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## EARLY HOMINID DISPERSIONS

**ABSTRACT:** *Modern humans have reached their present distribution through a process of dispersion that originated some two to three million years ago in Africa. Like most aspects of hominid evolution, this dispersion is best considered within a general framework drawn from a wider understanding of the ecology and evolution of the terrestrial mammal fauna.*

*New species originate in allopatry, within preferred habitats, and tend to remain within that habitat until new conditions provoke a fresh pattern of range fragmentation. Any dispersion of a new species is thus from a geographically restricted point of origin. The extent and rate of dispersion are therefore generally dictated by the rate of population expansion into new territories and the degree of habitat specialisation of the species. In the case of hominids, the development of technology and of increasingly sophisticated patterns of social organisation and behaviour will have impinged directly upon the 'natural' pattern of dispersion, removing the constraints of habitat specialisation. Changes in the pattern and range of dispersion may be seen with the first appearance of the genus *Homo* in Africa between 2.5 and 2.0 Ma (million years ago) and shortly after that with movement into the Levant and Caucasus, culminating by around 1.0 Ma with at least initial dispersions into the temperate and tropical regions of the Old World, most probably by *Homo erectus*. In this breadth of habitat exploitation the hominids more closely resemble the larger carnivores than any other family among the terrestrial mammals.*

*However, more permanent occupation of temperate Eurasia appears to have been a relatively late, Middle Pleistocene phenomenon. This pattern may in part have been dictated by the availability of food resources, which may in turn have been conditioned by the structure of the guild of larger carnivores. Only after 0.5 Ma did that guild reduce in size to resemble that of modern-day eastern Africa.*

**KEY WORDS:** *Human dispersion – Out of Africa – Earliest Europeans: Community evolution*

### INTRODUCTION

Modern humans, like the majority of other larger placental mammals, have reached their present distribution through a process of dispersion. Even the simplest map of hominid presence through time, based on a combination of archaeological and fossil evidence, will reveal a pattern of movement that originated some two to three million years ago in Africa and ended with virtually every piece of land occupied.

That alone is unremarkable, since every taxon has its origins. What complicates the picture for the hominid

palaeontologist is that this process of dispersion takes place in the context of considerable evolutionary change involving several taxa with differing distributions in time and space, and that the ultimate distribution of *Homo sapiens* is one of the widest achieved by any mammalian species. The number of dispersion events that led up to that ultimate distribution is itself the subject of considerable debate (Stringer, Gamble 1993). We also know, or can reasonably suspect from our knowledge of events during the historic period, that some element of volition is likely to have played a part in at least some of the movements. An obvious question is then raised: what constraints and



impetuses have operated on hominids to produce the chronological and geographical patterns of dispersion seen in the fossil record for various taxa?

Several years ago, I suggested that the initial hominid dispersions into temperate and cold environments of Eurasia could be profitably compared with similar patterns of movement by some of the larger carnivore species, most notably the lion, *Panthera leo* and the spotted hyena, *Crocuta crocuta* (Turner 1984). Although the evidence for the timing of movements on which that analysis was based has now been superseded (Turner 1992b), I argued then, and believe still, that most if not all aspects of hominid evolution are best considered within a general framework drawn from a wider understanding of the ecology and evolution of the terrestrial mammal fauna (Turner 1991, 1992a, Turner, Wood 1993a,b). Only in this way do we avoid the trap of overly particularist interpretations of our own past, with hominids always accorded special status and our evolution seen as something apart from the rest of the living world. My purpose here is to return to the comparative assessment of the earlier phases of hominid dispersion and to see what light can be shed on the matter by some recent developments in that more general framework, especially developments in our understanding of the opening and closing of dispersal routes.

I shall begin by saying something about communities and the distributions of species, in an effort to set the whole issue of species origin and dispersion within its widest possible context.

