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Craniofacial plasticity in ancient Peru

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With 4 figures and 6 tables

Summary: Numerous studies have utilized craniometric data to explore the roles of genetic diversity and environment in human cranial shape variation. Peru is a particularly interesting region to examine cranial variation due to the wide variety of high and low altitude ecological zones, which in combination with rugged terrain have created isolated populations with vastly different physiological adaptations. This study examines seven samples from throughout Peru in an effort to understand the contributions of environmental adaptation and genetic relatedness to craniofacial variation at a regional scale. Morphological variation was investigated using a canonical discriminant analysis and Mahalanobis D^2 analysis. Results indicate that all groups are significantly different from one another with the closest relationship between Yauyos and Jahuay, two sites that are located geographically close in central Peru but in very different ecozones. The relationship between latitude/longitude and face shape was also examined with a spatial autocorrelation analysis (Moran's *I*) using ArcMap and show that there is significant spatial patterning for facial measures and geographic location suggesting that there is an association between biological variation and geographic location.

Key words: craniometric data, cranial shape variation, genetic diversity, environmental adaptation.

Introduction

Craniometric studies within physical anthropology and skeletal biology have a long history back to the early twentieth century, when countless collections of cranial measurements and indices were collected globally (Boas 1912, Morton 1839, Newman 1943). However, without the development of multivariate statistics and technology to process and calculate these statistics, many of the early studies were limited in the extent to which meaningful interpretations could be made. Furthermore, investigations of global human variation involved matching cranial features and measurements to a racial typology, which has been rejected as studies of genetics and evolutionary mechanisms such as gene flow have shed light on the heritability of cranial shape (Armelagos et al. 1982, Kohn 1991, Sparks & Jantz 2002). More recent studies involving human variation based on craniometrics are primarily concerned with the roles of genetic diversity and environmental plasticity in population differences

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related to cranial shape (e.g., Betti et al. 2010, Pietrusewsky 2010, Relethford 2004, Ross & Ubelaker 2010).

A number of studies have demonstrated the genetic neutrality of craniometric variation, but the extent to which climate plays a role in cranial shape is still debated (Betti et al. 2010, Harvati & Weaver 2006, Relethford 2004, Roseman 2004, von-Cramon-Taubadel 2009a, von-Cramon-Taubadel 2009b). Hubbe et al. (2009) found that although cranial morphology is largely influenced by geographic distance, aspects of facial morphology are strongly correlated with climate. Selection due to climate was found to be strongest in groups living in extreme cold environments and the most highly correlated climatic aspect was temperature (Hubbe et al. 2009). South America is a particularly interesting region to examine cranial variation due to the variety of the ecological zones located in the area as a result of high elevations in the Andes Mountains. The rugged terrain in higher elevations in combination with the overall rise in topography initially created isolated populations and requires different physiological adaptations to ensure population survival (Sandweiss & Richardson 2008). Therefore, clear morphological differences between populations as a result of physiological adaptations and genetic distance should be present. A number of studies have been undertaken to examine cranial variation throughout Latin America on a regional scale, but rarely contain more than a few samples.

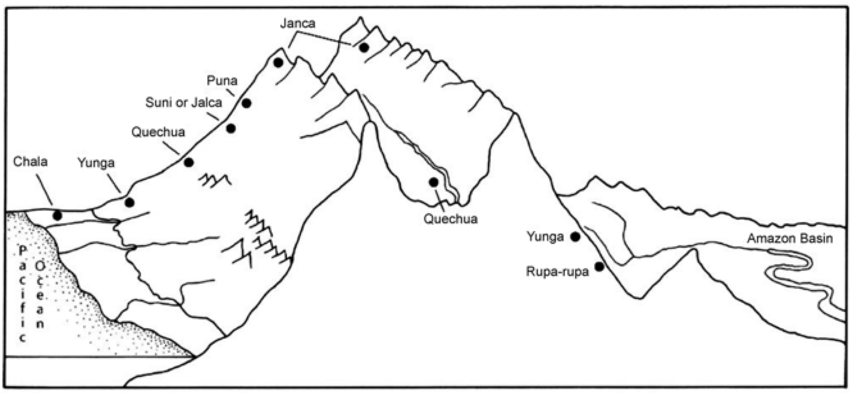
This study attempts to further examine cranial variation in Peru using a combination of seven samples from lowland coastal and highland groups throughout the northern and central regions. Using samples collected by Ross et al. (2008), Howells (1973), and Verano (1987), this paper will focus on the relationship between craniofacial variation, shifts in altitude, and geographic distance. Craniofacial variation will be evaluated using traditional craniometric analyses such as discriminant function analysis (DFA). The relationship between face shape and geographic distance will be examined using a spatial autocorrelation in ArcMap 10.1. Past research has shown that highland groups are morphologically similar to one another in relation to lowland groups, creating a coastal and highland differentiation. Furthermore, geographically close groups tend to be most similar to one another (Ditmar 1996, Haun & Cock Carrasco 2010, Ross et al. 2008, Sardi et al. 2006). Given that the lowland groups are located in a north-south direction along the coast, we expect that the degree of similarity between these samples will result in a north-south gradient of variation. Despite the geographic distance between the two highland sites, we also expect to see some degree of similarity between these groups as well.

