

Human Cranial Anatomy and the Differential Preservation of Population History and Climate Signatures

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ABSTRACT

Cranial morphology is widely used to reconstruct evolutionary relationships, but its reliability in reflecting phylogeny and population history has been questioned. Some cranial regions, particularly the face and neurocranium, are believed to be influenced by the environment and prone to convergence. Others, such as the temporal bone, are thought to reflect more accurately phylogenetic relationships. Direct testing of these hypotheses was not possible until the advent of large genetic data sets. The few relevant studies in human populations have had intriguing but possibly conflicting results, probably partly due to methodological differences and to the small numbers of populations used. Here we use three-dimensional (3D) geometric morphometrics methods to test explicitly the ability of cranial shape, size, and relative position/orientation of cranial regions to track population history and climate. Morphological distances among 13 recent human populations were calculated from four 3D landmark data sets, respectively reflecting facial, neurocranial, and temporal bone shape; shape and relative position; overall cranial shape; and centroid sizes. These distances were compared to neutral genetic and climatic distances among the same, or closely matched, populations. Results indicate that neurocranial and temporal bone shape track neutral genetic distances, while facial shape reflects climate; centroid size shows a weak association with climatic variables; and relative position/orientation of cranial regions does not appear correlated with any of these factors. Because different cranial regions preserve population history and climate signatures differentially, caution is suggested when using cranial anatomy for phylogenetic reconstruction. *Anat Rec Part A*, 288A:1225–1233, 2006. © 2006 Wiley-Liss, Inc.

Key words: craniofacial morphology; population history; neutral genetics; climate adaptation; human variation

Cranial morphology is commonly used to reconstruct hominin phylogenies and population histories (e.g., Howells, 1973, 1989; Lahr, 1996; Hublin, 1998; Gabunia et al., 2000; White et al., 2003; Strait and Grine, 2004). Despite this widespread use, its reliability in reflecting phylogeny and population history has been questioned (Collard and Wood, 2000; Hlusko, 2004). Integration among traits complicates phylogenetic reconstruction, while convergence, parallelism, reversals, and plastic

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response to the environment are often believed to influence cranial anatomy heavily. Different cranial regions are thought to be more or less susceptible to these processes. In humans, facial form, and particularly the shape of the nose, has been linked to climatic adaptation (Coon et al., 1950; Carey and Steegmann, 1981; Franciscus and Long, 1991; Roseman, 2004; Roseman and Weaver, 2004; Nicholson and Harvati, 2006) and to dietary or masticatory practices (Hylander, 1977; Skelton and McHenry, 1992; Lieberman et al., 2004; Sardi et al., 2006), probably through a combination of developmental responses to the environment and genetic adaptation. The size and shape of the neurocranium have also been related to climate differences (Beals et al., 1983; Roseman, 2004). On the other hand, the shape of the basicranium has been proposed to be the most genetically determined and evolutionarily conservative aspect of the cranium and is thought to be minimally influenced by environmental factors (Olson, 1981; Wood and Lieberman 2001). As such, it has been argued that the cranial base, and particularly the basal aspect of the temporal bone, preserves a stronger signal of phylogeny and population history, and that it should be preferentially used in phylogenetic analyses, while the face and neurocranium should be avoided (Olson, 1981; Harvati, 2001; Wood and Lieberman 2001; Lockwood et al., 2004). Until recently, however, these hypotheses remained largely untested, and researchers generally use all available cranial information to address phylogenetic/population history questions.

The advent of widely available and abundant genetic data for humans has recently made possible the direct testing of these ideas. Two studies (Roseman, 2004; Harvati and Weaver, 2006) have examined the relationship between distances based on cranial morphology and those based on neutral genetic loci among human groups for which both morphological and genetic data exist. Roseman (2004) explored the relationship between morphological distances based on linear cranial measurements. He used data collected by Howells (1973, 1989) from 10 modern human populations and neutral genetic distances among the same, or geographically similar, populations. Roseman (2004) found that distances based on some cranial measurements were strongly associated with neutral genetic distances: a few on the neurocranium or face, but the majority passing from the basicranium to the face. Two facial (nasal and zygomatic height) and some neurocranial breadth measurements were closely associated with temperature distances, calculated from the mean temperature during the coldest month of the year. Roseman (2004) concluded that both these facial measurements, as well as the general shape of the vault (brachycephalic vs. dolichocephalic), reflect climatic adaptation in at least some human groups, while most other measurements reflect neutral genetics or population history. This study did not explicitly address the question of which cranial region best reflects population history: linear measurements are often between landmarks found on two different cranial regions (i.e., from the basicranium to the face), making it impossible to assess the contribution of each individual region to the correlation with neutral genetics. Furthermore, the linear measurements used included size, also making it impossible to differentiate between the relative contribution of shape and size.

