THE EVOLUTION OF *HOMO SAPIENS* : AN EXAMINATION OF PATTERNS IN FOSSIL HOMINID DATA

by

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INTRODUCTION

The origin of the distinctive anatomical pattern characterising all living *Homo sapiens*, and of "racial" diversity, used to be a primary focus of palaeoanthropological research. However, with the wealth of Plio-Pleistocene fossils found over the last thirty years and perhaps also in reaction to the racist approach of certain authors working on human evolution, research has tended to be focussed on early hominids instead. Now, an increasing amount of attention is once again being given to the biological and behavioural changes which led to the appearance of *Homo sapiens* (GOWLETT, 1987; HUBLIN, 1987; LEWIN, 1987a). In this paper I will examine two of the models recently proposed to explain the origin of *Homo sapiens* (using the term as equivalent to "anatomically modern *Homo sapiens*"), and discuss the fossil evidence which leads me to conclude that only one of these models is compatible with that evidence. By concentrating on these two models, I do not wish to imply that only these models are worthy of discussion. There are numerous other possible scenarios for the evolution of *Homo sapiens* involving complex mixtures of migrations and gene flow, but such models are far more difficult to build testable hypotheses from, and are thus scientifically less satisfying and certainly no more plausible from existing evidence.

The two conflicting models for recent human evolution discussed here have been termed the "regional continuity" (multiple origins) and "Noah's Ark" (single origin) models (HOWELLS, 1976). In the first model, recent human variation is seen as the product of the early-middle Pleistocene radiation of *Homo erectus* from Africa. Thereafter, local differentiation led to the establishment of regional populations (referred to as "clades", but in fact primarily identified by a differential retention of symplesiomorphies) which successively evolved through a series of evolutionary grades to produce modern humans in different areas of the world. In contrast to COON's (1962) version of this model, Wolpoff and colleagues (WOLPOFF *et al.,* 1984; WOLPOFF, in press) emphasise the role of gene flow in maintaining grade similarities and preventing speciation, while allowing the persistence of regional features, particularly in peripheral areas. From this model, recent regional ("racial") features could have preceded the appearance of the *Homo sapiens* morphology, and the exact manner of its establishment would depend on gene flow and local selection.

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The single origin model proposes that there was a relatively recent common ancestral population for *Homo sapiens* which already displayed most or all of the anatomical characters shared by living people. Many recent proponents of this model have suggested Africa as the probable continent of origin of *Homo sapiens*, with an early late Pleistocene origin for the species and an initiation of African regional differentiation, a subsequent later Pleistocene radiation from Africa, and a final establishment of modern regional characteristics outside Africa (BRÄUER, 1984, in press; STRINGER, in press). Cladistic versions of the single origin model rely on the identification of a suite of derived features characterising *Homo sapiens*, and the recognition of these characters at an earlier date in the area of origin of the species (i.e. Africa), and at later dates elsewhere (STRINGER *et al.*, 1984; STRINGER and ANDREWS, 1984).

I will now review the fossil hominid record for the later middle and early late Pleistocene, and assess which model appears to match the pattern of *Homo sapiens* evolution most closely.

THE FOSSIL RECORD

Although the evidence is still disputed, an increasing number of adherents to both models of *Homo sapiens* origins (and to neither model) accept that Africa probably has earlier evidence of *Homo sapiens* morphological characters than any other area (with the possible exception of south west Asia, as discussed below). Claimed early late Pleistocene specimens which fall within the modern anatomical range in preserved parts are known from South Africa (Klasies River Mouth Caves and Border Cave) and from Ethiopia (Omo Kibish 1), while archaic specimens which lie close to the pattern of *Homo sapiens* in some respects are known from areas such as Ethiopia (Omo Kibish 2), Tanzania (Ngaloba) and Morocco (Jebel Irhoud). All these specimens appear to be associated with Middle Stone Age or Middle Palaeolithic industries.

