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MIGRATION AND CONTACT ZONES IN MODERN HUMAN ORIGINS: BABOON MODELS FOR HYBRIDIZATION AND SPECIES RECOGNITION

ABSTRACT: This paper uses data on species identification in modern baboon populations to critically examine the two conflicting models for the origins of modern humans: the recent African origins and the multiregional evolution ones. Informed by data on baboons, the paper examines the morphology of Middle and Late Pleistocene hominid remains from the circum-Mediterranean zone which suggest that this region served as an evolutionary contact zone which witnesses numerous repeated episodes of multi-directional migrations and gene flow. These past processes do not permit us to classify the hominid remains into discrete species.

KEY WORDS: Origin of modern humans – Polytypic species – Isolation – Contact zones – Hybridization

INTRODUCTION

The initial migration and subsequent radiation of hominids from the African continent approximately 1.0 Mya (million years ago) augmented the geographic and climatic boundaries of the human ancestral range. The crux of the debate surrounding the origin of *Homo sapiens* is one of defining the degree of population isolation relative to the degree of population mobility and contact that occurred after this primary dispersal. The migration of these groups of hominids, as fragments of a larger parent population, invokes the effects of random genetic drift, and their introduction into differing environments subsequently brings the forces of natural selection to bear upon these populations to varying degrees and in new ways. If these populations remained isolated from one another and differentiated enough over time via these processes, then one could argue that speciation could occur in one or more populations (i.e. as has been suggested via the use of the taxonomic designation *H. neanderthalensis* to describe Eurasian Middle Palaeolithic hominids). If, on the other hand, at least some of the populations received continuing

input from subsequent migrations of African groups into Eurasia, and/or these populations retained some degree of contact with one another via the process of gene flow, speciation would be less likely to occur. Thus, the concept of migration and the interpretation of its meaning is central to the contrast between the two prevailing models of modern human origins. Specifically, it can be argued that the Recent African Origins (RAE) model of modern human origins oversimplifies the phenomenon of migration. The purpose of this paper is to discuss a clarification of the migration "event" and an examination of the interpretations offered by both the RAE and Multiregional Evolution (MRE) models.

The RAE model describes a cladogenetic speciation event, around 150 kya (thousand years ago), in which a relatively static population of *H. erectus* in southern Africa becomes *H. sapiens*. This population of modern humans then migrates from its isolated point of origin into other regions of the Old World where it replaces, without interbreeding, resident populations of Neanderthals (in Europe) and other types of hominids elsewhere in Eurasia. Thus according to the RAE model, the migration of

H. sapiens must be envisioned as a singular event of considerable rapidity and magnitude within Eurasia. Hominid regional diversity prior to this event is regarded as a reflection of the existence and longevity of separate geographically based evolutionary lineages, and hence a multiplicity of hominid species throughout Eurasia. The new species of *H. sapiens* is seen to both genetically and culturally swamp the indigenous archaic lineages in a relatively short period of time (within less than 2–8 kya in western Europe if one relies on the accepted dates for Zafarraya, St. Césaire and Crô-Magnon). Recent human variation and diversity is therefore only as old as this migration of modern humans out of Africa and their establishment in new geographic regions.

The MRE model, on the other hand, denies the occurrence of cladogenetic speciation events within the last several hundred thousand years of hominid evolutionary history. In this model, the diversity of modern humans is seen to be of greater antiquity and is explained via a complex inter-relationship of genetic drift, local continuity, selection due to local environmental factors, and interregional genetic exchange of long duration. Humans are viewed as a successful, widely dispersed and polytypic species originating considerably prior to 200 kya and perhaps as far back as the initial migration of *H. erectus*. This view has recently found some support based on human mtDNA polymorphisms, which seem to indicate the presence of restricted, but significant gene flow among regionally diverse populations during this time (Templeton 1993, see also Wolpoff, this volume).

MIGRATION AND ISOLATION

How then does the RAE model hold up to scrutiny when one examines the movements of populations of *H. erectus* during the ca 900 ky prior to the speciation event it describes? I would argue that the RAE model is plausible only if the migration of *H. erectus* was a massive wave, which occurred extremely rapidly as either a singular event, or a chronologically compressed series of large-scale rapid expansions. The RAE model is predicated on the migration and radiation of the two species, *H. erectus* and *H. sapiens*, occurring in the same manner, with both magnitude and celerity. The inherent assumption appears to be that the founder populations of *H. erectus* all moved directly, in fact nearly instantaneously, to their final archaeologically detectable destinations and remained there, immobile and in virtual evolutionary stasis. It seems also to be implied that these populations were instantaneously isolated from one another, never coming into contact with a population that subsequently shifted in its course or destiny. Does the RAE model also assume that none of the original migrating peoples returned to the African continent or in that direction?

If, however, the migration of *H. erectus* occurred not as a solitary wave, but rather as continual, multiple migrations

of small groups over the course of a few thousand or hundred thousand years, then the existence of isolated populations becomes questionable. It seems equally plausible that a prolonged continuous exodus of peoples from Africa into Eurasia ensured that the latter populations were being constantly infused with a steady ration of the *H. erectus* parent population's gene pool. If the migrations of *H. erectus* were viewed as intermittent waves, then the incorporation of subsequent gene pools (essentially fragments of the original, more variable gene pool of the African population) could be accomplished.