Both these issues were explicitly addressed in our recent preliminary study of the relationship between cranial anatomy and population history/climate (Harvati and Weaver, 2006). In that analysis, we used 3D geometric morphometrics methods, which enabled us to distinguish between the effects of shape and (centroid) size and included 10 human populations for which both morphological and genetic data were available. The morphological data sets were partitioned into facial, vault, and temporal bone landmark sets. That analysis found that both temporal bone and neurocranial shape track neutral genetics (the latter more successfully). Facial shape was only weakly associated with neutral genetics and was instead related to climatic variables, as were vault and temporal bone size.

The results of Roseman (2004) and Harvati and Weaver (2006) are not directly comparable. Nevertheless, several similarities, as well as some apparent contradictions, between the two studies are evident: Roseman (2004) found most cranial measurements to reflect neutral genetics, even those that included parts of the face, while we found facial shape to be only weakly associated with neutral genetic distances; both studies found a climatic effect in the face and the vault, but in different aspects of their morphology (size vs. shape). A possible reason for these differences is that the linear measurements used by Roseman (2004) span multiple cranial regions, thereby incorporating information about the position and relative orientation of each region relative to the others. Such information may also be informative regarding population history but could not have been picked up in our previous work, where the shape and size of individual cranial regions were explored independently of one another. The degree to which measurements from the basicranium to the face reflect basicranial or facial shape in Roseman's (2004) study is also unclear. Furthermore, both studies were plagued by a small number of population samples, which limited the number of possible comparisons.

Here we address the inconsistencies in previous results by specifically testing for associations of neutral genetics and climatic variables with cranial shape, size, and relative position of three predefined regions (face, neurocranium, and temporal bone), as well as with total cranial shape. Our goal is to tease apart the contribution of each of these aspects of morphology to the observed relationships with neutral genetics and climatic variables. Further, we aim to improve on previous work by increasing the number of populations included. Although only three groups were added, this increase in samples resulted in almost double the number of between-population comparisons [78 in this study vs. 45 in both Roseman (2004) and Harvati and Weaver (2006)], thus increasing the reliability of our results. We also increased the number of climatic variables used so as to better represent temperature and humidity variation in each geographic locality. Although diet may also affect human craniofacial morphology (Hylander, 1977; Skelton and McHenry, 1992; Lieberman et al., 2004; Sardi et al., 2006), neither this nor our previous research were able to incorporate its effects explicitly. Very little information is available regarding the diets of the individuals in our samples, although all of them except the Australian, Greenland Inugsuk, and Khoisan individuals probably came from populations practicing some form of agriculture.

TABLE 1. Matched morphological and genetic samples with sample sizes

Morphological samples	Face	Temp.	Neur.	Genetic samples	<i>n</i>
W. African Dogon	32	33	33	Yoruba, Nigeria	25
E. African (Kenya, Somalia, Malawi)	11	13	14	Bantu North-East (Kenya)	12
S. African Zulu	20	22	22	S. African Bantu	8
S. African Khoi-San	29	30	30	San, Namibia	7
Austrian (Greiffenberg)	29	29	29	Tuscan, Italy	8
Italian	11	11	11	Italian	13
Greek	13	14	14	Sardinian, Italy	28
Syrian	16	18	20	Palestinian, Israel	51
North Chinese	17	19	20	Han, China	34
Thai	18	20	20	Cambodian	11
Greenland Inugsuk	30	30	30	Yakut, Siberia	25
S. Australian	29	31	31	Papuan, New Guinea	17
Melanesian (New Britain)	28	28	28	Melanesian (Bougainville)	19
Total	283	298	302	Total	258

