

13. Reliability of cranial morphology in reconstructing Neanderthal phylogeny

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Abstract

The usefulness of cranial morphology in reconstructing the phylogeny of closely related taxa is often questioned due to the possibility of convergence or parallelism and epigenetic response to the environment. However, it has been suggested that different cranial regions preserve phylogenetic information differentially. Some parts of the face and neurocranium are thought to be relatively developmentally flexible, and therefore to be subject to the epigenetic influence of the environment. Other parts are thought to be particularly responsive to selection for adaptation to local climate. The basicranium, on the other hand, and in particular the temporal bone, is thought to be largely genetically determined and has been argued to preserve a strong phylogenetic signal with little possibility of homoplasy. Here we test the hypotheses that cranial morphology is related to population history among recent humans, and that different cranial regions reflect population history and local climate differentially. Morphological distances among ten recent human populations were calculated from the face, vault and temporal bone using three-dimensional geometric morphometrics methods. The distance matrices obtained were then compared to neutral genetic distances and to climatic differences among the same or closely matched groups. Results indicated a stronger relationship of the shape of the vault and the temporal bone with neutral genetic distances, and a stronger association of facial shape with climate. Vault and temporal bone centroid sizes were associated with climate and particularly temperature; facial centroid size was associated with genetic distances. Temporal bone shape was more successful in tracking older population history than vault shape. Of the three cranial regions, it is therefore most appropriate for phylogenetic reconstructions among fossil humans. Analysis of temporal bone shape of both recent and Middle-Late Pleistocene humans showed Neanderthals to be morphologically very distant from both recent and fossil modern humans, indicating that Neanderthals represent a distinct evolutionary lineage.

Introduction

Among the major problems in phylogenetic reconstruction from skeletal morphology is the potential unreliability of morphological characters in reflecting phylogeny (among species) and population history (within species). Convergence, parallelism, reversals and epigenetic changes are often thought to overwhelmingly influence craniofacial anatomy and to erase any phylogenetic information it might have contained (see e.g., Lieberman et al., 1996; McCollum, 1999). This criticism has been leveled most recently by Collard and Wood (2000, 2001), who found that diverse cranio-dental datasets failed to reproduce molecular phylogenies in hominoids and papionins. These authors concluded that cranial morphology cannot be used to successfully reconstruct primate and human phylogenetic relationships.

This view, however, is not universally accepted, and some researchers have proposed a differential preservation of phylogenetic information in different cranial anatomical regions. Olson (1981) suggested that the basicranium is the most genetically determined and evolutionarily conservative aspect of the cranium, and as such should be highly phylogenetically informative. This view was echoed by Wood and Lieberman (2001), who also proposed that different cranial regions reflect phylogenetic information differentially. Since the basicranium develops from cartilaginous, rather than intramembranous, origin, they suggested that its development is genetically determined, so the resulting adult morphology is only minimally influenced by environmental factors. On this basis they argued that the basicranium is more phylogenetically informative and more appropriate for phylogenetic reconstruction than the facial or cranial vault regions, which are thought to be more developmentally plastic. Recent analyses of the complex three-dimensional shape of the petrous portion of the temporal bone have

provided tentative support for these hypotheses. Using three-dimensional geometric morphometrics, Harvati (2001) found that temporal bone shape tracks relationships among recent human populations better than the occipital and parietal regions of the skull. Lockwood et al. (2004) also analyzed three-dimensional temporal bone landmark coordinates to reconstruct the hominoid phylogeny, with results that closely matched the molecularly derived relationships.

Even if a cranial region reliably reflects underlying genetic variation, it will not be useful for phylogenetic reconstruction if it is particularly responsive to selection for adaptation to climate, other aspects of the local environment or behaviors. The face, in particular, has previously been linked to climatic adaptation (e.g., Coon et al., 1950; Roseman and Weaver, 2004) and to dietary and masticatory practices (e.g., Hylander, 1977; Rak, 1986; Smith, 1983), probably through a combination of epigenetic responses and genetic adaptation. The shape of the vault has also been linked to climatic adaptation (e.g., Beals, 1983; Roseman, 2004).

Here we tested the reliability of morphological evidence from three regions of the cranium – face, temporal bone and vault – in tracking population history by comparing morphological distances among recent human groups to those derived from a large number of microsatellites (neutral genetic loci, Rosenberg et al., 2002, see below). Ten globally distributed recent human groups represented in the genetic database (or their close neighbors) were also represented in our three-dimensional cranio-facial landmark database (two African, two Asian, two European, two Australasian, one Middle Eastern and one New World Arctic, see Table 1). Mahalanobis squared distance matrices (hereafter Mahalanobis D^2), corrected for unequal sample sizes, were calculated among the recent human groups based on landmark coordinates from each of the three cranial regions. The