For barriers to reproductive success to become established, how long would populations of a polytypic species have to be isolated from one another? Was there enough isolation, in the face of the possibility of multiple migrations to and from Africa, to engender a speciation event? In polytypic species such as *H. sapiens* and *H. erectus*, the effects of random genetic drift as a potential speciation mechanism are often neutralized to a large extent by gene flow. Humans are an extremely mobile and social species. The length of time required for temporarily separated populations of a polytypic species to become different enough to incur reproductive isolation is debatable, but probably considerable. From the time of their arrival, the early *H. sapiens* populations in Australia remained quite geographically and genetically isolated from the rest of the world's populations for at least 60 ky (Davidson, this volume). Yet, ample historical evidence demonstrates that European colonists were able to interbreed with the aboriginal populations at contact.

Most of those who support RAE, and therefore recognize *H. sapiens* as unique from other species of hominids in the Late Pleistocene, argue against any significant degree of gene flow between them and Neanderthals (e.g. Bräuer 1984, Stoneking, Cann 1989, Stringer, Gamble 1993). This contradicts what is known from more recent human migratory history (Sokal *et al.* 1991), where demic diffusion and the incorporation of resident gene pools appears to have been the norm. The statement by Templeton (1993: 65), that the geographical associations of mtDNA "strongly and clearly indicate that all Old World human populations were in genetic contact with one another throughout the entire period marked by the coalescence of mtDNA," argues against the persistent population isolation necessitated by the RAE model. Thus, restricted gene flow was probably occurring in significant enough proportions to prevent speciation.

CONTACT ZONES

When examining the evidence for population isolation, many of the discussions of modern human origins are concerned with comparing fossils from widely separated regions (e.g. southern Africa and western Europe). Much of the difficulty with these comparisons, and the confusion that has arisen regarding their interpretation, results from

underestimating the confounding compound factors of chronology, regional variation and adaptation when attempting to compare disparate populations. An examination of the fossil and archaeological evidence from contact zones, areas where the African and Eurasian continents are adjacent, can provide data from which the degree of isolation of Late Pleistocene hominids can be addressed adequately. The circum-Mediterranean in general, and the Levantine Corridor in particular (Bar-Yosef 1989, this volume), as the landed junction of three continents, would have been the region of first contact for populations of hominids migrating in and out Africa and Eurasia. I would argue that there is little evidence to suggest that this region maintained two hominid lineages, each with its own evolutionary tendencies and fate.

Recognition of discrete species within contact zones is dependent, not only on the degree of contact between regionally distinct populations, but also upon the duration of that contact (Wiley 1981). If the zone is wide, the forms are viewed as being geographic variants of the same evolutionary species; if the zone is ancient and narrow, the forms will probably maintain their identities in spite of gene flow and be regarded as discrete species. The circum-Mediterranean is a geographically wide expanse, and the hominids within this realm have been demonstrated to be of a highly variable morphology, often regarded as somewhat intermediate between European Neanderthals and contemporary southern African hominids.

Much debate has arisen concerning the attribution of the fossils from the Carmel Caves of Tabun and Skhul to type – Neanderthal or modern, *H. neanderthalensis* or *H. sapiens*. Certainly the association of the more modern Tabun C-2 mandible in the same layer as the Neanderthal-like Tabun C-1 skeleton has been viewed as troublesome. McCown and Keith (1939) dealt with the range of morphology among the hominids in Carmel caves of the Levant by considering them to be highly variable members of the same species, perhaps exemplifying a population enmeshed in the very process of evolution. The variability present within Tabun Cave and the stratigraphic uncertainties of the original excavation have caused some (e.g. Bar-Yosef 1993, Jelinek 1992) to assign the Tabun C-1 skeleton to layer B. However, Trinkaus (1993) has indicated that the stratigraphically questionable association of the Tabun C-1 "Neanderthal" and the Tabun C-2 "modern" mandible may be otherwise resolved. He notes that several right-side skeletal elements securely attributed to layer C are "virtually perfect mirror images of the same left bones of the Tabun C-1 skeleton and almost certainly derive from that skeleton (Trinkaus 1993: 620)."

Thoma (cf. 1965) was the first to assert that the Skhul hominids represented biological hybrids of Neanderthal and anatomically modern human populations. Arensburg (1991), in noting the extreme level of intra-population variation within the Skhul and Qafzeh sites, questioned the habitual designation of "Neanderthal" for such fossils as Amud, Shanidar, Kebara, and Tabun. Kramer *et al.*

(1992) have drawn attention to the high degree of both regional and within-site variability in the Levant; in a cladistic analysis of the Levantine Neanderthal and modern hominid crania, they have been unable to reject the idea that there is a single species of hominids in this region.

To the contrary, Rak (1993) views the more modern Tabun C-2 and Amud hominids, among others, as representative of the most primitive end of the spectrum, rather than as members of a highly variable population of long duration. He feels that the "modern" characteristics evidenced by these specimens are in fact generalized and pleiomorphic ones and, hence, they are "phylogenetically uninformative...[and] do not provide evidence of interbreeding" and that "[their] somewhat modern-looking face does not suggest that the anatomy appeared late..." (Rak 1993: 530).