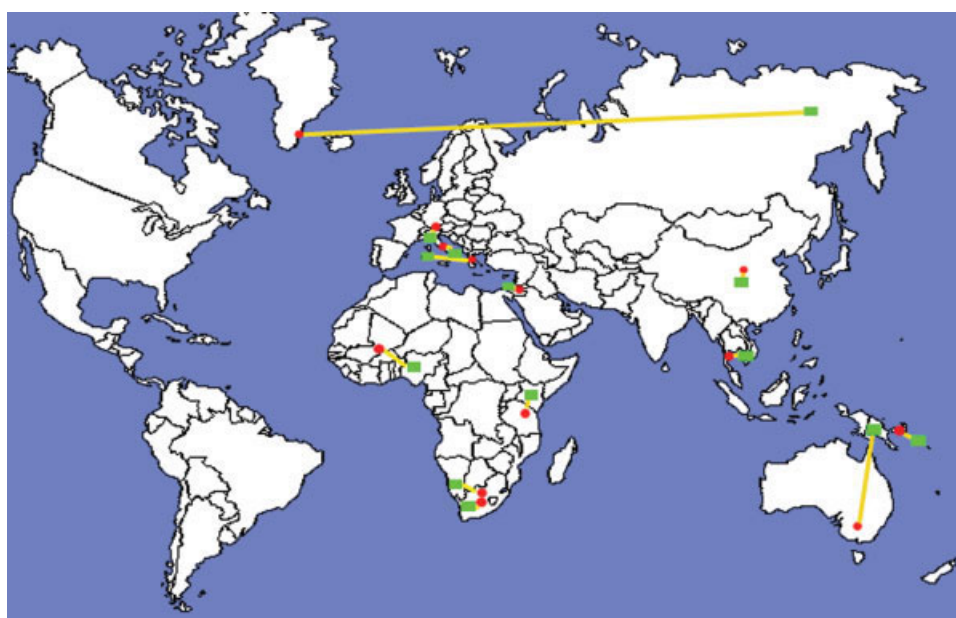


Fig. 1. Genetic (green rectangles) and morphological (red dots) modern human population samples used in the analysis. Yellow links indicate matched samples.

MATERIALS AND METHODS

Genetic and 3D geometric morphometric data were matched for 13 globally distributed recent human populations (Table 1, Fig. 1). These samples included only adult specimens, as determined by full eruption of the permanent dentition. When possible, an equal number of males and females were measured, but sex was in the vast majority of cases unknown and assessed morphologically. The exact matching of morphological samples with genetic ones was not always possible due to limitations in both data sets. Matching between geographic neighbors was therefore allowed in order to preserve a meaningful number of samples. As before (Harvati and Weaver, 2006), the geographic distance between the matched genetic and morphological samples was greatest in two cases: the Australian morphological sample was not represented in the genetic data set and was coupled with a sample from Papua, New Guinea, which is geographically

the closest group included in the genetic data set. Australian and Papuan New Guinea populations are thought to share a common origin and to be genetically similar (van Holst Pellekaan et al., 1998; Kayser et al., 2001). The Greenland Inugsuk morphological sample was matched with a Siberian population. These two groups are from similar latitudes and climatic conditions, an important consideration for the analysis of climatic variables. Previous work has shown that Siberian and Mongolian populations resemble New World groups, including the Inuit, in their cranial morphology (Howells, 1973, 1989). These groups are thought to share recent population history based on both archaeological and genetic evidence (Applet et al., 2000; Saillard et al., 2000; Helgason et al., 2006). It is important to point out that any error introduced by this imperfect matching of samples will bias the results toward not finding significant associations between morphology and neutral genetics (see also Roseman, 2004).

TABLE 2. Climatic variables used for each morphological sample

	Long	Lat	miT.	mxT.	mnT.	miVP	mxVP	mvVP	miP	mxP	mnP
South Australia	145.25	-35.25	8.7	24.0	16.35	89	143	113.58	8	13	11.25
Austria	11.75	47.25	-4.3	12.7	4.32	37	120	73.83	27	52	37.08
North China	110.25	35.25	-1.5	26.1	13.05	31	230	112.67	1	42	15.75
West Africa Dogon	-3.25	14.25	23.7	33.4	28.61	76	271	171.08	0	52	13.17
Greenland	-40.25	65.25	-11.1	4.2	-4.49	23	70	40.92	20	41	30.25
Greece	22.25	37.25	6.4	22.5	14.15	72	145	106.50	4	45	20.92
Italy	13.25	42.25	1.4	18.2	9.17	54	136	89.50	15	34	23.42
E. Africa	38.25	0.25	23.8	26.7	25.08	168	228	196.75	0	73	23.00
Khoisan South Africa	24.25	-25.25	12.4	26.0	20.15	93	204	146.92	1	25	10.67
Syria	38.25	35.25	5.7	29.2	17.73	68	137	96.33	0	12	5.92
Thailand	100.25	13.75	25.5	30.5	28.31	226	317	285.17	3	83	32.42
Melanesia	150.25	-5.75	25.0	26.0	25.62	251	270	262.83	99	189	135.00
Zulu South Africa	25.25	-30.25	8.6	23.9	16.67	59	138	94.67	3	26	11.08

Temperatures are reported in degrees Celsius; Vapor Pressures in hecta-Pascals*10; and Precipitation in millimetres per day*10.

The genetic data consisted of an expanded set of the data analyzed by Rosenberg et al. (2002) and Zhivotovskiy et al. (2003). They comprised 784 microsatellite loci from 258 individuals representing 13 populations closely matching the morphological samples (Table 1). These individuals represent a subset of those from the Human Genome Diversity Project-CEPH cell line panel (28). The samples were typed by the Mammalian Genotyping Service (Marshfield panel 10-52; <http://www2.marshfieldclinic.org/RESEARCH/GENETICS>).