Table 1. Morphological and genetic samples

<i>Morphological samples</i>	<i>Vault</i>	<i>Face</i>	<i>Temp.</i>	<i>Genetic samples</i>	<i>n</i>
W. African Dogon	33	32	33	Yoruba, Nigeria	25
S. African Khoi-San	30	29	30	San, Namibia	7
Australian, S. Australia	31	29	31	Papuan, New Guinea	17
Melanesian, New Britain	28	28	28	Melanesian, Bougainville	19
Italian	6	6	6	Italy	13
Greek	5	5	5	Sardinian, Italy	28
Syrian	20	16	18	Palestinian, Israel	51
Chinese, North China	20	17	19	Han, China	34
Thai	20	18	20	Cambodian	11
Inugsuk, Greenland	30	30	30	Yakut, Siberia	25
Total	223	210	220	Total	230

delta mu squared genetic distance (D_{dm}) was also calculated based on the microsatellite data to create a genetic distance matrix. The morphological distance matrices were then compared to the genetic distance matrix for the matched recent human groups using a Mantel test of matrix correspondence (Mantel, 1967; Smouse et al., 1986; Sokal and Rohlf, 1995). Importantly, the Mantel Test compares pairwise distances, so it does not assume a tree-like model for recent human population history. The morphological distance matrices were also compared to latitude, mean temperature and mean vapor pressure distance matrices for the location of origin of each recent human sample, in order to test the hypothesis that the morphology of these cranial regions reflects climatic adaptation.

We hypothesized that (a) cranial morphology reflects population history (as reflected by neutral genetic distances) in recent humans, (b) the temporal bone reflects population history best, and (c) the face also reflects adaptation to climate. Based on these hypotheses, we predicted that the morphological distances between our recent human samples would be significantly correlated with the genetic distances between the same groups; that the temporal bone distances would show the highest correlation coefficients with the genetic distances; and that the facial distances

would also be significantly correlated with climatic differences. Finally, the implications of the recent human analysis were applied to the problem of Neanderthal phylogenetic relationships.

Materials and Methods

SAMPLES

This analysis included ten globally distributed recent human populations for which both morphological and genetic data were available. Exact matching of the morphological and genetic samples was not always possible due to the limitations of both the morphological and the genetic datasets. Therefore, matching between populations that were not identical but instead relatively close geographic neighbors was allowed in order to preserve a meaningful number of samples in the analysis (Table 1). The matching was loosest in two cases. The Australian morphological sample was not represented in the genetic dataset and was matched with a sample from New Guinea, which is geographically the closest group included in the genetic samples. The Greenland Inugsuk morphological sample was matched with a Siberian population in the genetic dataset. These two samples match closely in terms of latitude and climatic conditions. Furthermore,

previous work has shown that Siberian and Mongolian populations approach New World populations, including Inuit groups, in their cranial morphology (Howells, 1989: 66–79).

DATA

Morphological Data

Morphological data were collected in the form of three-dimensional coordinates of osteometric landmarks on the cranium using a portable Microscribe 3DX digitizer and following the definitions of Howells (1973). All measurements were collected by Harvati. In geometric morphometrics landmarks are defined as homologous points that can be reliably and repeatedly located in all specimens under study (Bookstein, 1990; Valeri et al., 1998). Here they mostly represented standard osteometric points. Other landmarks were also included (their definitions are given in Table 2). The temporal bone dataset comprised thirteen landmarks from the right temporal bone; the facial dataset also comprised thirteen landmarks, both bilateral and midline; finally the vault dataset included eight bilateral and midline landmarks (Table 2). The three datasets overlapped minimally. Asterion was included in both the temporal bone and vault datasets, and glabella in both the vault and the face datasets. Where fossil specimens were included, minimal reconstruction was allowed during data collection for specimens with very little damage in a particular area of interest. Additionally, landmarks preserved only on one side were reconstructed by least-squares superimposing the specimens with their reflections using the Morpheus geometric morphometric software package (Slice, 1994–1999). The coordinates for each of the missing landmarks were then substituted from the fitted homologous landmark in the reflection.

The landmark coordinate data were processed using Generalized Procrustes Analysis, which superimposes the landmark configurations of the specimens and scales

Table 2. Landmarks included in the three morphological datasets

Temporal bone landmarks

1. Asterion, 2. Stylomastoid foramen, 3. Most medial point of the jugular fossa, 4. Most lateral point of the jugular fossa, 5. Lateral origin of the petro-tympanic crest, 6. Most medial point of the petro-tympanic crest at the level of the carotid canal, 7. Porion, 8. Auriculare, 9. Parietal Notch, 10. Mastoidale, 11. Most inferior point on the juxtamastoid crest (following Hublin, 1978), 12. Deepest point of the lateral margin of the articular eminence, 15. Most inferior point on the entoglenoid process

Vault landmarks

1. Inion, 2. Lambda, 3. Bregma, 4. Glabella, 5–6. Asterion right and left, 7–8. Anterior pterion right and left

Facial landmarks

1. Glabella, 2. Nasion, 3. Prosthion, 4–5. Frontomale temporale right and left, 6–7. Infraorbital foramen right and left, 8–9. Suture between the temporal and zygomatic bones on the superior aspect of the zygomatic process, right and left, 10–11. Suture between palatine pyramidal process and pterygoid plate of the sphenoid, right and left, 12–13. Malar root at alveolus, right and left.

them for size, so that the differences they exhibit are due to “shape” (Rohlf, 1990; Rohlf and Marcus, 1993; Dryden and Mardia, 1998; O’Higgins and Jones, 1998). Multivariate methods based on Procrustes-aligned specimens have been shown to have the highest statistical power among alternative geometric morphometric approaches (Rohlf, 2000). Superimposition was performed using the software Morpheus (Slice, 1994–1999). Specifically, specimen configurations were translated to a common origin, scaled to unit centroid size (the square root of the sum of squared distances of all landmarks to the centroid of the object), the measure of size used here, and rotated according to a least-squared best-fit criterion. Procrustes superimposition leads to points that lie in a hemispherical variant of Kendall’s shape space (Kendall, 1984; Rohlf, 1999; Slice, 2001). The present analysis was undertaken on differences among populations in the superimposed coordinates themselves.

