Reconstructing Recent Human Evolution

Christopher B. Stringer

References	**Article cited in:**
	http://rstb.royalsocietypublishing.org/content/337/1280/217#related-urls
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

Reconstructing recent human evolution

CHRISTOPHER B. STRINGER

The Human Origins Group, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

SUMMARY

The two most distinct models of recent human evolution, the multiregional and the recent African origin models, have different retrodictions concerning specific archaic–recent population relationships. The former model infers multiple regional archaic–modern connections and the ancient establishment of regional characteristics, whereas the latter model implies only an African archaic–all modern relationship, with recent (late Pleistocene) development of regionality. In this paper, four late archaic groups from Europe, southwest Asia, Africa and East Asia are compared with various fossil and recent *Homo sapiens* crania or cranial samples. The results of Penrose shape comparisons narrowly favour a late archaic African–modern special relationship over an East Asian–modern one, with European and southwest Asian Neanderthal groups much more distant. No specific archaic–recent regional relationships are indicated in the shape analyses, nor in separate examinations of patterns of regionality, which indicate a recent origin for present day regionality. The Skhul–Qafzeh sample provides an excellent shape intermediate between the archaic and recent samples.

1. INTRODUCTION

Debate on recent human evolution over the past few years has been focused on the contrasting models of multiregional evolution (regional continuity) and a recent African origin ('Out of Africa') to explain the evolutionary origins of anatomically modern *Homo sapiens* (hereafter *Homo sapiens* or modern humans). At their most basic, these different models have quite different retrodictions for the fossil record (Stringer & Andrews 1988; Wolpoff 1989).

From the multiregional evolution model, geographic 'clades' should be identifiable from the Early Pleistocene or earlier middle Pleistocene leading from local archaic populations to modern ones in the same regions. However, these 'clades' were not completely distinct genetically or phylogenetically, since they shared a common gene pool through gene flow and could even be regarded as representing early examples of our own species (*Homo sapiens sensu* Wolpoff & Thorne) following the last cladogenetic event, taken as the late Pliocene origin of what is usually termed *Homo erectus*. Grade changes can be recognized in the multiregional evolution of '*Homo sapiens*', with the gradual predominance of 'modern' morphological features occurring in the late Pleistocene.

In contrast, the recent African origin model has no specific retrodictions for middle Pleistocene hominid relationships. However, a monophyletic clade consisting of the (African) last common ancestor of all *Homo sapiens* plus all descendant hominids should be recognized. There would be no special clade relationship between regional *Homo sapiens* variants and non-*Homo sapiens* populations except via an Africa ancestor. There would be both a grade and clade relationship between *Homo sapiens* populations, with possible nested clades representing the results of late Pleistocene regional diversification.

Two related critical tests of the models concern the identification of a single or multiple archaic ancestral population for *Homo sapiens* in the late middle or early late Pleistocene, and the identification of specific regional affinities to modern *Homo sapiens* populations in any archaic samples. I have previously presented both phenetic and cladistic data in support of an African ancestral population for *Homo sapiens*. However, most of the evidence considered was from western Eurasia or Africa. Here I would like to use phenetic cranial data to investigate late middle Pleistocene: recent human relationships for all the major regions and to test whether one or more archaic populations are closest to recent populations as a whole or whether there are instead specific archaic–modern regional links. The main method used is the Penrose Shape Distance and it will be used to assess possible grade and clade similarities and differences in overall cranial shape comparing within and between archaic and modern samples. By comparing shape distances, it may be possible to assess which archaic group provides the best 'shape ancestor' for *Homo sapiens*.

I will also briefly examine the establishment of patterns of regionality in *Homo sapiens* as this provides a further test of the two evolutionary models. For the multiregional model these patterns had been established since the middle Pleistocene at least, and hence should be very evident even in early modern samples, whereas from the recent African model such patterns would have been poorly developed or absent in early *Homo sapiens*.

© 1992 The Royal Society and the author

2. CRANIAL SAMPLES

The comparisons given here will be presented for three different sets of material.

1. The first set consists of 'archaic' (i.e. non-anatomically modern) material from the late middle–early late Pleistocene of four regions: Europe (late Neanderthals), southwest Asia (late Neanderthals), Africa and China. The samples for crania used are as follows.

EuNea (actual or presumed European late Neanderthals): Saint-Césaire; Sala; La Chapelle-aux-Saints; La Quina 5; Forbes' Quarry; Feldhofer; Spy 1, 2; La Ferrassie 1; Guattari 1.

