Spatial Patterns and Evolutionary Processes in Southern South America: A Study of Dental Morphometric Variation

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ABSTRACT   The purpose of this article is to examine the patterns of evolutionary relationships between human populations from the later Late Holocene (1,500–100 years BP) of southern South America on the basis of dental morphometric data. We tested the hypotheses that the variation observed in this region would be explained by the existence of populations with different phylogenetic origin or differential action of gene flow and genetic drift. In this study, we analyzed permanent teeth from 17 samples of male and female adult individuals from throughout southern South America. We measured mesiodistal and buccolingual diameters at the base of the crown, along the cement–enamel junction. The results of multiple regression analysis and a mantel correlogram indicate the existence of spatial structure in dental shape variation, as the D^2 Mahalanobis distance between samples increases with increasing geographical distance between them. In addition, the correlation test results show a trend toward reduction of the internal variation of samples with increasing latitude. The detected pattern of dental variation agrees with the one expected as an outcome of founder serial effects related to an expansion of range during the initial occupation of southern South America. Am J Phys Anthropol 142:95–104, 2010.   © 2009 Wiley-Liss, Inc.

The origin and maintenance of evolutionary relatedness patterns among populations has long been the focus of studies aimed to understand the diversification of modern humans. These patterns are the result of microevolutionary processes such as gene flow and genetic drift, as well as expansion and population splitting, which act on heritable variation shaping the biological differentiation at intra- and interpopulational levels (Relethford and Lees, 1982; Sokal et al., 1989a; Templeton et al., 1995; Templeton, 1998). Therefore, the configuration and magnitude of biological relationships contain information about the relative contribution of underlying mechanisms that have modeled the variation at different spatial and temporal scales (Sokal et al., 1989a,b; Ramachandran et al., 2005).

One strategy to gain insight into microevolutionary processes is the quantification of distances between populations, which express their degree of similarity. Such relationships can be inferred on the basis of molecular and phenotypic traits. Since variation in polygenic traits emerges from complex interactions between genetics and environment, the ability of these traits to recover evolutionary relationships depends on their heritability, which should be as close to unity as possible (Cavalli-Sforza et al., 1994; Lieberman, 1999). In addition, polygenic traits should follow a random model of evolution (Relethford and Lees, 1982; Cavalli-Sforza et al., 1994; Relethford, 2004).

The patterns of evolutionary relationships among human populations from southern South America have played a central role in anthropological research, particularly within the debates about the peopling of the continent and the evolution of American aborigines (Imbelloni, 1937; Cocilovo and Guichón, 1985–1986; Lahr, 1995; Hernández et al., 1997; Moraga et al., 2000; Sardi, 2002; García-Bour et al., 2004; González-José et al., 2004). This is partially due to the fact that it is one of the last regions of the world to be colonized by modern humans, about 11–13 ka BP (Borrero, 1999; Lanata et al., 2008; Steele and Politis, 2008), and its populations are characterized by high levels of biological variation, which are thought to have originated in a short time, in comparison to the peopling of other areas of the world (Sardi et al., 2005; Bernal et al., 2006; Perez et al., 2007; Béguelin, 2009). Nevertheless, after more than 100 years of studies, there are still numerous controversies regarding the processes and events that could have shaped the patterns of evolutionary relationships among these populations.

The hypotheses proposed to explain the origin and maintenance of evolutionary relationships in this region were grouped into two propositions: a) different ancestral origins; b) local processes of diversification. Many researchers suggested that human groups inhabiting the southernmost confines of South America would be

descendants of the first settlers of the continent, the Palaeoamericans, who peopled America before the arrival of Amerindians, i.e., the Northeast Asian-descended populations (Imbelloni, 1937; Lahr, 1995; Neves et al., 1999; González-José et al., 2001b; Sardi et al., 2005). Conversely, other authors affirmed that the geographical and latitudinal pattern of morphological variation in this region could have emerged by local processes such as gene flow or genetic drift and that all the populations of southern South America would be derived from one Asian-descended population or a group of related Asiatic populations (Cocilovo and Di Rienzo, 1984–1985; Cocilovo and Guichón, 1985–1986; Rothhammer and Silva, 1990; Powell and Neves, 1999). Although it has been shown for several geographic regions that cranial plasticity is negligible and does not obscure population differences (e.g., Sparks and Jantz, 2002, 2003), recent cranial and postcranial studies in southern South America suggest that the great morphological differentiation of these aboriginal populations could be related to nonrandom factors such as natural selection (Pearson and Millones, 2005; Bernal et al., 2006; Béguelin, 2009) and/ or phenotypic plasticity (Sardi et al., 2006; Perez and Monteiro, 2009). Thus, nonrandom factors may perhaps obscure the evolutionary relationships of this region calculated using cranial and postcranial variation so that alternative sources of information would be required to elucidate them.