Because size is an important aspect of morphology which can be both phylogenetically informative and related to environmental factors (e.g., Shea et al., 1993), an analysis of centroid size of the three cranial regions examined was also undertaken. Centroid size, which was removed from the coordinate data during Procrustes superimposition, was analyzed separately for its relationship with neutral genetics and climatic factors.

Genetic Data

The genetic data consisted of an expanded set of the data analyzed by Rosenberg et al. (2002) and Zhivotovsky et al. (2003). They comprised 784 microsatellite loci from 230 individuals representing 10 populations, which closely matched the populations for the morphological datasets (Table 1). The individuals in these populations are a subset of those used in the Human Genome Diversity Project–CEPH cell line panel (Cann et al., 2002). The samples were typed by the Mammalian Genotyping Service (Marshfield panel 10–52; <http://www2.marshfield-clinic.org/RESEARCH/GENETICS>).

Climate Data

For the climate data, we first estimated approximate latitudes and longitudes for the populations in the study. Then, based on the latitude and longitude, we were able to obtain estimates of mean yearly temperature and mean yearly vapor pressure (a proxy for humidity) from the global climate dataset published by New et al. (1999, 2000). The global climate dataset was constructed by interpolating observations collected at thousands of climate stations spread throughout the world to obtain estimates for each cell in a 0.5° latitude by 0.5° longitude grid (New et al., 1999, 2000). These two variables, as well as latitude, were used here as climatic indicators.

ANALYSES

Morphology

The morphological distances among the modern human samples were estimated using Mahalanobis D^2 . This method represents the morphological variation among groups, scaled by the pooled within-group variation and accounting for covariance between variables (Neff and Marcus, 1980). Unlike other distance measures used with landmark data, such as Procrustes distance, Mahalanobis D^2 accounts for the covariation among landmark coordinates that is pervasive in biological datasets by weighting the distance by the inverse of the pooled within-group covariance matrix (see also Klingenberg and Monteiro, 2005). Additionally, by standardizing by the pooled within-group variation, Mahalanobis D^2 can be directly related to expected rates of morphological divergence predicted by population genetic theory for neutral evolution. This is because the neutral rate of morphological evolution is expected to be proportional to the within-population variation (Lynch, 1990).

For each of the three morphological datasets a principal components analysis was conducted on the superimposed coordinates. The principal components representing approximately 90% of the total variance were used as variables in calculating a Mahalanobis D^2 matrix of the recent human samples for each cranial region. Because the morphological samples used were not of equal size, a correction for unequal sample sizes was used (Marcus, 1993).

Centroid size was analyzed separately from shape information, and separately for each cranial region. The mean centroid sizes for the ten population samples were calculated. A squared distance matrix was created by calculating the squared difference in mean centroid size for all possible population pairs.

Genetics (Genetic Distance)

The genetic distances among the samples were calculated using the delta mu squared

(*Ddm*) statistic (Goldstein et al., 1995b). This distance measure is specifically designed for microsatellites, because it takes into account details of their step-wise mutation process. Under mutation-drift equilibrium, *Ddm* is expected to be linear with time, with a slope equal to twice the neutral mutation rate (Goldstein et al., 1995a, b). *Ddm* is a suitable distance for comparison with morphological Mahalanobis D^2 , because both these distances measure the squared pairwise differences between populations. Other genetic distances such as F_{ST} , or the R_{ST} for microsatellites (Slatkin, 1995), measure variation both among and within the population pairs and are thus not directly comparable to morphological Mahalanobis D^2 . The latter does take into account within population variation, but this is pooled-across all the populations in the sample, so there is a constant scaling of all the pairwise population comparisons.

Comparisons

The distance matrices were compared using a Mantel test of matrix correlation with NTSYSpc (Rohlf 1986–2000). This test measures the degree of relationship between two distance matrices. A permutation test is performed to assess if the relationship between the two matrices is significantly different from no relationship. Traditional tests of significance do not apply, because the matrix entries are not independent of each other. For the permutation test, one matrix is held rigid while the other is randomly permuted many times (here 10,000 times). The distribution of the matrix associations generated by the permutations can be used to construct a null distribution for tests of significance. It is also possible to compare three matrices for a partial Mantel test, which is analogous to a partial correlation among three variables (Mantel, 1967; Smouse et al., 1986; Sokal and Rohlf, 1995).

To examine the distance matrices in more detail, we conducted metric multidimensional

scaling on the genetic and morphological distances using MATLAB (The MathWorks, Natick, MA). Multidimensional scaling arranges “objects” (in our case populations) in a space with a particular number of dimensions (in our case 2), so as to reproduce the observed distances as closely as possible in a low-dimensional coordinate system (Johnson and Wichern, 1998). This allowed us to explore the structure of distance matrices from the different datasets on two-dimensional plots. Unlike tree-based methods of distance comparison, the use of multidimensional scaling does not assume a bifurcating branching pattern, which makes this method more appropriate for comparisons among recent human populations where both bifurcations and reticulation may have occurred.

