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SOME ASPECTS OF CRANIAL SIZE AND SHAPE, AND THEIR VARIATION AMONG LATER PLEISTOCENE HOMINIDS

ABSTRACT: *This paper investigates allometric relationships in later Pleistocene fossil humans using geometric morphometrics. The purpose is to re-evaluate variation of cranial size and shape and to differentiate pure shape change from size-induced trends. Cartesian coordinates were collected from 63 fossil specimens, mostly originals, as well as from a large modern sample. Based on Bookstein's relative warps analysis (Bookstein 1991, Rohlf 1993), shape variation was examined and related to centroid size. Results confirm on the one hand strong affinities between Near-Eastern Middle Palaeolithic humans and clearly modern populations, and reveal on the other a common archaic vault shape among the Neanderthals and archaic *Homo sapiens*. The role of allometric phenomena for facial morphology is also discussed. It is concluded that evidence for a gradual evolution towards modern *Homo sapiens* in Africa (Bräuer 1984) is poor.*

KEY WORDS: *Modern human origins – Cranial size and shape – Allometry – Geometric morphometrics*

INTRODUCTION

Cranial morphology still remains of major interest for the assessment of the evolutionary status of fossils, and numerous authors have stressed the importance of separating shape differences from those related to size (Bräuer 1984, Relethford 1984, Kidder *et al.* 1992, Aiello 1993). Recent advances in the field of morphometrics have given rise to a new approach that is summarized as "geometric morphometrics" (Bookstein 1991, Rohlf, Marcus 1993). It is claimed to be more powerful since it takes into account the geometry of the object under study (Rohlf, Marcus 1993) and produces a pictorial result of shape differences, making the morphological interpretation of statistics easier.

Within the background of the modern human origins debate, this paper attempts to improve knowledge of variation in cranial size and shape among later Pleistocene hominids from Europe, the Near East and Africa. Since opposing models on the origin of modern *Homo sapiens*

have been for a long time assessed by traditional multivariate morphometrics (e.g. Hemmer 1971, Bräuer 1984, Habgood, Walker 1986, Henke 1989, Corruccini 1992, Stringer 1994), we assume that size differences between fossil specimens dominate these models, whereas shape variation is insufficiently known. Therefore, it can be expected that the application of geometric morphometrics results in a re-evaluation of the origin and dispersal of the modern cranial form.

MATERIAL AND METHODS

In this study, we concentrate on cranial affinities between European, Near Eastern and African hominids during the later Pleistocene. The main fossil sample ($n=63$, cf. Table 1) includes crania assigned to archaic *Homo sapiens*, "classic" Neanderthals and Pre-Neanderthals, as well as to anatomically modern *Homo sapiens* from the Middle and Upper Palaeolithic. For exploratory purpose, two Asian

TABLE 1. Composition of the fossil and modern samples.

Fossil group	N	Specimens (the * designates casts)
<i>Homo erectus</i>	2	Sangiran 2 et 4
Archaic <i>Homo sapiens</i>	7	Eliye Springs*, Kabwe, LH18*, Ndutu*, Omo 2*, Singa, Zuttiyeh
Pre-Neanderthals	6	Biache 1, Forbes' Quarry, Saccopastore 1 et 2, Swanscombe, Tabun 1
"Classic" Neanderthals	8	La Chapelle-aux-Saints, La Ferrassie 1, Guattari 1, Neandertal 1, La Quina H5, Saint-Césaire, Amud 1, Shanidar 1*
Middle Pal. anat. modern <i>Homo sapiens</i>	6	Qafzeh 6 and 9, Skhul 4, 5 and 9, Omo 1
Upper Pal. and Epipal. <i>Homo sapiens</i>	34	
Modern <i>Homo sapiens</i>	210	Rumanians (n=27), Tasmanians (n=34), Melanesians (n=45), Africans (n=50), Japanese (n=54)
Total	273	

Homo erectus have also been included. All data were collected from original specimens, except for 6. A large representative sample of modern humans (n = 210) has been used to compare fossil variation with that seen today.