Environmental background

Within Peru lies a portion of the Andes, a series of interconnected mountain ranges that extend down the western coast of South America and result from the subduction zone between the Nazca and Antarctic Plates (Sandweiss & Richardson 2008). With the exception of the Himalayas in southern Asia, the Andes contain the only region in the world at a high enough elevation to cause physical stress on human occupants through increased isolation, extreme diurnal temperature ranges, lower atmospheric oxygen concentrations, and marginal resources. Due to sudden vertical changes in elevation, there is a high contrast between microenvironments from the coastal lowlands to the highest mountain elevations, requiring a range of physiological, technological, and social adaptations (Dillehay & Kolata 2004, Keatinge 1988). Peruvian geographer Javier Pulgar Vidal divided Peru into eight "natural regions" or ecozones based on altitude, climate, and land use that are organized from west to east. Sandweiss & Richardson (2008) have adapted this system to the Central Andes (Fig. 1). This modified system has been used to categorize our samples in order to further investigate smaller scale differences between ecozones.

Studies of cranial variation in the Americas

Examination of population variation has been a focus of physical anthropology for over 100 years. Scholars such as Hrdlicka, Boas, and Howells collected thousands of cranial measurements and indices globally in order to examine the shifts in cranial form across populations (Howells 1973, Howells 2007). Though many of the multivariate methods used today were not yet available, variation in craniofacial structure among population groups was identified. Many of these observed differences were used to create racial typologies (e.g., Mongoloid, Caucasoid, etc.) into which popula-



Chala – ranges from the coast to 500 m in elevation and is characterized by desert conditions due to a combination of airflow from the Humboldt Current and a rain shadow from the Andes. The desert is interspersed with river valleys that run perpendicular to the coastline and provide areas with terrestrial plant resources or irrigation opportunities. Nutrient upwelling from the current flow at the Pacific Coast also results in rich fisheries.

Yunga - ranges from 500-2300 m on the western side and 1000-2300 m on the eastern side. The eastern side contains forested slopes, river valleys, and regular, abundant precipitation. The western side contains more fertile river valleys where agriculture is possible.

Quechua – ranges from 2300-3500 m and contains the most agriculturally productive land. There is a smooth rise in slope and seasonal rainfall that allows for terracing. This zone is also significant because it is the start of elevations in which the concentration of atmospheric oxygen starts to decrease enough to affect humans. The combination of cold temperatures and hypoxic conditions require a physiological acclimation over a period of time in order to ensure survival (Baker 1969, Hurtado 1932).

Suni and *Puna* – range from 3500-4000 and 4000-4800 m, respectively, are at high enough elevations where there are extreme diurnal variations in temperature. The *suni* is characterized by steeper terrain and narrow rocky land, thus limiting the areas suitable for growing crops. The *puna* is the highest habitable ecozone and is characterized by high altitude grasslands.

Janca – The highest overall, including any areas over 4800 m in elevation. Although the area was visited by prehistoric peoples, this zone cannot be inhabited by humans due to low temperatures and oxygen and contains glaciers and snow caps that act as sources for the river systems at lower elevations.

Rupa-rupa – ranges from 400-1000 m on the eastern side and is characterized by warm, humid conditions and dense vegetation.

Omagua – Consists of the Amazon tropical forest and is characterized by hot, humid conditions, dense vegetation, and abundant rainfall.