Results

The results of the Mantel matrix correlation tests are reported in Table 3. Out of the three cranial shape datasets, the vault and the temporal bone shape distances were significantly associated with neutral genetic distances, although none of the correlations were very strong. Contrary to our predictions, the vault distances showed a stronger relationship to genetic distances than did the temporal bone distances. The weakest correlation with the genetic distance matrix, not reaching statistical significance, was found with the facial shape distance matrix. Neither temporal bone nor vault distances were correlated with any of the three climatic variables. As predicted, facial distances showed a relationship with climatic factors. They were significantly correlated with both latitude and mean temperature, but not with mean vapor pressure. The fact that facial distances were significantly correlated with both latitude and temperature is not surprising given that latitude and temperature are strongly associated with each other (Mantel test $r = 0.91$, $p = 0.001$). The relationship between

distances based on facial shape and genetic distances, however, was found to be stronger and statistically significant once the effects of latitude or temperature were adjusted for in a partial Mantel test (Table 3).

The results of the analysis of centroid size differed from the shape analyses. Although distances based on facial shape were not strongly associated with neutral genetic distances, facial size was found to be significantly correlated with the genetics distance

matrix. It also did not show a relationship with any of the climatic variables. Facial size remained significantly associated with genetics even when the effects of the three climatic variables were adjusted for in partial Mantel tests. Temporal bone and vault centroid sizes were not found to be associated with genetic distances, but instead showed a significant relationship with climate. These results were the inverse of what was found in the shape analysis. Vault centroid size was significantly

Table 3. Mantel test comparisons results. Statistically significant values are indicated by asterisks

<i>Mantel tests</i>	<i>Genetics</i>	<i>Latitude</i>	<i>Mean Temperature</i>	<i>Mean Vapor Pressure</i>
Facial Shape	$r = 0.2988^*$ $p = 0.0904^*$	$r = 0.4556^*$ $p = 0.0148^*$	$r = 0.4515^*$ $p = 0.0151^*$	$r = 0.0116$ $p = 0.4577$
Temporal Bone Shape	$r = 0.4879^*$ $p = 0.0266^*$	$r = 0.0335$ $p = 0.3535$	$r = 0.1079$ $p = 0.2400$	$r = -0.0890$ $p = 0.6021$
Vault Shape	$r = 0.5512^*$ $p = 0.0012^*$	$r = 0.0137$ $p = 0.4712$	$r = 0.0281$ $p = 0.4468$	$r = 0.0789$ $p = 0.3306$
Face Centroid Size	$r = 0.5254^*$ $p = 0.0270^*$	$r = 0.0703$ $p = 0.2455$	$r = 0.1459$ $p = 0.1526$	$r = -0.1199$ $p = 0.5746$
Temporal Bone Centroid Size	$r = 0.2857$ $p = 0.1211$	$r = 0.3627$ $p = 0.0793$	$r = 0.5076^*$ $p = 0.0410^*$	$r = 0.0315$ $p = 0.3587$
Vault Centroid Size	$r = -0.0672$ $p = 0.5698$	$r = 0.5286^*$ $p = 0.0154^*$	$r = 0.6612^*$ $p = 0.0051^*$	$r = 0.2451$ $p = 0.1050$
<i>Partial Mantel tests</i>		<i>Adjusted for Latitude</i>	<i>Adjusted for Mean Temperature</i>	<i>Adjusted for Mean Vapor Pressure</i>
Facial Shape vs. Genetics		$r = 0.3836^*$ $p = 0.0316^*$	$r = 0.4098^*$ $p = 0.0169^*$	$r = 0.3060$ $p = 0.0838$
Temporal Bone Shape vs. Genetics		$r = 0.4932^*$ $p = 0.0236^*$	$r = 0.5110^*$ $p = 0.0175^*$	$r = 0.4816^*$ $p = 0.0216^*$
Vault Shape vs. Genetics		$r = 0.5548^*$ $p = 0.0011^*$	$r = 0.5609^*$ $p = 0.0011^*$	$r = 0.5768^*$ $p = 0.0006^*$
Face Centroid Size vs. Genetics		$r = 0.5353^*$ $p = 0.0216^*$	$r = 0.5573^*$ $p = 0.0167^*$	$r = 0.5159^*$ $p = 0.0213^*$
Temporal Bone Centroid Size vs. Genetics		$r = 0.3432^*$ $p = 0.0282^*$	$r = 0.4182^*$ $p = 0.0067^*$	$r = 0.2964$ $p = 0.0998$
Vault Centroid Size vs. Genetics		$r = -0.0228$ $p = 0.5798$	$r = 0.0349$ $p = 0.4008$	$r = -0.0240$ $p = 0.5264$

correlated with temperature and latitude, while temporal bone centroid size was significantly correlated with temperature only. When the effects of latitude and temperature (but not vapor pressure) were adjusted for in partial Mantel tests, however, temporal bone size also became significantly correlated with the genetic distances.