The climatic variables were obtained from a global climate data set constructed by interpolating observations from thousands of climate stations around the world, published by New et al. (1999), using latitudes and longitudes approximated for each group (Table 2). Some samples represent localized populations and their approximate geographic position was relatively easy to estimate. However, others represent an assortment of specimens from a larger geographic region, such as the South Australian or East African sample. In these cases, latitude and longitude were estimated at the approximate center of the geographic distribution of our samples. As climatic indicators for each population, we used estimates of mean, minimum, and maximum yearly temperatures (hereafter mnT, miT, and mxT, respectively); total, minimum, and maximum yearly precipitation (tP, miP, mxP); and mean, minimum, and maximum yearly vapor pressure (mnVP, miVP, mxV; a measure of humidity). These indicators are listed for each population in Table 2.

The morphological data were collected by one of us (K.H.) as 3D coordinates of craniofacial osteometric landmarks [as defined in Howells (1973, 1989) and Harvati (2001, 2003)] using a portable Microscribe 3DX digitizer (Fig. 2, Table 3). The data were partitioned into three data sets, representing the face (13 bilateral and midline landmarks), the temporal bone (13 landmarks from the right temporal bone), and the neurocranium (8 bilateral and midline landmarks). The three data sets overlapped minimally: asterion was included in both the temporal bone and neurocranial data sets, and glabella in both the neurocranial and the facial data sets. Landmark coordinates were processed using generalized Procrustes analysis in the software package Morphueus et al. (State University of New York, Stonybrook, NY). Centroid size

was removed from the coordinate data during Procrustes fitting and was analyzed separately for its relationship with neutral genetics and climatic factors.

Superimposition was performed twice: once for each region separately (resulting in data sets reflecting shape only), and then for the three cranial regional data sets superimposed as a unit (resulting in data sets reflecting both shape and positional information). Based on these two superimpositions, we generated four sets of data: three shape data subsets, one for each cranial region, based on the Procrustes superimposed landmarks of that region alone; three shape/relative position data subsets, one for each cranial region, derived from the Procrustes superimposition of all 32 cranial landmarks but analyzed separately; a full cranial data set of all 32 landmarks superimposed together; and four centroid size data sets, one for each cranial region and for the entire cranium. Four analyses were therefore conducted: analysis 1, of shape of each cranial region; analysis 2, of shape and position of each cranial region; analysis 3, of shape of the entire cranium; and analysis 4, of centroid size of each cranial region and of the entire cranium.

We compared morphological distances among the modern human samples obtained from these data sets with genetic and climatic distances for their matched samples. Morphological distances were estimated using Mahalanobis D^2 [calculated on principal components representing 90-95% of the total variance and using a correction for unequal sample sizes (Marcus, 1993)]. This statistic represents the morphological variation among groups, scaled by the inverse of the pooled within-group covariance matrix. Unlike other distance measures used with landmark data (e.g., Procrustes distance), Mahalanobis D^2 accounts for nonindependence of landmark coordinates and within-group variation (Neff and Marcus, 1980; Klingenberg and Monteiro, 2005). Because the neutral rate of morphological evolution is expected to be proportional to the within-population variation, Mahalanobis D^2 can also be directly related to expected rates of morphological divergence predicted by population genetic theory for neutral evolution (Lynch, 1990). Population mean centroid sizes for each cranial region were calculated and a distance matrix of the squared differences in mean centroid size for all possible population pairs was created.

