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Circum-Mediterranean biological connections and the pattern of late Pleistocene human evolution

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Abstract
The isolation of human populations in Europe and in Africa is critical for models of modern human origins based on speciation events and total replacement of Neandertals and other archaic human groups by modern humans. Pleistocene human samples from Africa, west Asia and Europe are investigated to assess the morphological evidence for both isolation and regional interconnections. Four types of data are utilized: (1) results of a multivariate analysis of frontal bone shape, (2) distribution of patterns of supraorbital torus/brow ridge shape, (3) incidence of "cladistic" markers for Neandertals, and (4) occurrence of occipital buns. Environmental factors possibly influencing middle and late Pleistocene human evolution are also discussed. It is concluded that enough evidence exists for biological interconnections around the Mediterranean during this period to rule out regional isolation extensive enough to foster speciation. Thus, *Homo sapiens* has been a single, polytypic species since the Middle Pleistocene.

Key words: Evolution, Europe, gene flow, Neandertals, Near East, North Africa

One of the most basic issues in the on-going debate regarding the emergence of modern humans concerns the interpretation of regional variation in hominid fossils that date between approximately 200 kya and 50 kya. Supporters of both the Recent African Evolution (RAE) and Multiregional Evolution (MRE) models of modern human origins recognize the existence of significant regional diversity in hominid samples from this time span across the Old World but explain this diversity very differently. The Recent African Evolution model regards regional diversity as a reflection of the existence of separate, regionally based evolutionary lineages/species. According to this model, modern humans originated from the African lineage by 100 kya as a distinct species, which then radiated to Eurasia and replaced the indigenous archaic human lineages/species that evolved in these regions.[1] Multiregional Evolution denies the occurrence of speciation events within at least the last several hundred thousand years of human evolutionary history. It explains this diversity as resulting from a complex interplay of local genetic continuity, drift, interregional genetic exchange and local patterns of selection within a single species. In effect, MRE argues that *Homo sapiens* has been a widely-dispersed polytypic species since well before 200 kya.

Unfortunately, MRE continues to be misrepresented as supporting independent evolution of modern people from isolated regional lineages in several regions of the Old World (e.g. Howells 1993). In reality, MRE is the antithesis of this view and has always emphasized the importance of interconnections among regional lineages or clades (Frayer et al. 1993; Pope 1992; Smith 1992a; Smith et al. 1989a; Thorne and Wolpoff 1992; Wolpoff 1989, 1992). Because RAE views modern humans as the result of a distinct cladogenetic event (Stringer 1990, 1992a; Stringer and Andrews 1988; Tattersall 1993; see also Aiello 1993), it is *this model,* not MRE, that requires

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isolation. The African lineage would have to have been isolated for a time sufficient to establish the reproductive barriers required for cladogenesis. In our opinion, there are a number of indications from the pertinent fossil material which argue convincingly that this requisite isolation of African fossil hominids did not occur.

For many years, a distinct phenetic similarity has been recognized between the Kabwe (Broken Hill) 1 cranium and early European specimens like Petralona and Arago 21 (cf. Murrill 1975; Stringer 1983). Recently, Rightmire (1990) has recognized these specimens as part of the same lineage/species, which he designates as *Homo heidelbergensis*. Thus the isolation of the African lineage/species that presumably gave rise to mo-dern humans must have occurred after the time span of Kabwe/Petralona. The hominids that follow this time span in Africa are commonly placed in an African transitional group, reflecting their status as precursors of early modern Africans (Bräuer 1989, 1992; Smith 1992b; Smith et al. 1989a; Stringer 1990; Stringer & Andrews 1988). These specimens are listed in Table 1, and available data suggests an age of between 100 kya and 200 kya for them. Since the African transitional group exhibits a morphological pattern and trajectory that appears distinct from contemporary European and probably also Near Eastern hominids, it is reasonable to think that the isolation necessary for RAE must have been established during this period.