A basic photogrammetric setup has been used to ascertain raw data acquisition as far as fossil specimens are concerned, and outline drawings for the modern samples (cf. Frieß 1997, 1998 for technical details).

Cartesian coordinates have been recorded from the computer screen using tpsdig (Rohlf 1996). The photographic record has been tested by comparing a series of direct measurements with the same made on the screen. The mean difference between the two measurement series was less than 1 mm (Frieß 1997, 1998). This difference was statistically not significant, hence the raw data can be considered as being reliable.

Cranial shape was assessed by a series of 6 to 17 coordinate pairs (depending on the state of preservation) and recorded for each specimen in the lateral view. These landmarks mainly correspond to standard craniometric points, although few type II and III landmarks (Bookstein 1991) had to be used in order to describe the cranial vault. The morphometric analyses were performed on several fossil datasets, representing various landmark configurations and covering shape features of the vault, the face, as well as the frontal and occipital portions. In this paper, we will present analyses of the vault and the face.

As a global size variable, centroid size was calculated for each specimen using GRF-ND (Slice 1994). Shape variation of the samples was assessed by Bookstein's "relative warps analysis" using Rohlf's tpsrelw software (Rohlf 1997a). Relative warps are a principal components analysis of shape variation based on the procrustes distance between each specimen and the mean or consensus

configuration of landmarks. The principal components of shape variation in a given population can be shown as deviations from the consensus using cartesian transformation grids by calculating an interpolation function, the thin-plate spline. Hence, as a main difference with the basic thin-plate spline analysis (Bookstein 1991, Yaroeh 1996), the emphasis will be laid on within-group variation and not on the comparison of individuals.

Furthermore, based on the relationship between shape components and centroid size, allometry is analysed a posteriori. Here, we used regression and correlation to examine whether centroid size has any influence on shape components. The splines for visualizing allometries by means of regression were calculated using tpsreg (Rohlf 1997b). Statistica (version 5.1) was used for all statistical computations.

RESULTS

Variation in size

Analysis of variance (Anova) in modern human populations apparently indicates that size varies both with regard to sex and geographic origin, the latter being statistically dominant over sexual dimorphism. However, due to the relatively weak female sample size, sexual dimorphism cannot be definitely proven (cf. Table 2).

Mean differences with regard to sex and geographic origin are all significant at $p < 0.001$.

Between-group differences of phylogenetic units and chronological subdivisions reveal the existence of 3 major assemblages in terms of vault size, with *Homo erectus* showing the least size, followed by Pre-Neanderthals and finally by Neanderthals, archaic and anatomically modern

TABLE 2. Comparison of centroid size in extant humans. Mean differences with regard to sex and geographic origin are all significant at $p < 0.001$.

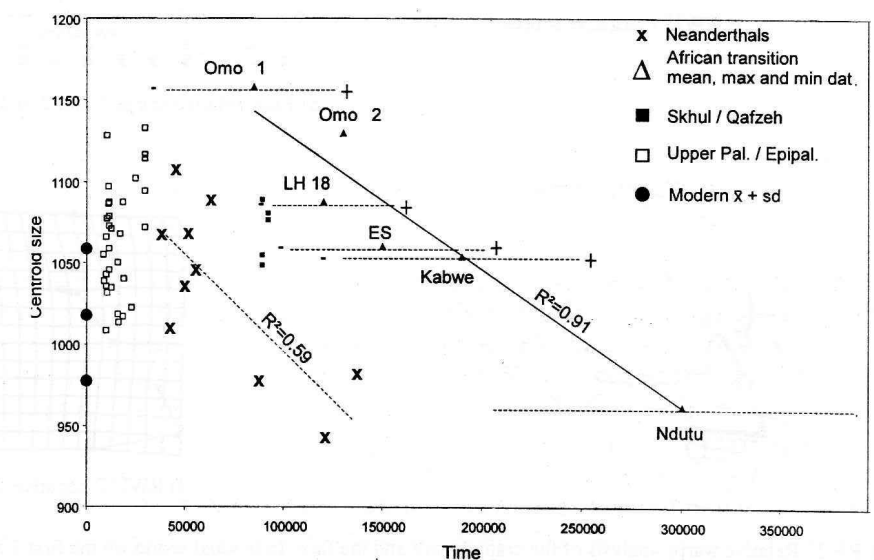
	Japanese	Melanesians	Tasmanians	Rumanians	Africans	♂ total	♀ total
Vault							
\bar{x}	1022.47	1021.87	1016.48	969.92	1036.61	1026.40	980.67
σ	36.43	33.53	39.92	31.58	35.88	37.15	38.37
N	54	45	34	27	50	122	34
Face							
\bar{x}	505.37	507.58	493.81	478.85	496.99	501.52	478
σ	17.61	20.80	29.62	20.56	22.58	22.94	22.96
N	52	45	22	20	49	112	24