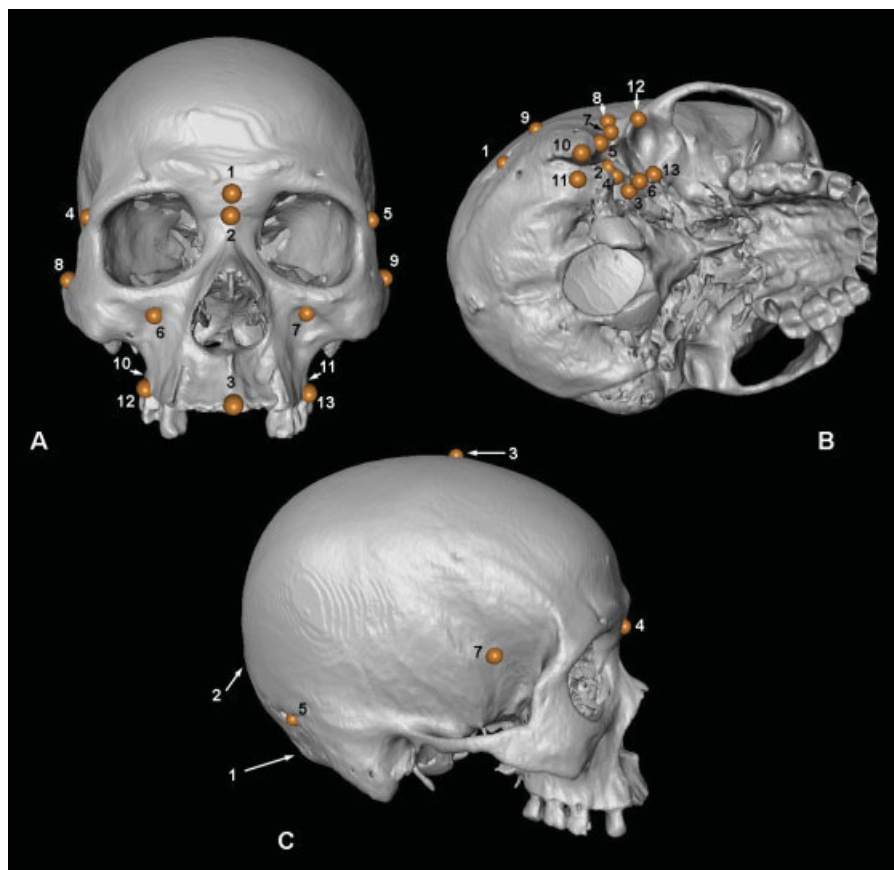


Fig. 2. Landmarks used in the analysis. Facial (A), temporal bone (B), and neurocranial (C) landmarks. Numbers match those in Table 3.

TABLE 3. Landmarks used in the analysis

Face

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.

Temporal bone

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, 12. Deepest point of the lateral margin of the articular eminence, 13. Most inferior point on the entoglenoid. process

Neurocranium

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

The genetic distances among the samples were calculated using the delta mu squared (Ddm) statistic (Goldstein et al., 1995a), which was specifically designed for microsatellites. Under mutation-drift equilibrium, Ddm is expected to increase linearly with time in diverging populations, with a slope equal to twice the neutral mutation rate (Goldstein et al., 1995a, 1995b). Ddm is a suitable distance for comparison with morphological Mahalanobis D^2 , because both of these distances measure the squared pairwise differences among populations. For the climatic distances, we built matrices of the squared differences in each of the climatic variables for all possible comparisons among population pairs.

The matrices were compared using a Mantel test of matrix correlation with NTSYSpc (Exeter Software, Setauket), which measures the degree of association between two distance matrices. A permutation test was performed to assess if the relationship between the two matrices was significantly different from no relationship (10,000 random permutations). Significance levels were set to $\alpha = 0.01$. It was also possible to compare the three matrices with a partial Mantel test, which is analogous to a partial correlation among three variables (Sokal and Rohlf, 1995). This test allowed us to control for the effects of a third variable during our comparisons. It was used to con-

TABLE 4. Mantel test results for the association of morphological distances with neutral genetic/climatic distances

	Genetics	Latitude	Mean temperature	Maximum temperature
Analysis 1: Shape of cranial regions				
Face	$r = 0.1702$ $P = 0.1895$	$r = 0.3581$ $P = 0.0365$	$r = 0.5236$ $P = 0.0030$	$r = 0.5550$ $P = 0.0079$
Temporal Bone	$r = 0.5633$ $P = 0.0004$	$r = 0.0619$ $P = 0.3277$	$r = 0.0501$ $P = 0.3639$	$r = 0.2028$ $P = 0.1340$
Neurocranium	$r = 0.4418$ $P = 0.0021$	$r = 0.0349$ $P = 0.4043$	$r = 0.1039$ $P = 0.2569$	$r = 0.0571$ $P = 0.3603$
Analysis 2: Shape and relative position of cranial regions				
Face	$r = 0.2388$ $P = 0.1015$	$r = 0.3795$ $P = 0.0301$	$r = 0.5207$ $P = 0.0071$	$r = 0.5507$ $P = 0.0117$
Temporal Bone	$r = 0.6054$ $P = 0.0001$	$r = 0.0484$ $P = 0.3606$	$r = 0.0952$ $P = 0.2546$	$r = 0.1144$ $P = 0.2273$
Neurocranium	$r = 0.4020$ $P = 0.0047$	$r = 0.0171$ $P = 0.4175$	$r = 0.1049$ $P = 0.2221$	$r = 0.05$ $P = 0.3449$
Analysis 3: Shape of entire cranium				
Cranium	$r = 0.4530$ $P = 0.0028$	$r = 0.3394$ $P = 0.0254$	$r = 0.4689$ $P = 0.0031$	$r = 0.4825$ $P = 0.0045$
Analysis 4: Centroid sizes				
Face	$r = 0.2619$ $P = 0.1034$	$r = -0.0351$ $P = 0.4467$	$r = -0.0353$ $P = 0.4781$	$r = -0.0131$ $P = 0.3930$
Temporal Bone	$r = 0.1478$ $P = 0.1904$	$r = 0.1798$ $P = 0.1275$	$r = 0.2904$ $P = 0.0720$	$r = 0.3941$ $P = 0.0406$
Neurocranium	$r = -0.0285$ $P = 0.5683$	$r = 0.1866$ $P = 0.0886$	$r = 0.3732$ $P = 0.0122$	$r = 0.3652$ $P = 0.0120$
Cranium	$r = 0.0529$ $P = 0.3826$	$r = 0.2847$ $P = 0.0757$	$r = 0.4181$ $P = 0.0416$	$r = 0.5034$ $P = 0.0297$

