

Relationship of Cranial Robusticity to Cranial Form, Geography and Climate in *Homo sapiens*

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ABSTRACT Variation in cranial robusticity among modern human populations is widely acknowledged but not well-understood. While the use of “robust” cranial traits in hominin systematics and phylogeny suggests that these characters are strongly heritable, this hypothesis has not been tested. Alternatively, cranial robusticity may be a response to differences in diet/mastication or it may be an adaptation to cold, harsh environments. This study quantifies the distribution of cranial robusticity in 14 geographically widespread human populations, and correlates this variation with climatic variables, neutral genetic distances, cranial size, and cranial shape. With the exception of the occipital torus region, all traits were positively correlated with each other, suggesting that they should not be treated as individual characters. While males are more robust than females within each of the populations, among the independent variables (cranial

shape, size, climate, and neutral genetic distances), only shape is significantly correlated with inter-population differences in robusticity. Two-block partial least-squares analysis was used to explore the relationship between cranial shape (captured by three-dimensional landmark data) and robusticity across individuals. Weak support was found for the hypothesis that robusticity was related to mastication as the shape associated with greater robusticity was similar to that described for groups that ate harder-to-process diets. Specifically, crania with more prognathic faces, expanded glabellar and occipital regions, and (slightly) longer skulls were more robust than those with rounder vaults and more orthognathic faces. However, groups with more mechanically demanding diets (hunter-gatherers) were not always more robust than groups practicing some form of agriculture. *Am J Phys Anthropol* 141:97–115, 2010. ©2009 Wiley-Liss, Inc.

Cranial robusticity in hominins includes aspects of cranial size, cranial bone thickness, and a suite of discrete characters, such as well-developed supraorbital elements and midline keeling. Many of the individual characters used to assess cranial robusticity in modern humans are also used as diagnostic characters to distinguish among *Homo* taxa and to reconstruct human phylogeny (e.g., *H. erectus*; Stringer, 1984; Bilsborough and Wood, 1986; Hublin, 1986; Rightmire, 1990; Bräuer and Mbua, 1992; Wood and Richmond, 2000; Dunsworth and Walker, 2002; Schwartz, 2004; Villmoare, 2005). Cranial robusticity in some populations of modern humans, particularly Aboriginal Australians, has also been used to support a close relationship with *H. erectus* from Java (e.g., Ngandong) under the multiregional model of modern human origins (Wolpoff et al., 1984; Frayer et al., 1993; Wolpoff, 1999). The assumption underlying these practices is that these traits have a strong genetic/hereditary component. However, it is also possible that cranial robusticity is influenced by functional or climatic variables.

Previous work by Lahr and Wright (1996) found that cranial robusticity is strongly influenced by the size, and, to a lesser extent, the shape of the cranium. This has been interpreted as supporting integration of cranial form and robusticity (Lahr and Wright, 1996; Churchill, 1998). At the same time, numerous studies have shown that cranial form is relatively homogeneous within single modern human populations (Howells, 1973, 1989; Hani-

hara, 1996; Hennessy and Stringer, 2002; Strand Violdarsdóttir et al., 2002), and that cranial shape in humans reflects neutral genetic distances among present-day populations (Roseman, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007). Taken together, these two observations suggest that cranial robusticity may track modern human population history. This would indicate that cranial robusticity is not under strong selection within *H. sapiens*.

Models derived from quantitative genetics are frequently applied to cranial morphometric data to assess a hypothesis of neutral evolution (e.g., Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007; Weaver et al., 2007). This study extends this practice to traits that capture cranial

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robusticity. The null hypothesis that will be tested here is that neutral evolutionary processes (particularly the effects of genetic drift) were responsible for the global patterning of cranial robusticity in modern humans. The primary assumptions of this model are that all genetic variance in a quantitative trait is 1) additive (no dominance or epistatic effects), and 2) selectively neutral within and among populations (Lande, 1992). Deviations from the null hypothesis of neutral evolution imply selection on these characters.

Ordinal data cannot simply be slotted into quantitative genetics models in a manner identical to morphometric data due to differences in the assumptions underlying categorical data. Fortunately, a similar model has been advanced for dichotomous or polychotomous characters, such as those used here to assess cranial robusticity. In this case, a discontinuous trait is assumed to have an underlying continuous character, termed the liability or the latent variable, with one or more thresholds (Wright, 1934; Falconer, 1965, 1989; Gianola, 1979, 1982; Falconer and Mackay, 1996; Lynch and Walsh, 1998; Konigsberg, 2000; Leigh et al., 2003). The threshold can be viewed as a certain accumulation of genetic and possibly environmental effects; when the liability exceeds the threshold value, one version of the trait is expressed while below this value an alternate expression of the trait occurs. To simplify this model, the distribution of this liability is assumed to be normally distributed in the population (Konigsberg, 2000), an assumption which is reasonable if the liability is multifactorial, with multiple genes contributing to the expression of the trait, and all factors having a relatively small effect (Falconer and Mackay, 1996). As mentioned above, the quantitative genetics model used here assumes an equal and additive genetic effects model. Although this assumption has not been evaluated explicitly for the characters being investigated here, it has been suggested that this assumption is met generally for morphological features (López-Fanjul et al., 2003). In regards to discrete cranial characters, Cheverud and Buikstra (1981a,b, 1982) found that epistatic traits have higher heritabilities than linear measurements in rhesus macaques. In contrast, Carson (2006a) found generally low heritabilities for nonmetric traits in a sample of modern human crania from Hallstatt, Austria whose family relationships were known. However, in both cases the discrete/meristic features were not identical to those examined here. Rather the discrete characters examined in these other studies were standard epistatic traits including accessory ossicles, foramina, and hyperostotic features, all with fairly clear cut categories of expression. Interestingly, one trait that Carson (2006a) investigated, the zygomaxillary tubercle, was also examined here. When measured as a dichotomous variable, this trait had one of the highest narrow sense heritabilities (0.49) of the traits examined; its value compared favorably with heritabilities for cranio-metric measures from the same sample presented in Carson (2006b).

In contrast to this nonadaptive model, several studies have linked a robust cranial phenotype to variation in masticatory (Endo, 1966, 1970; Russell, 1985) and paramasticatory (Spencer and Ungar, 2000) stresses. Mechanically demanding dietary regimes have been linked with variation in modern human craniofacial morphology (Larsen, 1981, 1982; Spencer and Demes, 1993; Spencer and Ungar, 2000), including the appearance of certain "robust" characters such as sagittal keeling and

supraorbital ridges (Hrdlička, 1910; Hilloowala and Trent, 1987; Lahr, 1995; Hernández et al., 1997). The transition from a hunter-gatherer to an agricultural lifestyle is characterized by a reduction in overall cranial robusticity and the size of the facial skeleton, the masticatory complex, and the occipital region, as well as shorter, rounder cranial vaults (e.g. Carlson and van Gerven, 1977, 1979; Larsen, 1982, 1995; y'Edynak and Fleisch, 1983; Sardi et al., 2006). These studies proposed that these changes were mainly a biomechanical response of the skull to reduced muscular activity related to a softer (i.e., agricultural) diet. Experimental evidence from other mammals has also supported the influence of diet on craniofacial morphology (Ciochon et al., 1997; Bresin et al., 1999; Lieberman et al., 2004). A more general argument has also been made that the supraorbital region may be better developed in primate taxa that generate greater forces in this region during mastication (Russell, 1985; Wolpoff, 1985; Bookstein et al., 1999; but see Hylander et al., 1991; Ravosa, 1991; Ross and Hylander, 1996). It is therefore possible that differences in masticatory stress may influence the size and morphology of the facial, supraorbital, and occipital regions that encompass many of the "robust" characters considered in this study.

Climate, particularly very cold conditions, appears to influence overall craniofacial morphology (Harvati and Weaver, 2006a,b; Gilligan and Bulbeck, 2007), especially in regards to nasal morphology (Carey and Steegmann, 1981; Franciscus and Long, 1991; Hernández et al., 1997; Lalueza et al., 1997; Roseman and Weaver, 2004). Studies of interpopulation variation in South America have also found that indigenous people from southern Patagonia and Tierra del Fuego (a cold, harsh environment) are more robust than South American populations at higher, warmer latitudes, concluding that cranial robusticity may be a response to cold climates (Bernal et al., 2006; Perez et al., 2007). The mechanism proposed by Bernal et al. (2006) and Perez et al. (2007) relates to increased hormone levels in cold adapted populations as demonstrated by Leonard et al. (2002), which may result in greater cortical bone growth throughout the organism. Similarly, Bulbeck (2001) reasoned that *in situ* evolution of cranial robusticity in Late Pleistocene/Holocene Australian fossils was an adaptation to the cold, extreme environmental conditions present in western New South Wales during the Last Glacial Maximum.

This study represents the first attempt to investigate the influence of numerous independent factors (e.g., climate, neutral genetic distances, cranial size, and cranial shape) on the expression of cranial robusticity within a broad geographic sample of modern humans. The results of this study will help inform our interpretations of variation in cranial robusticity in both modern and extinct hominin species.

MATERIALS AND METHODS

Sample

Patterns of intraspecific cranial shape and robusticity were examined in a large sample of modern human crania ($n = 281$) from the American Museum of Natural History, New York. This sample was designed to represent modern human geographic variation, as well as diverse subsistence activities, which can be subdivided into 14 main regional/genetic groups (Table 1). While some of the population sample sizes are small, our goal

TABLE 1. Fourteen corresponding morphological and genetic samples used in this study; number of individuals for each sex are indicated for the morphological populations used in the CLS, FLS, and MLS analyses (top to bottom)

Abbrev	Morphological population	M	F	U	Genetic population (no. of individuals)
WEur	Western Europe (Greifenberg, Austria; Baden-Württemberg, Germany)	22	14	0	France (53)
5.920	Oberkassel 2 ^a , Germany; Sclaigneaux, Belgium	21	14	0	
		11	14	0	
SEur	Southern Europe (Peloponnesus, Greece; Italy)	10	8	0	Italy (49)
5.911		8	8	0	
		6	6	0	
EEur	Eastern Europe (Galicia, Poland)	7	4	0	Russia (42)
5.907	Předmostí 2, Czech Republic	6	4	0	
		4	1	0	
SAm	Native South American (Tierra del Fuego)	2	3	0	Huilliche, Chile (20)
5.962	Cerro Sota Cave, Chile	2	2	0	
		3	2	0	
NAm	Native North American (Grand Gulch, Utah)	20	14	1	Pima, Mexico (25)
5.930		19	13	1	
		16	9	0	
Zeal	New Zealand (Maori)	10	11	0	New Guinea and Melanesia (36)
5.940		8	10	0	
		8	8	0	
Aust	Native Australian/Tasmanian	11	11	1	Australia (Aboriginal) (10)
5.908		10	9	1	
		9	10	1	
KSan	South African (Khoe-San)	4	5	0	Namibia (San) (7)
5.912		4	4	0	
		4	5	0	
EAF	East Africa	7	3	0	Kenya (12)
5.934		7	3	0	
		7	3	0	
WAF	West Africa (Ashanti)	6	4	0	Senegal ands Nigeria (49)
5.908		6	4	0	
		6	4	0	
Mong	Mongolia	8	6	0	Mongolia (10)
5.933		7	4	0	
		6	2	0	
SEAs	Southeast Asia (Indonesia, Philippines, Malaysia)	20	5	0	Cambodia (11)
5.908		20	5	0	
		18	4	0	
EAs	China	13	10	2	China (East and South) (54)
5.932		13	9	2	
		9	7	1	
Inui	Inuit (Point Hope, Alaska)	8	8	3	Chipewyan (Native Americans from Canada) (29)
5.959		7	7	2	
		6	7	1	

Logged centroid size based on CLS reported beneath group abbreviation.

^a Prehistoric specimens (Upper Paleolithic: Oberkassel 2 and Předmostí 2; Neolithic: Sclaigneaux and Cerro Sota Cave) are listed separately for each region below the main samples. Data were collected from casts for all prehistoric specimens.

was to sample broadly on a global scale rather than focusing on intrapopulation variation. The small size of the Tierra del Fuego sample is particularly regrettable, but this population is essential because it is one of two cold-adapted groups.

All specimens were adult, and males and females were approximately equally represented. Some of the discrete “robusticity” characters analyzed in this study are commonly used to differentiate between male and female crania, such as the development of the supraorbital and occipital regions. To avoid circularity, overall cranial size and the size of the mastoid process were used as indicators of sex because they were not scored as robusticity traits, and mandibles were used to confirm these assessments when present (most crania are not associated with postcranial remains). At least two observers assigned sex to each specimen. In those few cases where their assessments disagreed, sex was categorized as unknown. In addition, a few populations (Mongolians, Grand Gulch, and Australians) were sexed independ-

ently at an earlier time. There is little or no information regarding how these original sex assignments were determined and could be similarly based on cranial features. In the rare instances when there was disagreement between our assessments and those provided, ours took precedence. However, the high degree of accord provided additional independent confirmation of our sex assignments. Casts of several prehistoric (Upper Paleolithic or Neolithic) individuals were included in the analysis when sufficiently complete.