## COMMUNITIES

Although hominid evolution and dispersion take place as one element of a multifaceted change in the biota, it is important that we retain a clear perspective on the notion that it is somehow the community as a sum of more than the parts that actually evolves and disperses. As recent studies of vegetational changes in cyclically repeated interglacial periods have shown, this frequently invoked expectation of community evolution is simply not met when actual case histories are examined (Huntley, Webb 1989). Trees in particular, and especially broad-leaved taxa that became confined to southern refugia during glacial periods (Zagwijn 1992), each underwent very different migrations as they recolonised to form the woodland vegetation of central and northern Europe during the various interglacials (Zagwijn 1989). In the harsh conditions of the Siberian high Arctic, plant and animal communities show no sign of having undertaken a unified response to climatic change, so that "individual species response seems much more appropriate" as an interpretation of the radical restructuring of the biota that took place there during the course of the Pleistocene (Sher 1991: 221). Even the apparently regular alternation of glacial-cold adapted and interglacial warm-loving mammalian faunas in the Middle and Upper Pleistocene

of Europe was subject to what von Koenigswald (1992: 45) has referred to as "significant irregularities", perhaps exemplified by the appearance there of *Hippopotamus amphibius* and the water buffalo, *Bubalus murrensis*, in some but not all interglacial stages (von Koenigswald 1991). Biological communities, in other words, "are thus shown to be merely temporary assemblages of species brought together by the environmental conditions prevailing at any particular time" (Huntley, Webb 1989: 5).

Seen from this perspective, it is clear that the mammalian communities within which the hominids appeared and evolved must continue to be regarded as epiphenomena, made up of many species each with its own evolutionary history. Such generalisations as we may, quite properly, seek to apply to the study of hominid evolution are thus to do with responses by organisms to environmental stimuli, but those stimuli are to be seen operating on individuals and aggregations of individuals to produce taxon-specific responses. Thus the broad contemporaneity of the earliest European appearance of hominids and larger predators such as the lion and the spotted hyena, even if correct and even if from a similar region of ultimate origin (Turner 1991), is likely to have little to do with any notional entry of Lower Pleistocene hominids into the community of larger predators and the dispersion of that community as an entity. Instead, it reflects the similarity in the breadth of resource use in larger members of the *Carnivora* and carnivorous hominids equipped with technology. I shall return to this point below.

## DISTRIBUTIONS OF SPECIES

It is evident that no organism, and no species, can continue to inhabit an environment to which it is unsuited. That suitability can be measured in a number of ways, but it will essentially encompass aspects of physiology and behaviour and the extent to which the habitat can be modified.

Recent insights into the nature of species and the process of speciation show that sexually reproducing species are best understood to originate in preferred habitats to which the specific-mate recognition system (SMRS), which has the function of bringing mating partners in motile organisms together, is closely adapted (Paterson 1985, Turner, Paterson 1991). New species thereafter tend to stay within that habitat unless environmental changes produce range fragmentation. A new habitat encountered in such circumstances by a subset of the original population may then induce change in the SMRS, leading to incompatibility with organisms retaining the original SMRS and thus effecting a further speciation (Turner, Chamberlain 1989). I stress the may: speciation is not an inevitable outcome in such circumstances, but range fragmentation into allopatric communities is likely to be a necessary condition. However, since speciation is not an inevitable outcome of environmental changes, there is little point in simply



looking for the presence (or absence) of a continual pattern of evolutionary change (that is, speciation, extinction and dispersion), whether in species, lineages or clades, in relation to the detailed fluctuations of long-term environmental change, as recently proposed by Foley (1993) as a test of evolutionary mechanism. Instead, one should be looking for correlations between significant steps in environmental variables and evolutionary changes in resource and habitat specialist (stenobiomic) versus resource and habitat generalist (eurybiomic) lineages, a point usefully discussed in detail by Vrba (1987, 1992). Complexities such as the direction or nature of climatic change, seen by Foley as an impediment to interpretation and to the implication of climate as a driving force in hominid evolution, then become less relevant to the question of correlation with evolutionary events across clades. Rather, it is the interaction between the change itself, perhaps in terms of its intensity, and the lineage-specific characteristics of resource use that will determine whether or not members of a given lineage will participate in a given turnover event. The point made by Vrba (1985: 234) in this context is fundamental but essentially simple: if external forces provoke evolutionary turnover, not all lineages may react to a given externally-directed event but any that do will do so in concert.

