Research Article

The Role of Genetic Drift in Shaping Modern Human Cranial Evolution: A Test Using Microevolutionary Modeling

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The means by which various microevolutionary processes have acted in the past to produce patterns of cranial variation that characterize modern humans is not thoroughly understood. Applying a microevolutionary framework, within- and among-population variance/covariance (V/CV) structure was compared for several functional and developmental modules of the skull across a worldwide sample of modern humans. V/CV patterns in the basicranium, temporal bone, and face are proportional within and among groups, which is consistent with a hypothesis of neutral evolution; however, mandibular morphology deviated from this pattern. Degree of intergroup similarity in facial, temporal bone, and mandibular morphology is significantly correlated with geographic distance; however, much of the variance remains unexplained. These findings provide insight into the evolutionary history of modern human cranial variation by identifying signatures of genetic drift, gene flow, and migration and set the stage for inferences regarding selective pressures that early humans encountered since their initial migrations around the world.

1. Introduction

Recent studies have revealed that human cranial morphology, whether quantified using absolute linear dimensions or relative geometric morphometric techniques, largely reflects population history among humans [1–9]. Certain functional and developmental modules (FDMs) of the cranium have been identified as reflecting relationships based on neutral molecular markers [4–9]. In particular, patterns of variation in the 3D morphology of the temporal bone, upper face, basicranium, individual bones of the cranial vault [5–9], and to a lesser degree the mandible [10] have been demonstrated to reflect genetic distances among human populations. The assumption behind these findings is that the morphology of these FDMs is evolving largely neutrally, in a similar manner to neutral molecular loci, and can consequently be utilized in a similar manner to estimate genetic relationships among human specimens or samples in the absence of direct molecular data. The relationship between cranial morphology and genetic distances in humans indirectly suggests that human cranial morphology is evolving primarily neutrally;

however, the influence of selection has not been explicitly tested and therefore cannot be definitively discounted. Alternative methods exist for directly testing the impact of microevolutionary processes on morphology, through the use of microevolutionary modeling.

The patterns of phenotypic diversity within a species are central to inferring its modes of evolutionary diversification. Lande's quantitative approach to evolutionary theory can be applied to assess the relative effects of genetic drift and selection in a sample [11]. Lande's model is based upon the formula: $B_t = G(t/N_e)$, in which B_t is the between-population V/CV matrix during generation t, G is the additive V/CV matrix, and N_e is the effective population size [11]. For phenotypic data from contemporaneous groups, G is typically proportional to the within-group morphological V/CV matrix (W) [12–15]. Therefore, W can be substituted for G such that $B \propto W(t/N_e)$. Within a contemporaneous comparison, t and N_e will be constants, so the equation can be simplified further to $B \propto W$. In other words, if populations have diversified primarily through neutral evolutionary processes, then their within-group variance/covariance

(V/CV) matrices should be proportional to their between-group V/CV matrices [11, 16, 17]. Significant deviations from this pattern indicate that selection has impacted the morphology of a particular region, and the null hypothesis of neutrality is rejected [11, 16, 17]. This approach has been taken to evaluate the role of genetic drift in the evolution of cranial shape in New World Monkeys [18–21] and fossil hominins [22, 23]. Weaver and colleagues applied statistical tests based on Lande's model to human and Neandertal linear cranial dimensions and concluded that morphological divergence between the two species was consistent with a null hypothesis of drift [23]. However, to date, Lande's model has not been applied to the comparison of landmark-based cranial data among individual human populations with the purpose of assessing the impacts of selection and drift.

Several genetic models, including the Isolation by Distance (IBD) model [24–26] and the serial founder effect model [27, 28], predict that genetic divergence among demes increases with geographic distance between them. Therefore, one means of investigating the extent to which morphological diversity has been influenced by neutral or selective forces is to compare human craniometric variation to geographic distance. Human cranial morphology, as captured by linear dimensions, generally has an association with genetic distance on a global scale [2, 4]. However, Relethford [2] notes that the accordance of data to an IBD model does not definitively clarify the evolutionary history of the phenotype. Environmental conditions also grade geographically, and morphological clines can be adaptive. Thus, adherence of a phenotype to a cline does not conclusively indicate that neutral factors are dictating its variation.

In population genetics, adaptation is often identified by first accounting for variation that falls within the potential range of neutral evolution (e.g., [29–31]). This tenet derives from the Neutral Theory of Molecular Evolution, which argues that the majority of genetic variation is likely to be selectively neutral [29–31]. According to the Neutral Theory, the rate of divergence among groups will be determined by the mutation rate (μ), which is neutral [29]. Mutation generates new variation, and genetic drift acts upon it. There are two primary models in population genetics that describe neutral divergence patterns among groups [32–34]. According to the Constant Heritability (CH) model, the degree of heritability (h^2) of a character dictates the rate of neutral divergence among groups [32, 33]. Under the Mutation-drift Equilibrium (MDE) model, the expected genetic variance is calculated as $2N_e\sigma_m^2$, in which N_e is the effective population size and σ_m is the morphological variance. A population is considered to be in mutation-drift equilibrium when the rate of new mutations (causing new variation) is balanced by genetic drift (causing homozygosity). Therefore, morphological characters will reflect population history if populations approximate an equilibrium between mutation and genetic drift (MDE model), and/or new mutations impact the V/CV structure minimally (CH model). According to both models, the divergence rate among groups is determined by the strength of genetic drift, which is in turn dictated by N_e and h^2.