In order to compare the pattern of genetic distances to those shown by the three morphological distance datasets, multidimensional scaling plots were made for each of the distance matrices (Figure 1). Mean centroid sizes were also plotted by group for each of the three cranial regions (Figure 2). All of these were compared to the genetics multidimensional scaling plot (Figure 1a). The genetic distances showed a strong differentiation of the two African groups from the rest of the modern human populations along the first axis, with the South African Khoi-San being the most distinct population. The Eurasian samples fell close to each other on both axes, with two tight clusters representing the European/Near Eastern samples and the Asian populations, grouping also with the Greenland sample (matched with the Siberian group in the genetics dataset). Australians (matched with New Guineans) and Melanesians clustered together less tightly, and separated along the second axis from the Eurasian/New World samples, but not from the African groups.

The multidimensional scaling plot of facial shape showed a different pattern (Figure 1b). The first axis here clearly separated the two African and the Australian and Melanesian samples from the remaining groups, with the Greenland population further differentiated along the second axis. This pattern differed considerably from that shown by the genetic distances. It was consistent with a climatic influence on facial shape, as was found in the Mantel tests. Populations from tropical and subtropical climates (as defined by annual maximum and minimum temperatures) were found on the left of the first axis, while temperate

– cold climate groups (again defined by annual maximum and minimum temperatures) were found on the right side. The only exception was the Thai group, a tropical population, which showed an intermediate position, but closest to the Chinese sample. It is noteworthy that the present population of Thailand, which this sample represents, migrated south from China very recently in historical times. Facial shape therefore seems to reflect a combination of climate and population history.

The temporal bone multidimensional scaling plot (Figure 1c) separated the two African samples from all other groups along the first axis, with the Khoi-San being the most distinct. These features were consistent with the major African vs. non-African dichotomy shown by the genetic distances. However, temporal bone shape did not produce the same clusters within the remaining populations as found in the genetic distances: the Near Eastern sample here grouped with the Asian populations rather than the Europeans; Australians and Melanesians grouped together but were not separate from the Eurasian samples; and the Greenland Inugsuk were distinct from all other groups along the second axis, rather than clustering with the Asian samples. Temporal bone shape, therefore, successfully reflected the deepest separation found in the genetic distances, that between Africans and non-Africans, but not more recent population history.

The multidimensional scaling plot of the vault shape distances (Figure 1d) showed yet another pattern. Unlike the genetic pattern, the two African groups did not separate from the other samples, although the West African Dogon were most distinct along the second axis. Vault shape, however, did separate Australians and Melanesians from the Eurasian samples. It also showed the European and Near Eastern groups clustering tightly, and the Asian and Greenland samples falling relatively close to each other. Vault shape, therefore, unlike the temporal bone, appeared to reflect recent