AsNea (actual or presumed late southwest Asian Neanderthals): Shanidar 1, 5 (data from Trinkaus (1983) and personal communication); Amud 1.

AflmP (actual or presumed late middle Pleistocene African crania, excluding Omo-Kibish 1): Ngaloba–Laetoli hominid 18: Irhoud 1, 2; Eliye Springs ES-11693 cast; Singa; Omo Kibish 2.

DaMa (actual or presumed late middle Pleistocene Chinese crania): Dali (data from de Lumley & Sonakia (1985), Wu (1981) and a cast); Maba. Although not presented here, comparisons were also performed using Dali alone, with very similar results.

2. A set of early anatomically modern crania are also analysed, with samples as follows.

SQ (Skhul–Qafzeh): Qafzeh 3, 6, 9; Skhul 5, 9.

UP (European actual or presumed early Upper Palaeolithic): Vogelherd 1; Mladeč 1, 2, 5, 6 (casts or originals); Brno 2; Dolni Vestonice 3; Pavlov 1 cast; Predmosti 3, 4 (casts); Cro-Magnon 1, 2, 3; Grotte des Enfants 6 (cast); Abri Pataud 2.

AfTaf (North African Afalou and Taforalt): Afalou 9, 10, 29; Taforalt 11, 17.

RAus ('Robust early Australian') Cohuna (cast); Coobol Creek (a male individual).

Keil: Keilor (Australia) cast.

Wad: Wadjak 1 (Java, Indonesia) (Stringer/Parsons reconstruction).

UC: Upper Cave Zhoukoudian, 101, 102, 103 (casts, only selected data taken from the distorted and immature 102 cranium).

3. A third set of data consists of modern regional 'controls' consisting of overall means (= mean of male and female means) for the following *Homo sapiens* samples from Howells (1989).

No: Mediaeval Norse (110 individuals). Zalavar values had to be used for BRR, as this was not measured for the Norse sample.

Zu: South African Zulu (101 individuals).

Aus: Lower Murray River Australian (101 individuals).

SCr: Santa Cruz Island Native American (102 individuals).

Jap: South Japan (91 individuals).

3. METHODS OF ANALYSIS

The Penrose Size and Shape Statistic (Penrose 1954) provides a simple way of measuring overall similarity without resorting to complex multivariate procedures which include assumptions about the equality of variance–covariance matrices between different samples of populations or individual crania. An overall Penrose distance between any two samples is derived from the sum of the squared differences between the standardized means of each variable, divided by the number of variables. Standardization of means is necessary to prevent large measurements having an undue effect and is usually achieved by dividing by the overall standard deviation, but here I have preferred to standardize by logarithmic transformation, as this allows flexibility in sample composition without extensive recomputations, and provides very comparable results to standardizing by standard deviation. (See, for example, Stringer (1979).)

The size component is the square of the mean difference in size, and this can be subtracted from the overall Penrose distance described above to provide the shape component, which represents the variance among the measurement differences. The following

Table 1. *Measurements and abbreviations used (Howells 1973, 1989)*

(Measurements marked with asterisk were used in the size and shape analyses.)

GOL	glabello-occipital length
NOL	nasio-occipital length*
BNL	basion-nasion length*
BBH	basion-bregma height*
XCB	maximum cranial breadth*
XFB	maximum frontal breadth*
AUB	biauricular breadth*
ASB	biasterionic breadth
BPL	basion-prosthion length
NPH	nasion-prosthion height
NLH	nasal height
OBH	orbit height*
OBB	orbit breadth*
NLB	nasal breadth*
MAB	palate breadth, external*
MDH	mastoid length
ZMB	bimaxillary breadth*
SSS	bimaxillary subtense*
FMB	bifrontal breadth*
NAS	nasio-frontal subtense*
EKB	biorbital breadth
DKB	interorbital breadth*
FRC	nasion-bregma chord* (frontal chord)
FRS	nasion-bregma subtense*
FRF	nasion-subtense fraction*
PAC	bregma-lambda chord* (parietal chord)
PAS	bregma-lambda subtense*
PAF	bregma-subtense fraction*
OCC	lambda-opisthion chord* (occipital chord)
OCS	lambda-opisthion subtense*
OCF	lambda-subtense fraction*
NAR	nasion radius
SSR	subspinale radius
PRR	prosthion radius
ZMR	zygomaxillare radius
AVR	molar alveolus radius
BRR	bregma radius*
LAR	lambda radius

discussions will be based primarily on the shape distances.