Data collection

Morphological data. Two types of data were collected from each specimen. Eleven discrete traits were scored by a single observer (SF) for all specimens (Table 2 and Fig. 1). Character states for eight of the traits were defined previously by Lahr (1996) and Lahr and Wright (1996), while the other three, the malar tubercle, supra-mastoid crest, and anterior mastoid tubercle, were

TABLE 2. Robusticity character abbreviations, definitions, and character states

Trait	Abbrev	Definition	No. of Grades ^a
Sagittal keel	SK	The orientation of the parietal bones in the coronal plane. Grades range from moderate angling of the parietal bones to a distinct ridge or crest along all or part of the sagittal suture.	3
Infraglabellar notch	IN	The angle between the nasal bones and the frontal bone in profile. Grades range from small to large angles.	4
Supraorbital torus	ST	The supraorbital area ranging from flat or projecting to pronounced ridges that can often be divided into three portions (glabellar, superciliary, and trigone).	4
Zygomaxillary tuberosity	ZT	An elevation on the malar surface between its orbital and free margin. Grades range from smooth to a distinct ridge.	4
Zygomatic trigone	TR	The lateral portion of the supraorbital area formed by the frontal bone and the frontal process of the zygomatic. Grades range from small to pronounced.	4
Occipital torus	OT	Area between the superior and supreme nuchal lines. Grades range from a smooth nuchal region without visible supreme nuchal lines to a pronounced occipital torus.	6
Rounding of orbits	RO	Refers to the inferolateral orbital rim which can be either sharp or smooth, and the orbital floor can be depressed or elevated relative to the orbital rim.	3
Bregmatic eminence	BE	An eminence coinciding with the cranial vertex coupled with a slight elevation along the coronal suture.	2
Malar tubercle	MT	Area of contact between the zygomatic and frontal bone just inferior to the zygomaticofrontal suture. The angle of contact ranges from obtuse to acute. An obtuse angle usually lacks a tubercle; whereas an acute angle is most often associated with a small to large tubercle and cresting.	3
Supramastoid crest	SC	Cresting on the lateral surface of the temporal squama superior to the mastoid process (often continuous with the root of the zygomatic process anteriorly). Grades range from smooth to presence of crests extending superoposteriorly.	3
Anterior mastoid tubercle	AM	Absence or presence of a tubercle on the lateral surface of the mastoid process.	3

^a See Lahr (1996) for information about character states and scoring for SK, IN, ST, ZT, TR, OT, RO, and BE. Details about character scores for MT, SC, and AM can be found in Appendix A.

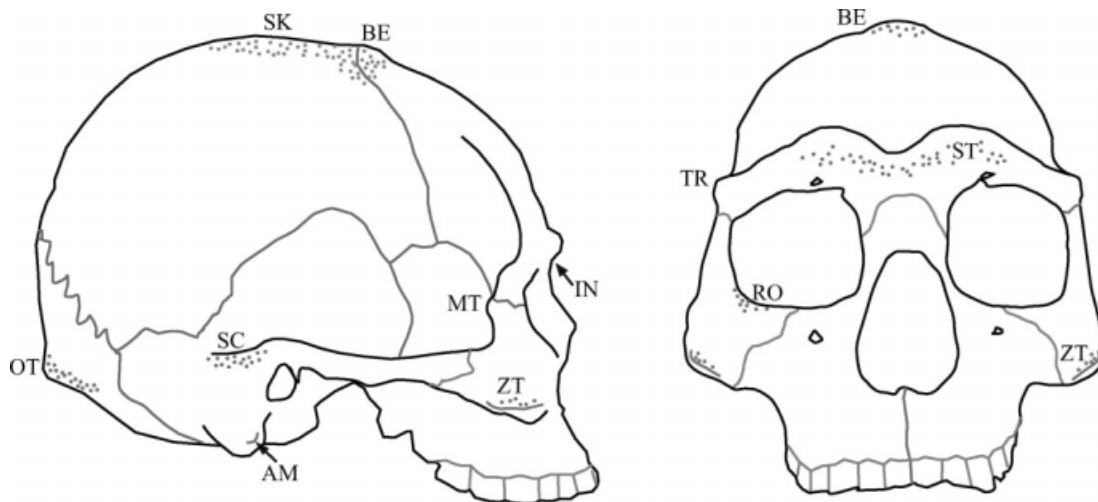


Fig. 1. All robusticity characters scored in this study. Trait abbreviations and definitions can be found in Table 2.

defined specifically for this study (Appendix A). Low grades corresponded to a more gracile expression of a given trait while higher grades indicated a more robust character state. The second data set consisted of three-dimensional (3D) landmarks acquired from each specimen with a Microscribe digitizer (Immersion Corp.) by

two of the authors (KB and SW). Multiple regressions indicated that differences due to interobserver error accounted for only 0.2% of the variation after controlling for differences among the regional/genetic groups; this small amount of interobserver error is not expected to influence the results of this analysis.

TABLE 3. Landmarks^a in cranial landmark set (CLS), facial landmark set (FLS), and masticatory landmark set (MLS), with abbreviations

CLS	FLS	MLS
Inion (INI), lambda (LA), bregma (BR), glabella (GL), alveolare (AL), alare (ALR), zygomaxillare (ZM), zygoorbitale (ZO), supraorbital notches (SON), anterior pterion (AP), porion (PO), asterion (AS), frontomolaretemporale (FMT), opisthion (OP), basion (BA), stylomastoid foramen (SF), maxillary tuberosity (MXT)	Glabella, midline post-toral sulcus (PTS), nasion (NA), anterior nasal spine (ANS), alveolare, infraorbital foramen (IF), alare, supraorbital notches, zygomaxillare, zygoorbitale, mid-torus superior (MTS), mid-torus inferior (MTI), frontomolareorbitale (FMO), jugale (JU), frontotemporale (FT), frontomolaretemporale, frontosphenomolare (FSM), malar root (MR), superior zygomaticotemporal suture (SZT), root of the zygomatic process (ZP), staphylion (ST), maxillary tuberosity	Alveolare, zygomaxillare, frontotemporale, staphylion, postglenoid (PG), inferior zygomaticotemporal suture (IZT), lateral prosthion (LP), lingual canine (LC), canine-P3 contact (CP3), M1-M2 contact (M1-2), distal M3 (DM3)

^a Landmark definitions can be found in Baab (2007). Landmarks illustrated in Figure 2.

For the shape data, all missing bilateral landmarks were reconstructed by reflecting their antimeres across the midsagittal line (reflected relabelling; Mardia et al., 2000; Harvati, 2003; McNulty, 2003; Gunz and Harvati, 2007); all other landmarks were averaged with their reflected configurations to remove bilateral asymmetry. For each subset of landmarks analyzed, the data were superimposed using generalized Procrustes analysis (GPA; Gower, 1975; Rohlf and Slice, 1990; Rohlf, 1999), thereby removing the effects of scale, translation, and orientation. GPA was performed in Morphueus et al. (Slice, 1998). Statistical analysis was then performed on the Procrustes superimposed landmark data. Centroid size, the square root of the sum of squared distances from each landmark to the centroid, was calculated for each specimen; logged centroid size was used as a proxy for overall size in subsequent analyses (Table 1). Three distinct subsets of landmarks were analyzed: cranial (CLS), masticatory (MLS), and facial (FLS) (Table 3 and Fig. 2). The MLS consisted of 20 landmarks that reflected the constrained lever model of mastication (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). These landmarks were identical to those of Singleton (2005) with the addition of frontotemporale to reflect the anterior position of the *temporalis* muscle, a major muscle of mastication. Singleton (2005) demonstrated the utility of this landmark set in elucidating the relationship between craniofacial morphology and mastication in mangabey monkeys. In addition, previous research indicates that chewing a softer, more processed diet results in reduction of the facial skeleton in modern humans, including the lower face, a pattern that should be reflected by this landmark set.

Polychoric correlation coefficients were calculated among all of the robusticity variables to investigate patterns of covariation among the various discrete robusticity characters. Polychoric correlations are maximum likelihood estimates of the product-moment correlations among ordered categorical variables, assuming an underlying bivariate normal distribution for the variables (SAS Institute, 2003). The polychoric correlation (equivalent to a tetrachoric correlation for dichotomous variables) is the preferred measure of association between two continuous characters (Krzanowski, 2000) and has been used previously in paleoanthropology in similar contexts (Konigsberg et al., 1993; Hanson and Pearson, 2007). Principal

components analysis (PCA) of the standardized robusticity scores was used to investigate covariation of these characters across groups. Multiple regression analysis was then used to assess the relationship between principal component scores and sex (scored as dummy variables; individuals of unknown sex excluded) and logged centroid size. All statistical analyses were performed in the SAS 9.1 statistical package (SAS Institute, Cary, NC).

Climatic and genetic data. Supplementary data on climate and genetic relatedness were collated for each of the 14 regional/genetic groups described above. Average values from 1961 to 1990 were used for average temperature, precipitation, vapor pressure, and wind speed (Table 4). Average values for minimum and maximum temperature were from either January or July depending on the hemisphere. These variables were interpolated from thousands of local climate stations corresponding to the latitude and longitude reported in Table 4 (<http://www.ipcc-data.org/java/visualisation.html>; see New et al., 1999, 2000 for more details). For groups sampled from more than one location, such as East Africa, an average location was determined and the climatic values for this location were used (Harvati and Weaver, 2006a; Smith et al., 2007).

Microsatellite data at 783 autosomal microsatellite loci were genotyped from 1,056 individuals across the world (Cann et al., 2002; Rosenberg et al., 2002, 2005; Ramachandran et al., 2005). An additional 422 Native Americans were typed for 678 of the same loci (Wang et al., 2007), resulting in the most complete set of microsatellite data available for modern humans. A smaller set of these loci were also typed for 10 indigenous Australians (<http://research.marshfieldclinic.org/genetics/home/index.asp>). Sample sizes for the genetic samples are tabulated in Table 1. Microsatellites are polymorphic loci in non-coding regions of the genome that consist of repeating units of DNA from one to five base pairs long. The number of repeated units varies among individuals and populations; these neutral genetic markers are commonly used in quantitative genetics to establish a model of neutral evolution.

Data analysis

Distance calculations. Interpopulation distances were calculated for all datasets. Mahalanobis D^2 distances for the robusticity data were computed via method M_3 of

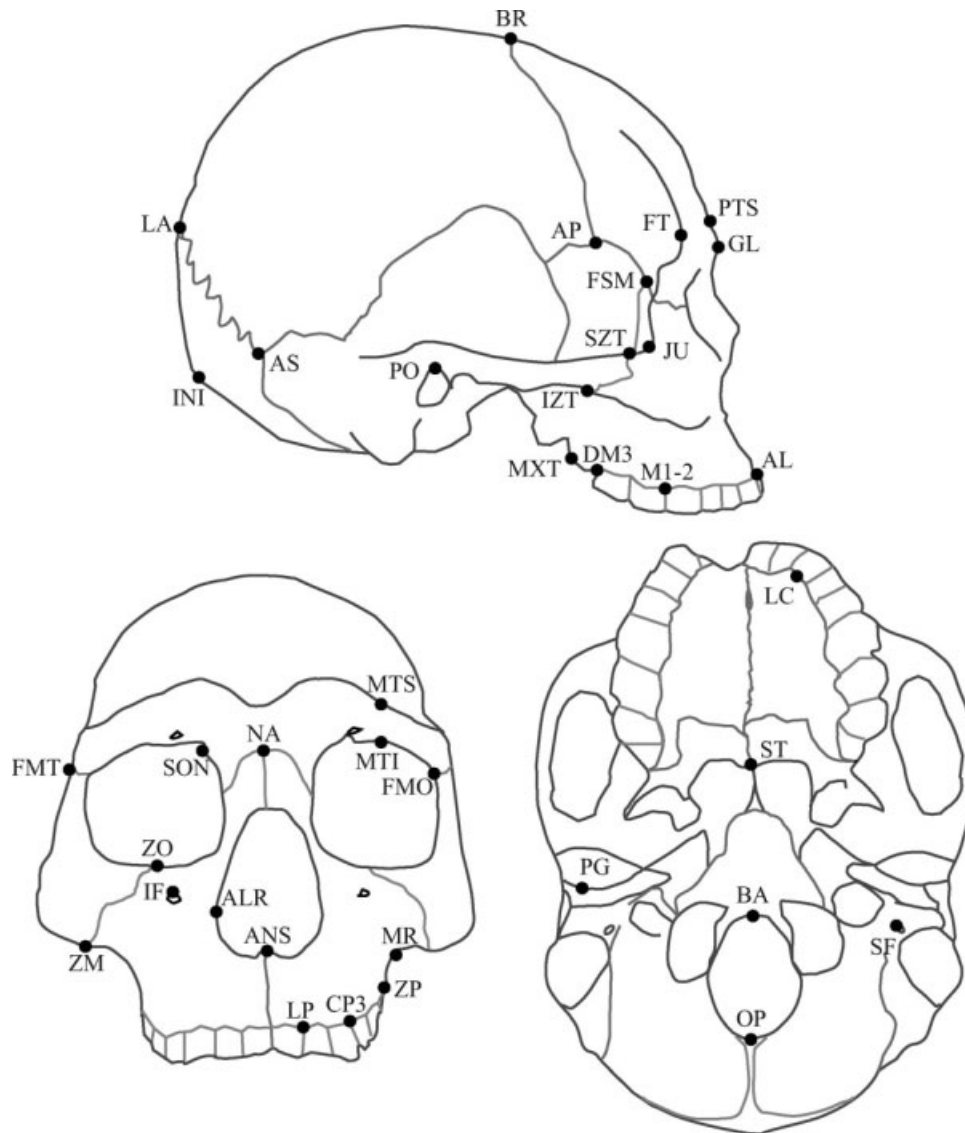


Fig. 2. All three-dimensional landmarks analyzed in this study. Trait abbreviations and definitions can be found in Table 3.