In this regard, tooth shape variation is considered to be one of the most reliable morphological indicators available for the assessment of evolutionary relationships because of the genetic and developmental characteristics of these elements. Teeth are less influenced by environment than other skeletal structures because they undergo a shorter period of development and attain their final morphology before eruption (Sperber, 2004). Recent studies also indicate that tooth shape is under strong genetic control (Cheverud et al., 1997; Leamy et al., 1999; Workman et al., 2002). In addition, previous studies performed on southern South American samples showed that the effect of nonrandom factors on dental shape variation is negligible, since between-population distances based on dental variables are significantly associated with molecular distances (i.e., mtDNA; see Bernal et al., 2008b), and the amount of intergroup dental variation matches the values expected under random processes (Bernal, 2008).

Accordingly, the purpose of this article is to examine the patterns of evolutionary relationships in human populations from southern South America dated as later Late Holocene (1,500–100 ^{14}C BP). Dental morphometric data were used to evaluate and discuss several hypotheses about the microevolutionary processes that could have shaped the patterns of evolutionary relationships in the region studied. The alternative hypotheses were evaluated following the model selection approach, in which several competing hypotheses are simultaneously confronted with the data (Smouse et al., 1986; Legendre et al., 1994; Johnson and Omland, 2004). This is a valuable alternative to traditional null hypothesis testing, especially when more than one hypothesis is plausible. In addition, Mantel correlogram analysis was used to describe the spatial structure of dental variation and discuss the underlying processes driving the pattern of biological distances (Legendre and Fortin, 1989; Sokal et al., 1989a; Legendre and Legendre, 2003).

Hypotheses about human biological variation in South America

Several hypotheses based on archeological and biological data have been proposed to explain the biological variation observed in this region. Below we summarize these hypotheses while attempting to incorporate their key concepts and expectations in relation to the dental shape variation among samples.

Hypothesis 1. The biological variation observed among populations in the region during the Late Holocene is the product of two routes of settlement in South America, one following the Atlantic shoreline and the other following the Andean mountains. This hypothesis is based on craniometric studies (Cocilovo and Di Rienzo, 1984–1985; Lalueza Fox et al., 1996; Pucciarelli et al., 2006; Ross et al., 2008). Under this hypothesis, the samples from the same route are expected to show greater similarities between each other than with those belonging to the other route.

Hypothesis 2. Biological differentiation was the result of two waves of migration. Early supporters of this hypothesis suggested that America was firstly peopled by an antique race (represented by skeletons of Lagoa Santa and ethnographical groups of Tierra del Fuego and Baja California), which was replaced by Asiandescent from which most of the modern Amerindians derived (Imbelloni, 1937). Recently, this hypothesis was formalized as the model of "two biological components" (Neves et al., 1999; González-José et al., 2001b). Based on these studies, we hypothesized that the biological variation in southern South America during the Late Holocene would be the product of two biological components, one representative of the first inhabitants of the continent, and a more recent one that gave rise to most modern Amerindians. Under this hypothesis, it is expected that the samples corresponding to the early component are differentiated from those of the latter one.

Hypothesis 3. The biological variation observed among populations in the region during the Late Holocene resulted from the establishment of a pattern of isolation by distance, as the product of a balance between drift and gene flow, with the first increasing and the second decreasing genetic divergence among populations (Cocilovo, 1981; Perez, 2006). Under this hypothesis, the biological distance among samples is expected to increase with the geographical distance.

Hypothesis 4. Biological variation among populations was structured as a product of multiple events of expansion of small hunter-gatherer groups during their initial settlement in the region (i.e. serial founder effect, Rothhammer and Silva, 1990; Moraga et al., 2000; García-Bour et al., 2004). Such a process could account for the latitudinal reduction of variation of haplogroups in South America, with a pattern of decreasing A and B haplogroups from north to south, whereas the haplogroups C and D tend to increase in the same direction. Under this hypothesis, the biological distance among samples is expected to increase along the main direction of peopling, whereas the internal variation of samples would decrease in the same direction.

Hypothesis 5. Biological variation resulted from factors acting differentially in different areas of Patagonia:

groups from Tierra del Fuego are different from continental populations due to their geographical isolation, while coastal groups from northern Patagonia show a pattern of variation resulting from gene flow limited by isolation by distance, and finally, the effect of the migration of populations from Chile, which results in a great similarity among these samples as suggested González-José (2003), is observable in the northwestern Patagonia and Pampean Regions.
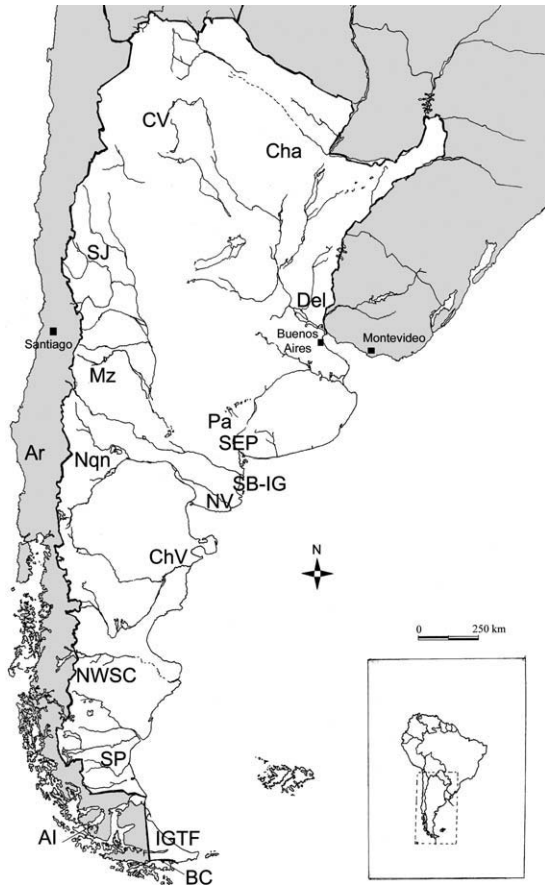
Hypothesis 6. The biological variation was the result of the establishment of different population dynamics on the north and south margins of the Chubut river. To the south of the Chubut river basin very low densities and higher population isolation are expected, particularly before the introduction of the horse in historic times, while north of this basin there is evidence of a probable process of geographical expansion from areas of higher population density, such as the lower valleys of north Patagonian rivers (i.e. Chubut, Negro and Colorado) and the Atlantic Coast (Barrientos and Perez, 2004; Perez et al., 2004; Barrientos et al., 2005; Béguelin et al., 2006). Under this hypothesis, a greater effect of genetic drift to the south and gene flow to the north of Chubut river would be expected.

MATERIALS AND METHODS
Samples

In this study, we analyzed the permanent teeth from 17 samples of male and female adult individuals from throughout southern South America (Fig. 1; Table 1). All the samples were assigned to later Late Holocene ($\sim$1,500–100 years ^{14}C BP) based on radiocarbon dating and contextual information (Table 1; Bernal, 2008). The samples come from groups that inhabited different geographic and ecological regions, distributed along 3,000 km (from 25° to 55° South latitude; Fig. 1). A detailed description of the samples analyzed is presented in Supporting Information Appendix 1.

Fig. 1. Map showing the location of the samples analyzed. Abbreviations are in Table 1.

TABLE 1. *Composition of the samples analyzed*

Samples[a]	Abbreviation	Region	n	Museum
Calchaqui valley	CV	Northwest	16	ME
Chaco	Cha	Chaco	14	MLP–ME
San Juan	SJ	Cuyo	23	MLP–ME
Center South Mendoza	Mz	Cuyo	11	MHNSR
Delta	Del	Pampean region	21	MLP
South East Pampa	SEP	Pampean region	12	MLP
Pampa	Pa	Pampean region	37	MLP
Negro valley	NV	Continental Patagonia	17	MLP
San Blas and Isla Gama	SB-IG	Continental Patagonia	20	MLP
Araucania	Ar	Araucanian region	18	MNHN
Neuquen	Nqn	Continental Patagonia	17	ME–SCN
Chubut valley	ChV	Continental Patagonia	26	MLP
North West of Santa Cruz	NWSC	Continental Patagonia	15	INAPL
South Patagonia	SP	Continental Patagonia	15	MRG
Tierra del Fuego	IGTF	Insular Patagonia	22	IPA
Austral Islands	AI	Insular Patagonia	20	IPA
Beagle Channel	BC	Insular Patagonia	13	MFM–IPA
Total			318	

[a] The specimens are housed at the Museo de La Plata (La Plata, Argentina, MLP), Museo Etnográfico "J. B. Ambrosetti" (Buenos Aires, Argentina, ME), Museo Regional Provincial "Padre Manuel Jesús Molina" (Río Gallegos, Argentina, MRG), Museo del Fin del Mundo (Usuahia, Argentina, MFM), Instituto Nacional de Antropología y Pensamiento Latinoamericano (Buenos Aires, Argentina, INAPL), Museo de Historia Natural (Santiago, Chile, MNHN), Secretaría de Cultural de Neuquén (Neuquén, Argentina, SCN), Museo de Historia Natural (San Rafael, Argentina, MHNSR), and Instituto de la Patagonia Austral (Punta Arenas, Chile, IPA).

Data collection and preliminary analyses

Sex and age estimations were made using cranial and pelvic features (Buikstra and Ubelaker, 1994). Sex estimation of pelvic structures was done using four morphological traits, following Phenice (1969) and Buikstra and Ubelaker (1994): ventral arch on the ventral surface of the pubis; subpubic concavity; medial aspect of the ischio-pubic ramus; and greater sciatic notch. However, most determinations were restricted to cranial traits because the majority of individuals were represented by skulls only. The traits scored in the skull were glabella, supraorbital margin, mastoid process, arcus superciliaris, crista supramastoidea, and overall aspect of mandible (Buikstra and Ubelaker, 1994; Graw, 2001).