One of the potential problems with the Penrose Size and Shape Statistic concerns the fact that (unlike methods such as the Generalized Distance Statistic of Mahalanobis) correlations between the variables are not taken into account. So in these analyses the potential number of variables (38) has been reduced by both practical considerations (missing values) in important specimens such as Jebel Irhoud and Dali, and by the removal of one of each pair of the remaining most highly correlated variables (e.g. glabello-occipital length, GOL, which is highly correlated with nasio-occipital length NOL, and biorbital breadth, EKB, which is highly correlated with frontomalare breadth, FMB). The remaining variables to be analysed are shown in table 1, and will be referred to by their abbreviations for the rest of this paper.

4. SHAPE ANALYSIS

A matrix of shape distances between the samples is shown in table 2, and it is immediately apparent that the four left hand columns generally display large shape distances compared with the columns to the right and especially with those between the recent samples. This is consistent with the inferred grade differences between the 'archaic' groups and the *Homo sapiens* samples because the archaic groups have another archaic group as first or second nearest neighbour (except for DaMa, where SQ is second nearest), while conversely all the anatomically modern groups have 'modern' nearest neighbours. If we first examine shape relationships between the archaic groups, EuNea and AsNea are similar to each other, comparable with shape distances obtained between the recent samples, while AflmP and DaMa are somewhat further apart, but still closely related. Although the first result was completely predictable, the second was (to me at least) unexpected, and I will return to its possible significance later. Distances between members of these two sets are larger, espe-

cially DaMa/EuNea and DaMa/AsNea. So whereas the four archaic groups seem at first glance to represent a common evolutionary grade when compared with *Homo sapiens*, they show internal diversity and an apparent separation into two subgroups.

When we move on to consider archaic–modern comparisons, the two archaic subgroups differ markedly in their relationships. Except for the AsNea/RAus and AsNea/UC comparisons, the relative ordering of relationshps to all the modern samples is (i) AflmP, (ii) DaMa, (iii) AsNea and (iv) EuNea, often with a substantial increase in shape distance when considering AsNea–modern and EuNea–modern comparisons. The nearest modern neighbours for the two Neanderthal groups are SCr and UC (EuNea) and UC and SQ (AsNea), but the shape distances are substantially smaller between DaMa, AflmP and these modern samples except in the case of UC where AsNea and DaMa have equivalent distances. There is no evidence here of the shape correspondence sometimes claimed between European Neanderthals and both Upper Palaeolithic specimens and recent Europeans. Because of the lack of any specific EuNea or AsNea shape similarities which would support a general multiregional model, I will now concentrate on the DaMa–modern and AflmP–modern relationships.

In a multiregional model we might expect the closest shape relationship between the archaic–recent groups to lie between AflmP and Zu, and between DaMa and Jap. However, the shape distance to Jap is actually the largest recent comparison, both for AflmP and DaMa. The AflmP–Zu distance is much smaller, but the smallest comparison is actually AflmP–SCr. If we compare the distance AflmP–Zu with the mean AflmP distance to the other recent groups, and we also compare the mean DaMa–Jap/SCr value (as possible clade members) with the other DaMa–recent comparisons, in each case the supposed regional clade distance is larger than the mean of the other corresponding shape distances. The shape relationships thus do not show any special archaic–recent regional correspondence, but reveal an overall ordering of

Table 2. *Shape distances (× 10⁴): 25 log vars*

	DaMa	AflmP	EuNea	AsNea	SQ	UP	AfTaf	RAus	Keil	Wad	UC	No	Zu	Aus	SCr
AflmP	9														
EuNea	23	14													
AsNea	29	18	6												
SQ	20	15	37	29											
UP	36	33	58	51	11										
AfTaf	34	29	59	48	7	5									
RAus	54	40	56	36	18	23	18								
Keil	36	26	43	32	11	13	13	19							
Wad	26	22	45	35	5	13	6	18	16						
UC	27	23	36	27	8	9	9	18	7	11					
No	35	32	51	42	11	5	6	23	14	9	5				
Zu	34	31	54	46	8	7	5	26	17	9	9	5			
Aus	25	24	41	34	8	7	7	22	17	8	5	3	3		
SCr	24	21	35	30	8	8	10	23	13	10	7	3	10	6	
Jap	40	38	64	54	11	6	5	26	17	14	11	5	4	7	7

Table 3. *Size and shape comparisons*

comparison	EuNea No	AflmP Zu	DaMa SCr	DaMa Jap	UP No	UP Jap	AfTaf Zu	AfTaf Jap	UC SCr	UC Jap	RAus Aus	Keil Aus	Wad Aus
size (all +)	9	8	11	7	2	3	3	5	10	7	14	13	20
shape	51	31	24	40	5	6	5	5	7	11	22	17	8

shape similarity of (i) AflmP; (ii) slightly more distant, DaMa; (iii) more distant, AsNea; and (iv) over 50% more distant than AflmP, EuNea.