Hanson and Pearson (2007) (Table 5). This approach assumes correlated latent continuous Gaussian variates underlying the ordinal outcomes (which are discretized according to cutoffs [threshold values]), and a hierarchical structure on the group means underlying the latent variates. The Mahalanobis distance is computed from the latent group means and common covariance matrix, and is essentially imputed through Gibbs sampling. A proper prior on the common covariance matrix was assumed based on maximum likelihood estimates from treating the ordinal data as continuous. This approach was used to avoid infinite parameter estimates stemming from several groups that had only one level of a measurement for a given robusticity character. The Mahalanobis distance calculations used for both the robusticity and shape data are based on the pooled variance-covariance for the entire sample rather than just the two samples being compared which reduced the effects of small samples.

To create a single distance measure related to climate, we calculated squared Euclidean distances among

groups based on the standardized mean climatic variables for each group (Table 6). For the shape data, principal components analysis of the Procrustes superimposed shape variables was performed, and the minimum number of components that accounted for 99% of the total variance were used to calculate Mahalanobis D^2 distances among the 14 groups (Tables 6 and 7). Our size distance matrix was based on the squared differences in centroid size (Table 8). Statistical analysis was performed in the SAS 9.1 statistical package (SAS Institute, Cary, NC).

For the genetic data, delta mu squared (D_{dm} ; Goldstein et al., 1995) distances based on the 348 loci common to all three data sets were generated in the Microsatellite Analyzer (MSA) software package (Dieringer and Schlötterer, 2003) (Table 8). As discussed by Harvati and Weaver (2006a), this measure of genetic distance is appropriate for comparison with the Mahalanobis D^2 distances generated for the robusticity data because both are squared intergroup distance measures. Distances between the native Americans and other genetic groups

TABLE 4. Climatic variables^a for 14 regional/genetic groups based on the given latitude and longitude

	Long.	Lat.	Ave. temp.	Min. temp.	Max. temp.	Ave. precip.	Ave. V.P.	Wind Spd.
Aust	145.0	-35.0	15.0	3.3	29	1.5	8.4	3.0
Eaf	35.5	-3.5	21.0	13.0	28.1	2.0	17.5	2.8
EAs ^b	115.0	35.0	14.4	-4.8	31.8	1.9	12.9	2.6
EEur	23.0	50.0	8.0	-6.6	22.9	1.9	9.1	3.4
Inui	-166.5	68.5	-4.6	-19.8	11.4	1.0	3.8	5.1
KSan	23.3	-32.4	16.9	3.9	31.8	0.7	10.3	2.9
Mong	105.0	46.0	3.0	-22.3	26.5	0.4	5.5	3.3
NAm	-111.0	38.0	10.5	-9.8	33.0	0.6	6.2	4.2
SAm	-70.0	-54.0	3.7	-1.0	12.9	1.4	6.1	5.1
SEAs	110.0	5.0	24.8	21.8	31.1	8.0	29.2	1.5
SEur	17.5	41.0	16.4	4.0	28.7	1.8	11.9	3.6
Waf	3.0	8.5	27.3	20.9	34.7	3.1	24.6	1.8
WEur	11.5	50.5	7.7	-4.8	21.3	1.8	8.7	3.2
Zeal	175.0	-40.0	12.6	3.8	21.5	3.3	12.2	3.5

^a Units are as follows: degrees Celsius (temperature), mm/day (precipitation), hectopascals (hPa; vapor pressure) and meters/second (wind speed).

^b The East Asia group consists of Chinese individuals collected from several localities (including Borneo and San Francisco), but the majority of specimens were collected from the northeast region of the country. The climatic data similarly reflect conditions in the northeast region of China.

TABLE 5. Mahalanobis D² distances for robusticity traits

Aust	0														
Eaf	3.72	0													
EAs	6.89	8.12	0												
EEur	4.52	5.93	6.70	0											
KSan	6.66	7.05	3.94	4.16	0										
Mong	8.25	9.74	2.13	5.83	3.31	0									
Zeal	4.98	6.85	5.31	4.17	5.82	5.38	0								
NAm	7.31	7.07	6.22	4.95	5.51	5.68	3.48	0							
SEAs	4.56	5.85	6.36	2.29	4.48	5.81	5.28	5.91	0						
SAm	6.40	6.32	6.42	4.27	5.17	6.43	4.15	3.97	5.13	0					
SEur	3.07	4.30	4.94	3.92	4.11	5.71	6.61	8.17	3.29	6.02	0				
Waf	4.47	3.62	7.28	4.21	6.16	8.05	4.80	4.45	4.03	4.09	4.96	0			
WEur	3.84	4.85	3.86	3.01	2.89	4.03	5.31	6.04	2.32	4.79	1.90	4.28	0		
Inui	7.85	6.16	5.87	4.29	3.71	5.20	4.63	4.76	4.88	4.92	6.13	4.97	4.57	0	
Aust	Eaf	EAs	EEur	KSan	Mong	Zeal	NAm	SEAs	SAm	SEur	Waf	WEur	Inui		

TABLE 6. Matrix of Mahalanobis D² distances for CLS (unshaded) and squared Euclidean distances based on climatic variables (shaded)

	Aust	Eaf	EAs	EEur	KSan	Mong	Zeal	NAm	SEAs	SAm	SEur	Waf	WEur	Inui
Aust	0	2.69	1.11	2.14	0.45	6.43	2.56	3.24	25.27	10.99	0.62	11.36	2.29	18.70
Eaf	29.38	0	3.13	6.64	2.41	15.23	3.71	9.71	14.97	16.97	1.95	3.93	6.67	28.97
EAs	37.66	39.59	0	2.95	1.14	6.14	3.83	4.07	22.02	15.22	1.65	9.76	3.38	21.65
EEur	35.40	33.59	26.99	0	3.87	2.90	1.68	3.33	30.97	5.29	2.42	19.25	0.11	9.09
KSan	43.91	33.27	45.88	39.66	0	7.70	4.57	3.56	26.03	14.28	1.03	9.81	4.14	22.68
Mong	64.70	60.09	16.57	37.00	59.64	0	8.90	3.24	47.61	9.54	7.90	30.90	3.35	8.36
Zeal	30.72	30.50	29.31	26.61	41.99	44.17	0	6.85	20.89	6.68	1.82	13.47	1.69	14.28
NAm	33.62	41.16	17.38	32.00	48.91	28.63	27.33	0	40.51	9.77	3.27	22.70	4.33	13.45
SEAs	21.11	19.73	13.76	17.63	34.47	32.37	11.54	16.82	0	49.41	23.29	7.50	31.05	66.69
SAm	36.43	38.77	38.14	36.08	52.60	59.51	27.19	28.55	21.96	0	9.83	36.59	5.19	3.16
SEur	36.51	26.03	20.95	10.98	44.11	31.47	14.42	26.70	13.13	34.78	0	10.42	2.84	18.35
Waf	30.36	20.27	38.81	48.96	40.85	68.49	31.60	42.09	20.31	41.60	34.93	0	19.36	52.93
WEur	46.60	42.97	24.53	12.76	44.16	23.34	35.36	28.42	24.20	51.72	14.26	62.26	0	9.18
Inui	44.21	59.76	15.06	40.62	57.73	24.38	34.24	11.34	26.31	40.45	33.62	53.86	35.88	0

have been increased due to a population bottleneck that occurred early in the settlement of the Americas (Mulligan et al., 2004; Wang et al., 2007; Halverson and Bolnick, 2008). Therefore, analyses were performed both with and without the American groups (i.e., Inui, NAm, SAm) (see also Smith et al., 2007). Distance matrices in Tables 5–8 correspond to the combined male–female sample.

Mantel tests. Mantel tests (Mantel, 1976; Smouse et al., 1986) were performed between the robusticity distance matrix and the other distance matrices (shape, size, genetic, and climatic) in the Excel add-in, PopTools (Hood, 2008). Each Mantel test results in a correlation coefficient (*r*) between the two sets of matrices. The significance test was calculated by randomizing the column and row labels in one matrix and recalculating the corre-

TABLE 7. Matrix of Mahalanobis D² distances for MLS (unshaded) and FLS (shaded)

	Aust	Eaf	EAs	EEur	KSan	Mong	Zeal	NAm	SEAs	SAm	SEur	Waf	WEur	Inui
Aust	0	39.72	47.86	76.50	81.59	90.55	83.00	54.77	45.91	123.93	75.50	44.99	55.46	89.30
Eaf	26.11	0	55.15	63.96	73.40	95.83	64.88	54.26	30.52	89.69	51.46	23.47	50.61	103.75
EAs	27.59	28.53	0	60.24	88.76	35.71	66.92	29.43	28.92	107.31	55.72	48.80	32.32	46.51
EEur	42.58	18.74	41.58	0	104.54	85.26	67.13	90.85	43.54	98.08	29.27	57.89	25.09	111.99
KSan	34.02	29.76	22.27	36.40	0	100.79	130.33	98.39	91.20	153.29	110.50	84.11	84.13	107.53
Mong	48.71	49.22	23.95	55.98	43.78	0	100.01	44.95	70.62	139.76	76.84	94.43	53.91	53.57
Zeal	26.63	18.72	20.64	14.49	29.28	34.70	0	95.98	50.74	95.48	43.83	66.47	64.49	109.30
NAm	23.15	26.32	11.18	39.37	29.77	18.76	19.31	0	50.92	131.40	75.35	71.04	50.36	53.20
SEAs	23.74	14.75	19.95	22.50	24.00	40.94	16.15	22.20	0	68.61	33.81	26.37	34.52	76.03
SAm	39.21	16.66	29.48	28.38	25.74	43.82	23.89	25.27	21.83	0	93.71	86.19	92.26	155.51
SEur	30.75	18.68	26.73	17.66	18.69	33.42	15.58	27.45	13.26	25.25	0	59.60	26.33	100.43
Waf	17.93	14.27	24.20	33.31	25.07	50.48	22.63	24.12	9.54	24.70	22.06	0	53.41	97.62
WEur	27.48	20.92	18.17	18.02	26.91	27.83	10.89	15.93	19.81	28.07	14.25	24.13	0	69.49
Inui	38.57	37.85	18.95	46.92	35.41	21.20	29.73	18.49	32.68	36.36	31.95	39.51	24.50	0

TABLE 8. Matrix of Ddm genetic distances (unshaded) and squared differences in centroid size (shaded)

	Aust	Eaf	EAs	EEur	KSan	Mong	Zeal	NAm	SEAs	SAm	SEur	Waf	WEur	Inui
Aust	0	92.87	78.00	4.07	1.78	85.10	141.28	62.35	0.07	427.56	0.34	0.00	14.94	363.96
Eaf	0.98	0	0.65	58.05	68.96	0.17	5.06	3.03	97.87	121.89	81.99	92.95	33.32	89.12
EAs	0.49	0.82	0	46.43	56.23	0.15	9.33	0.88	82.58	140.32	68.05	78.07	24.67	104.98
EEur	0.65	0.74	0.35	0	0.47	51.94	97.38	34.56	5.17	348.18	2.06	4.09	3.41	291.04
KSan	1.37	0.85	1.33	1.20	0	62.28	111.36	43.07	2.52	374.20	0.56	1.79	6.41	314.87
Mong	0.63	0.88	0.15	0.33	1.45	0	7.08	1.77	89.88	131.16	74.69	85.17	28.73	97.08
Zeal	0.45	0.89	0.60	0.68	1.27	0.74	0	15.92	147.42	77.29	127.77	141.37	64.33	51.72
NAm	1.19	1.30	0.71	0.86	1.92	0.70	1.22	0	66.45	163.36	53.49	62.41	16.25	125.02
SEAs	0.57	0.87	0.15	0.49	1.37	0.30	0.70	0.85	0	438.19	0.70	0.06	16.98	373.77
SAm	0.92	1.16	0.54	0.62	1.60	0.55	0.92	0.46	0.69	0	403.82	427.72	282.66	2.56
SEur	0.67	0.80	0.41	0.11	1.22	0.40	0.75	0.93	0.53	0.65	0	0.34	10.78	342.07
Waf	0.99	0.25	0.84	0.78	0.90	0.95	0.94	1.41	0.87	1.16	0.80	0	14.97	364.10
WEur	0.64	0.84	0.39	0.09	1.26	0.37	0.73	0.88	0.52	0.60	0.08	0.84	0	231.42
Inui	0.92	1.04	0.42	0.50	1.57	0.44	0.98	0.51	0.59	0.42	0.55	1.12	0.54	0

lation coefficient, creating a distribution of 10,000 coefficients under the null hypothesis. If the r value for the original matrix correlation exceeds 95% of the randomized values, then it is considered significant at the $\alpha = 0.05$ level (one-tailed test). The Bonferroni-Holm (stepwise) correction for multiple tests was performed and reported alongside the original P values (Holm, 1979). Correlations were calculated for males and females combined, as well as males and females separately. The Upper Paleolithic/Neolithic individuals were excluded from the single sex analyses because previous analysis has suggested a general decrease in cranial robusticity over time in modern humans (Lahr and Wright, 1996), making it difficult to assess sex for isolated specimens without larger comparative samples from that time period.