TABLE 3. Summary statistics for vault size in fossil hominids.

Group	HE (Sang 2)	PN	aHS	N	amHS	late UP	early UP
N	1	3	4	7	8	28	4
\bar{x}	899.78	967.67	1060.46	1060.78	1075.11	1061.66	1082.97
σ		20.82	69.09	32.75	39.30	33.18	41.23
Min		943.72	966.72	1010.63	1028.21	1008.12	1022.37
Max		981.45	1129.50	1107.68	1159.67	1132.56	1113.97

TABLE 4. Summary statistics for facial size in fossil hominids.

Group	late UP	early UP	am HS	PN	N	a HS (Kabwe)
N	21	3	5	3	5	1
\bar{x}	500.25	516.70	559.22	576.54	615.30	629.50
σ	21.86	18.85	28.96	26.01	26.08	
Min	464.22	495.09	524.20	548.66	584.56	
Max	543.37	529.76	594.05	600.15	654.16	

FIGURE 1. The evolution of global vault size, based on presumed absolute age estimations of later Pleistocene hominids. Note the linear increase in both archaic *Homo sapiens* and the Neanderthal lineage.

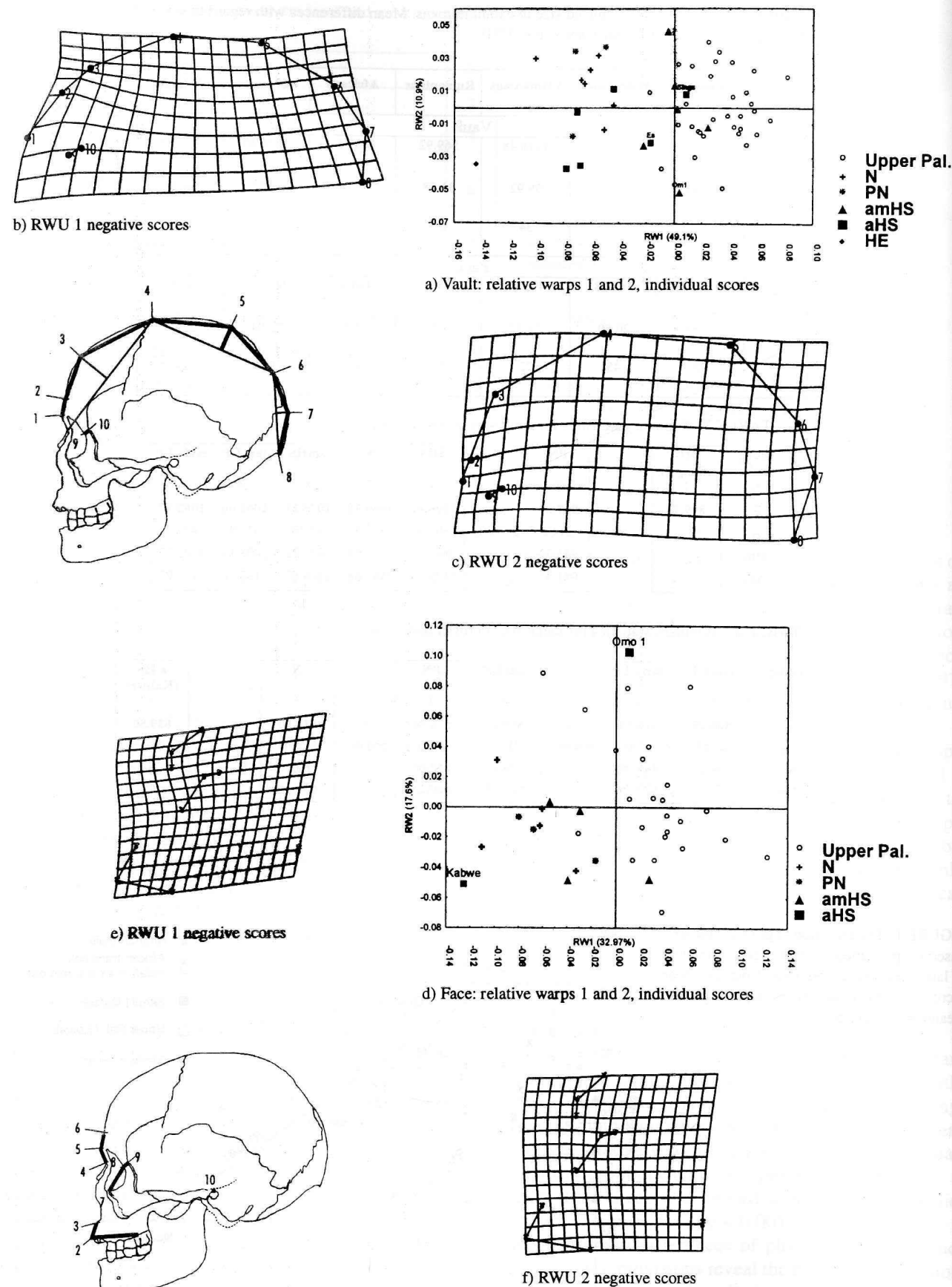


FIGURE 2. Relative warps analysis of the cranial vault and the face. Individual scores on the first 2 axes and the thin-plate splines associated with negative scores.

TABLE 5. Summary statistics of the relationship between centroid size and shape variables (partial warps) for the vault and the face of modern humans.

Analysis	Multiple regression				Multivariate test			
	R ²	F	df 1, 2	p	Wilks' Lambda	Fs	df 1, 2	p
Cranial vault	0.17	2.51	16, 193	<0.05	0.8276	2.513	16, 193	0.002
Face	0.31	5.0	16, 171	<0.01	0.6812	5.001	16, 171	2.045E-008