Turning now to the early modern specimens, SQ occupies a unique position in relation to the archaic and recent groups. Although SQ is closer to all the modern groups than it is to the archaic groups (with the exception of AflmP at a distance of 15 and RAus at 18), its relative proximity to the archaic groups means that it usually provides a shorter route for archaic–recent shape change than by the archaic–recent shape distance direct. Thus AflmP–Jap = a distance of 38, AflmP–SQ–Jap = 26. Wadjak, which is the nearest shape neighbour to SQ, does not have this effect, because it is more distant from the archaic samples.

Moving on to consider specific early modern–recent shape comparisons, we will now examine possible regional relationships for Europe (UP–No), East Asia (UC–Jap/SCr), Australia (RAus/Keilor/Wad–Aus) and Africa (AfTaf–Zu). The shape distance UP–No is favoured compared with the mean UP shape distance to the other recent populations, as is RAus–Aus, and Wad–Aus in their own regional comparisons. However, the UC–Jap/SCr mean distance is greater than the mean UC distance to the other recent samples, as is Keil–Aus compared with the rest. In the case of Keil and RAus, all the shape distances are relatively large, particularly so for RAus. For the latter sample, this result is comparable with that obtained for the Cohuna cranium alone in a previous study (Stringer 1974). Part of this distinctiveness might be due to artificial deformation of the cranium, as noted for parts of the early Australian sample (Brown, this symposium). In addition to the shape distinctiveness evident in early modern–Aus comparisons, there are also large size differences (see below).

The shape distances show, firstly, a predominance of grade over clade in comparing archaic and recent samples. This might have been expected using a phenetic technique, but it is surprising that even between the *Homo sapiens* groups there is such a poor signal of regionality when comparing such crania as Upper Cave and recent Japanese or Native Americans, or Keilor and recent Native Australians. Given the dating of the Upper Cave crania to 20–25 ka and Keilor to about 12 ka ago, these specimens are separated from the recent samples by less than 5 per cent of the total time proposed for the existence of their regional clades by Wolpoff (1989). When combined with the separate analysis of regionality given below, a major retrodiction of the general multiregional model is therefore falsified, and a retrodiction of the recent African model is supported: modern regionality is apparently a product of the late Pleisto-

cene. However, as will also be seen below, the retrodiction of the recent African origin model that the archaic African sample would be uniquely placed as closest to *Homo sapiens* is supported, but not as clearly as might have been expected. DaMa closely follows AflmP in shape distance for some comparisons (e.g. with UP, No, Aus, Jap).

So far I have been discussing Penrose shape distances only. However, it is instructive to compare size distances as well. Table 3 shows a comparison of some archaic and early *Homo sapiens* groups with recent samples for the 25 measurement analyses. Although shape distance generally predominates over size, it is evident that there have been major cranial size reductions in the evolution of some recent populations, especially in the SCr, Jap and Aus samples. Perhaps the most striking comparison is in Australasia, where there has been considerable Holocene size reduction, for reasons which are still not fully understood (Brown, this symposium). However, for the RAus comparison, in particular, sexual dimorphism is an important factor, because the sample consists of two large male individuals only. Whereas comparisons between the modern samples generally show a reasonable balance between size and shape distances, those between archaic and anatomically modern groups consistently show a predominance of shape differences over those of size. However, comparing the samples with the largest and smallest cranial dimensions in the whole analysis does give an exception to this generalization (AsNea and SCr have Size distance 36, Shape distance 30).

5. ROW STANDARDIZED CRANIAL DATA

Unlike methods of analysis such as Principal Components, Canonical Variates and Mahalanobis' Generalized Distance, the Penrose Size and Shape Statistic provide no straightforward method for determining the relative contributions of the different measurements used to the shape distances generated. However, an independent means of examining the most important contributors to shape difference comes from row standardization (Corruccini 1987). Here, cranial data are standardised through division by a mean (size) measure calculated from the individual row of measurements for each cranium or sample. After standardization, the measurements have been compared with a similarly standardised overall mean value for recent *Homo sapiens* (Howells 1989) to give the index 100 (standardized sample mean/standardized recent mean).