Although Rak's (1993) biogeographic model is presented perhaps more explicitly, the idea that the south-west Asian hominids are two distinct species separated by chronology and geography, has been the prevailing view of this region since the work of Bar-Yosef and Vandermeersch (1981) and their colleagues (Valladas *et al.* 1987, 1988). Bar-Yosef (1992, 1993) proposed a model whereby fluctuating environmental conditions were responsible for population ingress and egress in the Levantine Corridor. Thus "anatomically modern humans" (e.g. Skhul and Qafzeh in Israel, and Djebel Irhoud in Morocco) were present during warm and dry periods, while the "Neanderthals" were present during cool and wet periods. The former occupations correspond, then, to periods of aridity in the Sahara, which pushed the gracile African humans into the Levant; conversely, the latter are indicative of the glacial extremes of Europe, which pushed the Neanderthals into the same region at a different time. Alternating, not synchronous, occupation of the region leads Rak (1993) and Valladas *et al.* (1988) to negate any indication of sympatry, even though the archaeological cultures of the two hominid types are virtually indistinguishable (Hovers 1998, Shea 1989, Schoeninger 1982).

The functioning of this region as an evolutionary contact zone between Neanderthal populations to the North and African populations to the South of the Levant has been examined previously (Smith *et al.* 1995, Simmons *et al.* 1991, Simmons, Smith 1991, Simmons 1990, 1992a, 1992b, 1994). As Simmons *et al.* (1991: 265) concluded, there is "no convincing evidence that any of the Skhul hominids represent more of a "hybrid" population than does the Qafzeh 6 skull." The question I would now propose is whether the entire Levantine population of Late Pleistocene hominids should be considered hybrids.

Presumably, subsequent to their last recorded presence at Qafzeh some 92 kya, the gracile hominids exited the region. Where these hominids went, however, has not been satisfactorily explained. While the Skhul and Qafzeh sites are dated to 118–82 kya (Grun, Stringer 1991) and 92 kya (Valladas *et al.* 1988) respectively, the earliest dated site

with skeletal evidence of modern humans in Europe is at Mladeč, dated minimally some 40–50 ky later (Smith 1982, 1984). It is thus unclear at best where the anatomically modern *H. sapiens* lineage existed in the interim. Neither do Fogarty and Smith (1987) find support (contra Boaz *et al.* 1982) for the extreme climatic desiccation in North Africa that would have precipitated the exodus of modern peoples and their transit into south-west Asia and Europe.

North Africa, at the Straits of Gibraltar, presumably provided yet another place of early contact between regions and populations; Fogarty and Smith (1987) have illustrated that the absolute isolation of Europe during the Middle and Late Pleistocene was unlikely. The morphological similarity of the Jebel Irhoud and Gibraltar crania (Simmons, Smith 1991, Simmons 1994, Smith *et al.* 1995) demonstrate population continuity and hence a biological connection, between European and North African populations during that time. This contact was probably not extensive, as the depth of the Strait (Truwer 1980) would have prevented the formation of a land bridge *per se*. Yet if, as Stanley (1989) reports, the sea levels were at their maximum reduction at this approximate time, then Gibraltar would be distant from North Africa by only 10 km. It is certainly clear from population studies (Chamla 1980, Keita 1990) that some significant gene flow is discernible across the Strait by the terminal Pleistocene.

BABOON MODELS FOR HYBRIDIZATION

The fragmentary and incomplete nature of the human fossil record from the Middle and Late Pleistocene, as well as the imprecise chronology for that record, have made the interpretation of these migration and contact events exceedingly difficult. Yet the idea of contact zones in both the Levant and North Africa is all the more intriguing when one considers primate parallels. Much research has been conducted on the social organization (Nagel 1973, Gabow 1975), genetics (Shotake 1981, Shotake *et al.* 1977), and physical characteristics (Phillips-Conroy, Jolly 1981, 1986, Phillips-Conroy *et al.* 1991, Maples 1967) of hybridizing populations of baboon species in both Kenya and Ethiopia.

In the particular case of the Awash hybrid zone in Ethiopia (Phillips-Conroy, Jolly 1986), environmental pressures seem to cause population migration, in much the same manner as what Bar-Yosef (1992) and Rak (1993) have proposed for the hominid populations of the late Pleistocene Levant. Increasing aridity in the highlands forces hamadryas baboons into the riverine environment range of the anubis baboons. Antithetical to Rak and Bar-Yosef's models, however, these conditions actually produce an increased degree of contact between the two groups rather than alternating occupations of the same region. The formation of a hybrid zone, although climatically dependent and seemingly sporadic in nature, has created an enduring and stable contact zone between these populations, including genetic exchange the production of

fertile offspring. The baboons of the hybrid zone exhibit great phenotypic variability, and certain characteristics appear to be more conservative (stable) while others more frequently exhibit intermediate states of expression (Phillips-Conroy, Jolly 1981, 1986). The genetic data from these hybrid zones (Shotake 1981, Shotake *et al.* 1977) also support the existence of a wide, and even an expanding hybrid zone.

The Awash hybrid zone model is a fascinating and useful one for application to the Levantine and North African contact zones. As Stringer and Gamble (1993: 193) state: "Closely related biological species are often infertile, and may or may not produce fertile offspring when they hybridize. Neanderthals and Crô-Magnons would have been quite closely related, and genetically there may have been no barrier to Neanderthal/Crô-Magnon interbreeding. It would probably have been predominantly behavioural barriers that kept them distinct from one another. The two populations would have contrasted physically, and may have had major differences in language and gestural expressions. Hybrids, if they existed and were fertile, may have been discriminated against by the parent populations, ensuring that the flow of genes between the parent populations was restricted."