The view of species outlined above and the process of speciation that it suggests, have several implications for our understanding of patterns in the fossil record, particularly in relation to the deployment of speciation through time (Turner, Paterson 1991, Turner 1993). In the present context three major implications may be identified. First, since new species originate from a subset of the population of the parent species, they necessarily have a localised place of origin. Any subsequent distribution beyond the range of the subset must therefore be achieved by a dispersion (Tchernov 1992a). Population growth necessary to impel that dispersion will take time, and the speed of dispersion will be affected by the social structure of the species and the extent to which each generation must seek new territories (Turner 1984). Secondly, species with a narrow specialisation (stenobiomic) will be more tightly constrained in their range of territory, while environmental generalists (eurybiomic) will be much freer to move. It is no accident that some of the larger carnivores, constrained only by the availability of food in the shape of a sufficient supply of ungulates, have been among the most widely dispersed of the larger Plio-Pleistocene species (Turner 1990, 1992b). Thirdly, environmental specialists, even if they remain in the same place, will tend to encounter new habitats more frequently than generalists in conditions of environmental change, and will thus be likely to encounter conditions conducive to speciation (or to extinction) more frequently.

In the absence of physical barriers, habitat will therefore dictate where given species can and cannot exist. Habitat is largely determined by prevailing climatic conditions (van der Made 1992), and larger scale alterations to the range

of a species are therefore likely to occur with climatic change. In saying this I do not imply that tectonic events have no bearing on the problem, since physical contact can clearly be rendered possible or impossible by crustal movements and changes in elevation may themselves induce climatic change. I shall return to the subject of tectonic activity in the next section, since it has obviously played an important part in the question of earliest emergence from Africa. But important as these effects may be on a regional basis, the most important determinants of habitat during the Plio-Pleistocene seem to have been global in nature, induced by orbital fluctuations (Prentice, Denton 1988), and it is the wider habitat that is likely to have been of particular importance to the maintenance of populations in new regions.

In the absence of climatic change, population growth may still impel dispersion into previously unoccupied areas, and while this must be recognised as a confounding variable in any efforts to correlate past dispersions with climatic changes, such essentially biotically induced movements will usually only be successful if the habitat in the new area is sufficiently similar or if it can be modified successfully. The obvious feature of hominid evolution that makes all the difference to constraints on dispersion is the interaction of behaviour and technology to provide increasingly sophisticated ways of manipulating and modifying the habitat so as to permit occupancy in hostile circumstances, with eventual dispersion into the high Arctic as an evident case in point.

## EARLIEST HOMINID DISPERSIONS

The development of a stone tool technology can now be traced back in Africa to around 2.4 Ma, based on material from Hadar (Harris 1983) the Omo Shungura Formation (Merrick, Merrick 1976) and the Lokalalei Member at West Turkana (Kibunja *et al.* 1992). With the appearance of that technology, some of the hominids arguably became environmental generalists (eurybiomic) within the context of the overall range of hominoid ecology (Vrba 1988), and at the same time became capable of modifying their environment to some degree or other. As has already been stressed, it is in this context that we should understand any parallels between the distributions of hominids and larger predators, as species freed from the narrow constraints of habitat specialisation in the one case by an increasing intelligence and a developing technological repertoire and in the other by a generalised feeding strategy.

Our own genus, *Homo*, first appears in the fossil record at about the same time as the earliest tools, and shortly spread over eastern and southern Africa in the form of one or more of two possible species, *Homo habilis* and *Homo rudolfensis* (Turner, Wood 1993a). This dispersion seems to have marked the start of a transition from earlier, more spatially restricted distributions of species of the genus *Australopithecus*, the eastern African *A. afarensis* and the



South African *A. africanus*. Like *Australopithecus*, species of the robust genus *Paranthropus* (here considered a monophyletic clade) also appear to have been confined to one or other of these two African regions, despite the fact that other members of the larger mammal fauna have been found in both southern and eastern parts of the continent and point to the possibility of dispersions between the two areas during much of the later Pliocene (Turner, Wood 1993a: Tables 1–5).

