of anatomical modernity may thus correlate with this evolutionary shift during the African Middle Stone Age.

Where does this leave the issue of the Upper Palaeolithic or Mode 4 industries? If Mode 3 is an indicator of both Neanderthals and modern humans, and only the minor variants of these industries reflect detailed phylogenetic patterns, then Mode 4 cannot be a universal indicator of the spread of modern humans. This allows us to recognize diverse ends of the Mode 3 industries, reflected in the appearance of Mode 4 industries in Europe, or Mode 5 as in southern Asia or sub-Saharan Africa, and these should be seen as alternative technological trajectories. Second, the termination of Mode 3 is very ragged and geographically localized — abrupt and distinctive in Europe and the Middle East (Aurignacian); very late in North Africa; intermittent and local in sub-Saharan Africa; late and often directly to microliths in many parts of southern and eastern Asia. These varied developments reflect local adaptive strategies, greater potential for cultural variation, as well as further dispersals of modern human populations.

The 'Mode 3 hypothesis': concordant points

The model presented here clarifies certain apparent anomalies in the generally accepted 'Out of Africa' interpretation of later human evolution and prehistory.

1. The shared technology of Neanderthals and modern humans in the Levant is a plesiomorphy, representing a relatively recent common ancestor, although followed by considerable biological change.
2. The presence of 'advanced' behaviours in Neanderthals is not anomalous, given that they share a basic level of mental abilities with modern humans not present in other archaic populations.
3. The lack of correlation between the appearance of modern humans and the development of the Upper Palaeolithic technology is not significant; the Upper Palaeolithic represents one part of the potential for behavioural change within the modern human repertoire. Blades are regionally not globally important.

4. The absence of an Upper Palaeolithic in Australia is not indicative of separation of biological populations prior to the development of modern cognitive capacities.
5. The archaeological record shows that there are a number of potential routes of technological development that arise out of Mode 3 industries: microlithic blades and points, as well as the large punch blade tradition.
6. The Mode 3 hypothesis accounts for the extended temporal spread of the events associated with the evolution of modern humans, and provides a framework for interpreting these within their specific regional contexts rather than as lagged indications of universal human characteristics.

The 'Mode 3 hypothesis': unresolved issues and controversial aspects

While the model clarifies certain controversial issues, others become more prominent. Some of these are essentially empirical ones, where there is simply insufficient data to resolve ambiguities. One example is the later Chinese archaeological record. Morphologically a case can be made that *Homo heidelbergensis* populations spread into northern China. The model presented here would predict that if this was the case, Mode 2 industries should occur there. There has been considerable debate about the presence of bifaces in northern China, and whether these have affinities to the Acheulian of Europe and Africa. The answer would be significant to this hypothesis.

There are other examples of implications of the model that run counter to more orthodox interpretations.

1. The origins of Neanderthals are normally placed within Europe, with the original separation of African and European populations following the initial colonization of the continent by Mode 2 populations ~500 Kyr. This would imply a long period of isolation and regional evolutionary trajectories. According to the model we have presented here, the separation of Neanderthal and modern human lineages may be no older than 250 Kyr. If this is the case, then a number of implications follow. One is that the persistence of the Acheulian alongside the Middle Palaeolithic in Europe would indicate the presence of two distinct hominid populations (or even species). This raises the question of the nature of the interaction between them, and the ultimate fate of the *Homo heidelbergensis* populations. Was it a replacement event, did the true archaics of

Europe become extinct, or was there interbreeding between populations?

2. There is also the question of genetics. As discussed above, the mtDNA evidence and other genetic systems imply a source population for the ancestors of all living humans between 150 and 300 Kyr. This is close to the dates for the origins of Mode 3 and the dispersals that we have argued are associated with it. As Neanderthals are part of that dispersal, it does not follow automatically that they are not themselves descendants of the so-called African Eve. As they subsequently differentiated, however, this does not necessarily mean that they could interbreed with modern populations coming into Europe around 40 Kyr. The mtDNA gene acts only as a genealogical marker, and not as a genetic parameter of reproductive potential. Indeed, the level of morphological specialization of the Neanderthal lineage can be argued to reflect the evolution of a different species, *Homo neanderthalensis*.
3. The archaeological phylogeny discussed here also raises questions about the diversity of hominids within Africa. The period from 250–120 Kyr in Africa shows considerable variation in technologies. If these do represent relatively distinct hominids, then, as in Europe, it may imply that African *Homo heidelbergensis* co-existed with the Mode 3 population over a relatively long period of time, with implications for patterns of human genetic diversity.
4. The 'Mode 3 hypothesis' also raises taxonomic questions. Which populations are to be included within *Homo sapiens*? A case could be made for considering the ancestral Mode 3 population *Homo sapiens*. In that case, Neanderthals would be either a subspecies of *Homo sapiens* or a derived clade of such taxon. On the other hand, it could be argued that the development of Mode 3 industries and the mental capacities behind them did not mark the evolution of a new species, but reflected only differentiations within *Homo heidelbergensis*. In that case, genetic exchange with persistent Mode 2 populations in either forested Africa or Europe would have blurred the recency of the common ancestry between Neanderthals and humans. Both groups would then represent species derived from *Homo heidelbergensis* during Stage 6, and Mode 3 would map population movements but not phylogeny. A final option would be to consider the cognitive changes behind Mode 3 and its clear demographic success in relation to Mode 2 populations, as well as