Two-block partial least squares. One advantage of 3D landmark data over linear measurements is that shapes can be visualized. However, it was not possible to visualize what shapes are associated with a given pattern of robusticity using the Mantel test. Hence, two-block partial least-squares (2B-PLS) analysis was used to investigate the covariation between the standardized robusticity traits and mean-centered Procrustes superimposed coordinates. 2B-PLS calculates pairs of latent variables, one for each set of variables, that maximize the covariation between these two sets of observations (i.e., the shape coordinates and robusticity scores) (Rohlf and Corti, 2000). The 2B-PLS procedure is like that of a PCA, but is performed on the cross-covariance matrix rather than the within group covariance matrix (Book-

stein, 1991). As the goal of a 2B-PLS is to maximize covariance between the variable sets rather than variance within a set of variables (the goal of PCA), subsequent pairs of variables account for successively less of the total covariance. Unlike multiple multivariate regression, 2B-PLS does not assume that one set of variables is the predictor (and conversely, that the other set is the dependent variables), but rather both sets (blocks) are treated symmetrically (Zelditch et al., 2004). This is appropriate because an external set of conditions, developmental processes for example, may be responsible for any covariation observed between cranial shape and cranial robusticity. Only midline and right side landmarks were analyzed in the 2B-PLS analysis.

We present results for those pairs of latent variables that accounted for a substantive proportion of the total covariance (20% was chosen as an arbitrary cutoff); subsequent pairs of variables were not easily interpretable. A permutation test was performed to assess the significance of these dimensions as described by Rohlf and Corti (2000). The order of specimens in one block of variables was randomly reordered and the analysis was repeated; the procedure was performed a total of 10,000 times. If the squared covariance recorded for the original pair of latent variables exceeded 95% of the squared covariances for these permuted samples, then this was considered a significant result (Rohlf and Corti, 2000). The scores of each specimen on the latent variables can be plotted to graphically express the pattern of covariation captured by that dimension, and the shape variation associated with the shape component can be visualized by adding/subtracting the vector of weights to/from the

TABLE 9. Matrix of polychoric correlation coefficients among the 11 robusticity traits; coefficients $\geq |0.3|$ are in **bold**. See Table 2 for character definitions

SK	1										
IN	0.232	1									
ST	0.220	0.843	1								
ZT	0.254	0.466	0.592	1							
TR	0.333	0.484	0.566	0.499	1						
OT	-0.112	-0.032	0.106	0.145	0.100	1					
RO	0.084	0.267	0.298	0.314	0.175	0.167	1				
BE	0.428	0.358	0.352	0.277	0.657	-0.144	0.493	1			
MT	0.256	0.150	0.193	0.249	0.252	0.107	0.161	0.382	1		
SC	0.245	0.346	0.284	0.241	0.272	0.042	0.167	0.240	0.123	1	
AM	0.260	0.359	0.011	0.197	0.188	-0.105	0.008	0.395	0.067	0.431	1
	SK	IN	ST	ZT	TR	OT	RO	BE	MT	SC	AM

consensus landmark configuration. The 2B-PLS and permutation tests were performed by a routine written in SAS/IML (Interactive Matrix Language) by K.L.B.; results of the 2B-PLS were confirmed in MorphoJ (Klingenberg, 2008). Wireframe illustrations were generated using Morphueus et al. (Slice, 1998).

Hypothesis testing

By performing Mantel tests on each pair of distance matrices, it was possible to compare the correlations between robusticity and neutral genetic distances, size, shape, and climate. To test the null hypothesis of neutral evolution for cranial robusticity in modern humans, the Mahalanobis D^2 distances based on robusticity characters were compared to the Ddm distances derived from the microsatellite data. If the robusticity traits are the subject of neutral evolutionary processes, then the distance matrix based on these characters will be strongly correlated with that based on the neutral genetic markers (microsatellite data) (e.g., Roseman, 2004). Assuming that the morphological features being studied are adequately described by an equal and additive effects model; then statistically significant deviations from this neutral pattern indicate selection is acting on these characters.

If the expression of robusticity was strongly correlated with the size or shape of the cranium, this would imply functional or developmental integration of robusticity and cranial form. These functional/developmental factors may or may not be related to mastication as it is theoretically possible that these features form as a way to strengthen regions of the skull for reasons other than mastication-related stresses (e.g., protection from inter-individual violence). A functional hypothesis that specifically implicates forces associated with mastication would be supported by a stronger correlation between cranial robusticity and the MLS rather than CLS as the former more directly captures morphology associated with mastication, although it is also possible that changes in overall cranial shape may be related to mastication. A strong relationship between cranial robusticity and the climatic variables would support the influence of the local environment on the development of cranial robusticity.

RESULTS

Correlations among robusticity traits

Nearly all robusticity traits are positively correlated (Table 9). The polychoric correlation coefficients range from -0.144 (occipital torus and bregmatic eminence) to 0.843 (infraglabellar notch and supraorbital torus). The

highest positive correlations are among infraglabellar notch, supraorbital torus, zygomatic trigone, and zygomatic tuberosity. This pattern is not surprising given that three of the four traits (infraglabellar notch, supraorbital torus, and zygomatic trigone) are related to expression of the supraorbital elements. The two traits located in the mastoid region (anterior mastoid tubercle and supramastoid crest) are also strongly correlated. Several of the correlations involving the occipital torus are negative and all are quite low, indicating that this trait is neither strongly positively nor strongly negatively correlated with the other robusticity traits.

Principal components analysis

In deciding how many PCs to evaluate, we applied the common Guttman-Kaiser criterion (keep all PCs with eigenvalues >1.0 ; Kaiser, 1961), which results in the retention of the first three components. However, a more conservative criterion, the Scree Plot (Cattell, 1966), suggests that only PC 1 should be retained. Although PC 1 accounted for a proportionally larger percentage of the total variance in cranial robusticity (27%), the second and third components each explain 11% of the variance and may indicate that there is more than one relevant pattern of cranial robusticity (Table 10).

The first PC reflects overall levels of robusticity as all 11 traits load positively (Table 10), although the occipital torus has a loading near zero. This is consistent with the results of the correlation matrix in that the occipital region does not follow the same pattern as the other traits. The groups with the highest median (and mean) scores are New Zealand, Australia/Tasmania, North America, and South America, while the lowest scores belong to Mongolia, East Asia, Inuit, and Khoe-San (see Fig. 3). Analysis of variance (ANOVA) was used to assess whether groups had significantly different mean scores on each PC (Table 10). Several of the pairwise group contrasts between the highest and lowest scoring groups are significant, particularly those involving North America, New Zealand, and East Asia.

Size and sex account for about a third of variation in PC 1 scores ($r^2 = 0.36$, $P < 0.0001$), with both variables contributing significantly to the model. Males score significantly higher than females on PC 1 within all groups except the East and West Europeans, East and West Africans, and Khoe-San (Table 11), but males scored higher on average than females even in those groups that did not reach statistical significance. The r^2 values ranged from 0.36 (North America) to 0.98 (South America). Therefore, the large spread seen within each regional/genetic group along PC 1 is at least partially

TABLE 10. Results of PCA of the standardized robusticity scores from 260 individuals

Eigenvalue	PC 1	PC 2	PC 3
	3.01 (27.4%)	1.22 (11.1%) Trait loadings	1.19 (10.8%)
SK	0.26	-0.39	0.36
IN	0.42	0.14	-0.37
ST	0.45	0.25	-0.29
ZT	0.39	0.21	0.00
TR	0.38	-0.02	0.19
OT	0.03	0.55	0.32
RO	0.18	0.30	0.14
BE	0.20	-0.31	0.32
MT	0.20	0.03	0.55
SC	0.29	-0.18	-0.12
AM	0.25	-0.44	-0.26
Significant Group	<u>EAs</u> —Zeal, NAm,	<u>EAF</u> —Aust, EAs, KSan,	<u>Aust</u> —Inui, EAs, Zeal, Mong, NAm
Contrasts: ANOVA	SAM	SEur, Mong, WEur	
(with Bonferroni-Holm	<u>Nam</u> —Inui, WEur,	<u>EAs</u> —EEur, Zeal, NAm,	<u>EAs</u> —EEur, SEAs, SEur, WEur
Correction)	Mong	SEAs, Waf, Inui	
	<u>Zeal</u> —Inui, WEur	<u>Mong</u> —EEur, Inui,	<u>Nam</u> —WEur, SEAs, Eaf, SEur, EEur
		NAm, Waf, SEAs	
			<u>SEur</u> —Inui, Mong, Zeal
			<u>Zeal</u> —SEAs, WEur, EEur

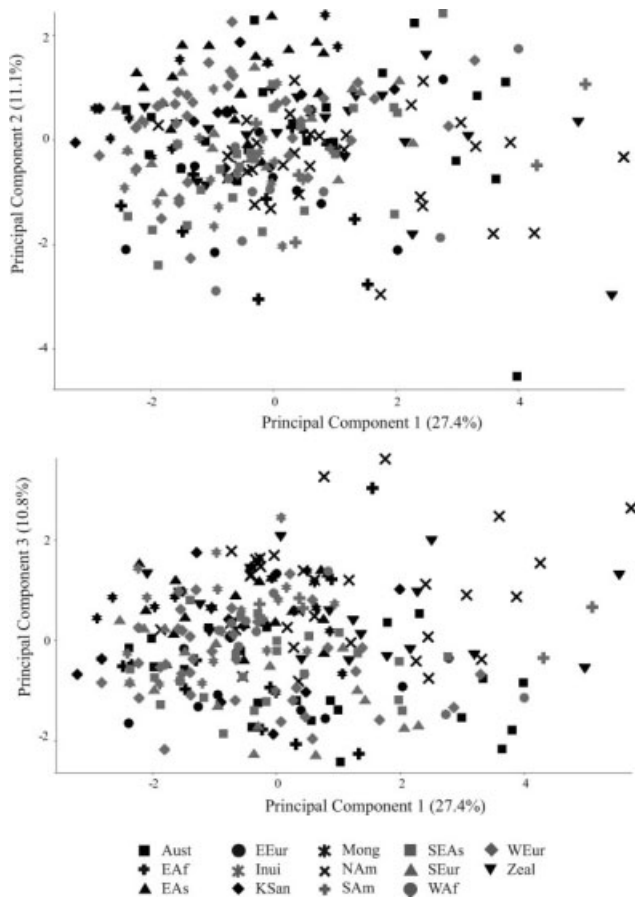


Fig. 3. Principal components analysis of robusticity traits: (a) PC 1 vs. PC 2 and (b) PC 1 vs. PC 3.

related to sexual variation in the expression of cranial robusticity.

The second PC has both high positive (occipital torus, rounding of orbits) and high negative (sagittal keel, anterior mastoid, bregmatic eminence) loadings, indicating

TABLE 11. Tests for significant sex differences on PC 1 within each genetic group

Group	r^2	P	Bonferroni-Holm adjusted P
Aust	0.64	<0.01	<0.01
EAFr	0.39	0.05	0.16
EAs	0.53	<0.01	<0.01
EEur	0.49	0.02	0.07
KSan	0.39	0.07	0.16
Mong	0.72	<0.01	<0.01
Zeal	0.65	<0.01	<0.01
NAm	0.36	<0.01	0.01
SEAs	0.40	<0.01	0.01
SAM	0.98	<0.01	0.01
SEur	0.54	<0.01	<0.01
W Afr	0.28	0.11	0.16
WEur	0.17	0.01	0.07
Inui	0.52	<0.01	0.02

increased robusticity in some aspects of cranial morphology but decreased robusticity in others. The highest scoring groups on PC 2 are East Asia, Mongolia, Australia/Tasmania, and the Khoe-San, while East Africa, West Africa, and Eastern Europe have low scores (Fig. 3a). Many of the pair-wise contrasts between the highest and lowest scoring groups are significant, particularly those that include East Africa, East Asia, and Mongolia (Table 10). It appears that while the East Asian populations are gracile overall (see above), they do display some characters typically considered as “robust” (e.g., the occipital torus). Only sex (not size) differences are significant on PC 2, but account for only 3% of the total variation ($P = 0.0224$).