Fig. 1. Cross section of the Andes showing the eight major eco-zones (Sandweiss & Richardson 2008).

tions were classified. Despite this general emphasis on racial typology, some early physical anthropologists noted differences between groups that could be attributed to environmental variation and geographic distance (Howells 2007, Newman 1943). As the use of cranial shape for racial classification was rejected, studies utilizing craniometric data shifted focus to the relationship between population structure, environmental adaptation, and cranial shape. However, until recently, larger scale studies still relied on single samples to represent large geographic areas. For example, the Yauyos sample from the Howells data set has been used as a Latin America representative in numerous studies (e.g., Relethford 1994, Relethford & Harpending 1994, Roseman 2004, Roseman & Weaver 2004). However, Ross et al. (2008) found that Yauyos were significantly different morphologically from three other Peruvian groups examined, and that the most environmentally similar groups were also the most biologically similar. Ross et al. (2002) also investigated the role of variation and environmental factors in the Americas to dispel the myth of a homogenized American "type" and found similar results indicating that there is a wide range of variation within the Americas.

More recently, a number of studies have undertaken research related to population structure and morphological variation both in relation to environmental change and across geographical space throughout the Americas. Ditmar (1996) examined seven cranial measurements in Andean populations and found that they clustered into three major morphological "types" corresponding to coastal Peru, Chile, and highland Bolivia and Argentina. Not only was a difference noted across environments, but also as one moved east to west. A similar east-west gradient was noted by both Pucciarelli et al. (2006, 2008), who examined variation across both North and South America, and Rothhammer & Silva (1989), who noted change moving from northwest South America towards the southeastern region. In order to assess inter-cemetery variation at Pacatnamu on the North Coast of Peru, Verano (1987) examined comparative samples from coastal and highland populations in relation to a sample from Pacatnamu and found that highland and coastal groups were distinct from one another and that geographic distance between samples correlated with biological distance. These studies have highlighted the significant range of variation in cranial shape throughout Latin America and demonstrate the unsuitable grouping of populations into a single "Latin American" or "Hispanic" category. By integrating multiple data sets from existing studies to create a larger study sample over a smaller geographic area, we are also able to examine the relationship between environmental factors, biological distance, and craniofacial shape at a finer scale or micro level.

Material and methods

The cultural periods of prehistoric Peru are divided into pre-ceramic and ceramic chronologies. Pre-ceramic culture begins with initial human occupation of the area and is divided into six major occupational periods reaching back to at least 11 500 BP and going up to the appearance of ceramic artifacts around 3800 BP (Keatinge 1988). The ceramic period spans from 3800 BP up to European contact in AD 1534 and is divided into an Initial Period, Early, Middle, and Late Horizons. The Initial Period and Early Horizons, which span 3800–2200 BP, are characterized by the emergence and expansion of the Chavín culture, shifts in settlement patterns, and evidence of agricultural intensification in the highlands and on the coast (Keatinge 1988, Pozorski & Pozorski 2008). The Middle Horizon, which begins ~AD 600, is marked on the north coast of Peru by migration of Moche groups in response to a series of drought events (Stanish 2001). In the highlands, the Wari and Tiwanaku cultures emerge as major powers dominating much of coastal and highland Peru and Bolivia (Butters & Castillo 2008, Goldstein 2005, Isbell 2008, Proulx 2008). The Late Intermediate Period spans AD 1000 to AD 1476, and is characterized culturally by the Chimu culture and development of Chan Chan as a major capital on the North Coast and the development of the Inca culture in the highlands around Cuzco (Keatinge 1988).

The seven samples used in this study date to the Middle and Late Horizons and were collected by the third author (Ross et al. 2008), Howells (1973), and last author (Verano 1987). The five lowland coastal samples consist of Makatampu, Jahuay, Pacatnamu, Malabrigo, and Ancon (associated with the *chala* ecological zone), while the highland sample includes Yauyos (*Suni* range) and Cajamarca (*Quechua* ecozone) (Fig. 2).