This earliest appearance of *Homo*, and the apparent split in the hominid clade at about this time, has been seen as one part of the larger-scale turnover in the mammalian fauna of Africa and Eurasia induced by the mid-Pliocene climatic changes that culminated in the event at around 2.5 Ma (Prentice, Denton 1988, Vrba 1988, Vrba *et al.* 1989, Turner, Wood 1993b, Turner 1995). By 1.8 Ma these earliest members of *Homo* had been joined, and eventually replaced, by *Homo erectus* (itself possibly preceded by *Homo ergaster* [Wood 1991]). Although the relationship between Asian and African *Homo erectus* is disputed by some, this is generally considered to be the oldest hominid species to appear in the fossil record outside the African continent (Turner, Chamberlain 1989). However, it may not have been the first to disperse (see below).

The earliest stone tools, essentially sharp-edged flakes and perhaps pounding implements (Kibunja *et al.* 1992), were augmented by around 1.4 Ma by more sophisticated, bifacially-worked items generally referred to as Acheulean (Asfaw *et al.* 1992). However, while the initial development of technology may have reduced the constraints upon the range of exploitable habitats for early hominids, it is unclear whether such technology was in itself necessarily sufficient to promote dispersion from the continent of origins. The timing of hominid first appearance outside Africa remains a subject of considerable dispute, with a time range of up to a million years after the first appearance of stone tools in Africa depending on acceptance of claims of earliest dates from elsewhere as usefully summarised in the volume edited by Bonifay and Vandermeersch (1991). Many of the supposedly earlier occurrences in western Europe in particular require substantial evaluation, based as they are on often disputed archaeological evidence rather than on hominid fossils.

In contrast, there is evidence for early Middle Eastern hominids based on Acheulean assemblages from 'Ubeidiya in Israel, now generally dated to around 1.4 Ma (Tchernov 1992b) and some possible pebble tools from the Erq-el-Ahmar Formation dated to 1.8–1.9 Ma (Verosub, Tchernov 1991). This has recently been augmented by claims for more primitive items dated to before 2.4 Ma based on specimens found below basalt exposures in Upper Galilee (Ronen 1991), although, as the latter author stresses, confirmation of these results is still awaited. Artefacts in the form of quartzite flakes have also been reported in deposits considered to date to 2.0 Ma from northern Pakistan (Dennell *et al.* 1988). In the meantime, the earliest non-African appearance currently given general credence

is the hominid mandible from Dmanisi in Georgia with a date of just after 1.6 Ma (Dzaparidze *et al.* 1992) based on volcanic deposits that immediately underlie the hominid-bearing level and the presence of an undoubtedly archaic mammalian fauna. The lithic assemblage from this site owes little to Acheulean forms (Bosinski *et al.* 1992). However, one should note in passing that among the biostratigraphic evidence supporting the date for Dmanisi has been the presence of the dirk-toothed cat, *Megantereon cultridens*. This species had until recently been thought to have gone extinct in Europe by around 1.2 Ma (Turner 1992b), but recent discovery of a specimen at the German site of Untermassfeld in Thuringia, dated to the Jaramillo event, now calls this support into question (Turner, unpublished data).

It would therefore seem that the first dispersion of hominids from Africa was achieved by populations still employing some of the earliest stone-tool technology, and it may have led to a relatively rapid episode of colonisation if the early dates from Israel and Pakistan prove to be correct. Even if these earliest claims are not upheld, the material from Dmanisi (if itself correctly dated) would seem to rule out alternative suggestions that earliest dispersions were dependent upon the development of bifacial implements and the increased technological repertoire that these might indicate. However, the presence of such items at 'Ubeidiya at close to 1.4 Ma might imply that their development led to a rapid and widescale adoption, although one should bear in mind that dating resolution at this age may render contemporaneity more apparent than real.