The third PC also has a mixed pattern of positive and negative loadings. The traits with the highest loadings are sagittal keel, occipital torus, malar tubercle, bregmatic eminence (all positive), infraglabellar notch and supraorbital torus (both negative). The North American and, to a lesser extent, New Zealand, groups score highest on PC 3, in contrast to Australia/Tasmania, Southern Europe, Eastern Europe, and East Africa (Fig. 3b). While both the North American and Australian/Tasmanian

TABLE 12. Results of Mantel tests based on 10,000 permutations^a

Correlation between Mahalanobis D^2 based on robusticity traits and:	r	P	Bonferroni-Holm adjusted P
All specimens			
Ddm genetic distances	0.139	0.159	0.636
Ddm genetic distances (no Americas)	0.165	0.177	0.636
Squared centroid size differences	0.097	0.228	0.636
Squared Euclidean distances based on all climatic variables	0.00	0.500	0.636
Mahalanobis D^2 distances based on CLS	0.294	0.012	0.072
Mahalanobis D^2 distances based on FLS	0.179	0.104	0.52
Mahalanobis D^2 distances based on MLS	0.334	0.006	0.042
Males only			
Ddm genetic distances	0.128	0.207	0.621
Ddm genetic distances (no Americas)	0.127	0.269	0.807
Squared centroid size differences	0.192	0.110	0.44
Squared Euclidean distances based on all climatic variables	-0.083	0.311	0.807
Mahalanobis D^2 distances based on CLS	0.321	0.011	0.077
Mahalanobis D^2 distances based on FLS	0.205	0.086	0.43
Mahalanobis D^2 distances based on MLS	0.283	0.021	0.126
Females only			
Ddm genetic distances	0.013	0.479	1.413
Ddm genetic distances (no Americas)	0.039	0.468	1.872
Squared centroid size differences	0.010	0.479	1.413
Squared Euclidean distances based on all climatic variables	0.176	0.169	1.014
Mahalanobis D^2 distances based on CLS	-0.012	0.471	1.413
Mahalanobis D^2 distances based on FLS	-0.115	0.265	1.325
Mahalanobis D^2 distances based on MLS	0.387	0.006	0.042

^a Robusticity-distance and size-difference matrices are based on the available specimens from the CLS analysis.

TABLE 13. Results of 2B-PLS between standardized robusticity scores and Procrustes aligned landmark (shape) data

	Dimension 1			Dimension 2		
	%	r	Loadings $\geq 0.3 $	%	r	Loadings $\geq 0.3 $
CLS	0.471	0.483	IN, ST, RO, SC, AM	0.198	0.483	SK, ZT, TR, OT, MT, <i>IN</i>
FLS	0.495	0.495	IN, ST, AM	0.316	0.506	SK, ZT, TR, OT, MT
MLS	0.566	0.599	IN, AM, <i>TR, OT, MT</i>	0.275	0.433	SK, ST, ZT, TR, RO

Only the results for the first two dimensions are shown. % is the proportion of total squared covariance, r is the correlation coefficient between the robusticity and shape vectors (all are significant at $P < 0.0001$); variables with negative loadings are in italics.

groups are fairly robust overall (as indicated by their high scores on PC 1), they exhibit significantly different patterns of character expression on PC 3. Together, size and sex explain only 8% of variation in PC 3 scores ($P < 0.0001$).

Relationship between external variables and cranial robusticity

The correlation coefficients from the Mantel tests are weak, ranging from -0.115 to 0.387 (Table 12). The null hypothesis of neutral evolution was rejected as the robusticity distances were not significantly correlated with neutral genetic distances.

The strongest (and only significant) correlations are between cranial robusticity and cranial (CLS) or masticatory apparatus shape (MLS). Cranial robusticity in the combined male-female sample is significantly correlated with the masticatory shape, and its correlation with overall cranial shape approached significance (Table 12). The relationship with masticatory shape was also significant in the female-only analysis, while the relationship between robusticity and overall cranial shape neared significance in the male-only comparison. Although signifi-

cant, the r values support only a weak correlation between these sets of intergroup distances.

Intergroup differences in cranial robusticity were not significantly correlated with overall cranial size or climate. Mantel correlations were also calculated between the robusticity Mahalanobis D^2 distances and the squared differences for each climatic variable (e.g., average temperature). None of these correlations were significant after the Bonferroni-Holm adjustment, and were therefore not reported, but both minimum temperature and average vapor pressure were significant in females before the adjustment (minimum temperature: $r = 0.295$, $P = 0.030$; average vapor pressure: $r = 0.301$, $P = 0.027$).

2B-PLS analysis

The only significant correlations involved cranial robusticity and shape. While the Mantel tests indicate that groups sharing a similar pattern of cranial robusticity also have similarly shaped crania, the details of this relationship remain unclear. However, we have information about both cranial robusticity and shape for each individual in the analysis. We can use 2B-PLS to explore this relationship across individuals in a more informa-

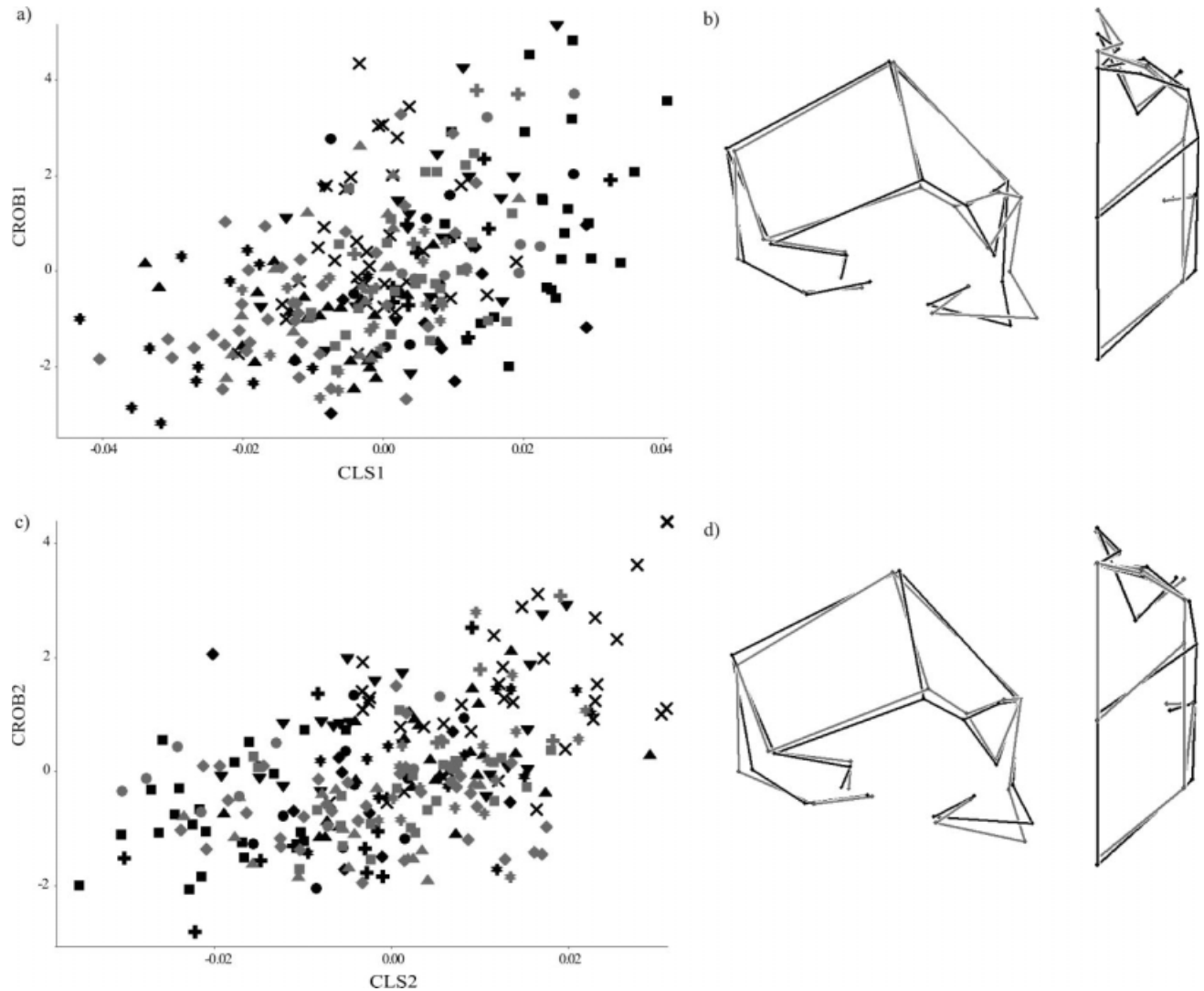


Fig. 4. Two-block partial least-squares analysis of cranial shape and cranial robusticity traits: (a) CROB1 vs. CLS1 and (c) CROB2 vs. CLS2. The shape change associated with (b) CROB1 and (d) CROB2 is shown in right lateral and superior views. The solid black line is the negative end of the component and the dashed gray line is the positive end. Legend same as in Figure 3.

tive manner. The summary statistics for the 2B-PLS analyses using the CLS, MLS, and FLS landmark sets are presented in Table 13. We used permutation tests on those dimensions (i.e., 2B-PLS latent variables) that accounted for 20% or more of the total covariance (the first two dimensions in all analyses). We found that these dimensions were highly significant in the CLS, FLS, and MLS analyses.

Shape of cranium (CLS) and robusticity. The first pair of latent variables explains almost half (47%) of the total covariation between robusticity traits and overall cranial shape, and the correlation between the shape and robusticity vectors (CLS1 and CROB1) is $r = 0.48$ (Table 13). The relatively low correlation value indicates that there is not a strong correspondence between the pattern of robusticity and the cranial shape of individual specimens, a similar result to that obtained by the Mantel test (Table 12). Individuals with high scores on both vectors are more robust overall (only the occipital torus trait has a negative loading), have more prognathic faces

in the midline, narrower cranial vaults at pterion and asterion, and stronger angulation of the occipital bone (Fig. 4b). The greater projection of glabella and the supraorbital tori (as measured at the supraorbital notch) is consistent with the high positive loadings of infraglabellar notch and supraorbital torus traits on this dimension. Only the Australian/Tasmanian group scored high along both the shape and robusticity dimensions (Fig. 4a). The opposite pattern of cranial shape and greater gracility is seen in low scoring groups, particularly the Mongolians. In general, groups have greater dispersion along the robusticity vector (y -axis) than the shape vector. This pattern is consistent with males and females in the same genetic group having similar cranial shapes but varying in their expression of cranial robusticity. On the other hand, no single group spans the entire robusticity vector (although the New Zealand and Australian/Tasmanian groups come closest), confirming that some groups are more robust than others regardless of sex.

The second dimension accounts for a fifth of the total covariation between robusticity and cranial shape; the

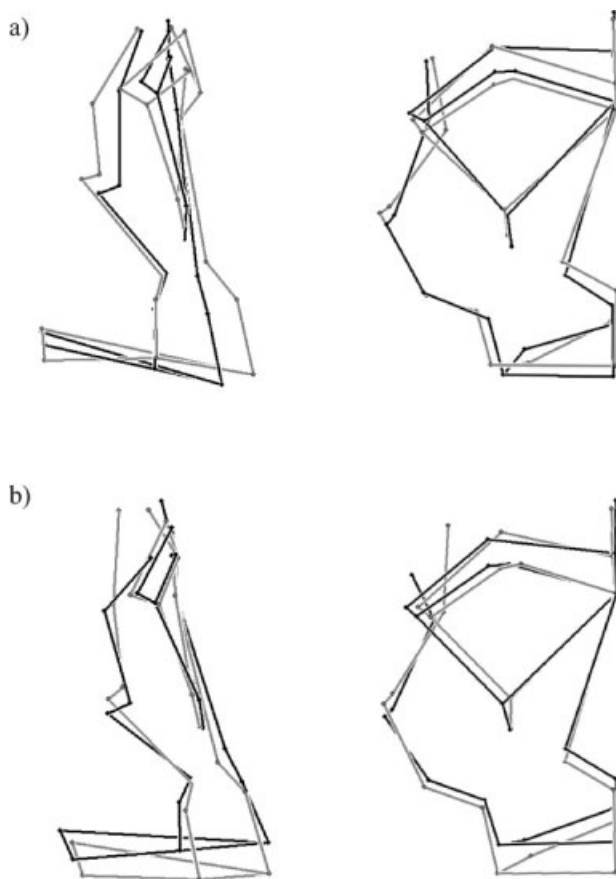


Fig. 5. Two-block partial least-squares analysis of facial shape and cranial robusticity traits. The scores along the pairs of latent variables are similar to that seen in Figure 4a,c, and are not replicated here. The shape associated with (a) the first and (b) second facial shape vectors are illustrated in right lateral and anterior views. The solid black line is the negative end and the dashed gray line is the positive end.

correlation between these vectors is $r = 0.48$. Higher scoring groups, particularly the North Americans (Fig. 4c), have a stronger expression of the sagittal keel, zygomaxillary tuberosity, zygomatic trigone, malar tubercle, and occipital torus but a weaker expression of the infraglabellar notch (Table 13). These groups have long orthognathic faces that are narrower across the supraorbital region but wider across the malars, and narrower cranial vaults with more tightly angled occipitals (Fig. 4d). The more posterior position of inion is consistent with the high positive loading of the occipital torus trait on this dimension. There is not a single group that scored very low on both vectors, although the East African and Australian/Tasmanian groups are among the lowest. The second pair of singular vectors highlights a similar pattern to that described above for PC 3.