This speculation concerning behavioural isolation and discrimination is contraindicated by the baboon data. In the Awash, the hamadryas and anubis baboons possess markedly different phenotypes and forms of social organization. Male hamadryas baboons form multi-female harems; anubis baboon social organization is based on multi-male groups. Although these forms may be adaptive, they are not environmentally specific (Jolly 1993). Hamadryas males migrate into anubis groups, establish residence, and become integrated into the host group's social structure (Phillips-Conroy *et al.* 1991). Anubis males may also migrate and attach themselves to hamadryas groups (Sugawara 1979). For the Awash baboons, neither the barriers of behaviour (gestural-expression and social organization) nor those of contrasting physical appearance have proved enough to restrict gene flow between the anubis and hamadryas populations. There is not "any reason to doubt that these hybrids are themselves fully fertile and socially integrated.... There is no evidence that Awash hybrids are at any social or ecological disadvantage" (Jolly 1993: 82).

No substantial barrier to gene flow and no problem of mate recognition correspond to the relatively sharp geographic demarcation of the anubis-hamadryas phenotypic transition in the Awash. There appears to be no indication of selective mating according to phenotype (Jolly 1993) and the hybrid zone has persisted for so long that there are relatively few, if any, "pure" types of these baboons among these populations (Phillips-Conroy *et al.* 1991). Thus, despite the assertions of Stringer and Gamble (1993), neither physical appearance nor behavioural variables are likely to have discouraged mating between

African and Eurasian Middle Palaeolithic hominids. Certainly, discrimination against hybrid offspring also presents no deterrent to social incorporation and evolutionary contributions to the gene pool among baboons. Human history records that neither cultural nor language barriers have proved to be consistently effective deterrents to genetic exchange at some level between members of different populations.

APPLYING AND ANALYZING THE MODEL

A series of multivariate morphometric analyses of frontal bone measurements is presented for the Awash baboons and the Levantine and North African hominids. The frontal squama measurements (Howells 1973) include the frontal chord, fraction, and subtense, and the minimum and maximum frontal breadth; the browridge measurements (Smith, Ranyard 1980) are those relating to browridge thickness at the medial, mid, and lateral orbit. Missing data were estimated according to the procedure outlined in Key (1983). For *Figures 1* and *3*, individual variables were log-transformed and average taxonomic distances (Sneath, Sokal 1973) were calculated and UPGMA clustering was performed on the data (see Simmons *et al.* 1991 for a complete description of the procedure). For *Figures 2* and *4*, the variables were log-transformed; scale-free, or shape variables, were subsequently created using the procedure described by Darroch and Mossiman (1985). Average taxonomic distances and UPGMA clustering were then performed on these shape data.

Single specimens are, by necessity, included in all analyses of fossil hominids; and thus similarities among populations are often explained on the basis of the characteristics of an individual, rather than on the range of variation present in all true populations. In addition, because the stratigraphic context and/or dating of these finds are often equivocal, researchers must be aware that they are examining not a single lifespan of a population, but multiple generations. In doing so, all researchers risk obscuring not only intra- with inter- species variation, or clade with grade, but confusing secular trends within a population with evolutionary trends in a species. The inclusion of the same analyses on the baboon specimens should shed some light on the interpretation of the hominid analyses. While the baboon sample is multi-generational, the hominid sample doubtless reflects a much wider time span.

The phenogram of the Awash baboons (*Figure 1*), which includes the effects of both size and shape, reveals a cluster of three of the four individuals identified as hybrids (Y) by the collectors when these animals were alive (C. Jolly, personal communication). What is also important to note, however, is the intermingling of the anubis (prefix A) and hamadryas (prefix H) baboons on either side of that hybrid grouping. Neither is there a distinct delineation between the males (suffix M) and females (suffix F). These results

are difficult to interpret satisfactorily without further knowledge of the exact genealogical relationships among these individual animals, but the analyses do tend to confirm observations of the extent of hybridization in the Awash baboon population. It is probable that the intermingling of those anubis, or anubis-like, and hamadryas, or hamadryas-like, baboons accurately reflects the duration of the hybrid zone and the lack of persistence of any "pure" individuals of either type. The analysis of these measurements was weighted most heavily on the frontal subtense, and all of the animals classified as hybrids (Y) have higher frontal elevations than the other individuals of either type. It is possible, although by no means provable, that this phenomenon is either a result of the first generation (F1) hybrid process (Jolly (1993) would argue that this is rather unlikely), or, the result of accumulated genetic changes in subsequent generations.

The phenogram of the Awash baboons (*Figure 2*), which is dependent on the scale-free, shape variables, results in a de-clustering of the hybrid specimens and a greater disassociation of anubis and hamadryas types. Because the hybrid cluster in *Figure 1* can be seen to have resulted from the characteristically greater frontal subtense measurements of that group, when size is effectively removed from the analysis, the cluster disappears. The lack of any distinctive clusters by type or sex in this analysis, probably reflects the longevity of the hybrid zone in a true manner.