Table 4 shows a comparison for four archaic and two *Homo sapiens* groups. It is interesting that row standardization minimizes what have traditionally

Table 4. *Size standardized cranial data. All comparisons are overall group means*

	GOL	NOL	BNL	BBH	XCB	XFB	AUB	ASB	BPL	NPH
EuNea/mod	100.4	101.8	104.0	88.7	99.8	97.9	100.8	103.0	109.7	115.1
AsNea/mod	100.0	102.1	102.6	89.7	97.9	97.6	102.7	102.2	104.1	118.5
lmPA/mod	102.6	100.2	98.4	89.4	98.0	96.8	104.8	104.7		105.3
DaMa/mod	108.2	106.2	107.2	85.0	103.6	94.4	112.6			
SQ/mod	98.9	98.2	98.0	93.5	100.3	97.4	101.5	103.1	107.2	104.8
UP/mod	102.4	103.4	97.0	96.4	98.3	102.2	100.9	99.6	102.0	96.9

	NLH	OBH	OBB	NLB	MAB	MDH	ZMB	SSS	FMB	NAS
EuNea/mod	110.5	99.5	101.3	112.0	106.2	67.6	106.4	146.8	103.4	127.1
AsNea/mod	113.7	95.5	101.6	113.5	103.7	83.9	103.9	141.1	103.3	128.5
lmPA/mod	87.7	96.4	104.4	110.3	111.2	63.3	104.6	116.1	109.6	102.9
DaMa/mod		96.6	102.4	119.3	109.4		109.7	102.6	106.7	97.1
SQ/mod	99.7	91.6	104.8	111.1	105.4	82.1	107.0	102.4	110.5	100.2
UP/mod	96.8	84.6	99.5	89.0	95.6	78.2	97.2	97.7	99.8	94.0

	EKB	DKB	FRC	FRS	FRF	PAC	PAS	PAF	OCC	OCS
EuNea/mod	99.5	113.4	93.8	75.0	106.3	88.1	67.7	85.2	87.3	110.1
AsNea/mod	102.3	111.7	92.9	66.4	108.8	90.4	81.3	89.6	92.4	104.3
lmPA/mod	111.0	132.6	97.7	86.1	111.2	96.0	68.7	94.4	90.8	108.7
DaMa/mod	104.6	117.9	97.9	93.3	102.9	92.9	70.8	87.7	87.2	119.4
SQ/mod	108.6	114.9	95.3	95.2	104.3	100.1	90.8	94.1	95.7	100.0
UP/mod	99.2	98.3	101.3	106.6	107.4	102.5	94.2	100.0	98.3	105.2

	OCF	NAR	SSR	PRR	ZMB	AVR	BRR	LAR	mean	s.d.
EuNea/mod	77.8	108.0	108.5	108.4	95.7	113.2	90.0	90.8	100.6	15.1
AsNea/mod	85.4	101.0	105.4	104.0	94.4	107.5	89.3	100.0	100.9	12.9
lmPA/mod	86.4	106.2	101.9	105.4	99.4	103.8	93.0	94.2	99.8	12.2
DaMa/mod	80.0						81.8		99.9	12.3
SQ/mod	106.8	96.6	97.5	101.1	93.4	97.6	96.1	96.3	100.0	6.4
UP/mod	101.4	104.2	102.7	101.6	106.9	100.2	99.3	96.3	98.9	5.7

been considered as some of the most distinctive Neanderthal features (e.g. long skull: GOL, NOL; broad skull: XCB; high orbits: OBH), but others are very much accentuated (e.g. high face and nose: NPH, NLH; prominent mid-face: SSS, NAS, AVR). DaMa, in particular, looks primitive in the low vault, broad at the base, with prominent occiput (BBH, BRR, AUB and OCS values). SQ and UP more closely approximate the modern values in most respects (BBH, NPH, NLH, FRS, PAC, PAS, OCC, OCF, PRR, AUR and BRR) but remain distinctive in the low OBH, and apparently primitive in total prognathism (higher BPL, PRR flatter frontal (FRF) and small mastoid (MDH)). The AflmP sample is generally archaic but has a distinctively low NLH, MDH, and high MAB, EKB, DKB (broader palate and upper face breadths). DaMa and AflmP are closer to *Homo sapiens* than are the Neanderthals in the lower SSS, NAS and higher FRC, FRS and PAC values. The former characters of transverse facial flattening are probably primitive retentions, whereas the latter (longer frontal and parietal, higher frontal) may reflect real synapomorphies in frontal and parietal shape.