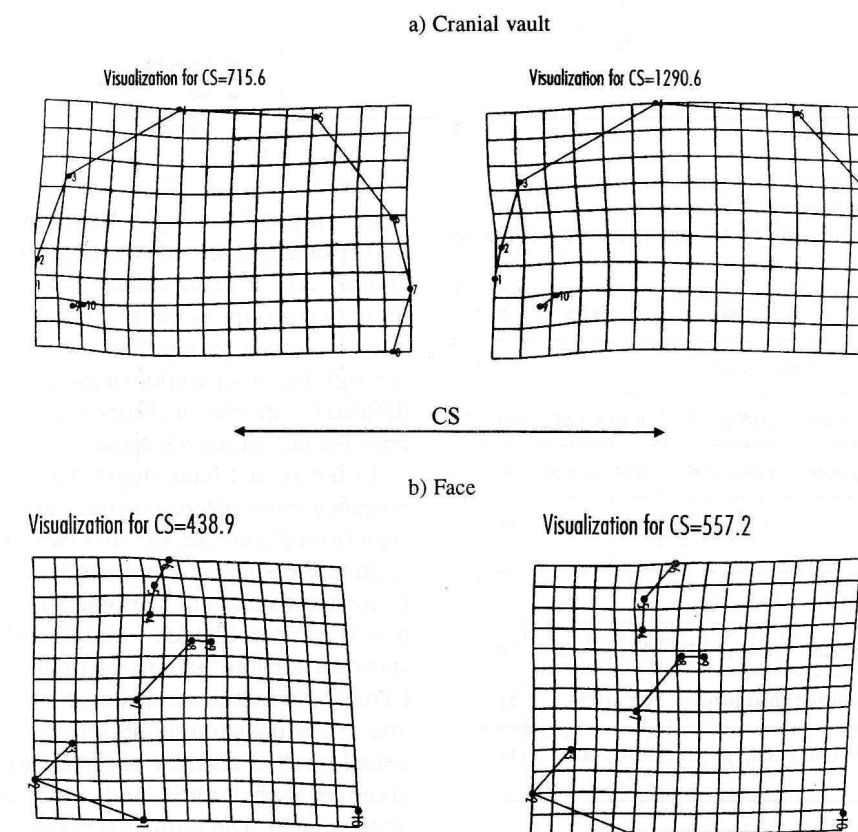


FIGURE 3. Thin-plate spline of the vault (a) and the face (b) associated with the regression of shape on centroid size (cs) in the modern sample.

Homo sapiens which all show statistically identical values for size (Table 3).

In terms of chronological or evolutionary trends, a global increase of size cannot be clearly inferred. Despite this absence of a generalized trend in the evolution of size, a strongly linear increase exists among the African transitional group as well as between Pre-Wurmian and "classic" Neanderthals, as is shown in Figure 1. Therefore, size increase should not be interpreted as a specifically modern trend.

Facial size (Table 4) unsurprisingly reveals that Neanderthals show the highest values, followed by both Pre-Neanderthals and the Skhul/Qafzeh group, whereas the Upper Palaeolithic and Epipalaeolithic show the lowest