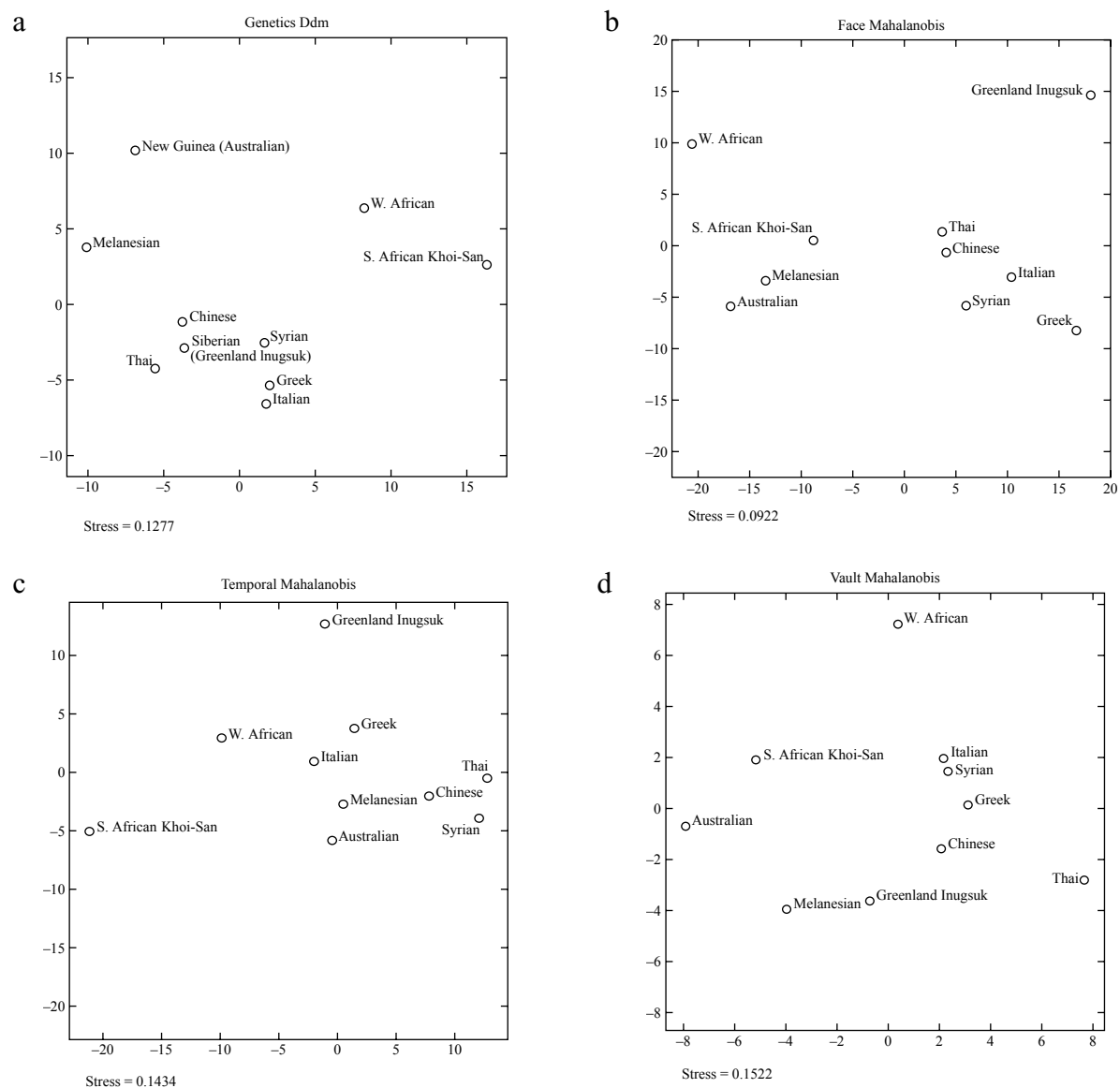


Figure 1. Multidimensional scaling plots of (a) genetic distance, in parenthesis shown matched groups from the morphological datasets, (b) face shape Mahalanobis D^2 , (c) temporal bone shape Mahalanobis D^2 , and (d) vault shape Mahalanobis D^2 among recent human samples.

population history among modern humans, rather than older events.

Face mean centroid size differences were found to be strongly correlated with genetic distances. When plotted by population (Figure 2a), they showed a separation between the two African samples and all other groups, with the Khoi-San being the smallest sample. West Africans were the second smallest, but

very close to the other samples. The remaining samples were not differentiated in a meaningful way. Since the Khoi-San were by far the sample with the smallest faces, they could be driving the association. Only with the addition of other small populations will it be possible to answer this question. Temporal bone centroid size again showed the African groups as the smallest, but less different than the others,

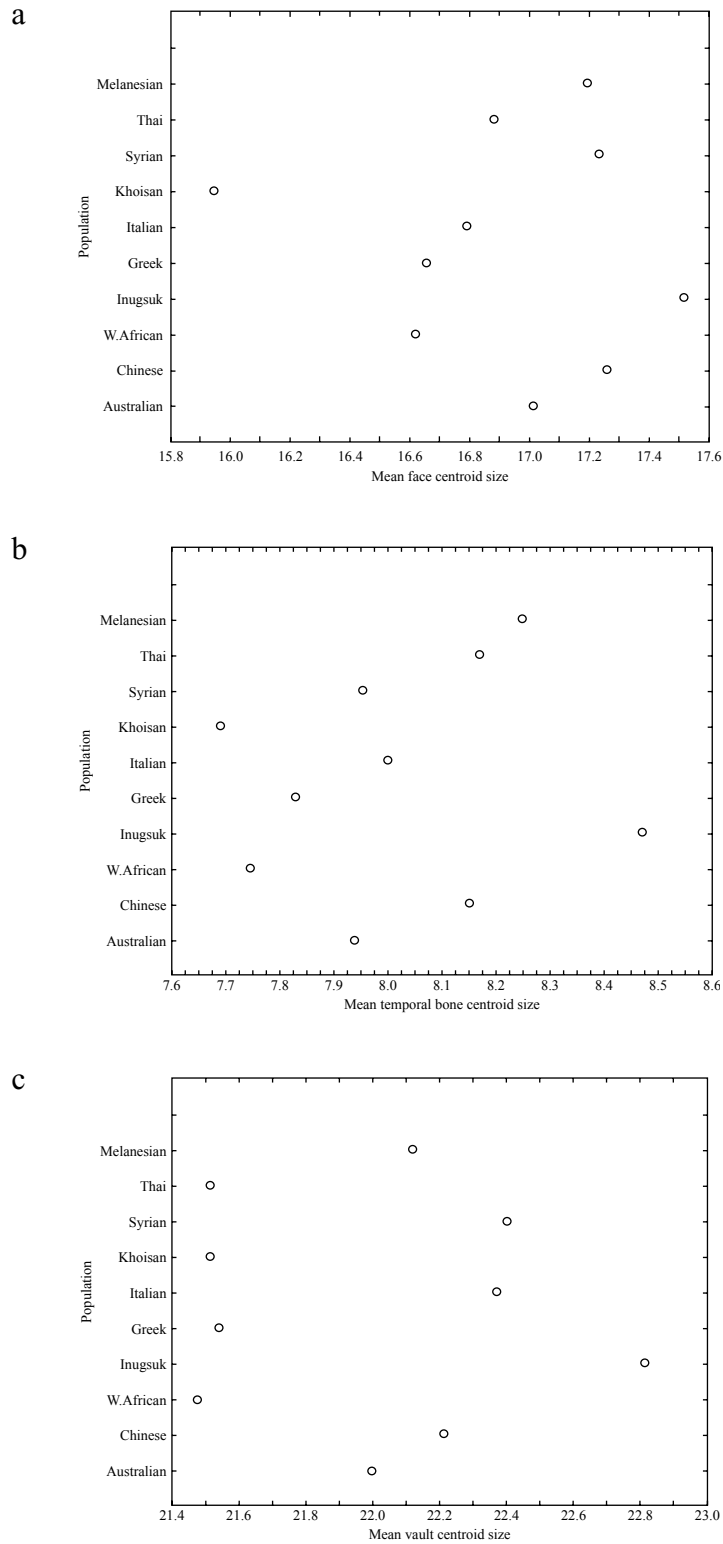


Figure 2. Mean centroid sizes for (a) face, (b) temporal bone and (c) vault, plotted by population.

and the Greenland sample as largest, with the remaining groups intermediate (Figure 2b). Vault centroid size also showed the Greenland group being the largest, and the African, Thai and Greek samples the smallest (Figure 2c).