the derived anatomical changes that originated Neanderthals and those that originated modern humans to reflect speciation events. In that case *Homo sapiens* and *Homo neanderthalensis* would be derived from a new species, for which the available name *Homo helmei* (Dreyer 1935) has been suggested, albeit to a differently composed sample (Stringer 1995). None of these issues is fatal to the model we have presented here, but they highlight the evolutionary significance of the origins of the Middle Palaeolithic/Middle Stone Age.

Conclusions

During the last half million years there may have been as many as four hominid species, of which *Homo sapiens* is but one. This relatively high level of biological diversity has been the inspiration for attempting to use the variability in the archaeological record as the basis for reconstructing the events that led to the evolution of *Homo sapiens*, its subsequent dispersal and the concomitant disappearance of other hominids. Archaeology, we have argued, can perhaps reach the parts of evolutionary history that other disciplines cannot. Interpreting the archaeological record in terms of evolutionary history, however, depends on the model employed. The conventional model would be what might be referred to as the local adaptive-functional diffusion model. According to this view, variation is a product of the interaction of general cognitive and technological capacities and local environmental demands. Geographical patterns are accounted for by a blend of cultural diffusion and local invention.

The alternative may be described as the dispersal-phylogenetic model — at a large geographical scale major differences in technology reflect affinities resulting from the expansion and contraction of populations. The dispersal-phylogenetic model is a working premise that allows us to explore the possibility that shared technologies indicate biological populations and their movements, and that differences across time and space indicate some form of biological discontinuity. From the point of view of the origins of modern humans debate, the key conclusion we would draw is that the development of Middle Stone Age technologies in Africa around 250 Kyr is of greater universal significance than the origins of the Upper Palaeolithic. The former may mark a major cognitive development associated with the biological changes leading to the evolution of modern humans; the latter is merely a regional shift in

behavioural patterns. Contrasts between the Middle and Upper Palaeolithic should not be underestimated: they represent a significant discontinuity in the archaeological record. But at a global scale continuities of Mode 3 industries also occur. Rather than undermining the 'Out of Africa' model of modern human origins, these continuities in fact provide further support by solving various anomalies.

The model presented here would transpose the relationship between morphological and behavioural evolution. Under current interpretations there is a considerable lag between the evolution of modern morphology and major behavioural transformations. The Mode 3 hypothesis would imply that evolutionary change occurred in the Middle Pleistocene which led relatively rapidly to an acceleration in encephalization, technological change, and dispersal of populations. The morphological developments leading to modern humans were one consequence of this change. Cognitive changes may well have been involved in these events, and within the model we have proposed these cognitive changes could have occurred over a period of more than one hundred thousand years. Such a broad chronological spread would account also for both the similarities and differences between modern humans and Neanderthals, and would furthermore help account for the uniformity of cognitive skills in living human populations.

The basis for this cognitive evolution remains unknown. Aiello & Dunbar (1993) have proposed that the brain size found in archaic hominids around 300 Kyr is at a critical threshold for maintaining social groups, and that this may have been a stimulus for the evolution of language. It is also the case that the costs imposed by brain sizes larger than 1000 cc are likely to have triggered much more human-like life history strategies (Foley & Lee 1991). The flexibility and efficiency of the Mode 3 technology may well have been a response to these biologically based developments, and in turn led to further ecological changes, some of which may have been critical in promoting evolutionary change in the African lineage during the stringent conditions of Stage 6. Furthermore, although the ancestors of modern humans in Africa and the ancestors of the Neanderthals in Europe evolved along different pathways, their shared ancestry during this period of rapid evolutionary change means that they may also have had a shared cognitive world. It does not, of course, follow that a shared cognition reduced the probability of extinction when the populations came into contact tens of thousands of years later.

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