We can estimate the divergence of these groups from the recent human mean by several different methods. One is to calculate the standard deviation for each data set in table 4. Although each one has a mean value close to 100 (reassuringly, because size standardization has been carried out), the standard deviations show considerable variation. SQ and UP have low values, EuNea a high value, and the three others are intermediate. AflmP is narrowly the least

divergent archaic sample, but the closely comparable DaMa standard deviation may well be atypically low because a number of measurements were not available for inclusion, some of which can be estimated to be very different from the modern mean. For example the apparent low facial height of Dali is certainly misleading because vertical crushing has considerably reduced the real NLH and NPH values. Values for both facial height and lower facial projection will have to be considerably increased if and when this fossil is reconstructed.

6. THE DESCRIPTION AND INTERPRETATION OF REGIONAL FEATURES

A fundamental problem in the study of supposed regional clade characters is that the characters used may be poorly defined or standardized. Although this is a serious issue, it is not one which I will address here. Another problem with many studies of 'regionality' used to support the multiregional model is that often only one region is examined at a time, with lists compiled of the characters in common between the archaic and recent representatives of the supposed local clade (see, for example, Wolpoff *et al.* (1984); Wolpoff (1989)). Moreover, the comparisons are often highly selective and ignore or minimise conflicting data. As a parallel example I could refer to metrical comparisons I have made between the Upper Cave and recent Japanese crania in 38 cranial measurements. If I selected the ten measurements where they

were similar to each other I could provide support for regionality. However, this would mean ignoring the 28 other measurements in which European early Upper Palaeolithic mean values were actually more similar than Upper Cave to those of recent Japanese crania! When proper interregional comparisons of supposed clade characters are made, the results are much more equivocal (see, for example, Groves (1989); Habgood (1989, 1992); Stringer (1992)). In such cases many of the characters either show inconsistency through variation within regions or even a higher frequency outside the supposed clade area.

Using cranial metrics rather than morphological characters provides an alternative method of looking at past and present regionality. This approach has been used descriptively with great success by Howells (1973, 1989). Suites of measurements in which certain regional populations are distinctive can be recognized, and individual crania can then be tested to see to which region they appear to be best assigned on the basis of their craniometric characteristics. For research still in progress, I have used size standardized data to test individual fossil crania, and their most probable regional affiliation using Howells' recent regional criteria are shown in the middle column of table 5. This approach is closest to a cladistic one, where distinctive regional characteristics are being selected albeit, in some cases, probable distinctive primitive retentions).

Table 5. *Primary regional affiliations of individual crania*

(Am = Native American, Eu = European/Egyptian, As = East Asian/Inuit, Aus = Australian/New Guinea, Af = Subsaharan African.)

	Row standardized: Howells variables sets	CRANID: 50 nearest neighbours
La Ferrassie 1	Aus	Af[a]
Jebel Irhoud 1	Aus/Am	Af[a]
DaMa	Aus	—
Qafzeh 6	Am	Aus
Qafzeh 9	Aus	Af
Skhul 5	Am	—
Mladeč 1	Aus	Eur
Predmostí 3	Aus	Aus
Predmostí 4	Aus	Eur
Cro-Magnon 1	Af	Aus
Grotte des Enfants 6	Aus	Eur
Abri Pataud	Aus	As
Afalou 9	As	Eu
Afalou 29	Af	Eu
Taforalt 11	Af	Af
Taforalt 17	Aus	Aus
Coobol Creek	Aus	Aus
Upper Cave 101	Aus	Aus
Upper Cave 103	Aus	Af
Wadjak	Aus	Af
Keilor	Aus	Af

[a] CRANID provided a warning in these cases that the crania were unusual by comparison with Howells' database. They were more than three standard deviations from the mean nearest-neighbour distance and from the mean distance from the overall centroid.

A completely separate method of investigating regionality (this time phenetically based) is provided by Richard Wright's CRANID package which uses Howells' cranial database to test the affinities of individual crania on the basis of 33 cranial measurements. Principal Components analysis is used to relate the samples in multivariate space and to provide the 50 nearest neighbour crania (of whatever population) using Euclidean distances. I have analysed most of the same crania listed in table 5 using CRANID, and have summarized the primary regional affiliation of the 50 nearest neighbours obtained, in the right hand column of the table. As can be seen if we omit the Skhul–Qafzeh specimens, of the 35 regional affiliations determined in table 5, only 11 could be considered as geographically appropriate. This shows the weak signals of modern regionality given out by these Pleistocene crania. Of the five possible regional affiliations, two predominate: Australian (19) and African (9). This is probably because the regional shape characters of low NPH (Australia and Africa), NLH (Australia), OBH (Australia), BRR (Australia) and SSS (Africa) are common in the Pleistocene samples.