Bold values significant at $P < 0.01$.

control for population history effects when testing for correlation between morphology and climatic variables (see also Roseman, 2004).

The previously observed relationships between climatic variables and facial shape, as well as neurocranial and temporal bone centroid sizes (Harvati and Weaver, 2006), could be driven by the inclusion of the Greenland Inugsuk sample. This sample is an outlier in both climatic and morphological distances. Therefore, these correlations could reflect the extreme facial morphology, and possibly adaptation, of human groups living in extreme climatic conditions, as observed also by Roseman (2004). Our Inugsuk sample is also the one that is least closely matched geographically to their genetic "equivalent" (Siberian) and could therefore also decrease the correlation between morphology and neutral genetics. Because of the possible large effect of the inclusion of the Siberian/Inugsuk sample on our results, we repeated the analyses excluding this matched population pair.

RESULTS

Results of the Mantel matrix correlation tests are shown in Tables 4 (all 13 sample pairs included) and 5 (Inugsuk/Siberian samples removed). Only variables that showed at least one significant comparison are shown.

Analysis of All Matched Sample Pairs

Out of the three morphological shape data sets (each region superimposed and analyzed separately; Table 4, analysis 1), only the neurocranial and temporal bone

shape distances were significantly associated with neutral genetic distances, the latter showing a stronger relationship. Facial shape distances were correlated with squared differences in mnT and mxT, but not with genetic distances or other climatic variables. The relationship between facial shape distances and mnT and mxT distances was still significant and somewhat stronger once the effects of genetics were held constant in a partial Mantel test ($r = 0.5495$, $P = 0.0033$, and $r = 0.5998$, $P = 0.0033$, respectively).

When the shape of each cranial region was examined together with its position and orientation relative to the other two bones (entire cranium superimposed as a unit, but each region analyzed separately; Table 4, analysis 2), the results were nearly identical to those reported for analysis 1. Temporal bone shape distances now showed a somewhat stronger association with neutral genetic distances, while the inverse effect was observed with neurocranial shape distances. Facial shape distances remained correlated with mnT, but not mxT distances, though both these comparisons were significant when the effects of neutral genetics were held constant in a partial Mantel test ($r = 0.5611$, $P = 0.0050$, and $r = 0.6159$, $P = 0.0058$, respectively).

Distances based on the shape of the entire cranium (full coordinates set; Table 4, analysis 3) were also significantly associated with neutral genetic distances, though less strongly than the temporal bone distances and approximately to the same degree as the neurocranial shape distances. Total cranial shape distances were also significantly associated with mnT and mxT distances (though only with mnT after accounting for the effects of neutral genetics in a partial Mantel test: $r =$

TABLE 5. Mantel test results for the association of facial shape and neurocranial, temporal bone and cranial centroid size distances with climatic distances after removal of the Inugsuk sample