Approaching the evolution of modern human cranial morphology from a population genetics framework, such as through the application of molecular-based models and microevolutionary modeling, provides a basis for understanding the patterns and variation that characterize humans today. Using an assumption of neutrality as the primary mode of microevolution unless demonstrated otherwise allows cranial form to be evaluated objectively, and deviations from the pattern expected under a neutral model can be investigated further and adaptive explanations sought out. This research expands upon previous studies investigating patterns of cranial morphology in modern humans, interpreting them in the context of geographic dispersion and migration, and revealing the microevolutionary processes which produced the variation in cranial shape observed among our species today.

2. Methods

2.1. Data Collection. Fifty-two landmarks capturing the shape of the basicranium and splanchnocranium were digitized in samples of sixteen modern human populations (Table 1). The three-dimensional coordinates of each landmark were recorded using a Microscribe G2 point digitizer (Immersion Corp.) and sent to a laptop computer. These landmarks are standard craniometric landmarks [35–37] and were selected for the current study following findings by Smith et al. [6, 7] that the morphology depicted by each set of landmarks overlying is significantly correlated with genetic distances in humans (Table 2). The landmarks were divided into subsets representing four different FDMs of the skull: the basicranium, upper face, mandible, and temporal bone. FDMs are portions of a morphological structure, in this case the skull, that share a common biomechanical function and/or developmental pathway.

The analyses of the basicranium, upper face, and temporal bone consisted of all 16 populations. However, due to the fragmentary nature of museum collections, many specimens were found to be missing mandibles. Consequently, the number of populations with adequate sample sizes to be included in the mandibular morphology analysis was reduced compared to the other analyses. Ten of the sixteen populations contained a sufficient number of mandibular specimens (Table 1); however, this reduced number is equivalent to those used in several other similar studies [4, 5, 7]. Sex determination was conducted by the author for each specimen, using traditional sexually dimorphic cranial traits [35], and approximately equal sex samples were then utilized for each population. Each population sample consisted exclusively of adult individuals, as indicated by the eruption of the third molars and/or fusion of the spheno-occipital synchondrosis. An approximation of the average geographic coordinates for each population was obtained using Google Earth.

2.2. Geometric Morphometric Analyses. Morphological coordinate data for each FDM were superimposed separately using Generalized Procrustes Analyses [38–41] in *MorphoJ* 1.02 [42]. During this step, all specimens were scaled,

TABLE 1: Human population samples included in the present study, with sample sizes and museum locations. AMNH, American Museum of Natural History, NMNH, National Museum of Natural History, BNHM, British Natural History Museum. *Subset of populations included in the analysis of mandibular morphology.

Population	Region	n	Museum locations
Cameroon*	Africa	44	AMNH
Khoisan*	Africa	43	AMNH, BNHM
Pare	Africa	27	AMNH
French	Europe	50	NMNH, BNHM
Russians	Europe	36	AMNH, NMNH
Han Chinese*	East Asia	50	AMNH, NMNH
Malay	East Asia	55	AMNH, NMNH
Japanese*	East Asia	40	BNHM, NMNH
Mongolian*	East Asia	44	AMNH
Siberian natives*	East Asia	51	AMNH, NMNH
Southern Indians*	South Asia	50	AMNH
Australian aborigines*	Oceania	48	AMNH, NMNH
Papua New Guineans*	Oceania	34	AMNH
Solomon Islanders	Oceania	31	AMNH, NMNH
Greenland Inuit*	North America	43	AMNH, NMNH
Mexican Indians	North America	44	NMNH

rotated, and translated, such that any remaining variation among them could be attributed directly to shape differences. Principal Components Analyses (PCA) were subsequently conducted, and Principal Component (PC) scores obtained. Mahalanobis D2 distances between pairs of populations were calculated based on the morphology of each FDM. In the context of geometric morphometric analyses of cranial morphology, D2 distances have been argued to be especially appropriate for estimating distances among groups due to their shared properties with the molecular distances with which they should covary if the morphology is evolving primarily neutrally (e.g., [43]). Patterns of morphological distances were also visualized using Multidimensional Scaling (MDS) plots, in which the relationships indicated by a distance matrix are forced onto three dimensions.

2.3. Geographic Comparisons.

Geographic distances between each pair of populations were calculated from their approximate average geographic coordinates using great circle distances, a haversine formula in which the distance between two points (D) is $D = 2R \arctan(\sqrt{\mathrm{hav}\theta}/\sqrt{(1 - \mathrm{hav}\theta)})$, in which θ is the central angle between the two points and R is the radius of the Earth. Additionally, following Ramachandran et al. [44], distance calculations included the consideration of migratory waypoints, geographic points through which early migrating humans would have likely passed in order to travel between continents. In accordance with Ramachandran et al. [44], the following waypoints were used: Anadyr, Russia (64N, 117E), Cairo, Egypt (30N, 31E),

Istanbul, Turkey (41N, 28E), Phnom Penh, Cambodia (11N, 104E), and Prince Rupert, Canada (54N, 130W). This adjustment in geographic distance calculation for intercontinental distances generates a more realistic estimate of the actual amount of migratory distance between two human populations, taking potentially insurmountable geographic barriers such as large bodies of water into consideration.

In order to compare the statistical association between geographic distance and morphological distance, a Regression Analysis was conducted separately between the great circle distances for each pair of populations and the Mahalanobis distances based on the 3D morphology of each of the FDMs. The alpha level was set at $\alpha = 0.05$ for significance, and the slope (β) was used to infer the degree of continuity between the variables. The R^2 value was interpreted as the degree of morphological variation explained by geographic patterning. Geographic distances were also visualized using a Multidimensional Scaling (MDS) plot in order to compare the distribution of populations to those based on morphology.