Shape of face (FLS) and robusticity. The overall patterns highlighted by the FLS 2B-PLS analysis were very similar to those reported for the CLS analysis (Table 13). The wireframes of the facial shapes associated with the first two dimensions again emphasize that different patterns of robusticity are associated with either prognathic (e.g., Australian/Tasmanian) or long orthognathic (e.g., Grand Gulch) facial morphologies (see Fig. 5).

Shape of masticatory system (MLS) and robusticity.

The first dimension accounts for 57% of the covariation between the masticatory landmarks and robusticity variables. The correlation between individuals' scores on the robusticity and shape vectors is higher than that seen in the CLS analysis ($r = 0.60$). There is a combination of high positive and negative loadings on MROB1. Higher scoring groups, such as the Australian/Tasmanians, East Africans, and Eastern Europeans (Fig. 6a), have a more robust expression of the infraglabellar notch and anterior mastoid traits but weaker expression of the zygomatic trigone, occipital torus, and malar tubercle. The shape associated with the positive end of the MLS1 vector includes an anteroposteriorly longer and more superiorly positioned palate, more posteriorly situated inferior zygomaticotemporal suture and postglenoid process, and a more anteroinferolateral location for frontotemporale (Fig. 6b). The Mongolian, North American, and East Asian groups have the lowest scores on the two vectors.

The second pair of latent variables is more clearly associated with an overall increase in robusticity. There is not, however, a high degree of correspondence between scores on the two vectors ($r = 0.43$), which is reflected in the greater scatter illustrated in Figure 6c compared with 6a. Whereas South Europe is among the lowest scoring groups on both the shape and robusticity vectors, the highest scoring groups on the robusticity vector (e.g., South America and New Zealand) are not the highest scoring groups on the shape vector (specifically Australia/Tasmania). The more gracile groups (e.g., South European) have more anteriorly positioned zygomatic bones (as indicated by the inferior zygomaticotemporal suture and zygomaxillare), more laterally located postglenoid processes and frontotemporale, and relatively larger cheek teeth (in the anteroposterior direction) that are more superiorly positioned.

DISCUSSION

The individual cranial traits investigated in this study generally showed a pattern of weak to moderate positive coexpression, with the exception of the occipital torus region, which has particularly low or even negative correlation coefficients. Based on the pattern of inter-correlation among these traits, Lahr and Wright (1996) argued against the use of robusticity characters in phylogeny because they are not independent of one another. The strongest correlation coefficients reported in this study are among traits from limited anatomical regions (e.g., the supraorbital region), and most of the coefficients were less than 0.3 (the average coefficient was 0.254; this increased to 0.304 when the occipital torus values were excluded). This suggests that while there may be some integration in the expression of these particular cranial features, this pattern is not particularly strong. The analyses above also revealed variation among groups in the patterns of expression of robust cranial traits (see below). It remains unclear to what extent the inter-correlation of these characters is related to underlying genetic, developmental, or functional mechanisms. The coexpression of these traits may indicate a pleiotropic effect or these characters may be linked developmentally or functionally such that small shifts in the developmental or functional regime would simultaneously affect these traits. One way to address this possibility would be to trace the appearance of these traits in ontogeny. If they develop chronologically before

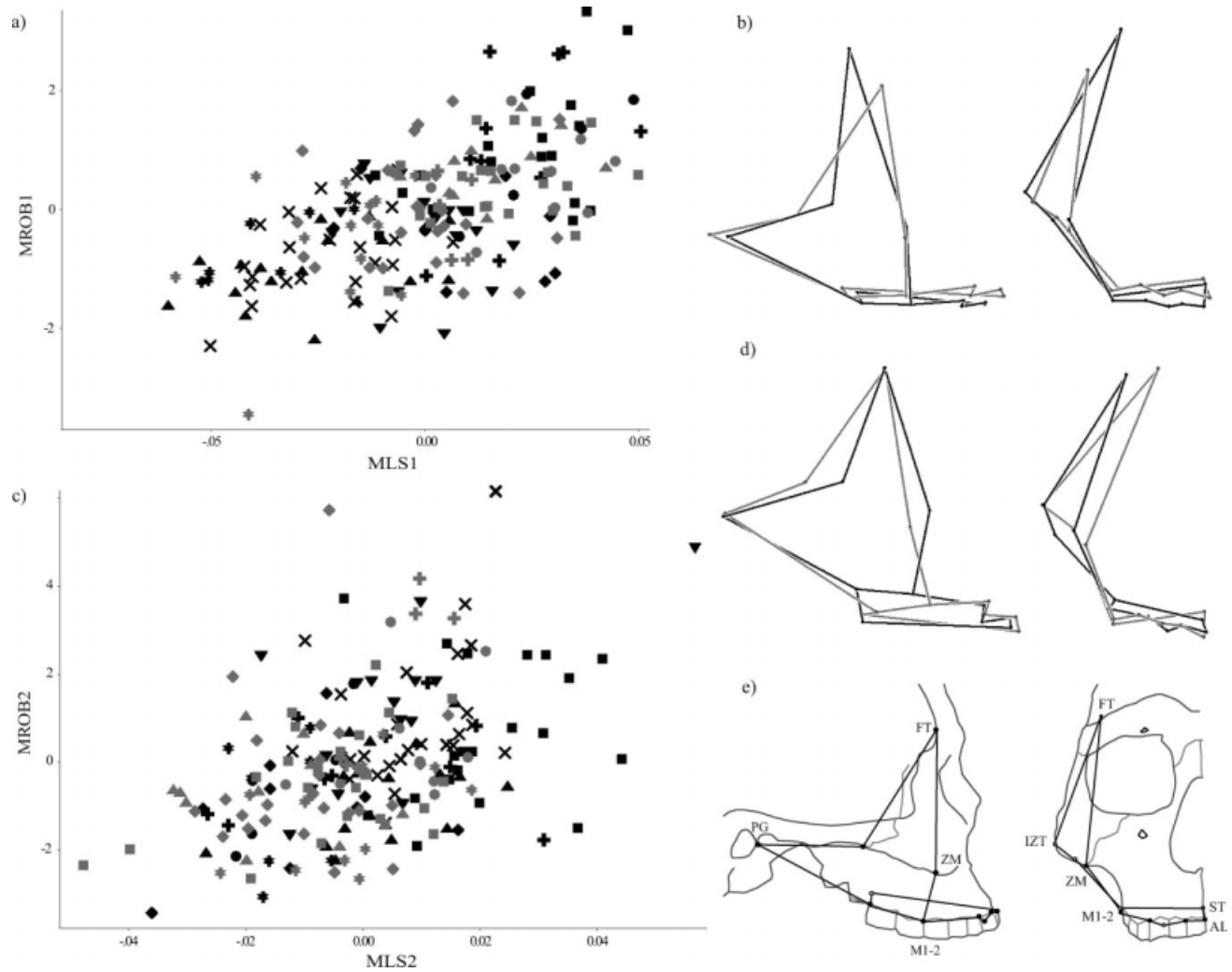


Fig. 6. Two-block partial least-squares analysis of mandibular landmarks and cranial robusticity traits: (a) MROB1 vs. MLS1 and (c) MROB2 vs. MLS2. The shape change associated with (b) MROB1 and (d) MROB2 is shown in right lateral and anterior views. The solid black line is the negative end and the dashed gray line is the positive end. Legend same as in Figure 3. To help orient the reader, (e) the wireframe was superimposed on an illustration of a human skull, and some of the landmarks were labeled.

the appearance of behaviors such as eating solid foods, then this would support developmental rather than functional integration.

This study does not find support for the argument that cranial robusticity and size are correlated (contra Lahr and Wright, 1996). This study differed in several ways from that of Lahr and Wright (1996); one major methodological contrast was the use of geometric morphometrics vs. linear morphometrics. The methods employed by Lahr and Wright (1996) were unable to statistically separate the effects of size and shape. They concluded that robusticity was related to cranial size because longer skulls with broader upper faces and more protruding maxillae were more robust than the opposite pattern. However, aspects of both size and shape are inherent in these measurements. In this study, we were able to study size (measured by centroid size) and shape (scale is removed in the superimposition process) independently. We found that while aspects of cranial shape are related to robusticity, overall cranial size is not. Differences in robusticity traits, sample composition, and ana-

lytical methods may also have contributed to differences between the two studies.

While several studies have demonstrated that cranial shape tracks neutral genetic distances (e.g., Roseman, 2004; Harvati and Weaver, 2006a), this study found that global patterns of cranial robusticity are not correlated with neutral genetic distances. These distances are thought to reflect neutral (i.e., random) evolutionary processes, primarily genetic drift, but also gene flow among populations. It is possible that the imperfect matches between morphological and genetic populations (e.g., Alaskan Inuit and Canadian Chipewyan; Table 1) decreased the correlation among these data sets. However, the correspondence between morphological and genetic populations in this study is comparable to that found in previous studies that demonstrated a significant relationship between cranial shape and neutral genetic distances (Harvati and Weaver, 2006a; Smith et al., 2007). This suggests that patterns of cranial robusticity were not shaped by neutral genetic processes.

While Aboriginal Australians have long been the standard bearers for robust cranial morphology, this study reveals that human populations exhibit more than one pattern of cranial robusticity. The results of this study emphasize a primary trend of variability from gracile to robust (except in the occipital torus region), but also highlight secondary patterns of differential cranial trait expression within populations. For example, the Native American group from Grand Gulch, Utah is characterized by robust expression of the sagittal keel, bregmatic eminence, occipital torus, and malar tubercle, but a more gracile supraorbital region in contrast to the pattern seen in Aboriginal Australians. A similar pattern was noted in native Americans from the Santa Barbara Channel, CA region by Walker (2008).

There was no support for a relationship between robusticity and climate (contra suggestions by Bulbeck, 2001; Bernal et al., 2006; Perez et al., 2007). This was true whether we examined individual climatic variables or multiple variables simultaneously. This analysis does not entirely rule out the influence of the environment on robust cranial morphology, but it appears to exclude global climate differences as a major factor. However, this conclusion is limited by the small number of cold climate populations in our study. If either the Tierra del Fuego or Inuit populations are outliers in terms of the expression of robusticity, then further sampling of cold adapted groups could reveal a relationship not detected here.

The strongest correlations were found between cranial robusticity and either cranial or masticatory shape. This may provide support for the functional model (relating mastication to robusticity), suggesting that future research into this relationship is warranted. The distances based on masticatory shape variables were significantly correlated with robusticity distances in both the combined male–female and female-only samples, and variation in the expression of robusticity was more strongly correlated with the masticatory landmarks than the cranial landmarks in the 2B-PLS analysis. However, the relationship between robusticity and shape highlighted by the 2B-PLS analysis was complex. González-José et al. (2005) found that masticatory morphology better differentiated between South American hunter-gatherers and farmers than did craniofacial shape as a whole. They attributed the smaller masticatory component to a reduction of mechanical stress associated with agriculture. In our analysis, however, those populations practicing hunter-gatherer subsistence activities (South Americans from Tierra del Fuego, Inuit, Khoe-San, and Aboriginal Australians) were neither consistently more robust, nor did they differ in the shape of their masticatory morphology, relative to the other groups. The latter may be due to deficiencies in the masticatory landmarks because they were designed for more large-scale differences in mastication/diet than observed among modern human populations. It is possible that a more extensive set of landmarks designed specifically with modern humans in mind may lead to a stronger correlation between robusticity and mastication. Interestingly, in the CLS 2B-PLS the shape associated with greater robusticity was similar to that described for groups that ate harder-to-process diets (Carlson and van Gerven, 1977, 1979; Larsen, 1995, 1997; Sardi et al., 2006). Specifically, crania with more prognathic faces, expanded glabellar and occipital regions, and (slightly) longer skulls were more robust than those with rounder vaults

and more orthognathic faces. Lahr and Wright (1996) described a similar cranial shape/robusticity pattern, emphasizing the relationship between longer, narrower crania with increased facial prognathism and greater robusticity. More detailed information related to subsistence and paramasticatory activities could clarify this potential relationship.