Discussion

The results of this analysis agreed with the predictions of our hypotheses in most cases, but also differed in some important ways. As predicted, facial shape distances showed the weakest relationship to genetics, and were instead more strongly associated with climate. When the effects of climate were adjusted for, however, the relationship between facial shape and genetics became stronger and statistically significant, suggesting an interaction of genetic and climatic factors influencing human facial form. Vault and temporal bone shape distances were both significantly correlated with genetic distances, but, contrary to predictions, the highest association was with vault shape. Vault shape differences among recent human groups, however, showed a different pattern from that found in the temporal bone shape, suggesting that these two cranial regions reflect different aspects of population history. The analysis of the vault shape was most successful in tracking recent events among recent humans, grouping together populations such as the Europeans and Near Easterners, and the Chinese and Thai. It failed to show the deep split between African and non-African groups observed in the genetic data. This major dichotomy was shown in the temporal bone shape analysis, which, however, was less successful in grouping samples with a recent common history. Centroid size for the three cranial regions was found to be correlated with genetic distances in the face, and in the temporal bone after accounting for the effects of climate. This result may be driven by the small size of the Khoi-San, one of the two African groups included here and

the smallest group in the recent human sample. However, it may also suggest that size may be phylogenetically informative and should not be *a priori* ignored in phylogenetic analyses. An extension of the present analysis to include additional small-bodied recent human populations is necessary to confirm this result. Finally, vault and temporal bone centroid size were found to be related to temperature (and the former also to latitude). This finding is consistent with previous studies indicating that cold-climate populations show larger brains on average than warm-climate groups among recent humans (Beals et al., 1983). Again, an extension of this analysis to include more cold-climate populations would be necessary to confirm this finding.

These results suggest that the temporal bone morphology tracks older events in population history more faithfully, while the vault reflects more recent affinities. This interpretation is consistent with the suggestion of greater developmental stability for the basicranium, which would necessarily result in slower change of this region's morphology, and for greater developmental plasticity for the vault, which would enable faster rates of morphological change (Wood and Lieberman, 2001). It is also consistent with the successful recovery of the hominoid molecular phylogeny using temporal bone three-dimensional shape (Lockwood et al., 2004). We therefore tentatively interpret our findings as indicating that temporal bone shape preserves old population history/phylogenetic signals, while vault shape preserves a more recent signal. The temporal bone would, therefore, appear to be the most appropriate of these three cranial regions for use in reconstructions of the phylogenetic relationships of Neanderthals and Pleistocene humans.

In light of this interpretation, the analysis of temporal bone shape was repeated with fossil human specimens from Europe, Africa and the Near East dated to the Middle and Late Pleistocene (see also Harvati, 2002, 2003a,

2004). The fossil samples included fourteen Neanderthal and seven Upper Paleolithic specimens, as well as Kabwe, Skhul 5 and Qafzeh 9 (Table 4). Mahalanobis squared distances were calculated among these samples, and are plotted in a multidimensional scaling plot in Figure 3. In this plot, Neanderthals fell on one end of the x-axis and recent humans on the opposite end, reflecting the great difference in temporal bone shape between these two hominin taxa. The Upper Paleolithic sample was very close to the recent human groups. Kabwe was placed close to the center, as might be expected for an older specimen that may represent the common ancestral taxon to both

Neanderthals and modern humans. This finding is in agreement with previous results of both temporal bone and overall morphology (e.g., Stringer, 1974; Harvati, 2002, 2003a, b, 2004). The position of the two early anatomically modern human specimens was more difficult to interpret. While this sample showed a very small morphological distance to the Upper Paleolithic specimens, its distances to the recent human groups were as great as that to the Neanderthals and Kabwe. These large distances may be due to the very small size of this sample, and may reflect the increased influence of error and deformation on small samples of fossils. Similar distances have been