We investigate this issue through a comparative analysis of fossil hominid remains from around the Mediterranean Sea, where Africa meets Asia (the Levantine corridor) and lies closest to Europe (via the Straits of Gibraltar). It is only in these areas of Afro-Eurasian proximity where the issue of contact versus isolation can be investigated. If African hominids are reproductively isolated from their Eurasian contemporaries during the span in question, we should expect to see a distinct separation of pertinent African and Eurasian archaic hominids. If not, there should be some difficulty in separating the samples into regional groups.

Four types of data are used in this analysis. First, we present a multivariate analysis of frontal bone shape (cf. Simmons et al. 1991; Simmons & Smith 1991). These data are selected because the frontal bone tends to be well-represented in fossil samples, thus providing larger sample sizes than would be available if more complete crania were used. Also, the form of the frontal is an excellent reflection of overall cranial architecture (Smith & Ranyard 1980; Smith et al. 1989b; Splitery 1980, 1985). Second, the *shape* of the supraorbital torus/brow ridge is assessed. These structures exhibit considerable size reduction during the late Pleistocene, but there are indications that reduction does not follow the same pattern in all regions. Third, we revisit the distributions of certain cranial features used by Santa Luca (1978) in what was the first "cladistic" attempt to define

Table 1. The African transitional group.

Site (Country)	Age estimate	Basis of estimate and source	Material processed
Jebel Irhoud (Marocco)	130-190 Kya	ESR (Grün & Stringer 1991)	2 crania (one with face), juvenile mandible and humerus, innominate fragment
Eliye Springs (Kenya)	?	surface find	crania
Florisbad (South Africa)	> 100 Kya	uranium series	anterior crania with patial face
Ngaloba (Tanzania)	129±4 Kya 108±30 Kya	uranium-thorium (Hay 1987)	cranium
Omo 2 (Ethiopia)	?	surface find (Butzer et al. 1969)	calvarium

Table 2. Frontal bone measurements used in the multivariate analysis. The source provides a description of the measurement.

	Measurement	Source
(1)	Frontal chord	Howells (1973)
(2)	Frontal subtense	Howells (1973)
(3)	Frontal fraction	Howells (1973)
(4)	Minimum frontal breadth	Howells (1973)
(5)	Maximum frontal breadth	Howells (1973)
(6)	Torus thickness - medial	Smith & Ranyard (1980)
(7)	Torus thickness - midorbit	Smith & Ranyard (1980)
(8)	Torus thickness - lateral	Smith & Ranyard (1980)
(9)	Torus projection - medial	Smith & Ranyard (1980)
(10)	Torus projection - midorbit	Smith & Ranyard (1980)
(11)	Torus projection - lateral	Smith & Ranyard (1980)

Neandertals. Do these traits unequivocally separate Neandertals from all non-Neandertals, as Santa Luca suggested, or is the situation more complicated? Finally, the incidence of occipital bunning among circum-mediterranean hominids is discussed as a indication of possible biological connection between certain samples.

Multivariate analysis of frontal bone shape

A battery of eleven measurements were taken on the frontal bones of 51 late Pleistocene specimens from Africa, western Asia, and Europe. These variables are listed in Table 2. Individual variables were log-transformed; missing data were estimated as is described by Key (1983); scale-free or *shape* variables were then created following the procedure of Darroch & Mossiman (1985); and average taxonomic differences are calculated and UPGMA clustering performed on the data (see Simmons et al. 1991 for complete details on the procedure).

Figure 1, a phenogram of African specimens, exhibits a separation of the African transitional group from both earlier and more recent specimens. However, the undated Omo Kibish 2 cranium, usually included with the African transitional group, sorts out here with more recent specimens. Interestingly, the only non-African specimen included in this analysis, the Gibraltar Forbes Quarry cranium (a European Neandertal), clusters with the transitional group.