values, identical to modern variation. In terms of diachronic variation, facial size seems to undergo a global reduction.

Variation in shape

The first principal component of shape variation (49.1%) allows for a relatively clear-cut distinction between modern and what can be called archaic vault shape. Near Eastern Middle Palaeolithic fossils from Skhul and Qafzeh show strong affinities with the modern specimens from the Upper Palaeolithic and Epipalaeolithic, while the archaic pool includes not only Neanderthals (*sensu lato*) but also most of the archaic modern humans used in this study and, at the extreme, the Sangiran 2 *Homo erectus*. The Singa and Eliye Springs archaic *Homo sapiens* fall roughly into the

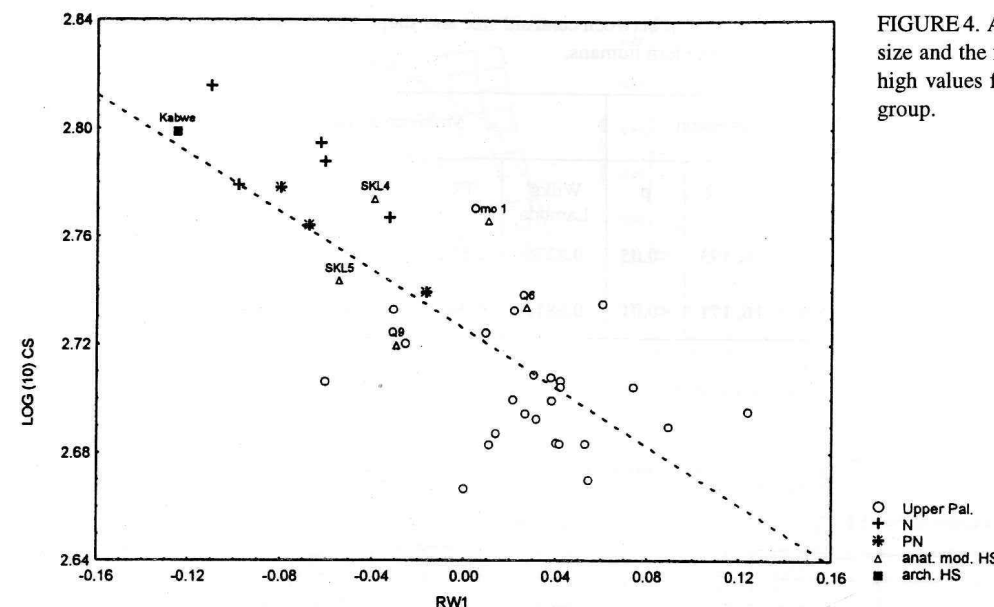


FIGURE 4. Allometric relationship between centroid size and the first relative warp of the face. Note the high values for size and shape in the Skhul/Qafzeh group.