Morphometric data for maxillary teeth, with the exception of third molars, were obtained. Teeth that were not completely erupted, obscured by crowding, presented carious lesions, or exhibited severe wear affecting the cervix were excluded from the analysis. Only measurements of the left teeth were used for statistical analyses; when measurement of the left side was not possible, data from the right antimere were substituted. Morphometric dental variation was studied using mesiodistal and buccolingual diameters. These diameters were measured at the base of the crown, along the cement–enamel junction, using a Mitutoyo Digimatic caliper with thin points—Paleo Tech Hillson/Fitzgerald Dental Caliper (Hillson et al., 2005). The mesiodistal cervical diameter for anterior teeth was defined as the distance between the most occlusal points of the cement–enamel junction curve on the mesial and distal sides. For posterior teeth, the measurement point was defined as midway along the cement–enamel junction on the mesial and distal sides of the crown. The buccolingual cervical diameter for anterior teeth was defined as the maximum distance at the cement–enamel junction from buccal to lingual. For posterior teeth, the measurement was taken on the cement–enamel junction at points midway along the buccal and lingual sides. All dental measurements used in this study were recorded by VB.

For further analyses, size standardization of the raw data was used, where each measurement was divided by the geometric mean of all the measurements for each individual in the sample (Darroch and Mosimann, 1985; see Jungers et al., 1995). The geometric mean was computed as the nth root of the product of all n variables [$GM = (X_1 X_2, \ldots, X_n)^{1/n}$, where X are the variables]. This size standardization procedure resulted in variables in the Mosimann family of shape ratios (Jungers et al., 1995). We used shape instead of size variables because previous analyses suggest that evolutionary history is the dominant factor driving dental shape diversification among human populations in southern South America, whereas the diversification of dental size is related to ecological factors (e.g. diet; Bernal et al., 2008b).

The existence of sexual dimorphism in tooth shape was previously evaluated using an ANOVA test of the standardized variables (Bernal, 2008). The results indicated no significant shape differences between sexes (Bernal, 2008); therefore, males and females were pooled in subsequent analyses to obtain larger sample size.

Assessment of intraobserver error was performed using a subsample comprising individuals from Chaco and Pampean Regions ($N = 120$ teeth). Mesiodistal and buccolingual diameters were measured twice on each tooth. The degree of intraobserver error was evaluated by means of the intraclass correlation coefficient (ICC; Shrout and Fleiss, 1979; Zar, 1999) and paired t test (Zar, 1999). Distributional normality of the two variables was tested by means of a Shapiro–Wilk test before the computation of ICC and paired t test (Weber and Skillings, 2000).

The samples of hunter-gatherers and agriculturalists employed in this study exhibited severe dental wear and postmortem tooth loss (Bernal, 2008). In consequence, a procedure to replace missing values was necessary to obtain complete data matrices adequate for multivariate analyses. The missing data were estimated using a method known as multiple imputation (Schaffer, 1999a,b). This method has been recently employed in anthropological research (Stefan, 2004; Stojanowski, 2004; Scherer, 2007). Measurements that were taken on too few individuals (less than 50%) were removed. Because all the measurements of anterior dentition displayed a large amount of missing data, only the mesiodistal and buccolingual diameters of Pm3, Pm4, M1, and M2 were analyzed. Individuals that had too few measurements (less than 50%) of posterior dentition were also removed. The dataset obtained after this procedure, comprising 318 individuals and 8 variables, had only 23% of missing data. To estimate missing values, we employed NORM, a multiple imputation program (NORM 2.03, Schaffer, 1999a,b), using the data augmentation procedure (Schaffer and Olsen, 1998).

Testing hypotheses

The hypotheses about the microevolutionary processes that shaped the patterns of dental shape variation among southern South American populations were investigated using R matrix and comparative methods (Relethford and Lees, 1982; Relethford and Blangero, 1990). With this approach we tried to identify processes on the basis of detected patterns, by means of the selection of models supposed to represent the underlying mechanisms.

Minimum biological distances between all pairwise samples (i.e. D^2 Mahalanobis distances; Mahalanobis, 1936) and within sample variation (heterozygocity) were derived from the R matrix, which represents the scaled variance–covariance matrix of population similarity (Relethford and Blangero, 1990; Relethford and Harpending, 1994). The value of heritability was estimated from a set of values for the posterior dentition obtained from the study of extant populations (Alvesalo and Tigerstedt, 1974; Sharma et al., 1985; Harzer, 1995; Dempsey and Townsend, 2001). Based on these works, we used heritability values between 0.55 and 1. Because the results obtained with different values of heritability did not change, we subsequently used the average heritability (0.65) of the set of values. Variation in effective population size does not generate significantly different results, and therefore the effective size was considered equal for all samples (Relethford and Blangero, 1990; Bernal, 2008). These analyses were performed using the Rmet v. 5.0 program (Relethford, 2008).