7. CONCLUDING REMARKS: ANCESTORS AND REGIONALITY

Returning to the tests of the multiregional and recent African origin models mentioned in the Introduction, can one or more archaic populations be identified as 'best shape ancestors' for *Homo sapiens*? From the phenetic shape analyses, the Neanderthal samples of Europe and Asia make unlikely ancestors for any of the modern cranial samples. Overall shape distances are too large, and the Neanderthal samples lose out in most comparisons with AfImP and DaMa (figure 1). From the row standardized data, the Neanderthals are no more distinct from the modern mean than AfImP and DaMa on a number of measurements, but where the Neanderthals do diverge (e.g. on NLH, SSS), they do so markedly. Comparing AfImP and DaMa in the shape analyses shows that AfImP is closer to every one of the other groups (modern or Neanderthal) than is DaMa. However for some of the modern groups (e.g. Aus, Jap) the differences are small. Bearing in mind the motley composition of the African sample, and the limitations of the Dali data (none of it obtained by me on the original fossil, which is not yet available for general study), we should remain somewhat cautious about the results (although the combination of Dali and Maba data seems to have little effect on the results). What the results do show, surprisingly for me, is that AfImP and DaMa share more similarities with each other in metrical data and shape than either share similarities with the Neanderthals or moderns (figure 1). So I conclude the 'best shape ancestor' test with a relatively confident statement that the two Neanderthals samples should be eliminated from consideration, but a less confident statement that the late archaic African sample remains the exclusive best ancestor for early and later *Homo sapiens*. If we can turn away from a universal multiregional model for modern human origins, we
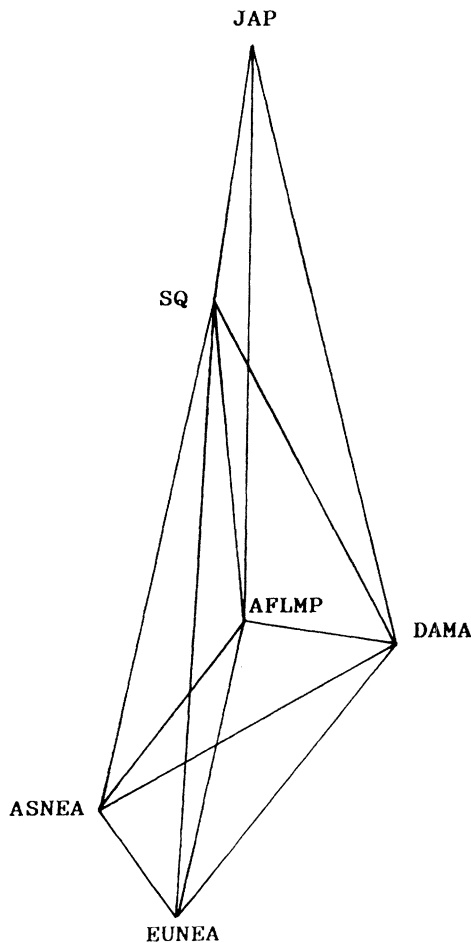
Figure 1. A two-dimensional approximation of shape distances between the four archaic samples (late Asian Neanderthals, late European Neanderthals, late archaic Africans, and Dali–Maba), Skhul–Qafzeh, and a recent sample (Japanese). The Skhul–Qafzeh sample is relatively closer to both the archaic and recent groups than can be shown in two dimensions.

cannot so easily exclude a dual African and East Asian ancestry model (see, for example, Habgood (1988)). But in such a case the DaMa sample appears most closely related to recent Australians (or Native Americans) rather than East Asians. However, if we do propose something like a special Dali–Australian relationship, it would still be necessary to infer the existence of an East Asian or Australasian intermediate population comparable to the Skhul–Qafzeh sample. It remains true that the most economical single route for shape changes from archaic–recent groups is via AflmP and SQ. Given recent age estimates for the Skhul–Qafzeh sample of 80–120 ka, these specimens may well lie close to the origin of all later *Homo sapiens*.