The phenogram of the hominids (*Figure 3*), based on the combined effects of size and shape, reveals a situation that is initially disconcerting to the idea of a hybrid zone. There are two main clusters of specimens, the upper one a "Neanderthal" grouping and the lower one a "modern" grouping. This analysis, too, however, is weighted most heavily on frontal subtense and frontal fraction to a lesser degree. What is in fact reflected in this phenogram is a division of the sample based on relative size and is thus not particularly informative. Essentially, the analysis merely reports that the Neanderthal-like hominids are larger, with less frontal elevation than the modern-like hominids. The effects of size are in effect concealing, rather than revealing, any other potential similarities among the individuals. Note also the unique position of Qafzeh 9 in this analysis, distinctive from either cluster.

The phenogram of the hominids (*Figure 4*) based on scale-free, shape variables presents an entirely different picture. No distinctive clustering of hominid "types" is disclosed by this analysis, which is weighted most heavily now on measurements of the browridge, particularly lateral and mid-orbital thickness. Instead, there is a great degree of intermingling of the Neanderthal-like and modern-like individuals. The upper-main cluster includes the Neanderthal-like Amud and Shanidar 5 specimens together with a group of Qafzeh and Skhul hominids; similarly, the lower main cluster groups a tight pairing of the geographically distant Qafzeh 6 and Jebel Irhoud 2 modern-like individuals with the more ancient Neanderthal-

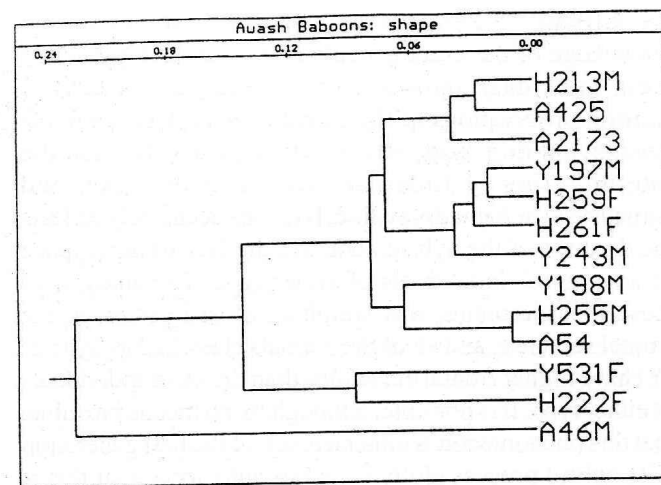


FIGURE 1. Size and Shape Phenogram of baboons from the Awash National Park hybrid zone, Ethiopia. A = anubis. H = hamadryas. Y = hybrid. Numbers indicate individual specimen identification followed by M = male or F = female.

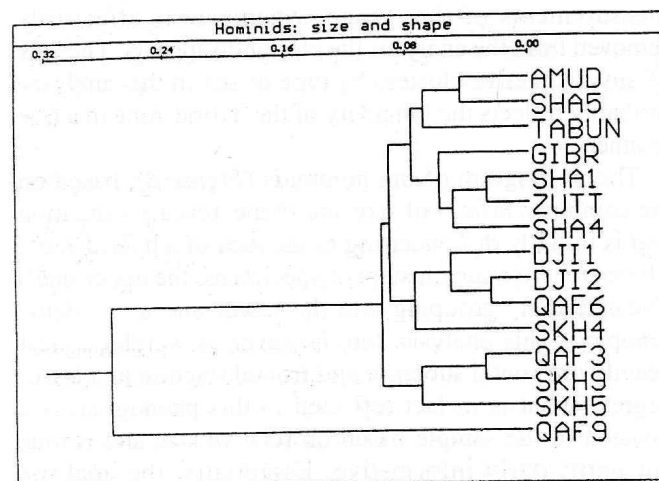


FIGURE 3. Size and Shape Phenogram of hominids from the Levant and north Africa.

like specimens from Tabun and Zuttiyeh. The other Shanidar hominids, as well as the Gibraltar and Djebel Irhoud 1 individuals, are represented in this cluster as well. The phenogram indicates no divisions based on site location and none based on hominid type; the Qafzeh hominids are part of all three clusters. As for the Djebel Irhoud hominids, despite their identical geographic association and their distance from all other hominids in this analysis except Gibraltar, their situation in the phenogram is interesting. The closest association of any hominids in the phenogram is that of Djebel Irhoud 2 with Qafzeh 6 (see also Simmons, Smith 1991). Again the solitary position of Qafzeh 9 in this analysis, too, must be noted and addressed.

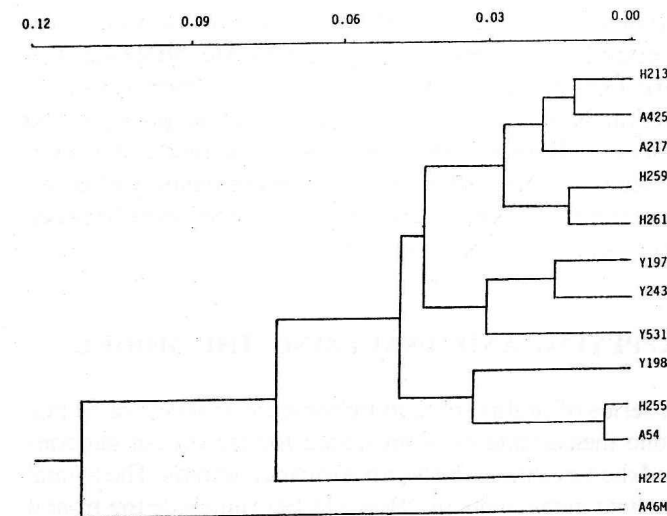


FIGURE 2. Scale-free Shape Phenogram of baboons from the Awash National Park hybrid zone, Ethiopia.