The phenogram of western Asian hominids, including Jebel Irhoud and Gibraltar (Fig. 2), presents a rather complex picture. Hublin (1989, 1992) recognizes a close relationship between the Jebel Irhoud and early modern western Asian specimens from Qafzeh and Skhul. This relationship is partly borne out by our analysis. Skhul 9, however, groups with archaic Near Easterners and Gibraltar clusters will the Qafzeh and Djebel Irhoud specimens rather with than the largely archaic group. Although not reported here, in a similar analysis of European hominids, the Jebel Irhoud hominids fall into the Neandertal group rather than with Modern European specimens. Within the Neandertal group, they cluster most closely with Gibraltar (Simmons & Smith 1991).

It could be argued that a multivariate analysis is of limited usefulness in approaching questions of interrelationships like those posed here. We agree that there are limitations to this type of analysis, but we believe it provides a useful representation of shape similarities among these specimens. It is important to note that results of other multivariate analyses have been used as forceful evidence *against* MRE (Howells 1989; Stringer 1992). Thus whatever limitations are assigned to the usefulness of our study should also apply to those supporting RAE. In any event, we do not believe that this issue should be approached entirely on the basis of multivariate analyses.

Supraorbital torus shape analysis

Supraorbital tori are characteristic features of archaic humans throughout the Old World, and reduction in size of these superstructures is widely accepted as part of the shift to modern human morphology (Bräuer 1984; Smith & Ranyard 1980; Splitery 1985; Wolpoff 1980). That reduction, however, does not seem to follow the same pattern throughout the Old World. In Africa, Europe and the Near East, there are at least two, and perhaps more, distinct patterns.

The European pattern has been documented by Smith & Ranyard (1980) and consists of a trend towards greater relative reduction of the midorbital segment of the torus (the part over the middle third of the eye orbit) from early to late

Neandertals in central Europe. Smith & Ranyard argue that this trend then continues, ultimately resulting in the separation into supraorbital trigones and superciliary arches characteristic of early modern Europeans and, ultimately, many other more recent human samples (Cunningham 1908). This European trend is reflected by a simple index of midorbital to lateral orbital toral thicknesses (Table 3), in which a smaller index value represents a relatively more reduced midorbital region.

In Africa, the pattern is different. Tori certainly reduce in size from Kabwe and Bodo through Ngaloba and Florisbad to Border Cave, but the reduction is more even across the torus. Thus the distinctive midorbit reduction characteristic of Europe is not evident. The values in Table 3 for these African hominids reveal a clearly separate shape trajectory than for Europe.

Near Eastern archaic specimens (Tabun and Zuttiyeh) reflect a rather primitive toral shape, similar to Bodo and Kabwe. The Skhul/Qafzeh hominid values are rather comparable to those of European Neandertals. Interestingly, the Jebel Irhoud specimens particularly Jebel Irhoud 1, conform to the European - Skhul/Qafzeh pattern rather than the African pattern.

Santa Luca's Neandertal features

In 1978, Santa Luca set out a series of features which were claimed to unequivocally separate Neandertals from other roughly contemporaneous hominids including the Skhul, Qafzeh, Jebel Irhoud and Omo samples. These features are pre-