	Genetics	Latitude	Mean temperature	Maximum temperature
Analysis 1: Shape of cranial regions				
Face	$r = 0.2456$ $P = 0.0929$	$r = 0.3764$ $P = 0.0219$	$r = 0.2239^a$ $P = 0.1125^a$	$r = -0.0546^a$ $P = 0.5802^a$
Temporal Bone	$r = 0.6396$ $P = 0.0001$	$r = 0.2495$ $P = 0.0868$	$r = -0.0102$ $P = 0.4697$	$r = -0.0901$ $P = 0.6664$
Neurocranium	$r = 0.4677$ $P = 0.0019$	$r = 0.4827^a$ $P = 0.0030^a$	$r = 0.2579$ $P = 0.0609$	$r = 0.1250$ $P = 0.2226$
Analysis 2: Shape and relative position of cranial regions				
Face	$r = 0.3036$ $P = 0.0372$	$r = 0.4103^a$ $P = 0.0098^a$	$r = 0.2325^a$ $P = 0.0915^a$	$r = 0.0369$ $P = 0.3533$
Temporal Bone	$r = 0.6645$ $P = 0.0001$	$r = 0.1970$ $P = 0.1221$	$r = 0.0559$ $P = 0.3505$	$r = -0.0646$ $P = 0.6149$
Neurocranium	$r = 0.4274$ $P = 0.0053$	$r = 0.5507^a$ $P = 0.0008^a$	$r = 0.3771$ $P = 0.0205$	$r = 0.131$ $P = 0.2068$
Analysis 3: Shape of entire cranium				
Cranium	$r = 0.5453$ $P = 0.0005$	$r = 0.3060$ $P = 0.0277$	$r = 0.2451^a$ $P = 0.0680^a$	$r = 0.0810^a$ $P = 0.2909^a$
Analysis 4: Centroid sizes				
Face	$r = 0.2398$ $P = 0.1259$	$r = 0.032$ $P = 0.3249$	$r = -0.1988$ $P = 0.9254$	$r = -0.1431$ $P = 0.8106$
Temporal Bone	$r = 0.1703$ $P = 0.1444$	$r = -0.0437$ $P = 0.5737$	$r = -0.1026$ $P = 0.7217$	$r = -0.1045$ $P = 0.7171$
Neurocranium	$r = 0.015$ $P = 0.4478$	$r = -0.1008$ $P = 0.7429$	$r = 0.1309$ $P = 0.1750$	$r = 0.0779$ $P = 0.2831$
Cranium	$r = 0.1820$ $P = 0.1501$	$r = -0.1142$ $P = 0.7537$	$r = -0.164$ $P = 0.8617$	$r = -0.1341$ $P = 0.7722$

Bold values significant at $P < 0.01$.

^aIndicates a change of significance in the associations from Table 4.

0.5749, $P = 0.0008$). None of the centroid size distances were significantly correlated with neutral genetic, latitude, or climatic distances (Table 4, analysis 4), although neurocranial centroid size showed a relationship approaching significance with mnT and mxT (also after accounting for the effects of neutral genetics: $r = 0.3723$, $P = 0.0136$, and $r = 0.3657$, $P = 0.0113$, respectively).

Analysis of Sample Pairs Excluding Inugsuk/Siberian Samples

Our results changed in some respects when the Inugsuk/Siberian paired samples were removed. These changes are summarized in Table 5 (entries with a superscript). Temporal bone and neurocranial shape and shape/positioning distances were still correlated with neutral genetic distances (Table 5, analyses 1 and 2), as was the shape of the entire cranium (analysis 3). The correlations in all cases were stronger than those reported for the analysis of all samples in Table 4. However, facial shape and shape/positioning distances (Table 5, analyses 1 and 2), as well as cranial shape distances (analysis 3), were no longer significantly correlated with the temperature variables. Interestingly, latitude showed a significant association with neurocranial shape and shape/positioning, as well as with facial shape/positioning, a strikingly different pattern from that seen in the total sample analysis. None of the centroid sizes were significantly correlated with either genetic or climatic distances.

DISCUSSION

Cranial Morphology and Population History

Similar to our previous work (Harvati and Weaver, 2006) and contrary to previous claims (e.g., Collard and Wood, 2000), we found that cranial morphology does preserve a population history signal, as reflected by the correlations between neutral genetic distances and most distances based on cranial morphology. Although these relationships were highly significant (α set to 0.01), their correlation coefficients were rather low, indicating that only part of the morphological variation can be explained in terms of neutral genetic differences. This result is not unexpected, given the many competing influences on the human cranium (adaptive, environmental). The lack of exact correspondence between genetic and morphological population samples also results in weaker correlations between morphology and genetics: removal of the Inugsuk and Siberian populations, the population pair most loosely matched in our analysis resulted in stronger correlations between neutral genetic and morphological distances.

This analysis also confirmed our previous finding of differential preservation of a population history among different cranial regions. While neutral genetic distances were associated with temporal bone, neurocranial, and total cranial shape distances, no such relationship was found with facial shape distances. However, while Harvati and Weaver (2006) found neurocranial shape to reflect human population history more closely than temporal bone shape, the reverse result was obtained here.

Although this finding may indicate a stronger population history signal in the shape of the temporal bone, it is also possible that these differences are due to the inclusion of additional samples in the present analysis. We previously argued (Harvati and Weaver, 2006) that the shape of the temporal bone may be most informative for older population history events and may mainly separate sub-Saharan African from non-sub-Saharan African groups. Further work including more population samples than are currently available is needed in order to address these questions conclusively.