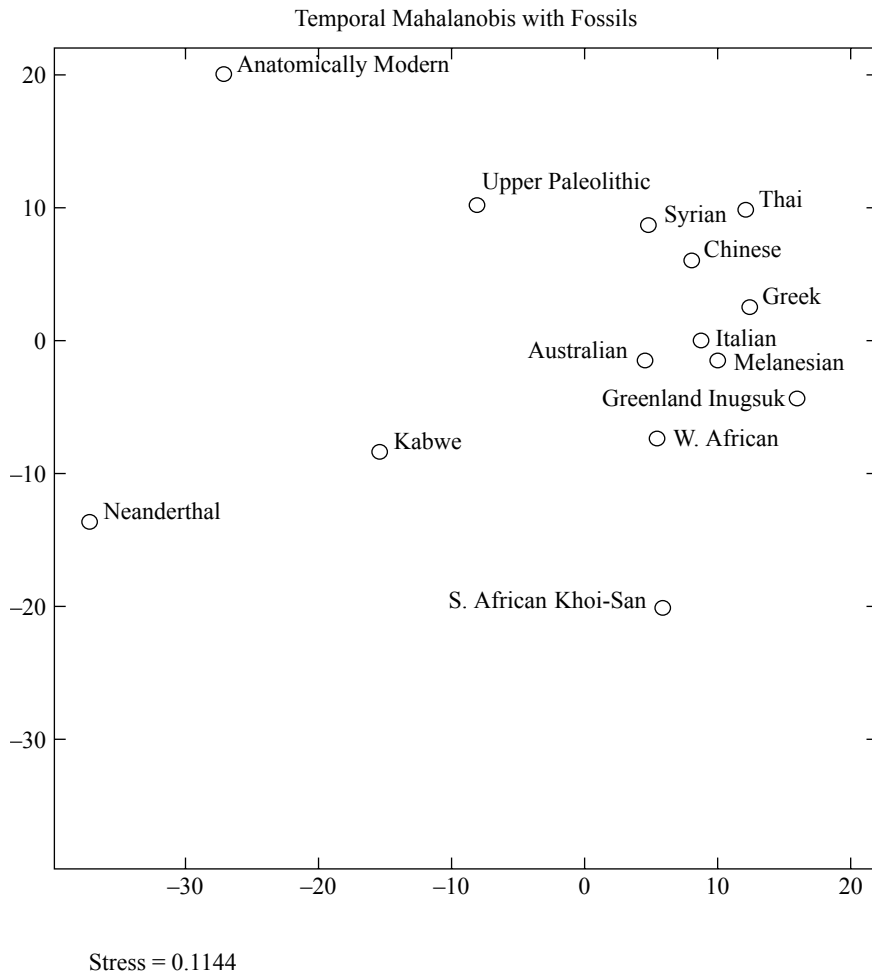


Figure 3. Multidimensional scaling plot of the temporal bone Mahalanobis D^2 among recent and Middle-Late Pleistocene humans.

Table 4. Fossil samples used

<i>Neanderthal</i>	Saccopastore 2, La Chapelle, La Ferrassie 1, La Ferrassie 2, Spy 1, Spy 2, La Quina 5, La Quina 27, Circeo 1, Gibraltar 1, Krapina C, Krapina 39-1, Amud 1, Shanidar 1 ¹
<i>Upper Paleolithic</i>	Cro Magnon 1, Abri Pataud, Předmostí 3 ¹ , Předmostí 4 ¹ , Mladeč 2, Mladeč 5 ¹ , Ein Gev
<i>Early Anatomically Modern</i>	Skhul 5, Qafzeh 9
<i>Middle Pleistocene</i>	Kabwe

¹ Specimens for which casts from the American Museum of Natural History Department of Anthropology were used.

found previously in studies of temporal bone morphology, as well as analyses based on other cranial and postcranial measurements (Stringer, 1974, 1992; Bräuer and Rimbach, 1990; Bräuer, 1992; Kidder et al., 1992; Pearson, 2000; Harvati, 2001, 2002, 2003a, b, 2004). They have been interpreted in terms of retention of primitive features in these specimens (Stringer, 1992).

Conclusions

The results of this analysis indicate that cranial morphology does preserve population history/ phylogenetic information, but that it does so differentially, as previously suggested by various researchers. Both vault and temporal bone shape were significantly correlated with neutral genetics (albeit not very strongly) while facial shape seemed to be affected both by climatic factors and population history. Contrary to expectations, the association between morphological and genetic distances was strongest in the shape of the vault, rather than that of the temporal bone. However, temporal bone shape appeared to be preserving older population history/phylogenetic signals, while vault shape seemed to register more recent events. Centroid size was also found to be correlated with genetic distances in some cases, and may also be phylogenetically important. It must be pointed out, however,

that these results are based on ten recent human groups only, and may be highly dependent on the individual properties of these groups. Further analysis is planned to include a greater number of population samples in order to further test these hypotheses.

Due to its greater preservation of older population history/phylogenetic information, we conclude that temporal bone shape is more appropriate for use in reconstructing the phylogeny of fossil humans. Analysis of temporal bone shape in a sample of fossil and recent humans showed Neanderthals to be distinct from recent humans and Upper Paleolithic specimens. The latter were very close to recent humans. No evidence for a close phylogenetic link between Neanderthals and any recent human group or Neanderthals and the Upper Paleolithic sample used here was found, even though limited interbreeding may have been possible (see Holliday, this volume; Serre and Pääbo, this volume). This result is consistent with other analyses of Neanderthal cranio-dental and postcranial morphology, development, genetics and behavior (e.g., Hublin, 1978; Holliday, 1997; Krings et al., 1997; Pearson, 2000; Ponce de León and Zollikofer, 2001; Rak et al., 2002; Klein, 2003; Bailey, 2004; Harvati et al., 2004; Mellars, 2004; Serre and Pääbo, this volume; Tattersall and Schwartz, this volume), and indicates that Neanderthals are best considered a distinct evolutionary lineage.

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