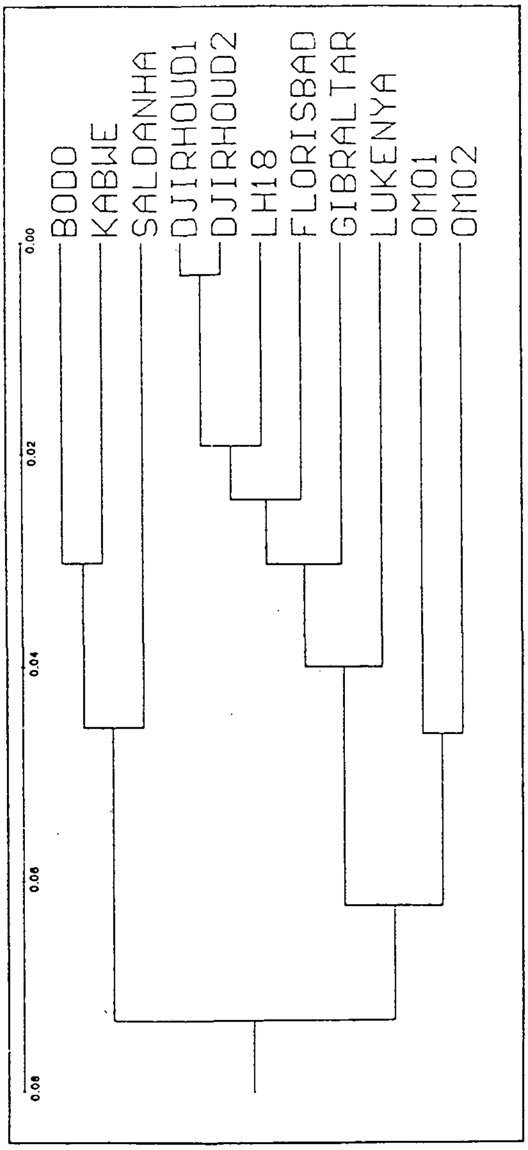

Fig. 1. Phenogram of the relationship of the African hominids and Gibraltar based on frontal bone metrics.

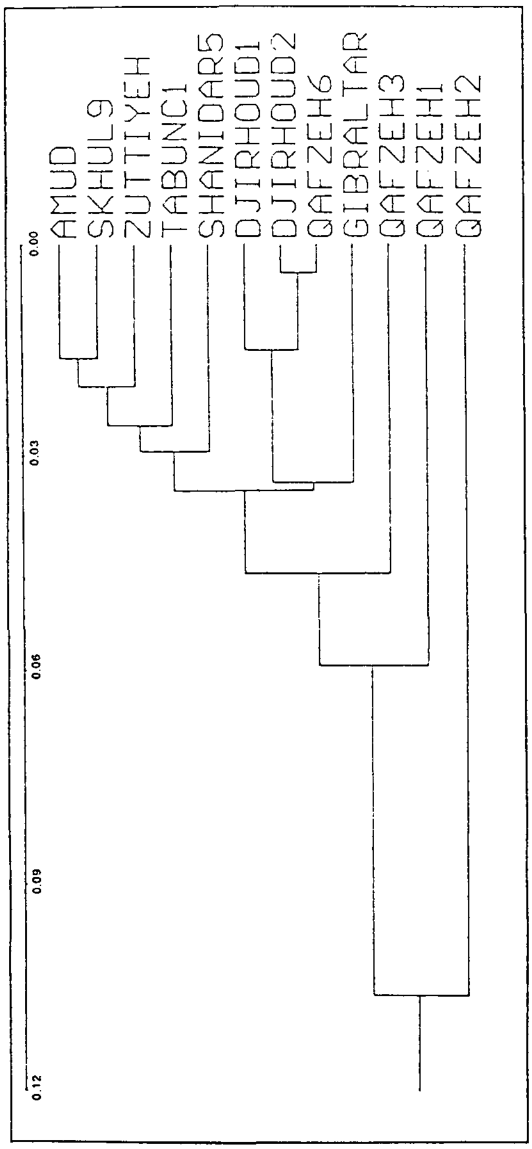

Fig. 2. Phenogram of the relationship of western Asian, North African and the Gibraltar frontal bone.

sence of (1) a mastoid tubercle (Hublin 1978); (2) an occipitomastoid crest of equal or greater inferior projection than the mastoid process; (3) a suprainiac depression; and (4) a horizontal occipital torus of relatively equal thickness, restricted to the central portion of the bone. Santa Luca reported all four features to be present in twelve Neandertals, including Krapina C, Saccopastore 1, Shanidar 1, Tabun C2 and Amud 1 (although he was uncertain about #2 for Amud 1). None were found in Qafzeh 6, Skhul 5 and 9, Jebel Irhoud 1, Omo 2, or Kabwe 1.