We tested the correspondence between the patterns of variation expected under different hypotheses and the dental shape variation observed among samples (i.e. D^2 Mahalanobis distance matrix). Our approach is based on a model selection method, which allows evaluating multiple alternative hypotheses while identifying levels of support for each one and selecting the model that has

the best adjustment to the data (Johnson and Omland, 2004). A similar methodology using craniofacial data from South America has been previously applied by other authors (González-José et al., 2001a; Fabra et al., 2007). First, we built five quantitative models based on the previously formulated hypotheses (see Supporting Information Appendix 2). These were expressed as design matrices and a geographic distance matrix built following the recommendations of Legendre et al. (1994) and Lapointe and Legendre (1992).

One-model "Two routes of settlement". The Andean route comprised samples from northwest Argentina, Cuyo, northwestern Patagonia, south-central Chile, and groups of marine hunters from Tierra del Fuego (SJ, CV, Mz, Nqn, Ar, BC, and AI). It also included a Pampa sample (Pa), since its settlement in that area would be recent. The coastal route included samples from Chaco, Delta, southeastern Pampa, the Atlantic coast of Patagonia, northwestern Santa Cruz, and hunters from Tierra del Fuego (Cha, SEP, Del, NV, SB-IG, ChV, SP, NWSC, IGTF). The distance between samples assigned to the same route was set as 0, while the distance between samples belonging to different routes was 1.

Two-model "Two biological components". Under this model, the ethnographic groups from southernmost South America (Yámanas and Alakaluf; corresponding to BC and AI samples) constitute relict populations of the first wave that peopled the continent. Therefore, the distance between the two samples of marine hunters in southern Patagonia (BC and AI) was set as 0, and the maximum distance of 1 was set between them and the remaining samples.

Three-model "Spatial structuring". This model represents the expected variation under two of the previously formulated hypotheses: 1) isolation by distance; and 2) the existence of multiple events of geographical expansion or serial founder effect. According to these hypotheses, the biological distance among samples increases with geographical distance. The matrix of geographical distances between samples was built from the linear distance in kilometers between the areas of geographic locations of the samples.

Four-model "Geographical isolation modified". Following González-José (2003), the four southernmost groups (AI, BC, IGTF, and SP) are more distanced from the northern ones (northern Patagonia and Pampa) with a maximum arbitrary value of 4, reflecting the highest degree of differentiation in Patagonia between Fueguians (samples AI, BC, and IGTF in this paper) and a group highly influenced by the Mapuches from Chile (sample Ar in this paper). A distance of 0 was assigned between the southernmost groups. Assuming the effect of gene flow to be limited by distance, the populations from the northern coast of Patagonia (SEP, NV, SB-IG, ChV, and NWSC) were separated by a distance of 1 from their closest southern or northern neighbors and by a sum of distances if the samples were not adjacent [e.g., d (SEP–NV) = 1; d (SEP–ChV) = 2]. This model was originally developed for Patagonian populations only; therefore, to establish relationships with samples from other regions, the biological distance expected was assumed to be proportional to geographical distance, since the expected distances from the original model are determined primarily by the geographical distance between samples.

Five-model "Different population dynamics at areas north and south of the Chubut river". In this model, we assigned a value of 1 to the maximum differentiation between two populations and intermediate values ranging between 0 and 1 to represent intermediate relationships. A value of distance 0 was assigned between samples from northern Patagonia and southeastern Pampas, 1 between these samples and those located south of the Chubut river, 1 for the samples from northern and southern Patagonia, and intermediate values were given among the remaining samples according to their geographic proximity.

We used the multiple regression of distance matrices for more than three matrices proposed by Smouse et al. (1986) and extended by Legendre et al. (1994) to simultaneously test the correspondence of D^2 Mahalanobis distance matrix against the set of models. This is an extension of the partial Mantel analysis to cases involving several explanatory matrices. The response and explanatory matrices are unfolded into vectors and a multiple regression is computed in which the response matrix is a function of the explanatory matrices. Thus, multiple regression allows evaluation of the independent contribution of each model (when the other matrices are held constant) to the matrix of biological distance among populations. This analysis differs from other approaches (e.g., when the relationship between biological and ecological variables is explored; see Sokal, 1984; Legendre, 1993) where only the geographic distance matrix is held constant to remove the effects of spatial variation in the relationship between populations. The models were expressed in different units of measurement, and then model matrices were z-standardized before regression analysis so that each matrix had a mean of zero and a variance of one (Legendre et al., 1994). In this way, standardized partial coefficients were obtained (Legendre et al., 1994). A Mantel permutational procedure was used to test the statistical significance of regression statistics (see Smouse et al., 1986; Legendre et al., 1994). This approach involves comparing the observed regression statistics to a null distribution of such statistics constructed by fixing explanatory matrices and randomly permuting the response or biological distance matrix, calculating a new statistic after each permutation. The regression was made using 9,999 random permutations for a one-tailed significance test, because we were interested in establishing whether the biological distance between groups increased as the distance predicted by the model increased. This analysis was performed using the REGRESSN program (Legendre, 2002). Previously, the effect of multicolinearity was tested using tolerance criteria, Spearman rank order, and Pearson's product–moment correlations among all matrices (Hair et al., 2005).