While ages of over 100 kyr have been claimed for the Klasies, Omo Kibish 1 and Border Cave hominids, these are in fact difficult to demonstrate convincingly from the existing evidence, although ages approaching 100 kyr are certainly possible. However, provided the specimens are not intrusive, an antiquity of at least 50-90 kyr is probable, and is enough to demonstrate the precocious appearance of modern human characteristics in the African continent. Although these specimens have been compared to recent African populations and found to be similar, there should be no expectation that they are specially related to any modern group, since morphological as well as genetic evolution would clearly be expected over the last 50 kyr. Ancestral populations of *Homo sapiens* may be represented at middle Pleistocene or assumed middle Pleistocene sites such as Florisbad and Eliye Springs, but possible synapomorphies between the assumed middle Pleistocene and early late Pleistocene samples are few compared with symplesiomorphies which can be demonstrated in facial shape and proportions. The precise evolutionary origins of the earliest *Homo sapiens* in Africa thus remain obscure.

The south west Asian record is one which contains clear evidence of both Neanderthal and *Homo sapiens* fossils associated with Middle Palaeolithic industries, and little or no evidence of transitional fossils. However, it is now becoming evident that the Qafzeh fossils actually predate many or all of the Neanderthals in the area (VALLADAS *et al.*, 1988). This means that the earliest appearance of humans of modern aspect in the area lies before 80 kyr, which places the earliest appearance of south west Asian modern humans comparably with the African first appearance suggested above. A local scheme of *Homo sapiens* evolution linking the probable middle Pleistocene Zuttiyeh partial skull with the Qafzeh hominids has been proposed (VANDERMEERSCH, 1981), but an African origin for the Qafzeh hominids is also possible (STRINGER, in press). What looks increasingly certain is

that the Neanderthals of south west Asia can have had nothing to do with the first appearance of *Homo sapiens* in the area.

In western Europe, there seems to be a clear pattern of morphological replacement of Neanderthals by *Homo sapiens* ("Cro-Magnons") between about 35-30 kyr ago. Neanderthal features which can be traced back into the middle Pleistocene from sites such as Ehringsdorf, Biache, Swanscombe and, less certainly, Petralona and Arago, are rapidly replaced (STRINGER *et al.*, 1984). The replacement event is coincident with the appearance of Aurignacian industries of the early Upper Palaeolithic, but the parallel appearance of the Châtelperronian industry may indicate adaptive cultural change or bow wave acculturation of late Neanderthals such as those known from Saint-Césaire. In central and eastern Europe there was apparently also a replacement event as indicated by the Aurignacian-associated *Homo sapiens* specimens from sites such as Mladeč, Stetten (Vogelherd) and Velika Pecina (providing a minimum radiocarbon age for a *Homo sapiens* frontal bone of c. 34 kyr). Archaeological evidence can be interpreted to show either an intrusive Aurignacian presence (from the east?) and parallel cultural change in local Neanderthals, producing industries such as the Szeletian, or local behavioural continuity.

Nevertheless, there are puzzling problems posed by the gracile Vindija Neanderthals from Yugoslavia, which some workers interpret as showing evolutionary trends towards a *Homo sapiens* morphology, and by the possibility of a transitional or hybrid form represented by the isolated Hahnöfersand frontal (BRÄUER, 1984; SMITH, 1984; STRINGER *et al.*, 1984). However, I now feel that this specimen is likely to be a rather robust modern *Homo sapiens*, without Neanderthal affinities. The somewhat unclear picture which emerges is of a time-transgressive (east-west) appearance of both the Aurignacian and its associated *Homo sapiens* fossils. Unfortunately it is impossible to take this association back to what may be the earliest occurrence of an Upper Palaeolithic industry in Europe – that known from Bacho Kiro, Bulgaria – since the associated remains are fragmentary and undiagnostic (KOZLOWSKI, 1982). However, it is possible that, paralleling the Qafzeh and Skhul evidence, Middle Palaeolithic-associated *Homo sapiens* did exist in eastern Europe and adjacent regions of Asia, on the basis of the immature human remains from Krapina (the A skull) and Starosel'ye in the Crimea.