There are two interesting exceptions to Santa Luca's trait package among these specimens. First, Santa Luca lists Krapina C as possessing a mastoid tubercle (1978: 628). However, neither this specimen nor any of the other 16 temporal bones from Krapina that preserve this area exhibit mastoid tubercles (Frayer 1992; Sothman & Smith 1994), although the Krapina hominids do ubiquitously exhibit the other three features (except for one occipital that lacks a suprainiac fossa). Second, in both Jebel Irhoud 1 and Amud 1 the cranial base is broken just medial to the mastoid process and digastric groove. Thus the occipito-mastoid crest is not preserved on either specimen. Santa Luca scores Jebel Irhoud 1 as non-Neandertal in mastoid projection, but indicates that Amud 1 probably conforms to the Neandertal form. Hublin (1992) also describes the Jebel Irhoud 1 mastoid as well defined and projecting below the occipito-mastoid crest. Our observations suggest that the form of the mastoid and that of the occipitomastoid area (as is indicated by contours of adjacent preserved bone) are very similar in Jebel Irhoud and Amud. Thus, if Jebel Irhoud is considered to exhibit a non-Neandertal pattern, the same diagnosis must also apply to Amud.

Occipital bunning

The presence of an occipital bun or "chignon" is a very common feature in European Neandertals (Smith 1991; Trinkaus & LeMay 1982) and appears early in ontogeny (Minugh-Purvis 1988). Modified buns also are essentially ubiquitous among the earliest modern Europeans from Europe (Smith 1982, 1984). Interestingly, buns are not present in the Near Eastern Neandertals or in the Skhul/Qafzeh hominids (Smith 1991; Trinkaus 1983, 1984). These features are also absent in Ngaloba, Eliye Springs, Omo 2, Omo 1, and Border Cave 1 (Smith, personal observation). However, bunning is well-developed on both Jebel Irhoud crania (Fig. 3). Thus, these north African specimens are the only non-European crania with occipital buns documented from this time period in the western Old World.

Table 3. Indices of midorbital to lateral thickness of the supraorbital tori /brow ridges of selected hominids. The index is calculated by midorbital thickness by the the lateral thickness. All measurements by FHS.

Specimen / Sample	Index
Krapina	$x = 0.85$ ($N=11$; $\sigma=0.08$)
Vindija	$X = 0.79$ ($N= 6$; $\sigma=0.04$)
Early Modern European	$x = 0.71$ ($N=13$; $\sigma=0.05$)
Kabwe 1	0.93
Bodo	1.02
Florisbad	0.93
Ngaloba	0.90
Border Cave	0.93
Jebel Irhoud 1	0.85
Jebel Irhoud 2	0.88
Zuttiyeh	0.97
Qafzeh 6	0.75
Skhul 5	0.85
Skhul 9	0.91
Tabun C1	1.09

Hublin (1992) has recently determined that the Jebel Irhoud hominids share no apomorphic features with Neandertals. Presumably this would also include occipital bunning, though he does not address this directly. It is certainly true that the expression of bunning is slightly different in the Jebel Irhoud crania than in European Neandertals, due to the differences in overall vault form outlined by Hublin (1989, 1992). Thus the occipital buns in Jebel Irhoud are more similar to those in early modern Europeans (like Mladec, Zlaty Kun, or Predmosti) than to Neandertals because of the greater similarity in posterior cranial vault morphology between them (see Smith 1982: 678). However, the shared presence of occipital bunning in the Jebel Irhoud and European hominids, combined with its absence in western Asian and other African hominids, should not be ignored. Other than some type of biological connection between Jebel Irhoud and European hominids, the only explanation for this situation would be parallelism. While this is a possibility, we regard it as highly unlikely, particularly given the distinctive neural growth pattern necessary to produce an occipital bun (Minugh-Purvis 1988; Trinkaus & LeMay 1982).

Interpreting the patterns

We believe that the patterns of distribution in these features reflect the complexity of human population dynamics around the Mediterranean during the last 200,000 years. Specifically, we interpret the morphology of the Djebel Irhoud hominids as indicating some biological connection to European, as well as Near Eastern, hominids. Further, we view the Near Eastern sample as exhibiting a strong biological relationship between archaic west Asians and the Skhul/Qafzeh people, a situation that is difficult to reconcile with speciation/total replacement models for the origin of modern humans. Additionally, we believe that circumstances like the absence of mastoid tubercles in the Krapina sample probably demonstrate the occurrence of genetic drift in late Pleistocene human populations. The action of drift is an important aspect of the multiregional perspective and underscores the complexity that we feel characterizes late Pleistocene human population dynamics.