In addition, a Mantel correlogram was computed to obtain a detailed description of the spatial structure of dental variation (Oden and Sokal, 1986; Sokal, 1986). To obtain a correlogram, the ordinary Pearson's product–moment correlation coefficient, r, statistic was calculated for a number of classes of geographical distances, and then these values were plotted against distance classes. This r value is monotonically related to the Mantel Z statistic and is generally preferred because it has the advantage of being expressed in standardized units so that the values can be compared among different matrices (Smouse et al., 1986; Legendre and Legendre, 2003). The number of classes in the correlogram was estab-

TABLE 2. Correlation matrix between the models and the D^2 Mahalanobis distance

	D^2	Model 1	Model 2	Model 3	Model 4	Model 5
D^2	1	0.111	0.087	0.378	0.352	0.145
Model 1	0.024	1	0.075	0.032	0.017	0.126
Model 2	0.121	0.116	1	0.281	0.166	0.236
Model 3	0.526*	0.021	0.281	1	0.958	0.453
Model 4	0.512*	0.008	0.221	0.943**	1	0.363
Model 5	0.161	0.109	0.227	0.430	0.393	1

Model 1: two routes of settlement; Model 2: two biological components; Model 3: spatial structuring; Model 4: geographical isolation modified; Model 5: different population dynamics at areas north and south of the Chubut river.
Spearman correlation above diagonal, and Pearson's product–moment coefficient below diagonal.
* $P < 0.05$; ** $P < 0.01$.

TABLE 3. Multiple regression with permutations

Model	b	t	P-perm
Model 1	−0.031	−0.407	0.350
Model 2	0.023	0.305	0.388
Model 3	0.568	6.763	0.000
Model 5	−0.078	−0.935	0.173

Model 1: two routes of settlement; Model 2: two biological components; Model 3: spatial structuring; Model 5: different population dynamics at areas north and south of the Chubut river.
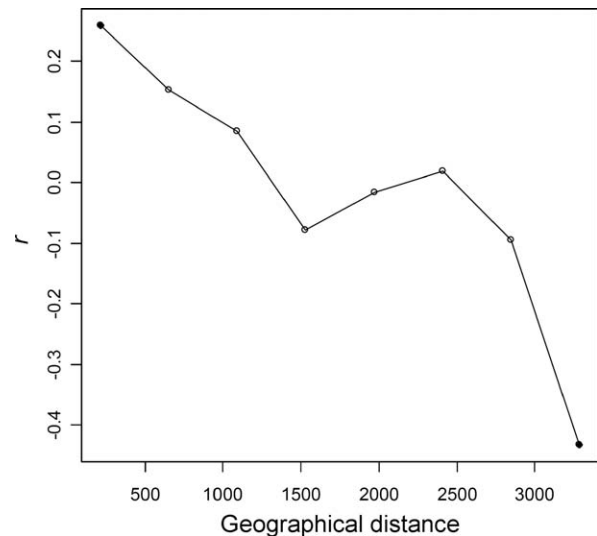
lished using Sturges rule (Sturges, 1926). The significance of each autocorrelation value was estimated using 10,000 permutations. We also performed a global test to evaluate the significance of the correlogram. This latter test was made by checking whether the correlogram contained at least one value, which was significant at the $\alpha' = \alpha/v$ significance level, where v is the number of tests, according to the Bonferroni method of correcting for multiple tests (Legendre and Fortin, 1989). The Mantel correlogram was performed using the ecodist 1.13 package in R 2.6.1 (R Development Core Team, 2008).

Finally, we tested the correlation between latitude and within-sample variation using Pearson's product–moment correlation.

RESULTS

Normality could not be rejected for any variable according to the Shapiro–Wilk test ($P < 0.05$). The results of intraclass correlation for the linear measurements taken with digital calipers indicate significant correlations for both mesiodistal (CCI > 0.94, $P < 0.01$) and buccolingual diameters (CCI > 0.93, $P < 0.01$). Moreover, the paired "t" values show nonstatistically significant differences between repeated measurements of both variables.