For the second test, that of regional affiliations, the results from tables 2, 3 and 5 are very clear. Archaic–modern regional affiliations are not reflected in these phenetic cranial shape analyses. Regionality appears to develop in the late Pleistocene, and a sample like the Skhul–Qafzeh crania seems a reasonable primitive modern template to which later regionality could be added. Samples of present day East Asians (e.g. Japanese) suggest that these populations are highly

derived away from any archaic or early modern ancestors. In contrast, the Australian sample (and to a lesser extent SCr) bears a closer overall resemblance to the Pleistocene material, perhaps because as Macintosh & Larnach (1976) proposed 'we could postulate the Aboriginal Australians as the earliest examples of evolving generalised modern *Homo sapiens* to arrive in their ultimate area of migration'.

Thus a model of universal multiregionalism is not supported by these analyses. If *Homo sapiens* originated in one region, that region was probably Africa, as represented here by the AflmP sample. However, if we take figure 1 and rotate it clockwise through 90°, we can obtain a different perspective on the AflmP–DaMa relationship. Is it possible that DaMa represents a more primitive version of AflmP, either an ancestral form or a relict population of an ancestral form? To answer that question depends on both the availability of better fossil samples and on an improved chronological framework for the African and Asian material. However, it seems unlikely to me that Dali represents a late Asian form of *Homo heidelbergensis*, as other analyses (not discussed here) show African (e.g. Bodo, Broken Hill) and European (e.g. Arago, Petralona) earlier middle Pleistocene fossils to be more similar to Neanderthals than to either AflmP or DaMa. Neither does Dali appear to be close to the Zhoukoudian *Homo erectus* sample in shape, from other more limited analyses.

REFERENCES

Corruccini, R.S. 1987 Shape in morphometrics: comparative analyses. *Am. J. Phys. Anthrop.* **73**, 289–303.

Groves, C.P. 1989 A regional approach to the problem of the origin of modern humans in Australasia. In *The human revolution: behavioural and biological perspectives on the origins of modern humans*, vol. I (ed. P. Mellars & C. B. Stringer), pp. 274–285. Edinburgh University Press.

Habgood, P.J. 1988 A morphometric investigation into the origin(s) of anatomically modern humans. Ph.D. thesis, University of Sydney.

Habgood, P.J. 1989 The origin of anatomically modern humans in Australasia. In *The human revolution: behavioural and biological perspectives on the origins of modern humans*, vol. I (ed. P. Mellars & C. B. Stringer), pp. 245–273. Edinburgh University Press.

Howells, W.W. 1973 *Cranial variation in Man.* Cambridge, Massachusetts: Peabody Museum.

Howells, W.W. 1989 *Skull shapes and the map.* Cambridge, Massachusetts: Peabody Museum.

de Lumley, H. & Sonakia, A. 1985 Première découverte d'un *Homo erectus* sur le continent indien á Hathnora, dans la moyenne vallée de la Narmada. *Anthropologie* **89**, 13–61.

Macintosh, N.W.G. & Larnach, S.L. 1976 Aboriginal affinities looked at in world context. In *The Origin of the Australians* (ed. R. L. Kirk & A. G. Thorne), pp. 113–126. Canberra: Australian Institute of Aboriginal Studies.

Penrose, L.S. 1954 Distance, size and shape. *Ann. Eugenics* **18**, 337–343.

Stringer, C.B. 1974 Population relationships of later Pleistocene hominids; a multivariate study of available crania. *J. archaeol. Sci.* **1**, 317–342.

Stringer, C.B. 1979 A reevaluation of the fossil human calvaria from Singa, Sudan. *Bull. Br. Mus. nat. Hist. (Geol.)* **32**, 77–83.

Stringer, C.B. 1992 Replacement, continuity, and the origin of *Homo sapiens*. In *Continuity or replacement: controversies in Homo sapiens evolution*. (ed. G. Bräuer & F. H. Smith), pp. 9–24. Rotterdam: Balkema.

Stringer, C.B. & Andrews, P., 1988 Genetic and fossil evidence for the origin of modern humans. *Science, Wash.* **239**, 1263–1268.

Trinkaus, E. 1983 *The Shanidar Neandertals*. New York: Academic Press.

Wolpoff, M.H. 1989 Multiregional evolution: the fossil alternative to Eden. In *The human revolution: behavioural and biological perspectives on the origins of modern humans*, Vol. I (ed. P. Mellars & C. B. Stringer), pp. 62–108. Edinburgh University Press.

Wolpoff, M.H., Wu, Z. & Thorne, A.G. 1984 Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from east Asia. In *The origins of modern humans* (ed. F. H. Smith & F. Spencer), pp. 411–83. New York, Liss.

Wu, X.Z. 1981 A well preserved cranium of an archaic type of early *Homo sapiens* from Dali, China. *Scientia Sin.* **24**, 530–539.