The present analysis also showed that information about the relative positioning and orientation of each cranial region with respect to the other two has no great or consistent effect on the correlations of morphological distances with neutral genetic distances (or climatic distances). Therefore, we tentatively conclude that it is the shape of each particular region, rather than their manner of integration (at least as reflected in their relative position and orientation), that is informative with regard to human population history. The discrepancy between previous results from linear measurements (Roseman, 2004) and from 3D coordinate data (Harvati and Weaver, 2006, this study) cannot be attributed to the effects of orientation or relative position, nor to those of size. It is possible that these differences ultimately stem from differences in the nature of the measurements used in the two studies (linear as opposed to 3D coordinates). Finally, the relationship of total cranial shape to neutral genetics was somewhat stronger than that between genetics and neurocranial shape, but weaker than that between genetics and temporal bone shape. This finding suggests that more information is not necessarily better in reconstructing human population history.

Since our analysis was confined to populations of a single species, it is not clear whether the observed relationships between cranial morphology, size, and integrational pattern on the one hand and population history on the other hand also apply to higher taxonomic levels or to different organisms. In order to shed light on this issue, our hypotheses must be tested using multiple species and genera of primates and other mammals.

Cranial Morphology and Climate

Our findings confirm the previously reported association of climatic variables with facial shape (Coon et al., 1950; Carey and Steegmann, 1981; Franciscus and Long, 1991; Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006; Nicholson and Harvati, 2006), even though our analysis included only a few landmarks around the nose, the part of the face most commonly linked to climate. Aside from the nasal area, the flat face and expanded zygomatics of Asian populations have been proposed to be related to cold-climate adaptation (Coon et al., 1950), but later studies have questioned the functional basis of this hypothesis (Steegmann, 1970). Our results suggest that a climatic signal may be present in the nonnasal aspects of facial morphology (as represented by our landmarks), although these may of course be associated with shape differences around the nasal aperture. However, the climatic signal observed here was largely driven by the inclusion of the Inugskul arctic human population (a finding similar to that of Roseman, 2004). When this group was excluded

from the analysis, no association was found with any of the temperature, precipitation, or vapor pressure variables. Interestingly, in this reduced sample analysis, both neurocranial shape and shape/positioning, as well as facial shape/positioning, were significantly correlated with latitude. This finding suggests that although the Greenland group may be characterized by a specific thermoregulatory adaptation, as suggested by Roseman (2004) for his Siberian sample, there might still exist a general clinal trend in human facial morphology. However, an alternative interpretation is that this association stems from the relatively strong relationship between latitude and neutral genetics found in this reduced sample ($r = 0.2896$, $P = 0.0398$; not significantly correlated with each other in the original sample: $r = -0.0318$, $P = 0.5499$).

Cranial size has been previously linked to climate, with larger crania found in cold-climate human groups (Beals et al., 1983; see also Roseman, 2004). This size effect has been related to the larger body and brain sizes found in cold climates (Beals et al., 1983). Our previous analysis supported this hypothesis, with neurocranial centroid size found to be associated with climate (Harvati and Weaver, 2006). The present study, however, found only a weak association between cranial centroid sizes and climatic variables, which approached, but did not reach, significance. This effect also disappeared when the Inugskul sample was removed from the analysis.

Our results tentatively support the proposed link between facial shape, and perhaps also cranial size, with climate in extreme cold-dwelling populations, possibly exhibiting thermoregulatory adaptations, as suggested by Roseman (2004). However, we cannot exclude a more general clinal effect of climate-related variation among human populations, as our samples were limited in their representation of cold-climate human populations. Further exploration of the climate-related aspects of facial shape and cranial size using geographically more dispersed samples will be able to shed additional light on the possible climatic adaptations of the human cranium.

CONCLUSIONS

Our results support the hypothesis that cranial morphology retains a population history signal, and that different aspects of cranial morphology can preserve different kinds of information. While human temporal bone shape tracks neutral genetics well, as previously predicted for the basicranial region, so does the shape of the neurocranium, often considered too developmentally plastic and environmentally influenced to retain any signal of population history. Human facial shape appears to retain a climatic, rather than a genetic, signature, but this climatic effect may be confined to arctic populations. The relative position and orientation of the three cranial regions to each other is not informative with regards to population history. Finally, the total cranial shape is less successful than the shape of the temporal bone alone in tracking population history, suggesting that more information is not necessarily better.

It is important to point out that these results may not apply when different organisms or higher taxonomic levels are considered and should be replicated with further analyses. However, our findings suggest caution and careful choice of anatomical features and regions in phylogenetic and population history reconstructions.

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