TABLE 6. Correlation coefficients for size and relative warp scores of the vault and the face, comparing within-group and between-group variation.

	RWU1	RWU2	RWU3	N
Cranial vault				
All groups	0.35 p=0.009	-0.05 p=0.7	-0.15 p=0.26	55
Upper Pal.	-0.34 p=0.05	0.03 p=0.83	-0.007 p=0.96	32
Non-Upper Pal.	0.61 p=0.002	-0.11 p=0.63	-0.31 p=0.14	23
Face				
All groups	-0.78 p=0.000	-0.06 p=0.72	0.21 p=0.18	38
Upper Pal.	-0.23 p=0.26	0.41 p=0.05	0.2 p=0.35	24
Non-Upper Pal.	-0.72 p=0.003	-0.03 p=0.89	0.51 p=0.06	14

modern group. Figure 2b shows the thin-plate splines associated with this axis. The main shape characteristics of the archaic group lie in a relatively low and elongated vault with strong supraorbital and occipital projections. It should be recalled that in the case of the Eliye Springs cranium, whose morphology in this regard appears to be as modern as Skhul 5 and Mladeč 5, the supraorbital region is not preserved. In this study, we used the intermediate reconstruction proposed by Bräuer and Leakey (1986) who describe its morphology as definitely not modern. If one does not take into account the supraorbital portion, it can still be stated that Eliye Springs, as does Singa, shows a rather high and rounded vault according to our results, whereas Bräuer and Leakey (1986) described it as flat.

On the second axis (10.9%), European Neanderthals show distinct scores from their Near Eastern counterparts as well as from archaic *Homo sapiens*, but Omo 2 lies close

to the range of European Neanderthals. Judging from the thin-plate spline associated with this component (Figure 2d), it occurs that the main difference between these two groups is the absence of an occipital bun in the African archaic group. The subsequent axes do not reveal any significant separation or grouping relative to commonly defined taxonomic or chronological units and thus account only for individual variation.

In terms of facial shape, the relative warps analysis reveals a more heterogeneous variation. In fact, as can be seen from Figure 3a, the first two axes (50.13%) lead to a relatively distant group of archaic faces having negative factor scores on both axes, but supposedly modern human fossils, such as Qafzeh 9 and Mallaha H37 (Natufian), do show an archaic pattern of facial shape. The combined Cartesian transformations of the first two axes (Figure 2e and f) reveal a strongly uniform shape change resulting in a well marked alveolar prognathism, a relatively reduced alveolar arch length, and a strong supraorbital torus development. The midfacial portion, as represented by the *processus frontalis* of the zygomatic bone, appears to retreat relatively to the supraorbital and alveolar parts.

Size effects

According to the statistical results from the regression of shape coefficients on the centroid size in the modern sample (Table 5), the latter has a rather weak, although highly significant influence on shape of the face. Transformations associated with increasing size mainly consist of a horizontal extension accompanied by a more pronounced supraorbital profile as well as a weaker occipital convexity (Figure 3a). It is noteworthy that facial allometry leads, besides the pronounced supraorbital arch, to an increased alveolar prognathism and a shortened alveolar arch (Figure 3b).

Due to insufficient sample size, allometric relationships in fossil humans were estimated by calculating correlation

coefficients between centroid size and the individual factor scores of the relative warps analysis. For the same reason, detailed within-group analysis was not performed. As is summarized in Table 6, the only significant correlations between size and shape, i.e. the principal components (RWU), were found on each first axis, which reveals itself to be a moderate function of size in the case of the vault and highly dependent of size in the case of the facial skeleton. In both analyses, these correlations can be mainly attributed to the specimens dated prior to the Upper Palaeolithic, that is the Neanderthal lineage, and the archaic to modern *Homo sapiens* transition.