Makatampu is located on the central coast and consists of 50 crania excavated from the site in the 1940s (Ross et al. 2008). The site dates to AD 1–800, a period broadly characterized by replacement of the Chavín by the Moche on the North Coast, the Nazca to the south, and the Lima culture on the central coast. Based on associated Wari-style ceramics, the Jahuay sample, which consists of 54 isolated crania collected from a looted cemetery on the central coast, has been assigned to this period. The Pacatnamu sample consists of 133 surface crania collected from nine Early and Late period cemeteries, as well as 28 excavated burials from various areas of the site. The Early period cemeteries also date to the Middle Horizon and are contemporary with the Jahuay sample, while the Late Period cemeteries date to the Late Intermediate Period and are contemporary with the Malabrigo sample. The Malabrigo sample was collected from a looted cemetery on the North Coast in the Chicama Valley and has also been dated to the Late Intermediate Period by associated ceramics (Verano 1987).

Fig. 2. Map of Peru and the locations of the samples used in this study (lowland sites indicated by circle and highland sites indicated by triangles).

Ancon (n = 47) is a lowland site on the central coast that was excavated for the Columbian Exposition of 1893 and dates to the Late Intermediate Period (Ross et al. 2008, Weinstein 2005).

The Cajamarca sample consists of two collections – Maqui-Maquis and Rumi Lanchi. The two collections are closely associated and are some of the only samples from the northern sierra (~ 2700 m) region of Peru (Verano 1987). The Maqui-Maquis sample consists of isolated crania collected from several caves dated to the Early Intermediate period and is earlier than the Early Period at Pacatnamu. The Rumi Lanchi sample consists of crania excavated from rock tombs less than 10 km from Maqui-Maquis. The two samples are temporally distinct; Rumi Lanchi dates to the Late Intermediate Period and is contemporary with the Late Period at Pacatnamu and the Malabrigo sample (Verano 1987). However, Ericksen (1962) concluded that this site represented regional continuity and thus the samples were combined for this study. Yauyos, the Latin American representative from the Howells data set, consists of 110 crania collected by Julio C. Tello from burial caves in the central highlands (Howells 1973). The total sample size for study is 507 individuals (Table 1).

Selection of cranial traits for this study was based on the consistency between the Ross and Verano data sets, meaning only measurements that were available for all seven of the samples were included in the analysis, thus limiting the measurements used to 10 (Table 2). Undeformed adult crania were selected by Ross et al. (2008) and Verano (1987) for their samples. The measurements used in this study have been thoroughly tested and are part of the standard forensic set, which allows for incorporation of data from various sources with mini-

Table 1. Sample composition.

Group	N (M/F)	Temporal range	Ecological zone	Reference
Ancon	47 (37/2)	AD 1000–1476	Central Coast (*Chana)*	Ross 2008
Cajamarca	56 (26/30)	AD 1–100, AD 1000–1200	North Highland (*Quechua)*	Ross 2008
Jahuay	54 (29/25)	AD 800–1000	Central Coast *(Chana)*	Verano 1987
Makatampu	50 (29/21)	AD 1–800	Central Coast *(Chana)*	Ross 2008
Malabrigo	51 (27/23)	AD 1100–1470	North Coast *(Chana)*	Verano 1987
Pacatnamu	139 (67/72)	AD 600–1050, AD 1100–1370	North Coast *(Chana)*	Verano 1987
Yauyos	110 (55/55)	Pre-Contact No conclusive dates exist	Central Highland *(Suni)*	Howells 1973

Table 2. Measurement descriptions.

Measurement	Descriptions
Basion-Prosthion Length (BPL)	Moore-Jansen et al. 1994:51 #6.
Nasion-Prosthion (NPH)	Howells 1973: 174.
Nasal Height (NLH)	Howells 1973: 6 #14; Moore-Jansen et al. 1994:54 #13.
Orbital Height (OBH)	Moore-Jansen et al. 1994:55 #16.
Orbital Breadth (OBB)	Howells 1973: 175; Moore-Jansen et al. 1994:55 #15.
Nasal Breadth (NLB)	Howells 1973: 176; Moore-Jansen et al. 1994:54 #14.
Maxillo-Alveolar Breadth (MAB)	Howells 1973:176; Moore-Jansen et al. 1994:51 #7.
Biorbital Breadth (EKB)	Howells 1973:178; Moore-Jansen et al. 1994:55 #17.
Interorbital Breadth (DKB)	Moore-Jansen et al. 1994:55 #18.
Frontal Chord (FRC)	Howells 1973:181; Moore-Jansen et al. 1994:55 #19.