While this study examined a wide range of factors previously implicated in the expression of robust cranial morphology, there are additional explanations that may be considered in future research. Particularly active/mobile individuals or populations may express cranial robusticity to a greater degree than sedentary ones. Experimental evidence in armadillos and pigs indicated that increased exercise resulted in thicker cranial bones (Lieberman, 1996), and it has been shown that exercise causes the release of growth hormone (GH), which in turn has been implicated in increased bone mass (Vogl et al., 1993; Banu et al., 2001; Forwood et al., 2001). While hormones such as GH are thought to influence craniofacial growth (Cónsole et al., 2001), it is unclear whether this explanation can be extrapolated to the development of more localized cranial superstructures. Hunter-gatherer populations are thought to lead more physically demanding lives than sedentary, agricultural ones (Larsen, 1982, 1984; Perzigian et al., 1984; Larsen and Ruff, 1994; Carlson et al., 2007, but see Bridges, 1989; Kelly, 1995), but this study indicates that they are not always more cranially robust. Of the four hunter-gatherer populations included in this study, the South Americans and Aboriginal Australians are fairly robust, but the Khoe-San and Inuit are not.

Protection of the contents of the skull may also influence the development of robust cranial superstructures and cranial bone thickness. Boaz and Ciochon (2004) hypothesized that the thick skull bones and strongly developed cranial superstructures ubiquitous in *H. erectus* are the result of selection against injury during inter-population violence. Interpersonal violence was also posited to explain the presence of relatively thick cranial vault bones in some Aboriginal Australians (Brown, 1987; 1994). More detailed ethnographic information detailing the occurrences of interpersonal violence for each of the populations studied would be necessary to completely address these questions.

Extrapolation of these results to fossil hominins suggests that caution should be exercised when treating the types of traits analyzed here as independent characters as most are positively correlated; this coexpression may relate to developmental or functional integration. The PCA confirmed that males are generally more robust than females (Table 11), but this pattern was more apparent within single populations—males were more robust than females from the same groups, but not necessarily more robust than females from other groups. Therefore, these features should only be used to establish sex for individual fossil hominins when a reasonable sample of individuals is uncovered from the same time period and locality. The results of this analysis also raise doubts about whether variation in robusticity can be used to infer population history or local climatic adaptations within a population. While the possibility that the expression of robusticity is related to elevated activity levels or the processing of a more difficult-to-process diet cannot be ruled out, there is also not strong evidence to support these claims.

CONCLUSIONS

This study represents the first statistically rigorous test of a range of hypotheses regarding the expression of cranial robusticity. Positive coexpression of robust cranial traits may support a relatively simple genetic basis or developmental/functional integration, although varying patterns of “robust” cranial morphology were observed in different populations. Shape of the overall cranium and the masticatory apparatus are the only factors examined here that are significantly correlated with robusticity, but the relationship is weak. These results are partially consistent with those obtained by Lahr and Wright (1996), the only other study to explore robusticity at a global level. Our results indicate that unlike cranial shape, variation in robusticity did not reflect either climate or neutral genetic distances. The relationship between the masticatory landmark configuration and robusticity suggests that cranial robusticity may be influenced by masticatory/paramasticatory function. The possibility also remains open that variation in activity levels or behavior (e.g., interpersonal violence) contributed to the observed pattern of cranial robusticity in modern humans, and these should be carefully examined in future research.

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APPENDIX A

Trait	Abbrev.	Definition of grades	No. of grades
Malar tubercle	MT	<ol style="list-style-type: none"> 1. Contact between frontal bone and zygomatic bone inferior to the zygomaticofrontal suture forms no angle; tubercle absent 2. Obtuse angle is formed; smooth tubercle present 3. Acute angle is formed; tubercle present and often associated with cresting 	3
Supramastoid crest	SC	<ol style="list-style-type: none"> 1. The lateral surface of the temporal squama superior to the mastoid process is smooth; no cresting 2. Some elevation is present, extending superoposteriorly; no crest 3. Crest present, extending superoposteriorly 	3
Anterior mastoid tubercle	AM	<ol style="list-style-type: none"> 1. Lateral surface of the mastoid process is smooth 2. Weak to moderate tubercle present 3. Strongly expressed tubercle present 	3

LITERATURE CITED

- Baab KL. 2007. Cranial shape variation in *Homo erectus*. Ph.D. dissertation. New York: City University of New York.
- Banu J, Orhii PB, Okafor MC, Wang L, Kalu DN. 2001. Analysis of the effects of growth hormone, exercise and food restriction on cancellous bone in different bone sites in middle-aged female rats. *Mech Ageing Dev* 122:849–864.
- Bernal V, Perez SI, Gonzalez PN. 2006. Variation and causal factors of craniofacial robusticity in Patagonian hunter-gatherers from Late Holocene. *Am J Hum Biol* 18:748–765.
- Bilsborough A, Wood BA. 1986. The nature, origin and fate of *Homo erectus*. In: Wood B, Martin LB, Andrews P, editors. *Major topics in primate and human evolution*. Cambridge: Cambridge University Press. p 295–316.
- Boaz NT, Ciochon RL. 2004. Dragon Bone Hill: an ice-age saga of *Homo erectus*. New York: Oxford University Press.
- Bookstein FL. 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge, England: Cambridge University Press.
- Bookstein FL, Schaefer K, Prossinger H, Seidler H, Fieder M, Stringer CB, Weber GW, Arsuaga JL, Slice D, Rohlf F, Recheis W, Mariani J, Marcus L. 1999. Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. *Anat Record* 257:217–224.
- Bräuer G, Mbua E. 1992. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J Hum Evol* 22:79–108.
- Bresin A, Kiliaridis S, Strid KG. 1999. Effect of masticatory function on the internal bone structure in the mandible of the growing rat. *Eur J Oral Sci* 107:35–44.
- Bridges PS. 1989. Changes in activities with the shift to agriculture in the southeastern United States. *Curr Anthropol* 30:385–394.
- Brown P. 1987. Pleistocene homogeneity and Holocene size reduction: the Australian human skeletal evidence. *Archaeol Oceania* 22:41–71.
- Brown P. 1994. Cranial vault thickness in Asian *Homo erectus* and *Homo sapiens*. *Cour Forsch Inst Senckenberg* 171:33–46.
- Bulbeck D. 2001. Robust and gracile Australian crania: the tale of the Willandra Lakes. In: Simanjuntak T, Prasetyo B, Handini R, editors. *Sangiran: man, culture and environment in Pleistocene times*. Jakarta: Yayasan Obor Indonesia/The National Research Centre of Archaeology/École Française d'Extrême-Orient. p 60–106.
- Cann HM, Toma C, Cazes L, Legrand M-F, Morel V, Piuuffre L, Bodmer J, Bodmer WF, Bonne-Tamir B, Cambon-Thomsen ACZ, Chu J, Carcassi C, Contu L, Du REL, Ferrara GB, Friedlaender JS, Groot H, Gurwitz D, Jenkins T, Herrera RJ, Huang X, Kidd J, Kidd KK, Langaney A, Lin AA, Mehdi SQ, Parham P, Piazza A, Pistillo MP, Qian Y, Shu Q, Xu J, Zhu S, Weber JL, Greely HT, Feldman MW, Thomas G, Dausset J, Cavalli-Sforza LL. 2002. A human genome diversity cell line panel. *Science* 296:261–262.
- Carey JW, Steegmann JR. 1981. Human nasal protrusion, latitude, and climate. *Am J Phys Anthropol* 56:313–319.
- Carlson DS, van Gerven DP. 1977. Masticatory function and post-Pleistocene evolution in Nubia. *Am J Phys Anthropol* 46:495–450.
- Carlson DS, van Gerven DP. 1979. Diffusion, biological determinism, and biocultural adaptation in the Nubian Corridor. *Am Anthropol* 81:561–580.
- Carlson KJ, Grine FE, Pearson OM. 2007. Robusticity and sexual dimorphism in the postcranium of modern hunter-gatherers from Australia. *Am J Phys Anthropol* 134:9–23.
- Carson EA. 2006a. Maximum-likelihood variance components analysis of heritabilities of cranial nonmetric traits. *Hum Biol* 78:383–402.
- Carson EA. 2006b. Maximum likelihood estimation of human craniometric heritabilities. *Am J Phys Anthropol* 131:169–180.
- Cattell RB. 1966. The scree test for the number of factors. *Multivar Behav Res* 1:629–637.

- Cheverud JM, Buikstra JE. 1981a. Quantitative genetics of skeletal nonmetric traits in the Rhesus macaques on Cayo Santiago. I. Single trait heritabilities. *Am J Phys Anthropol* 54:43–49.
- Cheverud JM, Buikstra JE. 1981b. Quantitative genetics of skeletal non-metric traits in the rhesus macaques on Cayo Santiago. II. Phenotypic, genetic, and environmental correlations between traits. *Am J Phys Anthropol* 54:51–58.
- Cheverud JM, Buikstra JE. 1982. Quantitative genetics of skeletal non-metric traits in the rhesus macaques on Cayo Santiago. III. Relative heritability of skeletal non-metric and metric traits. *Am J Phys Anthropol* 59:151–155.
- Churchill SE. 1998. Cold adaptation, heterochrony, and Neandertals. *Evol Anthropol* 7:46–61.
- Ciochon RL, Nisbett RA, Corruccini RS. 1997. Dietary consistency and craniofacial development related to masticatory function in minipigs. *J Craniofac Genet Dev Biol* 17:96–102.
- Cónsole GM, Oyhenart EE, Jurado SB, Riccillo FL, Pucciarelli HM, Gómez Dumm CLA. 2001. Effect of undernutrition on cranial components and somatotroph-lactotroph pituitary populations in the squirrel monkey. *Cells Tissues Organs* 168:272–284.
- Dieringer D, Schlötterer C. 2003. Microsatellite Analyser (MSA): a platform independent analysis tool for large microsatellite data sets. *Molec Ecol Notes* 3:167–169.
- Dunsworth HM, Walker A. 2002. Early Genus *Homo*. In: Hartwig W, editor. *The primate fossil record*. Cambridge: Cambridge University Press. p 419–426.
- Endo B. 1966. Experimental studies on the mechanical significance of the form of the human facial skeleton. *J Faculty Sci Univ Tokyo (Section V, Anthropol)* 3:1–106.
- Endo B. 1970. Analysis of stress around the orbit due to masseter and temporalis muscles respectively. *J Anthropol Soc Nippon* 78:251–266.
- Falconer DS. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. *Ann Hum Genet* 29:51–76.
- Falconer DS. 1989. *Introduction to quantitative genetics*. New York: Wiley.
- Falconer DS, Mackay TFC. 1996. *Introduction to quantitative genetics*. Harlow, England: Pearson Education.
- Forwood MR, Li L, Kelly WL, Bennett MB. 2001. Growth hormone is permissive for skeletal adaptation to mechanical loading. *J Bone Miner Res* 16:2284–2290.
- Franciscus RG, Long JC. 1991. Variation in human nasal height and breadth. *Am J Phys Anthropol* 85:419–427.
- Frayser DW, Wolpoff MH, Thorne AG, Smith FH, Pope GG. 1993. Theories of modern human origins: the paleontological test. *Am Anthropol* 95:14–50.
- Gianola D. 1979. Heritability of polychotomous characters. *Genetics* 93:1051–1055.
- Gianola D. 1982. Theory and analysis of threshold characters. *J Anim Sci* 54:1079–1096.
- Gilligan I, Bulbeck D. 2007. Environment and morphology in Australian Aborigines: a re-analysis of the Birdsell database. *Am J Phys Anthropol* 134:75–91.
- Goldstein DB, Linares AR, Cavalli-Sforza LL, Feldman MW. 1995. An evaluation of genetic distances for use with microsatellite loci. *Genetics* 139:463–471.
- González-José R, Ramírez-Rozzi F, Sardi M, Martínez-Abadías N, Hernández M, Pucciarelli HM. 2005. Functional-cranial approach to the influence of economic strategy on skull morphology. *Am J Phys Anthropol* 128:757–771.
- Gower JC. 1975. Generalized procrustes analysis. *Psychometrika* 40:33–51.
- Greaves WS. 1978. The jaw lever system in ungulates: a new model. *J Zool* 184:271–285.
- Gunz P, Harvati K. 2007. The Neanderthal “chignon”: variation, integration, and homology. *J Hum Evol* 52:262–274.
- Halverson MS, Bolnick DA. 2008. An ancient DNA test of a founder effect in Native American ABO blood group frequencies. *Am J Phys Anthropol* 137:342–347.
- Hanihara T. 1996. Comparison of craniofacial features of major human groups. *Am J Phys Anthropol* 99:389–412.
- Hanson TE, Pearson OM. 2007. Fitting Manova models with missing continuous or ordinal data using reference priors. *Commun Stat Simulat* 36:621–630.
- Harvati K. 2003. The Neanderthal taxonomic position: models of intra- and inter-specific craniofacial variation. *J Hum Evol* 44:107–132.
- Harvati K, Weaver TD. 2006a. Human cranial anatomy and the differential preservation of population history and climate signatures. *Anat Rec A* 288:1225–1233.
- Harvati K, Weaver TD. 2006b. Reliability of cranial morphology in reconstructing Neanderthal phylogeny. In: Harvati K, Harrison T, editors. *Neanderthals revisited: new approaches and perspectives*. Dordrecht: Springer. p 239–254.
- Hennessy RJ, Stringer CB. 2002. Geometric morphometric study of the regional variation of modern human craniofacial form. *Am J Phys Anthropol* 117:37–48.
- Hernández M, Lalueza C, García-Moro C. 1997. Fuegian cranial morphology: the adaptation to a cold, harsh environment. *Am J Phys Anthropol* 103:103–117.
- Hilloowala RA, Trent RB. 1987. Supraorbital ridge and masticatory apparatus II: Humans (Eskimos). *Hum Evol* 3:351–356.
- Holm S. 1979. A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70.
- Hood GM. 2008. PopTools version 3.0.2. Available on the internet URL at: <http://www.cse.csiro.au/poptools>.
- Howells WW. 1973. Cranial variation in man. *Pap Peabody Mus Am Archaeol Ethnol* 67:1–259.
- Howells WW. 1989. Skull shapes and the map: craniometric analyses in the dispersion of modern Homo. *Pap Peabody Mus Am Archaeol Ethnol* 79:1–189.
- Hrdlička A. 1910. Contribution to the anthropology of central and Smith Sound Eskimo. *Anthrop Pap Am Mus Nat Hist* 5:177–280.
- Hublin J-J. 1986. Some comments on the diagnostic features of *Homo erectus*. *Anthropos (Brno)* 23:175–187.
- Hylander WL, Picq PG, Johnson KR. 1991. Masticatory-stress hypothesis and the supraorbital region of primates. *Am J Phys Anthropol* 86:1–36.
- Kaiser HF. 1961. A note on Guttman’s lower bound for the number of common factors. *Br J Psychol* 14:1–2.
- Kelly RL. 1995. *The foraging spectrum: diversity in hunter-gatherer lifeways*. Washington, DC: Smithsonian Institution Press.
- Klingenberg CP. 2008. MorphoJ: faculty of life sciences, University of Manchester, UK. Available at: http://www.flywings.org.uk/MorphoJ_page.htm.
- Konigsberg LW. 2000. Quantitative variation and genetics. In: Stinson S, Bogin B, Huss-Ashmore R, O’Rourke D, editors. *Human biology: an evolutionary and biocultural approach*. New York: Wiley. p 135–162.
- Konigsberg LW, Kohn LAP, Cheverud JM. 1993. Cranial deformation and nonmetric trait variation. *Am J Phys Anthropol* 90:35–48.
- Krzanowski WJ. 2000. *Principles of multivariate analysis: a user’s perspective*. Oxford: Oxford University Press.
- Lahr MM. 1995. Patterns of modern human diversification: implications for Amerindian origins. *Yearb Phys Anthropol* 38:163–198.
- Lahr MM. 1996. *The evolution of modern human diversity*. Cambridge: Cambridge University Press.
- Lahr MM, Wright RSV. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *J Hum Evol* 31:157–191.
- Lalueza C, Hernández M, García-Moro C. 1997. La morfología facial de las poblaciones fueguinas: ¿reflejo de una adaptación al frío? *An Inst Patagon Ser Cs Hum* 25:45–58.
- Lande R. 1992. Neutral theory of quantitative genetic variance in an island model with local extinction and colonization. *Evolution* 46:381–389.
- Larsen CS. 1981. Skeletal and dental adaptations to the shift to agriculture on the Georgia Coast. *Curr Anthropol* 22:422–423.
- Larsen CS. 1982. The anthropology of St. Catherines Island. 3. Prehistoric human biological adaptation. *Anthrop Pap Am Mus Nat Hist* 57:157–270.