The uncertainties over the timing of initial dispersions from Africa make it impossible to seek a correlation with any one particular external agency that may have driven the movements. The taxonomic questions that surround the African fossil record at around 2.0 Ma themselves scarcely add clarity to the search for ultimate causes. For the present, we must therefore attempt to assess the initial dispersion of the *Hominidae* in wider terms, in the reasonable expectation that any external agency will have impinged on more than just our own family.

## LARGER DISPERSION PATTERNS

Mammalian dispersions between Africa and Eurasia have taken place at various times during the past few millions of years since the early Miocene contact between plates provided a land bridge (Thomas 1985, Tchernov 1992b). Hominids are therefore certainly not unique in having moved out of Africa. However, tectonic events and climatic changes have continued to play a major role in the formation of the physical and biotic environment of the region, and the route to Eurasia through the Levant has been subjected to progressive displacement and desiccation. Since the early Pleistocene the exchanges have therefore been selective. The extent of other possible Pliocene contact points, such as the land bridge at



Gibraltar which is widely presumed to have been present during the end-Miocene Messinian crisis, is unclear, although the Lower Pleistocene presence of the African giant *papionine* *Theropithecus* cf *T. oswaldi* and *Hippopotamus* at the Spanish site of Cueva Victoria have been used to argue for some contact with north Africa at that time (Agusti, Moya-Sola 1992). The latter at least may of course have arrived in Iberia simply by swimming, while the precise geography of the Gibraltar portal may have permitted earlier Miocene taxa to disperse from Africa onto what then became an island between Africa and the Iberian Peninsula proper before it joined to the latter during the Pliocene. Direct Plio-Pleistocene contact between Africa and south-western Europe would not therefore be indicated by the presence of African taxa in Iberia (J.-P. Suc, pers. comm.), although the presence of the genus *Hippopotamus* rather than *Hexaprotodon* in southern Spain would suggest that the time of contact was post 2.5 Ma in that particular case (Turner, Wood 1993b). But in any event, relatively few species do appear to have moved either out of Africa or into it during the Pleistocene, a fact reflected in the scarcity of North African taxa recorded at the Israelian Lower Pleistocene site of 'Ubeidiya (Tchernov 1992b: Tables 4a,b) and the hominids in that sense may be seen as members of a minority if they were indeed dispersing out of Africa at that time.

However, it should be stressed that Pleistocene restrictions on the movement of species through the Levant and into and out of Africa may imply greater significance for the claimed later Pliocene Levantine occurrences of hominids. During late Pliocene times it seems that exchanges did take place between eastern Africa and the southern Levant via the Bab-el-Mandab Afro-Arabian landbridge at the southernmost end of the Red Sea, despite the fact that widening of the Red Sea was by that time leading to the break-up of the connection (Tchernov 1992b). As Tchernov points out, the faunal assemblage from Bethlehem (Hooijer 1958) does contain open-country species, and in particular a giraffe, quite typical of an eastern African lowland savannah landscape and one in which later Pliocene hominids would have been very much at home. However, in the same paper Tchernov (1992b: 116) appears to be in error in suggesting that the Levant as a whole had little in common with southern Europe, since the same Bethlehem fauna contains several taxa, such as the racoon dog, *Nyctereutes megamastoides*, the Etruscan rhinoceros, *Stephanorhinus etruscus*, and the bovid *Gazella torticornis*, well-known in Villafranchian faunal assemblages. Overall, the Levantine evidence may therefore be taken to indicate some late Pliocene Afro-Eurasian contact.