mal interobserver error (Moore-Jansen & Jantz 1994, Ousley & Jantz 1998). In order to examine the full range of biological variation within the groups and to increase sample sizes, males and females were pooled. Sardi et al. (2005) concluded that sex variation is negligible within each sample population in among group comparisons. Missing values were estimated using the computer program *NORM: Multiple imputations of incomplete multivariate data under a normal model* (Schafer 1999), a simulation procedure that uses a type of Markov chain Monte Carlo technique to generate random draws where the distribution of each draw depends on the previous (http://www.stat.psu.edu/~jls/misoftwa.html#misoftwa.html#mi). The general guidelines followed were not to accept any case for data replacement that had more than 20 % of missing values or no more than 2 variables per individual.

To examine the between-group variation, a canonical variates analysis (CVA) was conducted. In a CVA, linear combinations of predictor variables that summarize between-population variation are used to examine interrelationships among the samples in order to graphically represent the differences on canonical axes, which maximize the differences (Ross 2004). CVA was selected over exploratory analyses such as PCA (principal components analysis) as the samples are of known origin/provenance and the data are traditional craniometric data, which do not require a dimension reducing technique (Ross 2004). To measure the among-group differentiation, a Mahalanobis D^2 matrix was also calculated. An unweighted pair-group method with arithmetic average (UPGMA) clustering analysis was performed using the distance matrix (Sneath & Sokal 1973) in order to visually assess the relationships among the groups. These analyses were performed using the SAS system for Windows Version 9.3 (2011).

To examine the relationship between facial morphology including the frontal chord and geographic distance based on latitude and longitude, a spatial autocorrelation analysis was performed using the Spatial Autocorrelation tool in ArcMap 10.1 (ESRI 2012). The tool uses Global Moran's *I* to measure the degree to which a set of spatial feature locations and data values tend to cluster or disperse in space. Spatial autocorrelation measures the dependence of the values of the craniometric variables on the same craniometric variables as a function of spatial lags – in this case latitude and longitude – using Global Moran's *I* (Sokal 1979, Sokal & Uytterschaut 1987, Fortin et al. 2002). Moran's *I* is a product-moment coefficient, which varies from –1 (negative autocorrelation) to 1 (positive autocorrelation) and in the absence of spatial autocorrelation with an *expected value* close to zero (Fortin et al. 2002). After the spatial autocorrelation tool calculates the Moran's *I* index it calculates the Expected index and these two values are then compared (ESRI 2012). The resulting z-score and *p*-values reflect the overall variance of the features and dataset, which indicate whether differences are significant or not (ESRI 2012).

Results

Craniometrics

The first three significant canonical axes are presented in Table 3, which account for 87 % of the total variation. These indicate that approximately 52 % of the among-group shape variation is accounted for by the first canonical variate (CAN1), 22 % is accounted for by CAN2, and 13 % by CAN3. The total canonical structure and correlation between the original variables and the canonical variates is presented in Table 4. The total canonical structure suggests that the variation on CAN1 is associated with nasal breadth (NLB), CAN2 is associated with basion-prosthion height (BPL), and CAN3 with nasal height (NLH).

When CAN1 is plotted against CAN2 (Fig. 3) there is no obvious clustering, however, the axes divide the samples into two major groups. Along CAN1, Jahuay, Malabrigo, and Pacatnamu fall on the positive side of the axis, which coincides with a broader nasal aperture, while the remaining samples fall on the negative side suggesting

Table 3. Significant canonical axes.

	Canonical Correlation	Eigenvalue	Proportion	Cumulative	Likelihood Ratio	Approximate F-value	Num DF	Den DF	Pr > F
1	0.651234	0.7364	0.5236	0.5236	0.31538518	10.58	60	2577.6	<.0001
2	0.488900	0.3141	0.2233	0.7470	0.54764402	7.06	45	2203.9	<.0001
3	0.434105	0.2322	0.1651	0.9121	0.71965962	5.31	32	1819.7	<.0001
4	0.245732	0.0643	0.0457	0.9578	0.88676869	2.89	21	1419.1	<.0001
5	0.229484	0.0556	0.0395	0.9973	0.94375661	2.42	12	990	0.0042
6	0.061477	0.0038	0.0027	1.0000	0.99622058	0.38	5	496	0.8650

Table 4. Total Canonical Structure.