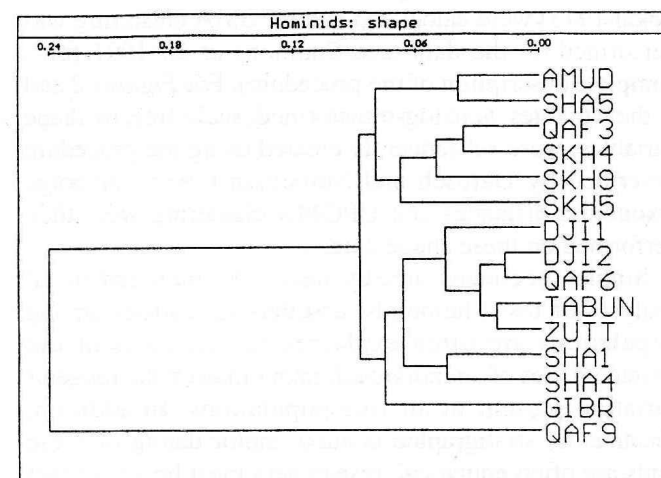


FIGURE 4. Scale-free Shape Phenogram of hominids from the Levant and north Africa.

Despite the wide range of geography and chronology that characterizes the hominid sample (Zuttiyeh and Gibraltar at the ancient end of the spectrum and Amud at the recent end), Qafzeh 9 stands out as somehow different from the others. One possible explanation is the fossil's stratigraphic separation from the other Qafzeh hominids included in this analysis (Vandermeersch 1981). The 92 kya date for the Qafzeh hominids is an average of TL dates from all the hominid bearing layers which is justified on the basis of the perceived rapid rates of deposition involved in the formation processes of this site (Valladas *et al.* 1988). Research on ostrich egg shell dating by Brooks (1993) may suggest, however, that the rate of deposition was not as rapid as once thought, and that indeed a considerable

amount of time may have elapsed between the demise of Qafzeh hominids 3 and 6 and the existence of Qafzeh 9. Perhaps Qafzeh 9 is a "purer" African-like modern human migrant. It does seem to share some uniquely African traits including extreme gracility and restricted alveolar prognathism. Both Bräuer (1984, 1989) and Stringer and Andrews (1988) have indicated its close affinities to the geographically diverse African anatomically modern *H. sapiens* group, including Border Cave, Omo 1, and Klasies River Mouth. Once the relative chronology is resolved, the position of Qafzeh 9 may be more explicable.

CONCLUSIONS

The Levantine Corridor, and to some degree the Straits of Gibraltar, have been junctions of migrating populations throughout historical times. These analyses have demonstrated that, while the environmental conditions proposed by the Bar-Yosef (1989) and Rak (1993) biogeographic models are not contested, the view that these conditions necessarily predicate population isolation and predispose those populations to speciation and the maintenance of separate gene pools is highly equivocal. Indeed, the role of these areas as evolutionary contact zones appears to have been extant in prehistoric as well as in historic times. What is known about the morphological and behavioural affinities of the late Pleistocene population of the Levant and North Africa reflects sporadic, but continuing multi-directional migrations and gene flow. The net effect is the incorporation of genetic material. The result is the inability to recognize discrete differences between these populations. The extreme variability at the intra-population level (e.g. within Skhul, Qafzeh, or Tabun) coupled with the remarkable similarity at the inter-population and inter-regional level (e.g. between individuals from Qafzeh and Djebel Irhoud) provides good evidence of a wide and enduring hybrid zone, similar to that exhibited by the Awash baboons.

Much like the Awash baboon hybridization model, the situation of the circum-Mediterranean exemplifies the ephemeral nature of sub-specific, or regional variation. The persistence of differentiated populations of "Neanderthals" and "anatomically modern humans" is only found at the extremes of the cline extending from Europe to the southern portion of Africa, and only after *ca* 85 kya (Brooks 1993). The Levantine and North African hominids discussed in this paper existed both prior to and subsequent to that time of isolation, and no evidence supports the recognition of discrete species in these regional contact zones. In sum, the Neanderthal-like and modern-like variants in the hybrid zones of the Levant and North Africa cannot be demonstrated to maintain their own evolutionary tendencies and historical fate. Hence, they cannot be demonstrated to be the products of speciation events nor can they be unique evolutionary species themselves.