It is worth ending this section by pointing out that any appearance of hominids in the Levant (and perhaps beyond) at or about 2.0 Ma could then be seen as part and parcel of the train of events set in motion by the earlier climatic changes. In other words, it may not be necessary to seek a separate explanation. Of course, we need to need to

introduce a note of caution into the search for correlations and mechanisms, otherwise we may simply end up with over-generalised explanations whereby everything is simply referred back to a previous event. But, as has been stressed elsewhere (Turner, Wood 1993b, Turner 1990, 1995) the climatic changes that culminated at 2.5 Ma do seem to have had a particularly marked effect on the subsequent vegetational and faunal histories of both Africa and Eurasia, and cannot simply be seen as a single event in the development of the biota. Unless we are prepared to think in terms of follow-on effects stemming from changes in the determinants of evolutionary trajectories, we shall fail in our efforts to understand the mechanisms that underlie speciation, extinction and dispersion in the fossil record.

## THE EARLIEST EUROPEAN HOMINIDS

It is clear from the foregoing discussion that the hominid mandible from Dmanisi is of particular interest to those interested in the question of what hominid species first colonised Europe in view of its geographic position and age. Despite the uncertainties raised by the discovery of *Megantereon cultridens* elsewhere at a substantially later date than that claimed for the assemblage there, the deposit from which the specimen comes is certainly of Lower Pleistocene age, while the site is almost perfectly located on the crossroads between Africa, Europe and Asia. The mammalian assemblage appears to represent a fauna of typically European Villafranchian species, with the presence of the Etruscan bear, *Ursus etruscus*, the machairodont cats, *Homotherium cultridens* and *Megantereon cultridens*, the Etruscan rhinoceros, *Stephanorhinus etruscus*, the zebrine horse, *Equus cf stenonis*, and a number of cervids and bovids (Vekua, Gabunia 1992). However, several elements of the assemblage are also shared with 'Ubeidiya, and a notable inclusion is a specimen of ostrich, providing an interesting link with Africa.

The hominid specimen from Dmanisi has been initially described as having a mosaic of characters that include some *Homo erectus* features (Gabunia *et al.* 1992), although mandibles are notoriously hard to deal with taxonomically and whether this suggestion stands the test of time remains to be seen. However, the species of hominid that first colonised western Europe is uncertain, since the earliest fossil specimen from the region, the Mauer mandible, is unquestionably later than the evidence for Lower Pleistocene occupation afforded by the TDG deposits at Atapuerca usefully summarised by Aguirre (1998), and later than the material from Dmanisi by at least several hundred thousand years whatever we take the age of the latter to be (Zöller 1991). But even the correct designation of later, Middle Pleistocene hominids such as Mauer, together with skulls such as Steinheim and Petralona, is unclear. The use of terms such as "archaic"



*Homo sapiens* to describe the earliest known European fossils makes little taxonomic sense (Stringer 1985, Tattersall 1986) even if one would not wish to go so far as Tattersall suggests in splitting the sample into formally-named taxa. Indeed it would seem to me, in view of what we can now understand about species and the process of speciation, that a proliferation of what were presumably eurybiomic hominid species during the Middle Pleistocene is inherently unlikely.

Most logically, I would argue, the earliest colonists were therefore probably *Homo erectus*, given that only that species is known elsewhere during the Lower Pleistocene and that there is as yet no convincing case for a Pliocene presence in Europe and thus of *Homo habilis*, *Homo rudolfensis* or even any representative of *Australopithecus* (and certainly no evidence for *Paranthropus*). But whether the transition to the non *erectus*-like morphology that has led to the introduction of the unfortunate designation "archaic" *Homo sapiens* for Middle Pleistocene specimens occurred soon after initial colonisation is unclear. I suspect that it did not, simply because the archaeological evidence for intensive and permanent occupation of the temperate zones of Eurasia is a Middle Pleistocene phenomenon, and I have suggested that Lower Pleistocene attempts were largely sporadic and unsuccessful (Turner 1992a).

Europe presented a very different environment for latest Pliocene and earlier Pleistocene hominids from of the African savannah in which they had evolved. Throughout the Pleistocene Europe was a temperate and frequently glacial or periglacial region, dominated by colder and more arid conditions than today except at the peaks of the interglacials (Gamble 1986, Turner 1992a, Zagwijn 1992). During much of the glacial periods that came to dominate the past million or so years it was a region of treeless vegetation (Zagwijn 1992: Fig. 1). In such circumstances, a high dependence on animals as a food source would have been inevitable since plant foods would simply not have provided an adequate, year-round supply, and the ability to function and obtain such resources in cold conditions would have been a pre-requisite for occupation. The ability to make clothing and to construct shelters would have been essential, but obtaining food was probably no simple matter either.