2.4. Lande's Method.

The likelihood that the patterns of cranial variation observed in humans today can be explained by genetic drift can be assessed by comparing among- and within-population V/CV matrices [16]. The V/CV matrices for each FDM were calculated in *Statistica 9.1* using a Multiple Analysis of Variance (MANOVA) in which the morphological traits were treated as dependent variables and the populations as independent variables. Each V/CV matrix was subsequently simplified into its Principal Components for comparative purposes. Following Ackermann and Cheverud [19], PC scores were calculated for each population mean by multiplying population means by the standardized eigenvectors: $Y = XE$, in which Y is the PC score of a population mean, X is the matrix of population means, and E is the matrix of standardized eigenvectors. For each PC, the among-population variance was calculated as the variance among the population mean PC scores.

If the morphology of an FDM has diversified primarily through genetic drift, then Lande's model predicts that the between-group variation will be proportional to the within-group variation ($B \propto W$). Here, this model is applied by comparing the within-population variances to the among-population variances. A Regression Analysis was conducted between the within- and among-population variances. For each FDM, a slope of $\beta = 1.0$ is consistent with the hypothesis of drift, while any significant deviations from 1.0 are suggestive of nonneutral patterns of microevolution.

As an additional test of whether the covariance structure was similar among and within populations, a Mantel test [45, 46] of these covariance matrices for each FDM was conducted in PopTools, an add-on for Microsoft Excel. FDMs, found to have significant correlations ($P < .05$), were interpreted as having similar covariances among and within populations. It should be noted, however, that this test considers only the lower diagonal of a matrix, and therefore the variances within each variable are not incorporated nor tested. As a result, it should not be considered a direct test of

TABLE 2: Cranial landmarks included in each functional and developmental module.

Landmark	Description
Basicranium	
Basion	Midline point on the anterior margin of the foramen magnum
Condylar foramen	The posterior point on the margin of the condylar foramen
Condyle anterior	Most anterior points on the occipital condyles
Condyle posterior	Most posterior points on the occipital condyles
Inferior nuchal	Midline point on the inferior nuchal line
Inion	Most posterior point on the external occipital protuberance
Mastoidale	Most inferior point on the mastoid process
Opisthion	Midline point at the posterior margin of the foramen magnum
Temporal Bone	
Anterior articular	Most anterior point on the articular surface of the articular eminence
Auriculare	A point on the lateral aspect of the root of the zygomatic process at the deepest incurvature
Entoglenoid	Most inferior point on the entoglenoid process
Jugular	Most lateral point of the jugular fossa
Lateral eminence	Point on the center of the lateral margin of the articular surface of the articular eminence
Lateral ovale	Most lateral point on the margin of the foramen ovale
Mandibular fossa	Deepest point within the mandibular fossa
Mastoidale	Center of the inferior tip of the mastoid process
Medial articular	Most inferior point on medial margin of articular surface of the articular eminence
Petrous apex	Apex of petrous part of the temporal bone
Porion	Most superior point of the external auditory meatus
Postglenoid	Most inferior point on the postglenoid process
Supraglenoid gutter	Point of inflection, where the braincase curves laterally into the supraglenoid gutter, in the coronal plane of the mandibular fossa
Tympanic	Most inferolateral point on the tympanic element of the temporal
Zygion	Most lateral point on the zygomatic arch
Face	
Dacryon	Point on the medial orbit at which the frontal, lacrimal, and maxilla intersect
Ectoconchonion	The intersection of the most anterior surface of the lateral border of the orbit and a line bisecting the orbit along its long axis
Frontomalare Temporale	Most laterally positioned point on the frontozygomatic suture
Glabella	Most anterior midline point on the frontal bone
Nasion	Point of intersection between the frontonasal suture and midsagittal plane
Orbitale	The lowest point on the margin of the orbit
Mandible	
Condylion laterale	Most lateral point on the mandibular condyle
Coronoid process	Most superior point on the coronoid process of the mandible
Gnathion	Most inferior midline point on the mandible
Gonion	A point along the rounded posteroinferior corner of the mandible between the ramus and the body
Infradentale	Midline point at superior tip of the septum between the mandibular central incisors
M1-M2 contact	Projected (laterally) onto the alveolar margin
Mandibular notch	Most inferior point in the mandibular notch
Mesial P3	Most mesial point on mandibular P_3 alveolus, projected onto the alveolar margin
Pogonion	Most anterior point on the mental eminence

Lande's method but instead a means of further investigating covariance structure.

Alternate methods for investigating the proportionality of between- and among-group variance/covariance structure exist. Most notably, Flury [47] proposed a hierarchical method of testing for common principal components (CPCs) among matrices, which has been employed as a test for Lande's model [48, 49]. However, it has been noted that this approach may generate spurious results in analyses involving large samples, since even small deviations in biological variation can appear statistically significant and cause the null hypothesis of neutrality to be rejected [18, 20]. Therefore, that approach was not employed here.

3. Results

3.1. Morphological Variation among Populations and Geographic Distance Comparisons. The matrices and multidimensional scaling plots of Mahalanobis D2 distances among populations indicated variation in the degree of similarity among groups in the morphology of the various FDMs (Figure 1). In general, most populations grouped roughly according to continent (Figure 1); however, the various continental groups exhibited differing degrees of dispersion and overlap with other groups.

The three populations from Oceania (Australians, Papuans, and Solomon Islanders) were highly divergent in the morphology of the temporal bone, and basicranium as a whole. In fact, the D2 distances among the Oceanic populations were among the highest recovered for these FDMs. Despite some geographic patterning, the MDS plots revealed overlap between continental groups in basicranial and temporal bone morphology, and the African and Oceanic populations did not cluster together (Figures 1(a) and 1(b)).

The D2 distances based on facial morphology suggested some shared structure between the populations from Africa and those from Oceania (Figure 1(c)). The East Asian populations grouped together, as did the European samples. The New World groups were similar along two of the three dimensions, but the Inuit showed the greatest morphological affinity to the native Siberians.