The similarity of the Djebel Irhoud crania to Europeans is seen in three areas: frontal bone shape, supraorbital torus form, and occipital bunning. In the first two, however, Jebel Irhoud is also quite similar to the west Asian specimens from Skhul and Qafzeh, a connection emphasized by Hublin (1989, 1992). Given the available chronology, it is difficult to say where the beginnings of the midorbital reduction seen in Europeans, Skhul/Qafzeh and Jebel Irhoud originated. But it is clear that this is a derived morphological pattern, in that earlier humans from Africa (Bodo, Kabwe), the Near East (Zuttiyeh, Tabun C1), and Europe (Petralona, Arago 21) lack this pattern. Except for Jebel Irhoud, members of the African transitional group and Border Cave retain a primitive brow ridge shape that lacks midorbital reduction. Thus, no matter what the phylogenetic pathway, the fact that Jebel Irhoud, Skhul/Qafzeh, and European Neandertals share an apparently derived

Fig. 3. The Jebel Irhoud 1 cranium.

morphology indicates that these samples were biologically related during the period in question.

The Djebel Irhoud crania also share the presence of occipital buns with European Neandertals and early modern Europeans. In this case, however, this feature is not shared with any west Asian specimen. Thus, it would appear that the shared presence of bunning establishes a direct biological connection between North African and European fossil samples in the Pleistocene. The only other possibility is to explain this as a parallelism, but two factors argue against such an explanation. First, as previously discussed, the apparent complexity of the biological basis of bunning would render parallelism unlikely. Second, parallelism would be more convincing an explanation if the Jebel Irhoud specimens were not in such close proximity to Europe, where occipital buns are common, and if there were other isolated instances of occipital buns in other specimens during the late middle or early late Pleistocene.[2]

For the Near East, our data indicate that the morphological separation between Neandertals and the Skhul/Qafzeh hominids is by no means an absolute one. The frontal data do not completely segregate the two groups, though some degree of distinction is certainly evident (Fig. 2). In general, the placement of the Skhul/Qafzeh hominids in our study mirrors the results of two other recent multivariate assessments, which pointed out the somewhat archaic nature of their crania (Corruccini 1992; Kidder et al. 1992). Additionally, certain aspects of the morphology of the Tabun C2 and Amud 1 specimens are not typical for Neandertals. As we note earlier in this report, Amud's mastoid projection is similar to Jebel Irhoud 1's and therefore is not any more reminiscent of a Neandertal than is the latter's. The Tabun C2 mandible is very similar to those from Skhul, particularly in symphyseal anatomy, and is quite unlike the presumably contemporary Tabun C1 mandible (cf. McCown & Keith 1939: Figs. 143-148).

It has been argued that the Near East represents something of a "contact zone" between Neandertal populations to the North and more modern groups (Bar-Yosef 1992, 1993; Rak 1993; see also Smith 1991). Such an explanation makes a great deal of sense to us, particularly in light of the documented differences in morphological trajectory between Europe and Africa during this period (Bräuer 1989, 1992; Smith 1992b; Smith et al. 1989). Rak (1993) has divided a rather elaborate "biogeographic" model to explain the variation and morphological overlap exhibited by the hominid fossils while continuing to recognize two separate species. We prefer to explain this situation as indicating that Neandertals and the Skhul/Qafzeh people, while certainly distinct at some level, are members of the same biological species, who engage in significant genetic exchange when they are in contact, both Neandertals and the Skhul/Qafzeh people are part of the same species, *Homo sapiens*, which was polytypic then just as it is now.