Turning now to eastern Asia, where China has the only reasonable fossil record, there are unfortunately few representatives of Neanderthal-grade hominids, and hence there is a large morphological and chronological gap between the probable late middle Pleistocene archaic fossils from Yinkou, Maba and Dali, and the earliest known *Homo sapiens* fossils from sites such as Liujiang and Upper Cave Zhoukoudian (of late Pleistocene age, probably less than 20 kyr). Nevertheless a unilinear evolutionary sequence from the Lower Cave Zhoukoudian and Hexian *Homo erectus* fossils through to *Homo sapiens* populations has been proposed. Suggested Asian "clade" features seem to be predominantly primitive retentions such as a transversely flattened face and lingual shovelling of the upper incisors, and the clear non-*Homo erectus* morphology of the immediate post-*Homo erectus* fossils seems to present more of a contrast between them than is indicated by equivalent fossils further to the west. More data are required from this area to test properly the competing models of regional continuity or African origin, particularly in providing more complete fossils in the time range 20-100 kyr, and in integrating palaeoanthropological data with developing interpretations of the extensive archaeological data.

For the south east Asian and Australasian areas there is also a dearth of later middle-early late Pleistocene evidence which could bridge the morphological gap between the (assumed) middle Pleistocene Ngandong sample from Indonesia, which many assign to *Homo erectus*, and the earliest *Homo sapiens* fossils from Niah Cave, Borneo, and Mungo, southern Australia. The Niah cranium may date to c. 40 kyr, in which case it is the oldest dated *Homo sapiens* fossil in the area, but direct accelerator dating would be required to confirm this. The Mungo specimens are more securely dated to between 24-30 kyr. Both

the Niah Cave and Mungo specimens are gracile, and cannot easily be related to preceding archaic or *Homo erectus* populations in the area. However, the presence of much more robust late Pleistocene-early Holocene populations in Australia is indicated by large skeletal samples from sites such as Kow Swamp and Coobol Crossing. These samples show considerable morphological variation and most of them postdate the gracile Mungo fossils, but perhaps the most robust of all, the calvaria from Willandra Lakes (WLH-50), may be of comparable age.

Several scenarios of Australasian *Homo sapiens* evolution have been proposed recently (WOLPOFF *et al.*, 1984; HABGOOD, 1985, in press; STRINGER, in press). One model suggests an initial colonisation by fully evolved *Homo sapiens* from outside the area as part of an expansion of early modern humans. The variation in later Pleistocene Australians would have to be seen as derived from a fairly gracile morphology, involving in some cases the reversal of general evolutionary trends towards gracility in the evolution of *Homo sapiens*. A second model also proposes one founder population, but this time it would have been the more robust group, perhaps represented by WLH-50, locally derived from Indonesian middle Pleistocene *Homo erectus*. A third model combines elements of both the other models, in that the robust populations are seen as derived from Indonesian *Homo erectus*, and the graciles from eastern Asia. This last model suggests that modern Australians are derived from these two sources. Each of the models has explanatory problems, but it is possible that the extent of early Australian cranial variation has been overestimated by some workers, particularly where local microevolution and artificial cranial deformation have been contributory factors (BROWN, 1987).

MODELLING REGIONAL CHANGES AND THE PATTERN OF *HOMO SAPIENS* EVOLUTION

It is very difficult to illustrate the patterns of human evolution expected from the model of regional continuity, but to convey some important points about it, I have constructed a simple table depicting several aspects of cranial evolution according to this model. The parallel grade changes which are supposed to occur in separate geographical areas during the evolution of *Homo sapiens* are represented by changes in frequency or degree of expression of certain characters, as presented in schematic form in table 1. Of necessity, various dates have been estimated and averaged for the sake of simplicity. Here it has been assumed, for the benefit of discussion, that the cranial features shared between populations in time and space are homologous, and that evolutionary changes produced homologous results in each area. However, such assumptions may not be correct, and it is implicit in the African single origin model that these changes are not, in fact, all homologous.

The cranial features used are concerned with total facial prognathism (FAPR, assessed where possible using the midsagittal prosthion and nasion angles), supraorbital torus development (SUTO, both vertical thickness, projection and continuity), transverse facial flattening (FAFL, using the nasiofrontal and subspinale angles), occipital protrusion (OCPR, the development of an occipital bun or hemibun) and midsagittal frontal flattening (FAFL, using the frontal angle between nasion and bregma).