With regard to mandibular morphology, the African populations clustered together, as did the East Asian populations (Figure 1(d)). However, the Oceanic populations were again widely divergent both from each other and from their Pacific neighbors in East Asia. The Inuit fell near the East Asian samples in dimensions 1 and 2 but exhibited a negative score along dimension 3.

The great circle distances including waypoints among populations indicated the migratory distances required for each group to migrate to the center of the other's average geographic location (Table 3, Figure 2). The Regression Analyses between great circle distances and morphological distances revealed variation in the relationship between geography and shape for each FDM (Table 4). Morphological D2 distances based on the basicranium and mandible had moderate ($R = 0.322$ and 0.358, resp.) and significant ($P = .0003$ and $.0156$, resp.) correlations with great circle geographic distances.

The morphological patterns of temporal bone shape were significant ($P = .0367$) but low ($R = 0.191$). Basicranial D2 distances, on the other hand, were nonsignificant ($R = 0.110$, $P = .152$). The R^2 values of all comparisons were low (0.012–0.128).

3.2. Lande's Model. The Regression Analysis of the PCs representing within- and among-population V/CVs indicated differences in the associations between these factors for the various FDMs (Table 5). For three of the four FDMs evaluated—the basicranium, face, and temporal bone—the slope was not significantly different than 1.0 (Table 5). The R^2 values for these three FDMs indicated that a substantial proportion of variation was shared (86.5–95.6%) between the within- and among-population variances.

For mandibular morphology, however, a different pattern emerged. The slope of the regression equation was $\beta = 0.746$, although the correlation between the two variables was nonsignificant ($P = .254$) and the 95% confidence interval ranged widely from $\beta = 0.275$–1.217. The R^2 value was 0.335 (Table 5).

The Mantel tests of within- and among-population covariances revealed highly significant correlations ($P < .001$) between the patterns for all four FDMs (Table 6).

4. Discussion

FDMs of the skull known to reflect population history in humans are generally assumed to be evolving primarily through neutral microevolutionary processes, such as genetic drift, gene flow, and mutation. As such, their patterns of variation behave very much like neutral molecular loci in that variation should accumulate at a relatively constant rate and grade geographically along clines. However, cranial morphology is affected by a number of complex and varied influences, including functional constraints and pressures of the masticatory apparatus, remodeling of osseous tissue, and indirectly through climate and diet, in ways that neutral genetic markers are not. As such, it is perhaps unreasonable to expect any functional aspect of morphology to behave according to a strict molecular model; however, the application of this framework can provide a starting point for identifying microevolutionary signatures that can be subsequently explored further.

The application of Lande's model [16] to subsets of cranial data indicated that the null hypothesis of predominantly neutral evolution cannot be rejected for the basicranium, temporal bone, and upper face, cranial regions which have been found previously to reflect population history [5–8]. The 3D shape of the temporal bone and face also track geography, with populations located in greatest proximity to each other sharing the most morphological affinities. However, despite the significance of these correlations, their R^2 values are low, suggesting that much of the variance is unexplained by this factor alone.

Basicranial morphology was found to have a nonsignificant relationship with great circle distances. One possible explanation for this result is that, while this FDM is generally evolving primarily neutrally across humans as a species, a few

Table 3: Matrix of great circle distances using waypoints among human populations included in this study.