The results of the correlation test and tolerance criteria indicate high and significant association between the models "Spatial structuring" and "Geographical isolation modified" ($r = 0.943$; Table 2). This would indicate that even though the "Geographical isolation modified" model is more complex in terms of the processes that have acted to shape the pattern of interpopulational variation, it does not contain independent information on geographical distance to account for the biological distances observed. Therefore, only one of these two models should be selected to perform regression analysis. We chose the "Spatial structuring" model because of its relative simplicity and higher correlation with the matrix of D^2 Mahalanobis distances (Table 2).

The multiple regression analysis indicated that the "Spatial structuring" model presents the best adjustment to the matrix of biological distances, with a slope significantly different from 0 (partial $b = 0.57$; Table 3). The slope values for the other models were low and not significantly different from 0. These results indicate that they do not provide independent information to explain the biological variation observed among populations.

Fig. 2. Geographic patterns of dental variation, as described by Mantel Correlogram. x axis: geographic distance between samples in km; y axis: correlation coefficients (r). Filled circles indicate significant r values.

The results of the implementation of the Bonferroni correction ($\alpha = 0.05/8 = 0.0065$) indicate that the entire correlogram is significant, since some of the individual values exceed the level of correction. Because there is a positive and significant autocorrelation between geographical distances corresponding to the first class (less than 220 km) and a significant and negative autocorrelation between geographical distances corresponding to the last class (more than 3,000 km), the correlogram indicates higher similarity between samples at low geographical distance and lower similarity at successively greater geographical distances (see Fig. 2), as is usually observed for clinal patterns. However, the value of the last interval should be considered cautiously, since it only includes seven pairs of distances (Legendre and Fortin, 1989). The area of significant positive autocorrelation is comprised by the first interval, i.e. between samples located at distances less than 220 km. This indicates that populations located at short distances exhibit great morphological similarity.

Finally, we found negative correlation between within-sample shape variation and latitude ($r = -0.516$, $P < 0.05$). This result indicates that within-sample shape variation decreases in north–south direction.

DISCUSSION

The data set obtained represents an important source of information about dental metric variation in South

America, which was largely unknown until now. Particularly, the results of this study stress the relevance of dental shape data for the analysis and assessment of hypotheses regarding microevolutionary processes of human populations from this region.

The results of the multiple regression analysis support the existence of spatial structure in dental shape variation among southern South American samples. This analysis showed that the geographical distance between samples showed the highest adjustment to the D^2 Mahalanobis distance. In addition, the estimation of the correlation between these two variables showed a positive and significant value ($r = 0.53$; $P < 0.01$; 10,000 permutations). According to this model, the biological distance between samples increases with increasing geographical distance between them. The remaining models evaluated in this work did not provide independent information to explain the pattern of biological distances between samples.

Several previous studies based on craniometric and molecular data are consistent with the results of this work in showing that the biological distance between samples from southern South America is clearly associated with geographical distance (Cocilovo and Di Rienzo, 1984–1985; Rothhammer and Silva, 1990; Moraga et al., 2000; Schurr, 2004; Bernal et al., 2006; Perez, 2006). In addition, the pattern of dental variation found in this study agrees with the pattern of frequencies of certain mtDNA haplogroups. Moraga et al. (2000) analyzed the mtDNA of three Aboriginal groups in Chile (Yamana, Pehuenches, and Mapuches) using restriction fragment length polymorphism (RFLP) and the sequence of the D-Loop region. Their results indicate the existence of a north–south gradient in the diversity of haplotypes of the D-loop region sequence and the diversity of haplogroup C. This trend coincides with the decrease in the frequency of haplogroups A and B from North to South America, while haplogroups C and D tend to increase in the same direction (Merriwether et al., 1995; García-Bour et al., 2004; Schurr, 2004; Dejean et al., 2007).

The goodness of fit approach followed in this article was useful to eliminate specific models that displayed very low adjustment to the data. However, as Templeton (2007) has noted, such an approach only refers to hypothesis compatibility. Accordingly, the existence of spatial structuring of biological distances in this region is compatible with different underlying processes, such as gene flow restricted by geographical distance (i.e., isolation by distance model: IBD; Wright, 1943; Cavalli-Sforza et al., 1994; Relethford, 2004) or serial founder events (Excoffier, 2004; Ramachandran et al., 2005; Wegmann et al., 2006).

Generally, human populations tend to occupy discrete habitats with multiple dimensions, characterized by a certain concentration of resources that result in aggregate distributions (i.e., local populations, subpopulations, or demes; Cavalli-Sforza et al., 1994). As a result of this spatial structure, gene flow will be more frequent between nearby populations, leading to some degree of genetic uniformity at smaller geographical scales, while at greater distances restricted gene flow leads to genetic differentiation by genetic drift (Slatkin, 1993; Cavalli-Sforza et al., 1994; Peterson and Denno, 1998; Hutchison and Templeton, 1999). Therefore, when the level of mobility is moderate, the structuring of biological variation following a model of IBD is expected.