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REFERENCES

- ARENSBURG B., 1991: From Sapiens to Neandertals: Rethinking the Middle East. *Amer. J. of Phys. Anthropol.* 44, Supplement 12 (abstract).
- BAR-YOSEF O., 1989: Geochronology of the Levantine Middle Palaeolithic. In: P. Mellars, C. B. Stringer (Eds.): *The Human Revolution*. Pp. 589–610. Edinburgh University Press, Edinburgh.
- BAR-YOSEF O., 1992: Middle Palaeolithic chronology and the transition to the Upper Palaeolithic in southwest Asia. In: G. Bräuer, F. Smith (Eds.): *Continuity or Replacement*. Pp. 261–272. A. A. Balkema, Rotterdam.
- BAR-YOSEF O., 1993: The role of western Asia in modern human origins. *Philosophical Transactions of the Royal Society (London)* B 337: 197–200.
- BAR-YOSEF O., VANDERMEERSCH B., 1981: Notes concerning the possible age of the Mousterian layers in Qafzeh Cave. In: J. Couvin, San Laville (Eds.): *Préhistoire du Levant*. Editions du Centre national de la recherche scientifique 598: 281–85.
- BOAZ N. T., NINKOVITCH D., ROSSIGNOL M., 1982: Paleoclimatic setting for *Homo sapiens neanderthalensis*. *Naturwissenschaften* 69: 29–33.
- BRÄUER G., 1984: A Craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In: F. H. Smith, F. Spencer (Eds.): *The Origins of modern humans*. Pp. 327–409. Alan R. Liss, New York.
- BRÄUER G., 1989: The evolution of modern humans: a comparison of the African and non-African Evidence. In: P. Mellars, C. B. Stringer (Eds.): *The Human Revolution*. Pp. 124–155. Edinburgh University Press, Edinburgh.
- BROOKS A., 1993: *The African evidence*. Paper presented at "The Human Tide – Human colonization and the Palaeolithic Archaeological Record". An international symposium sponsored by the Wenner-Gren Foundation for anthropological research and INQUA, 15–19 June 1993, Moscow, CIS.
- CHAMLA M. C., 1980: The Settlement of non-Saharan Algeria from the Epipaleolithic to modern times. In: I. Schwidetzky,