|	Australia	Cameroon	China	France	India	Inuit	Japan	Malay	Mexico	Mongolia	Pare	PPNG	Russia	San	Siberia	Solomon
Australia	0	17337	8962	16434	9121	21859	13208	5276	20621	10226	17913	3384	13494	19758	12571	3644
Cameroon	17337	0	10026	6740	8462	20012	12767	12053	18774	9705	3110	16563	6367	3058	10732	17540
China	8962	10026	0	8611	3646	13233	3053	3678	11995	1264	10602	8188	5380	12447	3708	9165
France	16434	6740	8611	0	7871	17722	11034	11150	16484	8028	7316	15660	2691	9161	8609	16637
India	9121	8462	3646	7871	0	16703	6517	3837	15465	4496	9038	8347	5856	10883	7000	9324
Inuit	21859	20012	13233	17722	16703	0	11595	16575	6304	12211	20588	21085	13789	22433	9742	22062
Japan	13208	12767	3053	11034	6517	11595	0	7924	10357	3062	13343	12434	7355	15188	3279	13411
Malay	5276	12053	3678	11150	3837	16575	7924	0	15337	4942	12629	4662	8210	14474	7287	5650
Mexico	20621	18774	11995	16484	15465	6304	10357	15337	0	10973	19350	19847	12551	21195	8504	20824
Mongolia	10226	9705	1264	8028	4496	12211	3062	4942	10973	0	10281	9452	4519	12126	2554	10429
Pare	17913	3110	10602	7316	9038	20588	13343	12629	19350	10281	0	17139	6943	2699	11308	18116
PPNG	11702	16563	8188	15660	8347	21085	12434	4662	19847	9452	17139	0	12720	18984	11797	989
Russia	16061	6367	5380	2691	5856	13789	7355	8210	12551	4519	6943	12720	0	8788	4692	13697
San	19758	3058	12447	9161	10883	22433	15188	14474	21195	12126	2699	18984	15561	0	13153	19961
Siberia	12571	10732	3708	8609	7000	9742	3279	7287	8504	2554	11308	11797	4692	13153	0	12774
Solomon	3644	17540	9165	16626	9324	22062	13411	5650	20824	10345	18116	989	13697	20274	12774	0
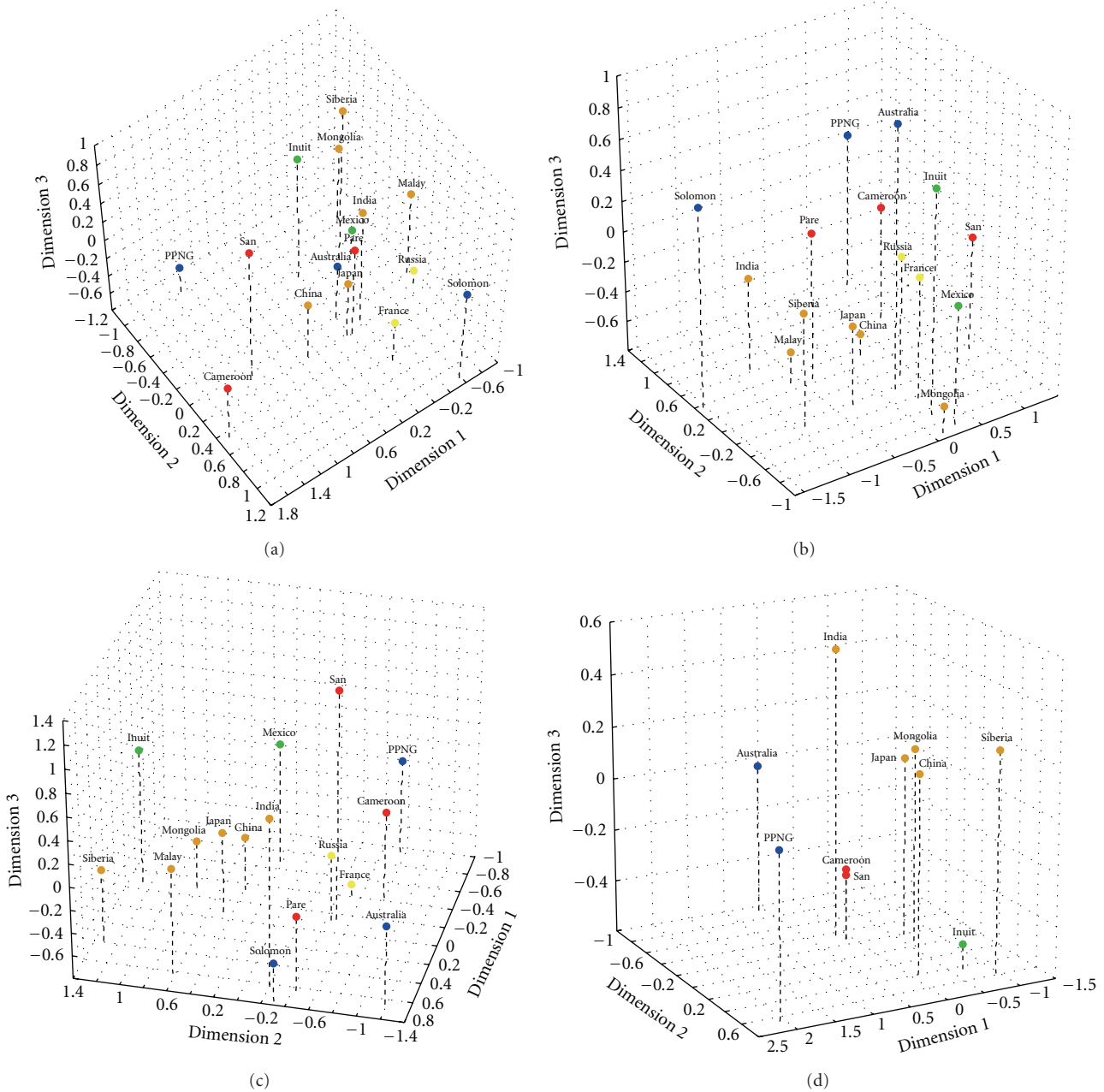
FIGURE 1: Multidimensional scaling (MDS) plot of Mahalanobis D2 distances among populations based on three-dimensional morphology of the: (a) basicranium, (b) temporal bone, (c) face, and (d) mandible. All plots use the following color scheme: Africa = red; Asia = orange; North America = green; Europe = yellow; Oceania = blue.

populations may still be differentially affected by selection. In fact, this FDM contains some potentially adaptive aspects of morphology, in particular with respect to climate. Three samples in this study could be characterized as "cold-adapted," the Inuit, Siberian natives, and, to a lesser degree, the Mongolians. These three groups cluster together on the MDS plot (Figure 1(a)), indicating affinities in basicranial morphology, as captured by the current set of landmarks. It has been noted that extremely cold climates may have a disproportionate effect on the basicranial morphology of populations exposed to them, causing them to differ from

expected patterns of morphology [6, 46]. The functional pressures of a diet of tough and partially frozen items and paramasticatory behaviors may result in adaptive and plastic responses in the morphology of the masticatory apparatus, including the temporomandibular joint (TMJ), as these factors result in extensive stress on the masticatory apparatus [48–52]. Ethnographic literature has documented the Inuit practice of using the anterior dentition as a "third hand" [53], contributing to additional stresses to be accommodated by the skull. The skeletal structure of the Inuit skull has been modeled as a series of adaptations
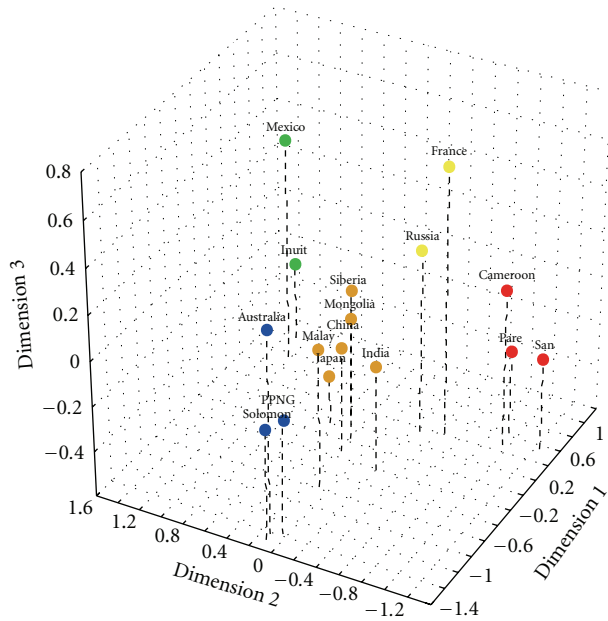
FIGURE 2: Multidimensional scaling (MDS) plot of geographic great circle distances among populations, incorporating waypoints. Geographic regions are depicted as follows: Africa = red; Asia = orange; North America = green; Europe = yellow; Oceania = blue.