However, the expansion of modern humans into South America through multiple and successive dispersion events of small groups from North to South (a process known as expansion of range; Slatkin, 1993) is an alternative way of producing a correlation between geographic and biological distances. Geographical expansion events—expansion from a single direction or one side [see Sokal et al. (1989a,b)]—may occur through many steps, with each such migration involving a sampling from the previous subset of the original population. This sampling would have led to a stepwise increase in biological distance (i.e., a clinal pattern; Sokal et al., 1989a) and a concomitant decrease in genetic diversity. This process is frequently called serial founder effect (Ramachandran et al., 2005).

The shape of the Mantel correlogram obtained here was compared with those generated by simulating processes such as migration from different sources and directions, isolation by distance, and natural selection (Sokal et al., 1989a). The shape observed in the correlogram is compatible with a clinal pattern, i.e., there is higher morphometric similarity at small geographical distances and large differences at greater geographical distances (see Fig. 2). This correlogram differs from the pattern obtained by isolation by distance, which generally has an asymptotically decreasing shape (Sokal et al., 1989a; Barbujani, 2000). Therefore, the Mantel correlogram suggests an important effect of processes such as expansion or migration from a single direction or one side (Sokal et al., 1989a,b).

The expansions of range lead to several events of random sampling (i.e., serial founder events) resulting in a gradient of reduction of biological diversity within populations away from the center of expansion in the direction that the groups are moving, unless gene flow rates are extremely high (Barbujani, 2000; Excoffier, 2004; Ramachandran et al., 2005; Wegmann et al., 2006). Consequently, this hypothesis is also supported by the results of correlation test, which show a trend of decreasing internal dental variation of samples from north to south, i.e., the main direction of peopling in the region (Borrero, 2001a; Miotti and Salemme, 2004; Lanata and Garcia, 2005).

The results presented here are consistent with a process of expansion from a single direction or one side, and accordingly in the following paragraphs we discuss other lines of evidence that give independent support to this hypothesis.

The initial human dispersion into Patagonia has been characterized as a discontinuous and hierarchical process, which occurred during the Pleistocene/Holocene transition (11–13 ka BP). At the time, small groups of hunter-gatherers explored and colonized an uninhabited area in a context of climatic instability (Clapperton, 1992; Heusser, 1993; Dillehay, 2000; Borrero, 2001a; Miotti and Salemme, 2004; Lanata and Garcia, 2005; Dejean et al., 2007). The scarcity of sites dated between 10 and 12 ka BP indicates that human populations were small, mobile, and scattered. Particularly, the spatial distribution of the early archeological sites shows a remarkable concentration in certain spots such as the Deseado Central plateau in the south-central area of the Patagonian Region, the Magellan Basin, and the region of the Pacific Rim at the western side of the Patagonian Andes, whereas other areas remained uninhabited (Miotti and Salemme, 2004). In addition, palynological, faunal, and glaciological information indicates that not all areas were suitable for human occupation, and so the ones that became occupied were those more highly ranked in

terms of food and other resources such as water (Borrero, 2001b; Miotti and Salemme, 2004). As a consequence of this habitat fragmentation, the differential occupation of space by populations persisted even during the middle and late Holocene.

From a demographic point of view, the populations of hunter-gatherers of this region were characterized by low densities (Borrero, 2001b; Goñi et al., 2000–2002; Neme et al., 2005). Even during the later Late Holocene, some areas remained uninhabited or were discontinuously occupied (Franco and Borrero, 1996; Aschero et al., 2005). This is also supported by ethnohistoric sources indicating that the number of individuals in Continental Patagonia, from the Negro valley to the Magellan Strait, was around 4,000 to 10,000 during the XVI century (Bernal, 2008).

The organizational properties of these hunter-gatherers could also have contributed to the discontinuous pattern of occupation observed (Borrero, 1999, 2001a). Ethnographic information leads to the expectation that the hunter-gatherer settlers were characterized by a type of structure in which individuals formed a series of nested units, i.e. hierarchic structure (Johnson, 1982; Hamilton et al., 2007). Under these circumstances, dispersion into unknown areas most likely occurs through the fission of groups leading to the emergence of new groups formed by members of younger generations who move into new spaces, retaining some degree of contact with their groups of origin (Kelly, 2003). However, the low population density, lack of knowledge about their environment, and the existence of barriers that restricted the movement of individuals could have facilitated further isolation among groups.

In summary, the spatial structuring of both biological distances and within-sample variation indicate that on a wide geographical scale, dental variation agrees with the pattern expected as the product of serial founder effect related to an expansion in north–south direction. Molecular and archeological data also suggest that such a process characterized the peopling of Patagonia. The conditions of relative isolation and low demography in Patagonia through the Holocene could have facilitated the maintenance of patterns of biological variation established during the initial occupation of this area. Therefore, the differentiation produced by the serial founder effect would not have been significantly altered by the posterior gene flow among populations, whose effect was likely important only at small geographical distances.

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