Variable	Can1	Can2	Can3
BPL	0.016121	**–0.538059**	–0.237030
NPH	–0.191862	–0.429904	0.366076
NLH	–0.095327	–0.118800	**0.488952**
OBH	0.178858	–0.446567	0.259341
OBB	0.227674	–0.433801	–0.004685
NLB	**–0.618963**	0.045295	–0.431588
MAB	–0.019113	–0.219578	0.433322
EKB	0.440798	–0.145461	–0.160437
DKB	0.385113	0.336737	–0.349313
FRC	–0.190775	0.242235	0.054961

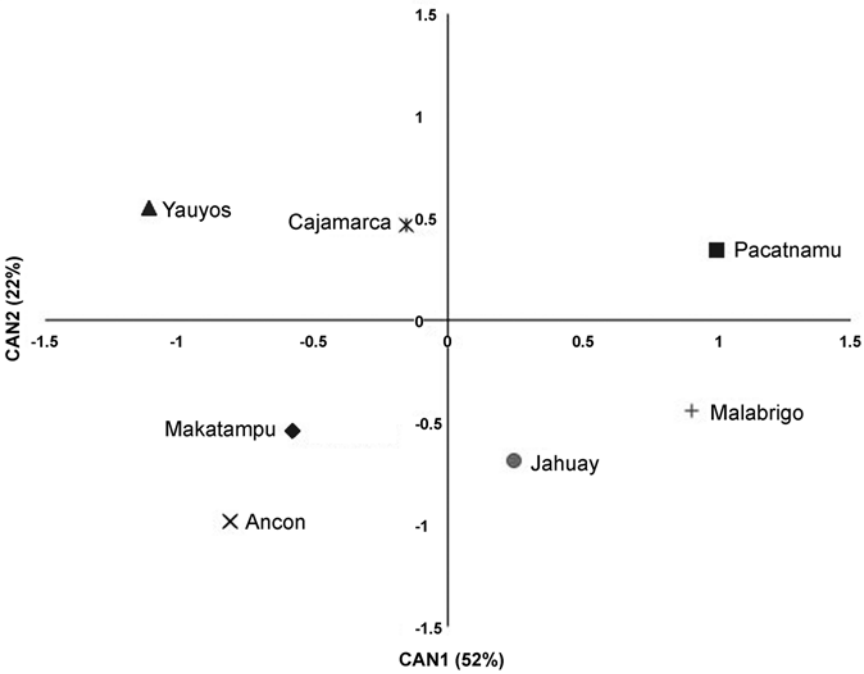


Fig. 3. CAN1/CAN2 plot.

a narrower nasal aperture. Along the CAN2 axis, Yauyos, Cajamarca, and Pacatnamu fall on the negative side with a shorter basion-prosthion height, while the remaining samples falls on the positive side, characterized by a greater basion-prosthion height. There is no clear overall pattern related to environmental zones. However, the two highland sites cluster fairly close together in the upper left quadrant, as well as two groups (Makatampu and Ancon and Pacatnamu and Malabrigo) that are geographically close to one another.

Mahalanobis squared distances (Table 5) indicate that all samples are significantly different from each other based on the associated *p*-values presented on the lower diagonal of the table. The D^2 values show that the most similar groups are Pacatnamu and Malabrigo, Jahuay and Malabrigo, and Ancon and Makatampu, followed by Cajamarca and Pacatnamu. The most morphologically dissimilar are Yauyos and Malabrigo. The squared distances were also used to generate a dendrogram (Fig. 4) that illustrates three major clusters: Ancon and Makatampu, Yauyos and Cajamarca, and Pacatnamu and Malabrigo. The first two clusters are more similar to each other than they are to the other groups and Jahuay is most similar to the northern coastal groups.

Spatial autocorrelation

The Global Moran's *I* spatial autocorrelation results are presented in Table 6. A positive autocorrelation coefficient implies similarity of localities at a given distance for the variable in question (e.g. EKB), while a negative autocorrelation implies dissimilarity. The patterns expressed can be clustered, dispersed or random. All of the patterns expressed with relation to latitude/longitude and cranial variables were significant, positive, and clustered with the exception of frontal chord (FRC), which was random. The measurements z-scores indicate that there is less than one percent likelihood that these clustered patterns could be the result of random chance, which was calculated from the overall variance of the dataset, variables and the variance between the Expected index and the Observed (Moran's *I*) index.