TABLE 4: Results of Regression Analysis of geographic great circle distances and Mahalanobis D2 distances based on the morphology of each functional and developmental module (FDM). Significant correlations are indicated in bold.

FDM	R	R^2	P value
Basicranium versus geography	0.110	0.012	.1516
Temporal bone versus geography	0.191	0.037	**.0367**
Face versus geography	0.322	0.103	**.0003**
Mandible versus geography	0.358	0.128	**.0156**

TABLE 5: Results of Regression Analysis of within- and among-population variance/covariance (V/CV) matrices. Significant correlations are indicated in bold.

FDM	β	95% confidence	R^2	P value
Basicranium	0.960	0.798–1.122	0.895	**.0096**
Face	0.995	0.926–1.065	0.956	**.0048**
Mandible	0.746	0.275–1.217	0.335	.2539
Temporal bone	0.940	0.801–1.079	0.865	**<.0001**

to generate and dissipate powerful occlusal forces, one of which involves a thickened tympanic plate [48, 49]. These factors have also been documented to affect some aspects of facial morphology; however, the facial landmarks utilized here specifically avoid the oral cavity and its associated alveolar bone. The extent of cold adaption in the basicranial

TABLE 6: Results of Mantel test comparing among- and within-population covariances. All correlations were significant.

FDM	R	P value
Basicranium	**0.998**	**<.001**
Face	**0.999**	**<.001**
Mandible	**0.868**	**<.001**
Temporal bone	**0.999**	**<.001**

morphology of the populations under consideration in the present study is difficult to tease apart definitively from geographic distance or population history, however, because the current cold-adapted populations are located comparatively closely to each other and share a fairly recent common ancestry [44]. Future studies incorporating cold-adapted samples from more distantly related groups, such as those from northern Europe, could shed additional light on this topic by separating out the effects of extreme climate in high latitudes from genetic relatedness.

One apparent deviation from geographic patterning in morphology is the widely divergent shape of the basicranium, temporal bone, and face among the three Oceanic populations. While these groups are located within a reasonably circumscribed geographic area (Australia, Papua New Guinea, and Solomon Islands), they are quite morphologically distinct. However, this is not surprising given that they are separated from each other by large bodies of water, which could have hindered the degree of possible gene flow among these groups by necessitating watercraft travel between islands. Additionally, several studies have suggested that Melanesia was likely colonized multiple times [54–58] and that speakers of the Papuan and Oceanic language groups have maintained a substantial degree of differentiation [54–56, 58]. Geographic distance is frequently used as a proxy for genetic distance, but, in cases of multiple colonization events of a region by genetically differentiated groups, this assumption may be unfounded. Friedlaender and colleagues found that molecular distances for populations within Melanesia are substantially higher than a worldwide average and show essentially no relationship with geographic distances [58]. Similarly, molecular studies have revealed substantial genetic delineation between Australian indigenous peoples and Papuans, which has been interpreted as separate colonization events from different ancestral stock [54–56]. In the case of basicranial and temporal bone microevolution, it is clear that simple geographic distances cannot explain the patterns of morphology among Oceanic groups, just as it does not explain their genetic relationships.

Genetic drift is rejected as the predominant mechanism influencing mandibular shape in *Homo sapiens*. This finding is consistent with previous studies that have attempted to approach this question in an alternate manner [7, 10]. Interpretations as to the utility of mandibular morphology for reconstructing population history have been varied and depend upon which populations are evaluated and the type of molecular data used for comparison. Smith [7] found that the shape of the mandible in nine human populations

did not significantly correspond with their genetic distances based on short tandem repeat (STR) data; however, in a comparison to molecular distances based on *Alu* insertion polymorphisms and using a smaller number of populations, the association became statistically significant. Additionally, Nicholson and Harvati [10] found that mandibular shape tracks loosely with geography, and that functional demands such as diet and climate also play a role. These studies highlight the complexity of the patterns of mandibular morphology currently present in our species and the variety of microevolutionary processes that likely contributed to its current distribution.

Overall, the shape of the human skull, whether quantified using linear measurements or three-dimensional landmarks, reflects population history to a large degree [1–9]. Much of the microevolutionary history of this region, in particular the temporal bone and upper face, has involved largely neutral mechanisms and therefore reflects population history. However, simple geographic distance models [24–28] cannot explain the extent of the variation observed in individual FDMs, and specific functional aspects of the skull, such as the masticatory system, require selective explanations and interpretations. A population genetics framework provides a starting point for inferring the multicausal mechanisms of human cranial evolution, understanding these processes and their impacts, and retracing human evolution.

The subtext of many studies investigating human cranial evolution goes beyond understanding how the morphological variation has evolved. In the absence of molecular data in the paleoanthropological record, many researchers wish to identify phylogenetically informative aspects of morphology that can be used as a proxy for genetic data to address questions about hominin phylogenetic relationships and relative genetic distances among individual hominin specimens. Research into the relationship between cranial morphology and genetic relationships in humans is a crucial step in this process; however, the assumption that the patterns characterizing *Homo sapiens* will also apply to nonhuman species has not been tested. Future studies investigating similar factors in other catarrhine primates can elucidate this question by using phylogenetic bracketing. Cranial FDMs found to be evolving predominantly neutrally and reflecting genetic relationships both within humans and among other Old World primates can be evaluated in the hominin fossil record to confidently infer phylogeny.