The role of environmental factors in the evolution of *Homo sapiens*

Environmental factors must certainly be considered in discussion of human population connections or isolation during the Pleistocene. In the 1950s, Howell (1951, 1952, 1957) suggested that environmental changes associated with the last Pleistocene glaciation in Europe led to the isolation of European "pre-Neandertals" and the subsequent emergence of "classic" Neandertals. More recently, the increasingly harsh environmental conditions in Europe, combined with reduction of the conditions fostering isolation, have been implicated in the spread of Neandertals into the Near East (e.g. Bar-Yosef 1992, 1993). Additionally, Boaz et al. (1982) have argued that climatic dessication in North Africa virtually forced the migration of modern people into western Asia and Europe.

All of these environmental effects probably influenced middle and late Pleistocene human evolution to some extent. However, Fogarty & Smith (1987) have shown that complete isolation of Europe was unlikely to have occurred during this period and that the conditions in North Africa were not so inhospitable as to cause the type of exodus envisioned by Boaz et al. (1982). Certainly there was enough restriction to gene flow to promote the morphological trends evident in Neandertals, which resulted from adaptation to the European glacial environment, but there is no reason to assume from the environmental data that this European gene pool was totally isolated. Indeed the similarities between European and west Asian Neandertals, extending back to at least 120 kya, are testament to the existence of a biological connection.

We believe there was also contact between European and North African Pleistocene human groups at the Strait of Gibraltar. This is reflected mainly in the morphological similarity of the Jebel Irhoud and Gibraltar crania demonstrated in this report and elsewhere (Simmons & Smith 1991). The extent of such contact was probably not extensive, because the Strait is minimally over 100 fathoms (183 meters) deep at its shallowest point (Truver 1980). However, if sea levels are lowered around 100 meters, apparently the maximal reduction during this approximate time period (Stanley 1989), the minimum distance between the Iberian Peninsula and North Africa is only about 10 km.

Relatively small, but not insignificant, amounts of gene flow across the Strait is evident by the end of the Pleistocene (Chamla 1980; Keita 1990). Archaeological similarities between Spain and North Africa indicate possible connections extending back to the Mousterian and Acheulean (Alimen 1975; Butzer 1971; Hublin et al. 1987; but see Hublin 1992). Thus although some water crossing would be necessary, at least some degree of biological connection across the Strait of Gibraltar during the Mousterian is defendable, if not probable. As Bordes has speculated: "la terre est in vue: au Riss, même s'il n'était pas à sec, il devait être plus étroit que de nos jours, et avec un radeau il est aussi traversable que la Congo, par example" (1984: 108).

Concluding statement

In our opinion, the data presented here suggest that at least some degree of biological connection was maintained among most regional human populations throughout the middle and late Pleistocene in the western Old World. This is evident in the hominid fossils from the circum-Mediterranean, where the continents meet. Degree of geographic distance and the effect of various environmental factors certainly influenced the extent of these connections throughout this period, but we maintain that isolation was never extensive enough to allow for speciation events during this period in our evolutionary past.

On the other hand, we recognize that our evidence for regional connections and interbreeding between groups is revealed mainly in morphological details rather than in total morphological patterns. Neandertals are certainly distinct at some level from African hominids; and if present chronological frameworks are accurate, modern human morphology to seems to appear earlier in Africa/West Asia than in Europe. Thus we are inclined to believe that the emergence of modern people in regions like Europe is strongly influenced by adjacent regions. The exact nature of that influence is open to considerable debate (e.g. Aiello 1993; Bräuer 1989, 1992; Frayer et al. 1993; Smith et al. 1989), but we are convinced that any model of modern human origins based on the existence of multiple species and the total replacement of archaic species by a modern one can be clearly refuted by the fossil evidence.

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Notes

1 Not all advocates of an African origin for modern human origins agree that modern humans resulted from a speciation event (e.g. Bräuer 1989, 1992), however all argue that continuity outside Africa is either non-existent or of negligible significance.

2 Pope (1992) has claimed that Jinniushan from China exhibits evidence of an occipital bun, but this structure is not evident in available photographs.

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