Discussion and conclusion

The first three canonical variates account for the majority of the overall variation between the samples used. Each sample was found to be significantly different from the others, and as a result when both CAN1 and CAN2 are plotted (Fig. 3), no obvious clustering related to environmental zone occupation is apparent. On both plots (Figs 3 and 4), the samples that are in the closest proximity to one another geographically are also closest to one another on the plots. However, relative distances do not appear to be correlated, as illustrated by the Jahuay and Yauyos samples, which are geographically close despite being located at different altitudes. Relationships between high and low altitude groups are illustrated by Fig. 4, where Cajamarca and Yauyos, the two highland groups, cluster together despite being located at the northern and southern margins of our sample area, respectively. The remaining coastal groups cluster into pairs based on geographical proximity with the exception of Jahuay, which despite being located on the southern coast, clusters with the northern coastal sites.

Table 5. Mahalanobis Squared Distances. The *p*-values for each distance are located below the diagonal.

Squared Distance to group from group	Makatampu	Pacatnamu	Yauyos	Ancon	Cajamarca	Jahuay	Malabrigo
Makatampu	0	4.18173	3.38911	1.56845	2.14035	4.20292	4.10304
Pacatnamu	<.0001	0	4.68968	5.18402	2.12885	2.77935	0.96909
Yauyos	<.0001	<.0001	0	2.73346	2.13290	3.91613	5.26978
Ancon	<.0001	<.0001	<.0001	0	3.35339	2.73979	3.39128
Cajamarca	<.0001	<.0001	<.0001	<.0001	0	3.58024	2.80156
Jahuay	<.0001	<.0001	<.0001	<.0001	<.0001	0	1.67698
Malabrigo	<.0001	0.0001	<.0001	<.0001	<.0001	<.0001	0

Table 6. Spatial Autocorrelation analysis.

	Moran's Index	Expected Index	Variance	z-score	*p*-value
BPL	0.006	–0.002	0.0000	2.668	0.008
DKB	0.079	–0.002	0.0000	26.20	0.0000
FRC	0.001	–0.002	0.0000	1.038	0.2994
EKB	0.056	–0.002	0.0000	19.91	0.0000
MAB	0.021	–0.002	0.0000	4.57	0.0000
NLB	0.072	–0.002	0.0000	23.65	0.0000
NLH	0.013	–0.002	0.0000	4.72	0.0000
NPH	0.036	–0.002	0.0000	12.30	0.0000
OBB	0.016	–0.002	0.0000	5.72	0.0000
OBH	0.008	–0.002	0.0000	3.23	0.0000