However, as far as the cranial vault is concerned, the apparent allometric relationship is widely due to the extreme position in size and shape of the Sangiran 2 specimen. Once this fossil is excluded from the analysis, no statistically significant allometry can be detected. In any case, it can be concluded from these results that the differences between modern and more archaic vault morphology can be explained, above all, by shape rather than by size. Conversely, facial shape shows a strong allometric component (Figure 4), leading to pronounced archaic features when face size increases.

DISCUSSION AND CONCLUSION

According to Kidder *et al.* (1992) it is necessary to identify the limits of variation of cranial size and shape encountered in modern populations in order to establish at what time modern cranial shape appeared during evolution. Our results indicate that the evolution of the modern cranial vault was primarily due to a shape change, whereas size increase seemed to be an unspecific trend occurring in the African transition but also in the Neanderthal lineage. When vault shape, as revealed by relative warps, is related to time, there seems to be no gradual evolution from specimens like Nduku to late archaic and anatomically modern *Homo sapiens* (Omo 1, Skhul and Qafzeh). The latter, however, fall inside the range seen in Upper Palaeolithic cranial shape, a result that supports models of a Near Eastern origin of modern humans (Vandermeersch 1981, Mann 1995). Most of the African archaic *Homo sapiens* used in this study share archaic shape features with other groups such as Neanderthals (*sensu lato*), but do not expose clearly modern cranial shape. However, they also share the same size with Neanderthals, as well as with the Skhul/Qafzeh group, and it can be concluded from this that numerous preceding studies using standard multivariate statistics, i.e. without size control (Mosimann 1970), resulted in shape description that was affected by residual size.

Two specimens considered as belonging to archaic *Homo sapiens*, Singa and Eliye Springs, revealed a position in shape space close to Upper Palaeolithic fossils. We prefer to be cautious concerning this result, because these specimens might not be suitable for comparison given the

pathology of Singa (Spoor *et al.* 1998) and the incomplete state of preservation of the supraorbital region in Eliye Springs (Bräuer, Leakey 1986). As far as the Omo 1 specimen is concerned, its modern cranial shape claimed by others (Day, Stringer 1991) is supported by our results, but as long as the fossil is lacking reliable absolute dating, it cannot be considered as the best proof of any African origin model (*cf.* Smith 1992).

Considering size only, it is interesting to note the important variation inside the Neanderthal lineage and the African transitional group. "Classic" Neanderthals can be easily differentiated from Pre-Neanderthals solely by their increased vault size, whereas their shape is merely the same. From the morphometric point of view, any evolutionary trend towards "neanderthalization" (Condemi 1992) cannot be confirmed, except in terms of increasing size. Moreover, given the sexual dimorphism of size among modern humans, the same can be expected in fossil groups, so that the observed size differences inside the Neanderthal lineage could be attributed to the fact that most Pre-Neanderthals used here are claimed to be females. Similar patterns of sexually related size variation cannot be ascertained for the African transitional group, where size range is biggest compared to the other groups used here. Explanations might be given by taxonomic considerations, or simply by the greater time range, but cannot be definitely affirmed at this state of our research.

The evolution of the face tends to show strong allometric changes of shape, in the sense that size heavily influences the expression of archaic morphological traits, i.e. strong alveolar prognathism, shortened alveolar arch length, zygomatic retreat and a heavily pronounced supraorbital torus. These features, although sometimes considered as being a Neanderthal apomorphy (Rak 1986, Trinkaus 1987), can be detected in some of the specimens that show clearly modern cranial vault shape, for example Qafzeh 9, Skhul 4 and 5 and Mallaha H37. But given the centroid size of these fossils, this morphology should be interpreted as a size dependent general plesiomorphic trait, rather than an apomorphy. This is also supported by the comparison with modern populations who reveal similar allometric shape changes in the face.

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