- Larsen CS. 1984. Health and disease in prehistoric Georgia: the transition to agriculture. In: Cohen MN, Armelagos GJ, editors. *Paleopathology at the origins of agriculture*. Orlando, FL: Academic Press. p 367–392.
- Larsen CS. 1995. Biological changes in human populations with agriculture. *Ann Rev Anthropol* 24:185–213.
- Larsen CS. 1997. *Bioarchaeology: interpreting behavior from the human skeleton*. Cambridge: Cambridge University Press.
- Larsen CS, Ruff CB. 1994. The stresses of conquest in Spanish Florida: structural adaptation and change before and after contact. In: Larsen CS, Milner GR, editors. *In the wake of contact: biological responses to conquest*. New York: Wiley-Liss. p 21–34.
- Leonard WR, Sorensen MV, Galloway VA, Spencer GJ, Mosher MJ. 2002. Climatic influences on basal metabolic rates among circumpolar populations. *Am J Hum Biol* 14:609–620.
- Leigh SR, Relethford JH, Park PB, Konigsberg LW. 2003. Morphological differentiation of *Gorilla* subspecies. In: Taylor AB, Goldsmith ML, editors. *Gorilla biology: a multidisciplinary perspective*. Cambridge: Cambridge University Press. p 104–131.
- Lieberman DE. 1996. How and why humans grow thin skulls: experimental evidence for systemic cortical robusticity. *Am J Phys Anthropol* 101:217–236.
- Lieberman DE, Krovitz GE, Yates FW, Devlin M, St. Claire M. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J Hum Evol* 46:655–677.
- López-Fanjul C, Fernández A, Toro MA. 2003. The effect of neutral nonadditive gene action on the quantitative index of population divergence. *Genetics* 164:1627–1633.
- Lynch M, Walsh JB. 1998. *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer Associates.
- Mantel N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220.
- Mardia KV, Bookstein FL, Moreton IJ. 2000. Statistical assessment of bilateral symmetry of shapes. *Biometrika* 87:285–300.
- McNulty KP. 2003. *Geometric morphometric analyses of extant and fossil hominoid craniofacial morphology*, Ph.D. dissertation. New York: City University of New York.
- Mulligan CJ, Hunley K, Cole S, Long JC. 2004. Population genetics, history, and health patterns in Native Americans. *Annu Rev Genomics Hum Genet* 5:295–315.
- New M, Hulme M, Jones P. 1999. Representing twentieth-century space-time climate variability: I, development of a 1961–90 mean monthly terrestrial climatology. *J Clim* 12:829–856.
- New M, Hulme M, Jones P. 2000. Representing twentieth-century space-time climate variability. part II: development of 1901–96 monthly grids of terrestrial surface climate. *J Clim* 13:2217–2238.
- Perez SI, Bernal V, Gonzalez PN. 2007. Morphological differentiation of aboriginal human populations from Tierra del Fuego (Patagonia): implications for South American peopling. *Am J Phys Anthropol* 133:1067–1079.
- Perzigian AJ, Tench PA, Braun DJ. 1984. Prehistoric health in the Ohio River Valley. In: Cohen MN, Armelagos GJ, editors. *Paleopathology at the origins of agriculture*. London: Academic Press. p 347–366.
- Ramachandran S, Deshpande O, Roseman CC, Rosenberg NA, Feldman MW. 2005. Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *Proc Natl Acad Sci USA* 102:15942–15947.
- Ravosa MJ. 1991. Interspecific perspective on mechanical and nonmechanical models of primate circumorbital morphology. *Am J Phys Anthropol* 86:369–396.
- Rightmire GP. 1990. *The evolution of Homo erectus: comparative anatomical studies of an extinct human species*. New York: Cambridge University Press.
- Rohlf FJ. 1999. Shape statistics: procrustes superimpositions and tangent spaces. *J Classif* 16:197–223.
- Rohlf FJ, Corti M. 2000. Use of two-block partial least-squares to study covariation in shape. *Syst Biol* 49:740–753.
- Rohlf FJ, Slice D. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39:40–59.
- Roseman CC. 2004. Detecting inter-regionally diversifying natural selection on modern human cranial form using matched molecular and morphometric data. *Proc Natl Acad Sci USA* 101:12824–12829.
- Roseman CC, Weaver TD. 2004. Multivariate apportionment of global human craniometric diversity. *Am J Phys Anthropol* 125:257–263.
- Rosenberg NA, Mahajan S, Ramachandran S, Zhao C, Pritchard JK, Feldman MW. 2005. Clines, clusters, and the effect of study design on the inference of human population structure. *PLoS Genet* 1:e1–e70.
- Rosenberg NA, Pritchard JK, Weber JL, Cann HM, Kidd KK, Zhivotovsky LA, Feldman MW. 2002. Genetic structure of human populations. *Science* 298:2381–2385.
- Ross CF, Hylander WL. 1996. In vivo and in vitro bone strain analysis of the circumorbital region of Aotus and the function of the postorbital septum. *Am J Phys Anthropol* 101:183–215.
- Russell MD. 1985. The supraorbital torus: a most remarkable peculiarity. *Curr Anthropol* 26:337–350.
- Sardi ML, Novellino PS, Pucciarelli HM. 2006. Craniofacial morphology in the Argentine Center-West: consequences of the transition to food production. *Am J Phys Anthropol* 130:330–343.
- Schwartz JH. 2004. Getting to know *Homo erectus*. *Science* 305:53–54.
- Singleton M. 2005. Geometric morphometric analysis of functional divergence of mangabey facial form. *J Anthropol Sci* 82:29–45.
- Slice DE. 1998. *Morpheus et al.: software for morphometric research*. Department of Ecology and Evolution (Stony Brook, New York): State University of New York.
- Smith HF, Terhune CE, Lockwood CA. 2007. Genetic, geographic, and environmental correlates of human temporal bone variation. *Am J Phys Anthropol* 134:312–322.
- Smouse PE, Long JC, Sokal RT. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst Zool* 35:627–632.
- Spencer MA. 1998. Force production in the primate masticatory system—electromyographic tests of biomechanical hypotheses. *J Hum Evol* 34:25–54.
- Spencer MA. 1999. Constraints on masticatory system evolution in anthropoid primates. *Am J Phys Anthropol* 108:483–506.
- Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. *Am J Phys Anthropol* 91:1–20.
- Spencer MA, Ungar PS. 2000. Craniofacial morphology, diet and incisor use in three Native American populations. *Int J Osteoarchaeol* 10:229–241.
- Strand Vidarsdóttir U, O'Higgins P, Stringer CB. 2002. A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *J Anat* 201:211–229.
- Stringer CB. 1984. The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Cour Forsch Inst Senckenberg* 69:131–143.
- Villmoare B. 2005. Metric and non-metric randomization methods, geographic variation, and the single-species hypothesis for Asian and African *Homo erectus*. *J Hum Evol* 49:680–701.
- Vogl C, Atchley WC, Cowley DE, Crenshaw P, Murray JD, Pomp D. 1993. The epigenetic influence of growth hormone on skeletal development. *Growth Dev Aging* 57:163–182.
- Walker PL. 2008. Sexing skulls using discriminant function analysis of visually assessed traits. *Am J Phys Anthropol* 136:39–50.
- Wang S, Lewis CM Jr, Jakobsson M, Ramachandran S, Ray N, Bedoya G, Rojas W, Parra MV, Molina JA, Gallo C, Mazzotti G, Poletti G, Hill K, Hurtado AM, Labuda D, Klitz W, Barrantes R, Bortolini MC, Salzano FM, Petzl-Erler ML, Tsuneto LT, Llop E, Rothhammer F, Excoffier L, Feldman MW, Rosenberg NA, Ruiz-Linares A. 2007. Genetic variation and population structure in Native Americans. *PLoS Genet* 3:e185.

- Weaver TD, Roseman CC, Stringer CB. 2007. Were Neanderthal and modern human cranial differences produced by natural selection or genetic drift? *J Hum Evol* 53:135–145.
- Wolpoff MH. 1985. On explaining the supraorbital torus. *Curr Anthropol* 26:522.
- Wolpoff MH. 1999. *Paleoanthropology*. Boston: McGraw-Hill.
- Wolpoff MH, Wu XZ, Thorne AG. 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In: Smith FH, and Spencer F, editors. *The origins of modern humans*. New York: Alan R. Liss. p 411–484.
- Wood BA, Richmond BG. 2000. Human evolution: taxonomy and paleobiology. *J Anat* 197:19–60.
- Wright S. 1934. An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics* 19:506–536.
- y'Edynak G, Fleisch S. 1983. Microevolution and biological adaptability in the transition from food-collecting to food-producing in the Iron Gates of Yugoslavia. *J Hum Evol* 12:279–296.
- Zelditch M, Swiderski D, Sheets DH, Fink W. 2004. *Geometric morphometrics for biologists: a primer*. New York: Elsevier Academic Press.