- B. Chiarelli, O. Necrasov (Eds.): *The Physical anthropology of European populations*. Pp. 257–269. Mouton, The Hague.
- DARROCH J. N., MOSSIMAN J. E., 1985: Canonical and principle components of shape. *Biometrika* 72: 241–252.
- FOGARTY M. E., SMITH F. H., 1987: Late Pleistocene climatic reconstruction in North Africa and the emergence of modern humans. *Hum. Evol.* 2: 311–319.
- FRAYER D., WOLPOFF M. H., THORNE A. G., SMITH F. H., POPE G. G., 1993: Theories of modern humans origins: The Paleontological test. *Amer. Anthropol.* 95,1: 14–50.
- GABOW S. A., 1975: Behavioral stabilization of a baboon hybrid zone. *The American Naturalist* 109(970): 701–712.
- GRUN R., STRINGER C. B., 1991: Electron spin resonance dating and the evolution of modern humans. *Archeometry* 33: 153–199.
- HOVERS E., 1998: The Origins of modern human behavior: A Levantine point of view. *J. of Hum. Evol.* 34,3: 8–9.
- HOWELLS W., 1973: *Cranial variation in man*. Papers of the Peabody Museum of archaeology and ethnology 67. Harvard University Press, Cambridge.
- JELINEK A., 1992: Problems in the chronology of the Middle Paleolithic and the first appearance of early modern *Homo sapiens* in southwest Asia. In: T. Akazawa, K. Aoki, T. Kimura (Eds.): *The Evolution and dispersal of modern humans in Asia*. Pp. 253–275. Hokusen-sha, Tokyo.
- JOLLY C., 1993: Species, subspecies, and baboon systematics. In: W. H. Kimbel, L. B. Martin (Eds.): *Species, species concepts, and primate evolution*. Pp. 67–107. Plenum Press, New York.
- KEITA S.O.Y., 1990: Studies of ancient crania from northern Africa. *Amer. J. of Phys. Anthropol.* 83: 35–48.
- KEY P., 1983: *Craniometric relationships among plains Indians*. University of Tennessee, Department of Anthropology, Report of Investigations 34.
- KRAMER A., CRUMMETT T., WOLPOFF M., 1992: Morphological diversity in the Upper Pleistocene hominids of the Levant: Two species? *Mitekufat Haeven*, Supplement 1: 65.
- MCCOWN T.D., KEITH A., 1939: *The Stone Age of Mount Carmel: The fossil human remains from the Levallois-Mousterian*. The Clarendon Press, Oxford.
- MAPLES W., 1967: An Analysis of the taxonomic status of the Kenya baboon (*Papio doguera* and *Papio cynocephalus*). August 1967. Doctoral Dissertation. University of Texas, Austin.
- NAGEL U., 1973: A Comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19,2–3: 104–166.
- PHILLIPS-CONROY J., JOLLY C., 1981: Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. *Amer. J. of Phys. Anthropol.* 56: 115–129.
- PHILLIPS-CONROY J., JOLLY C., 1986: Changes in the structure of the baboon hybrid zone in the Awash national park, Ethiopia. *Amer. J. of Phys. Anthropol.* 71: 337–350.
- PHILLIPS-CONROY J., JOLLY C., BRETT F., 1991: Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. *Amer. J. of Phys. Anthropol.* 86: 853–868.
- RAK Y., 1993: Morphological variation in *Homo neanderthalensis* and *Homo sapiens* in the Levant: a biogeographic model. In: W. H. Kimbel, L. B. Martin (Eds.): *Species, species concepts, and primate evolution*. Pp. 523–536. Plenum Press, New York.
- SCHOENINGER M., 1982: Diet and the evolution of modern human form in the Middle East. *Amer. J. of Phys. Anthropol.* 58: 37–52.
- SHEA J., 1989: A Functional study of the lithic industries associated with hominid fossils in the Kebara and Qafzeh Caves, Israel. In: P. Mellars, C. B. Stringer (Eds.): *The human revolution*. Pp. 611–635. Edinburgh University Press, Edinburgh.
- SHOTAKE T., 1981: Population genetic study of natural hybridization between *Papio anubis* and *P. hamadryas*. *Primates* 23: 285–308.
- SHOTAKE T., NOZAWA K., TANABE Y., 1977: Blood protein variations in baboons 1. Gene exchange and genetic distance between *Papio anubis*, *Papio hamadryas*, and their hybrid. *Japanese Journal of Genetics* 52,3: 223–237.
- SIMMONS T., 1990: Comparative morphometrics of the frontal bone in hominids. August 1990. Doctoral Dissertation. University of Tennessee, Knoxville.
- SIMMONS T., 1991: North African and Levantine hominid affinities: Frontal squama and browridge morphometry. *Amer. J. of Phys. Anthropol.* Supplement 12: 162.
- SIMMONS T., 1992a: The concept of hybridization in modern human origins. 3rd International congress on human paleontology. Jerusalem, Israel. *Mitekufat Haeven*, Supplement 1: 109.
- SIMMONS T., 1992b: Evaluating the concept of hybrid zones in modern human origins. *Amer. J. of Phys. Anthropol.* Supplement 14: 152.
- SIMMONS T., 1994: Neanderthals and modern humans in the contact zones: evolutionary schematics and model predictions. In: M. Nitecki, D. Nitecki (Eds.): *Origins of anatomically modern humans*. Pp. 201–225. Interdisciplinary contributions to archaeology series. Plenum Press, New York.
- SIMMONS T., SMITH F. H., 1991: Human population relationships in the Late Pleistocene. *Curr. Anthropol.* 32,5: 623–627.
- SIMMONS T., FALSETTI A., SMITH F. H., 1991: Frontal bone morphometrics of southwest Asian Pleistocene hominids. *J. of Hum. Evol.* 20: 249–269.
- SMITH F. H., 1982: Upper Pleistocene hominid evolution in south-central Europe: A review of the evidence and analysis of trends. *Curr. Anthropol.* 23: 667–703.
- SMITH F. H., 1984: Fossil hominids from the Upper Pleistocene of central Europe and the origin of modern Europeans. In: F. H. Smith, F. Spencer (Eds.): *The Origins of modern humans: a world survey of the fossil evidence*. Pp. 137–209. Alan R. Liss, New York.
- SMITH F. H., RANYARD G., 1980: Evolution of the supraorbital region in Upper Pleistocene fossil hominids from south-central Europe. *Amer. J. of Phys. Anthropol.* 53: 589–610.
- SMITH F. H., FALSETTI A. B., SIMMONS T., 1996: Circum-Mediterranean biological connections and the pattern of Late Pleistocene human evolution. In: H. Ullrich (Ed.): *Man and environment in the Palaeolithic*. Pp. 197–202. Etudes et recherches archéologiques de l'Université de Liège [E.R.A.U.L.], Liège. No. 62.
- SNEATH P., SOKAL R., 1973: *Numerical Taxonomy*. W. H. Freeman, New York.
- SOKAL R., ODEN N., WILSON C., 1991: Genetic evidence for the spread of agriculture in Europe by demic diffusion. *Nature* 351: 143–145.
- STANLEY S. M., 1989: *Earth and life through time*. 2nd Edition. W. H. Freeman, New York.
- STONEKING M., CANN R., 1989: African origin of human mitochondrial DNA. In: P. Mellars, C. Stringer (Eds.): *The human revolution*. Pp. 17–30. University of Edinburgh Press, Edinburgh.
- STRINGER C., ANDREWS P., 1988: Genetic and fossil evidence for the origin of modern humans. *Science* 239: 1263–1268.
- STRINGER C., GAMBLE C., 1993: *In Search of the Neanderthals*. Thames and Hudson, New York.
- SUGAWARA K., 1979: Sociological study of a wild group of hybrid baboons between *Papio anubis* and *Papio hamadryas* in the Awash Valley, Ethiopia. *Primates* 20: 21–56.
- TEMPLETON A., 1993: The "Eve" hypothesis: a genetic critique and reanalysis. *Amer. Anthropol.* 95,1: 51–72.
- THOMA A., 1965: Le Déploiement évolutif de l'*Homo sapiens*. *Anthropol. Hungar.* V,1–2: 179.
- TRINKAUS E., 1993: Comment on "Seasonal mobility among hunter-gatherers," by D. Lieberman. *Curr. Anthropol.* 34,5: 620–2.
- TRUVER S., 1980: *The Strait of Gibraltar and the Mediterranean*. Alphen aan den Rijn (Sijthoff and Nordhoff).
- VALLADAS H., JORON J., VALLADAS G., ARENSBURG B., BAR-YOSEF O., BELFER-COHEN A., GOLDBERG P., LAVILLE H., MEIGNEN L., RAK Y., TCHERNOV E., TILLIER A. M., VANDERMEERSCH B., 1987: Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel. *Nature* 330: 159–160.
- VALLADAS H., REYES J., JORON J., VALLADAS G., BAR-YOSEF O., 1988: Thermoluminescence dating of Mousterian 'Proto-Crô-Magnon' remains from Israel and the origin of modern man. *Nature* 331: 614–616.
- VANDERMEERSCH B., 1981: *Les Hommes fossiles de Qafzeh (Israel)*. Editions du Centre national de la recherche scientifique, Paris.
- WILEY E. O., 1981: *Phylogenetics: the theory and practice of phylogenetic systematics*. John Wiley and Sons, New York.

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