Scavenging is likely to have been a significant means of obtaining food in such circumstances, and successful colonisation would therefore have depended strongly on the structure of the larger carnivore community or guild, members of which would have been in direct competition for available carcasses (Turner 1992a,b). Only after ca 0.5 Ma do we see a shift in that community in Europe towards the structure of the modern-day carnivore guild of eastern Africa, with the loss of two large species of carcass-destroying hyenas, and it is only around that time that the archaeological evidence from Europe begins to show evidence of more intensive occupation. I consider that correlation to be significant, and the structure of resource availability to have been a direct constraint upon successful,

permanent occupation by the first hominids to disperse into Europe.

There have been suggestions that the first major appearance of hominids in the temperate zones of western Eurasia in particular may have occurred at around 0.9 Ma, perhaps in parallel with the extinction in Africa of the robust australopithecines and the change that marks the end of the European Villafranchian faunal span and all driven by a further marked shift in global climate (Vrba *et al.* 1989). It seems clear that oxygen-isotope stage 22 did indeed see a marked switch in the bipolar ice sheet system, and thus in climate, with the establishment of the intense glacial-interglacial sequence of the Middle and Upper Pleistocene. However, some qualification is required. On the one hand, the end of the Villafranchian is a major faunal horizon, but it is now thought to have been underway prior to the climatic changes marked by stage 22 (Agusti *et al.* 1992) and is best seen as a rather extended event involving the dispersion of various taxa from Central Asia in to Europe (Sher 1992). On the other hand, we can see something of the eventual effect of that climatic shift in the subsequent appearance of the fully cold-adapted taxa such as *Coelodonta antiquitatis* (woolly rhinoceros), *Rangifer tarandus* (reindeer), *Ovibos moschatus* (musk ox) and the more specialised forms of *Mammuthus* (mammoth) in Europe (Turner 1992a: Tables 1-4). In the case of hominid incursions, while these may very well have commenced at or about 0.9 Ma, it is reasonably clear that such appearances really represent no more than initial attempts at colonisation rather than "the earliest massive geographic expansion" of Vrba *et al.* (1989: 142). The interesting point is that when more intensive occupation of temperate regions did take place it was probably successful because of the nature of the resource distribution produced by the earlier climatic developments, one that could be exploited with the available technology. Thus, as in the case of the 2.5 Ma event, while climate does indeed appear to be profoundly implicated in the biotic changes that took place around and subsequent to stage 22, it is clear that there is no single, once and for all response.

## CONCLUSION

Allopatric speciation in subsets of an original population implies a clear point of origin for hominid species, with the first representatives of our own genus, *Homo*, appearing in Africa at close to 2.5 Ma. Hominid dispersion, including that of *Homo*, can be seen as part of a larger pattern of dispersion by members of the terrestrial mammalian fauna, one resulting in an emergence from Africa via the Levant perhaps some time between 2.4 and 1.6 Ma. The effect of tectonic and climatic changes on the Levantine route during the Plio-Pleistocene suggests that a late Pliocene dispersion should be given serious consideration.

Earliest dispersions into the Levant and Eurasia appear to have been achieved by hominids equipped with a lithic



technology little changed from that recorded in Africa from 2.4 Ma. If the earliest Levantine and Pakistan dates are upheld, then the initial development of lithic technology may correlate with a fairly rapid dispersion, and would imply the presence of a pre-*Homo erectus* species such as *Homo habilis*. However, the earliest appearance of hominids in western Europe is more likely to have been achieved by *Homo erectus*, although whichever species first attempted to colonise the region appears to have been unable to do so on a permanent basis until the Middle Pleistocene.

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