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References

[1] J. H. Relethford, "Global analysis of regional differences in craniometric diversity and population substructure," *Human Biology*, vol. 73, no. 5, pp. 629–636, 2001.

[2] J. H. Relethford, "Global patterns of isolation by distance based on genetic and morphological data," *Human Biology*, vol. 76, no. 4, pp. 499–543, 2004.

[3] R. González-José, S. V. Van Der Molen, E. González-Pérez, and M. Hernández, "Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration," *American Journal of Physical Anthropology*, vol. 123, no. 1, pp. 69–77, 2004.

[4] C. C. Roseman, "Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 35, pp. 12824–12829, 2004.

[5] K. Harvati and T. D. Weaver, "Human cranial anatomy and the differential preservation of population history and climate signatures," *Anatomical Record A*, vol. 288, no. 12, pp. 1225–1233, 2006.

[6] H. F. Smith, C. E. Terhune, and C. A. Lockwood, "Genetic, geographic, and environmental correlates of human temporal bone variation," *American Journal of Physical Anthropology*, vol. 134, no. 3, pp. 312–322, 2007.

[7] H. F. Smith, "Which cranial regions reflect molecular distances reliably in humans? Evidence from three-dimensional morphology," *American Journal of Human Biology*, vol. 21, no. 1, pp. 36–47, 2009.

[8] N. Von Cramon-Taubadel, "Congruence of individual cranial bone morphology and neutral molecular affinity patterns in modern humans," *American Journal of Physical Anthropology*, vol. 140, no. 2, pp. 205–215, 2009.

[9] N. von Cramon-Taubadel, "Revisiting the homoiology hypothesis: the impact of phenotypic plasticity on the reconstruction of human population history from craniometric data," *Journal of Human Evolution*, vol. 57, no. 2, pp. 179–190, 2009.

[10] E. Nicholson and K. Harvati, "Quantitative analysis of human mandibular shape using three-dimensional geometric morphometrics," *American Journal of Physical Anthropology*, vol. 131, no. 3, pp. 368–383, 2006.

[11] R. Lande, "Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry," *Evolution*, vol. 33, pp. 402–416, 1979.

[12] J. M. Cheverud, "A comparison of genetic and phenotypic correlations," *Evolution*, vol. 42, no. 5, pp. 958–968, 1988.

[13] D. A. Roff, "The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture," *Heredity*, vol. 74, no. 5, pp. 481–490, 1995.

[14] D. A. Roff, "The evolution of genetic correlations: an analysis of patterns," *Evolution*, vol. 50, no. 4, pp. 1392–1403, 1996.

[15] K. R. Roots and J. P. Gibson, "Realized sampling variances of estimates of genetic parameters and the difference between

genetic and phenotypic correlations," *Genetics*, vol. 143, no. 3, pp. 1409–1416, 1996.

[16] R. Lande, "Genetic variation and phenotypic evolution during allopatric speciation," *American Naturalist*, vol. 116, pp. 463–479, 1980.

[17] D. Lofsvold, "Quantitative genetics of morphological differentiation in Peromyscus. II. Analysis of selection and drift," *Evolution*, vol. 42, pp. 54–67, 1988.

[18] R. R. Ackermann and J. M. Cheverud, "Phenotypic covariance structure in tamarins (genus *Saguinus*): a comparison of variation patterns using matrix correlation and common principal component analysis," *American Journal of Physical Anthropology*, vol. 111, no. 4, pp. 489–501, 2000.

[19] R. R. Ackermann and J. M. Cheverud, "Discerning evolutionary processes in patterns of tamarin (genus *Saguinus*) craniofacial variation," *American Journal of Physical Anthropology*, vol. 117, no. 3, pp. 260–271, 2002.

[20] G. Marroig and J. M. Cheverud, "A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of New World Monkeys," *Evolution*, vol. 55, no. 12, pp. 2576–2600, 2001.

[21] G. Marroig and J. M. Cheverud, "Did natural selection or genetic drift produce the cranial diversification of neotropical monkeys?" *American Naturalist*, vol. 163, no. 3, pp. 417–428, 2004.

[22] R. R. Ackermann and J. M. Cheverud, "Detecting genetic drift versus selection in human evolution," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 52, pp. 17946–17951, 2004.

[23] T. D. Weaver, C. C. Roseman, and C. B. Stringer, "Were neandertal and modern human cranial differences produced by natural selection or genetic drift?" *Journal of Human Evolution*, vol. 53, no. 2, pp. 135–145, 2007.

[24] S. Wright, "Isolation by distance," *Genetics*, vol. 28, pp. 114–138, 1943.

[25] N. E. Morton, S. Yee, D. E. Harris, and R. Lew, "Bioassay of kinship," *Theoretical Population Biology*, vol. 2, no. 4, pp. 507–524, 1971.

[26] L. L. Cavalli-Sforza, P. Menozzi, and P. Piazza, *The History and Geography of Human Genes*, Princeton University Press, Princeton, NJ, USA, 1994.

[27] N. Von Cramon-Taubadel and S. J. Lycett, "Brief communication: human cranial variation fits iterative founder effect model with African origin," *American Journal of Physical Anthropology*, vol. 136, no. 1, pp. 108–113, 2008.

[28] L. Betti, F. Balloux, W. Amos, T. Hanihara, and A. Manica, "Distance from Africa, not climate, explains within-population phenotypic diversity in humans," *Proceedings of the Royal Society B*, vol. 276, no. 1658, pp. 809–814, 2009.