Hominid samples used to assess the character states are as follows:

i) Africa: 300+ kyr Bodo, Ndutu, Thomas Quarries, Salé; 200 kyr Broken Hill, Saldanha; 100 kyr Omo Kibish 2, Ngaloba, Florisbad, Eliye Springs, Djebel Irhoud; 80 kyr Klasies, Border Cave, Omo Kibish 1; 30 kyr Dar-es-Soltane 5, Nazlet Khater, Afalou, Taforalt; 0 kyr sub-Saharan African crania.

ii) For Europe: 300+ kyr Arago, Petralona, Bilzingsleben; 200 kyr Swanscombe, Ehringsdorf, Biache; 100 kyr Saccopastore, Krapina, La Chaise; 50 kyr La Ferrassie, La

Chapelle-aux-Saints, La Quina, Neanderthal, Spy, Saint-Césaire; 30 kyr Cro-Magnon, Stetten, Mladeč, Predmostí; 0 kyr recent European crania.

iii) For S.W. Asia: 150 kyr Zuttiyeh; 80 kyr Qafzeh; 50 kyr Tabun, Amud, Shanidar; 0 kyr recent Middle Eastern crania.

iv) For East Asia: 300+ kyr Zhoukoudian Lower Cave, Hexian; 150 kyr Dali, Yinkou, Maba; 20 kyr Zhoukoudian Upper Cave, Liujiang; 0 kyr recent "Mongoloid" crania (Asian/Amerindian).

v) For Australasia: 300+ kyr Indonesian *Homo erectus*, especially Sangiran 17; 200 kyr Ngandong; 30 kyr Mungo, Willandra Lakes WLH-50, Keilor; 0 kyr recent Australian crania.

The conventionally recognised first appearance of anatomically modern *Homo sapiens* in each area is shown by a transverse dotted line above the relevant sample, although it must be remembered that in an area such as eastern Asia the earliest well-dated occurrences are unlikely to represent the real time of first appearance. In South West Asia, the complex situation brought about by the new Qafzeh dates means that there is a subsequent intrusion of a Neanderthal sample, presumably followed by the reappearance of anatomically modern humans in the late Mousterian (if that is where the Skhul sample belongs) or early Upper Palaeolithic. Arrows added across the diagram indicate possible population links between the early modern humans of Africa and South West Asia at c. 80 kyr and between the Neanderthals of Europe and South West Asia at c. 50 kyr.

As can be seen from this table, many of the cranial characters change in parallel (in the regional continuity model this is seen as due to similar selection pressures or to gene flow). There are consistent "trends" for a **decrease** in facial prognathism (FAPR), supraorbital torus development (SUTO), transverse facial flattening (FAFL) and frontal flattening (FRFL). However, in the case of occipital protrusion (OCPR) the character changes in three geographical regions are for an **increase** in the degree of protrusion. Supposed local "clade" features in Asia (transversely flat face) and Australasia (greater facial prognathism, supraorbital torus development, frontal flattening) are shown to be primitive retentions which could be derived from other archaic populations in other areas.

Clearly, what is needed to support the model of regional continuity is a demonstration of genuine clade (shared derived or synapomorphous) features, and examples can be demonstrated from table 1. In Europe, transversely flat midfaces are transformed from a more primitive condition in the middle Pleistocene (c. 400 kyr FAFL 2-3) to a derived condition of midface projection (FAFL 0) in the Neanderthals (c. 50 kyr ago). This seems to provide a potential synapomorphy with recent Europeans (FAFL 1), but the intervening early *Homo sapiens* sample shows a contrasting and apparently more primitive transverse facial flattening (FAFL 2)! A better synapomorphy between European Neanderthals and early *Homo sapiens* might be provided by the development of a high degree of occipital protrusion ("bunning" – OCPR in table 1), but the uniqueness of this character to the European clade is called into question by its similar prevalence in the North African samples dated at c. 30 kyr which are not considered to have evolved from Eurasian Neanderthals, even by proponents of regional continuity. Instead, the possibility of homoplasies in occipital growth must be considered (TRINKAUS and LeMAY, 1982).