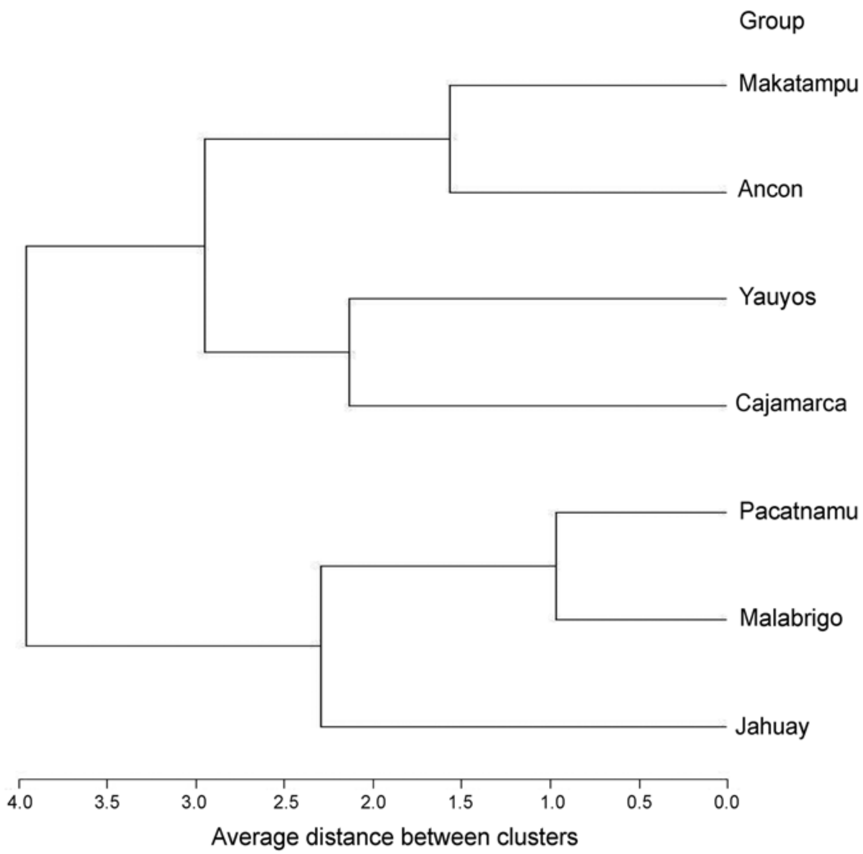


Fig. 4. Dendrogram generated from squared distances.

The results of this study show a different pattern than Ross et al. (2008) and Verano (1987). Ross et al. (2008) found that maxillary breadth, cranial length, and orbital height contributed the most to the variation. These differences are due in part to the present study primarily examining facial variation, whilst Ross et al. (2008) incorporated facial and neurocranial measures. However, the contribution of maxillary breadth to overall variation remains consistent between the two studies. A broader biorbital breadth and broader maxillae is associated with a broader face overall. The broad maxilla found in Ross et al.'s (2008) paper was associated with the Makatampu and Cajamarca samples. Interestingly, the Makatampu and Cajamarca samples are characterized by narrow biorbital breadth in this study. The results of this analysis also indicate that as biorbital breadth decreases, nasal breadth increases. This would suggest that these samples have broader maxillae, but a face that narrows superiorly.

The spatial autocorrelation results show that all facial measures have a clustered spatial pattern meaning that geographical distance is consistent with biological distance. Interestingly, the only measure that was not significant and was found to be a random pattern was frontal chord. This is consistent with findings that the face and base of the skull are more stable, while the vault is more plastic (Enlow 1990, Ross & Ubelaker 2009, Ross & Williams 2010). The variation seen among the groups therefore is the result of a combination of genetic and environmental factors, though the differences between highland and coastal environments do not appear to play a large role given the lack of clear differentiation between the samples. Because the samples do not exhibit clear temporal overlap, the degree of admixture and potential gene flow between samples cannot be further determined as some samples contain material from multiple time periods even though it has been hypothesized that there is regional continuity. Interestingly, however, there is a considerable amount of spatial patterning for the facial variables coinciding with geographical location suggesting local adaptation or limited migration.

There are other potential environmental factors that could be contributing to the observed differentiation in face shape, including subsistence-related masticatory stress. A number of studies have suggested that the craniofacial region responds strongly to diet composition, though there is no clear association with subsistence strategy. Rather, the influences of masticatory loading on face shape appear more strongly associated with localized variation in the hardness, toughness, and particle size of foods (González-José et al. 2005, Paschetta et al. 2010, Sardi et al. 2005). The samples used in this study are all representatives of agricultural groups for which common dietary staples include quinoa, potato, maize, beans, squash, and peppers, as well as a mixed marine fish and terrestrial mammal diet (Verano & DeNiro 1993). Specific dietary information is not available for all of the samples studied here, but isotopic and archaeological data from Pacatnamu support a diet consisting of maize, beans, squash, chili pepper, and various fruits, and a mixed marine and terrestrial protein component consisting of camelids, fish and shellfish. Discrepancies between Early and Late Period samples suggest an increase in the amount of marine resources consumed over time (Verano & DeNiro 1993). Though it is possible that there are some localized staples that may contribute to differences in masticatory loading between the samples, the current lack of site-specific archaeological and isotopic data prevent us from examining this possibility further.

In conclusion, the variation seen among prehistoric Peruvian groups in this study is related to a combination of among-group variation as a result of geographic proximity to one another, which was supported by the spatial autocorrelation analysis. Further archaeological evidence of interaction between groups, as well as larger samples of highland individuals would allow for investigation of the various potential factors at play in the range of cranial variation seen in this study. Inclusion of southern and eastern Peruvian samples would also present a broader regional picture of variation across the full range of environmental zones.

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