[29] M. Kimura, "Evolutionary rate at the molecular level," *Nature*, vol. 217, no. 5129, pp. 624–626, 1968.

[30] M. Kimura, *The Neutral Theory of Molecular Evolution*, Cambridge University Press, Cambridge, UK, 1983.

[31] J. L. King and T. H. Jukes, "Non-Darwinian evolution," *Science*, vol. 167, pp. 788–798, 1969.

[32] R. Lande, "Natural selection and random genetic drift in phenotypic evolution," *Evolution*, vol. 30, no. 2, pp. 314–334, 1976.

[33] M. Lynch and W. G. Hill, "Phenotypic evolution by neutral mutation," *Evolution*, vol. 40, pp. 915–935, 1986.

[34] M. Turelli, J. H. Gillespie, and R. Lande, "Rate tests for selection on quantitative characters during macroevolution and microevolution," *Evolution*, vol. 42, pp. 1085–1089, 1988.

[35] J. Buikstra and U. H. Ubelaker, *Standards for Data Collection from Human Skeletal Remains*, Arkansas Archaeological Survey, Fayetteville, Ark, USA, 1994.

[36] W. M. Bass, *Human Osteology: A Laboratory and Field Manual*, Missouri Archaeological Society, Columbia, Mo, USA, 4th edition, 1995.

[37] C. A. Lockwood, W. H. Kimbel, and J. M. Lynch, "Morphometrics and hominoid phylogeny: support for a chimpanzee-human clade and differentiation among great ape subspecies," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 13, pp. 4356–4360, 2004.

[38] J. C. Gower, "Generalized procrustes analysis," *Psychometrika*, vol. 40, no. 1, pp. 33–51, 1975.

[39] F. J. Rohlf and D. Slice, "Extensions of the Procrustes method for the optimal superimposition of landmarks," *Systematic Zoology*, vol. 39, pp. 40–59, 1990.

[40] C. R. Goodall, "Procrustes methods and the statistical analysis of shape (with discussion)," *Journal of the Royal Statistical Society B*, vol. 53, pp. 285–340, 1991.

[41] I. L. Dryden and K. V. Mardia, *Statistical Shape Analysis*, John Wiley & Sons, Chichester, UK, 1998.

[42] C. P. Klingenberg, *MorphoJ*, Faculty of Life Sciences, University of Manchester, Manchester, UK, 2008.

[43] M. Lynch, "Methods for the analysis of comparative data in evolutionary biology," *Evolution*, vol. 45, no. 5, pp. 1065–1080, 1991.

[44] S. Ramachandran, O. Deshpande, C. C. Roseman, N. A. Rosenberg, M. W. Feldman, and L. L. Cavalli-Sforza, "Support from the relationship of genetic and geographic in human populations for a serial founder effect originating in Africa," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 102, no. 44, pp. 15942–15947, 2005.

[45] N. Mantel, "The detection of disease clustering and a generalized regression approach," *Cancer Research*, vol. 27, no. 2, pp. 209–220, 1967.

[46] P. E. Smouse, J. C. Long, and R. T. Sokal, "Multiple regression and correlation extensions of the Mantel test of matrix correspondence," *Systematic Zoology*, vol. 35, pp. 627–632, 1986.

[47] B. Flury, *Common Principal Components and Related Multivariate Methods*, John Wiley & Sons, New York, NY, USA, 1988.

[48] P. C. Phillips and S. J. Arnold, "Hierarchical comparison of geneticvariance-covariance matrices. I. Using the flury hierarchy," *Evolution*, vol. 53, no. 5, pp. 1506–1515, 1999.

[49] W. L. Hylander, "The adaptive significance of Eskimo craniofacial morphology," in *Orofacial Growth and Development*, A. A. Dahlberg and T. Graber, Eds., pp. 129–169, Mouton, The Hague, The Netherlands, 1977.

[50] A. Balicki, *The Netsilik Eskimo*, Natural History Press, Garden City, NJ, USA, 1970.

[51] J. K. So, "Human biological adaptation to arctic and subarctic zones," *Annual Review of Anthropology*, vol. 9, pp. 63–82, 1980.

[52] S. C. Antón, "Tendon-associated bone features of the masticatory system in Neandertals," *Journal of Human Evolution*, vol. 31, no. 5, pp. 391–408, 1996.

[53] G. De Poncins, *Kablooma*, Reynal, New York, NY, USA, 1941.

[54] S. Van Holst Pellekaan, M. Frommer, J. Sved, and B. Boettcher, "Mitochondrial D-loop diversity in Australian riverine and Australian desert Aborigines," *Electrophoresis*, vol. 18, no. 9, pp. 1538–1543, 1997.

[55] S. M. Van Holst Pellekaan, M. Frommer, J. A. Sved, and B. Boettcher, "Mitochondrial control-region sequence variation

in aboriginal Australians," *American Journal of Human Genetics*, vol. 62, no. 2, pp. 435–449, 1998.

[56] A. J. Redd and M. Stoneking, "Peopling of Sahul: mtDNA variation in Aboriginal Australian and Papua New Guinean populations," *American Journal of Human Genetics*, vol. 65, no. 3, pp. 808–828, 1999.

[57] G. R. Summerhayes, "Island Melanesian pasts—a view from archaeology," in *Genes, Language, and Culture History in the Southwest Pacific*, J. S. Friedlaender, Ed., pp. 10–35, Oxford University Press, New York, NY, USA, 2007.

[58] J. S. Friedlaender, F. R. Friedlaender, F. A. Reed et al., "The genetic structure of Pacific Islanders," *PLoS Genetics*, vol. 4, no. 1, article e19, 2008.