Overall, to summarise the picture provided by table 1, it is evident that either the local continuity or recent African origin models can be accomodated by such data. However, provided the relative dating of the early *Homo sapiens* fossils is accepted, all the (assumed homologous) morphological changes required to produce the earliest *Homo sapiens* morphologies can most economically (parsimoniously, with minimum reversals or parallelisms) be provided by assuming that the early *Homo sapiens* groups in Africa or

South West Asia at c. 80 kyr are the most appropriate ancestors for those appearing subsequently elsewhere (indicated by the shaded areas). What remains to be determined is whether the Qafzeh sample could represent a genuine ancestral population for subsequent Eurasian *Homo sapiens*, or whether the hypothetical dispersal of *Homo sapiens* across Eurasia originated from different populations which **succeeded**, rather than preceded Neanderthals in the region.

There is a remaining problem concerning the origin of the more robust of the range of Australian early *Homo sapiens* morphologies. Here, the morphology of the archaic Ngandong hominids (placed at c. 200 kyr) provides a possible alternative (and local) antecedent, but it remains to be demonstrated that the apparent archaic-modern synapomorphies are homologous, rather than (as I prefer to believe) homoplastic, similarities. Additionally, the Ngandong specimens may yet prove to be considerably younger in age; thus narrowing the time available for an evolutionary transition.

CONCLUDING REMARKS

If it is accepted that Africa and South West Asia have the oldest known *Homo sapiens*, must it be assumed that the previous evolution of *Homo sapiens* could only have occurred in those regions? The answer from the fossil evidence alone must be "not necessarily" since the predominantly plesiomorphous morphologies of preceding African hominids are matched both by the known parts of the Zuttiyeh skull in South West Asia and by what is so far known of the archaic hominids from Chinese sites such as Yinkou and Dali. More study and analysis of the fossil data are required, but reference must also be made to the growing body of genetic data (LEWIN, 1987b). These data match well with the earliest known presence of modern human fossils in Africa (and the immediately adjacent area of Israel). However, it must then be assumed that while the evolution of modern *Homo sapiens* occurred in Africa, modern genetic data from North Africa reflects considerable recent gene flow from Eurasia rather than the original "African" gene pool which was there in the Pleistocene (and which can still be traced further South). This does not seem an unreasonable assumption, but must be tested by further genetic analyses.

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TABLE 1

A representation of later Pleistocene regional changes in cranial morphology

AGE (kyr)	AFRICA FAPR	SUTO	FAFL	OCPR	FRFL	EUROPE FAPR	SUTO	FAFL	OCPR	FRFL	S.W. ASIA FAPR	SUTO	FAFL	OCPR	FRFL	E. ASIA FAPR	SUTO	FAFL	OCPR	FRFL	AUSTRALIA FAPR	SUTO	FAFL	OCPR	FRFL
300+	3	3	3	3	3	2-3	3	2-3	3	3						-	3	3	3	2	3-4	3	3	3	3
200	2	3	1-3	3	3	2	2-3	1-2	2-3	2											-	2	2-3	3	3
											-	2	3	-	2	2	2	3	3	2					
100	2	1-2	2-3	2-3	1-2	2	2	1	2	2															
	-	0-1	2-3	3	0-1	←→					2	1	2	3	0-1										
50						2	2	0	1-2	2	2	2	0	2-3	2										
30	0-2	0-1	2	2-3	0-1	1	0-1	2	2-3	0-1						0-1	0-1	2-3	3	0-1	1-2	0-2	1-2	3	0-2
0	0	0	2	3	0	0	0	1	3	0	0	0	1	3	0	0	0	3	3	0	1	1	1	3	1

FAPR = facial prognathism; SUTO = supraorbital torus development; FAFL = transverse facial flatness; OCPR = occipital protrusion; FRFL = midsagittal frontal flatness. Modern *Homo sapiens* morphology represented by shaded areas.