



ELSEVIER

Contents lists available at ScienceDirect

HOMO - Journal of Comparative Human Biology

journal homepage: www.elsevier.com/locate/jchb

Craniofacial variation, body size and ecological factors in aboriginal populations from central Patagonia (2000–200 years B.P.)



Valeria Bernal^{a,b,*}, Marien Béguelin^{b,c}, Florencia Gordón^{a,b}, Virginia A. Cobos^{a,d}, Paula N. Gonzalez^{a,b}, Federico P. Lotto^a

^a División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata 1900, Argentina

^b CONICET, Buenos Aires, Argentina

^c Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Río Negro, Argentina

^d Consejo Interuniversitario Nacional, Argentina

ARTICLE INFO

Article history:

Received 5 August 2013

Accepted 17 November 2013

ABSTRACT

Previous studies have shown that ecological factors had a significant role in shaping the patterns of craniofacial variation among South American populations. Here, we evaluate whether temperature and diet contributed to facial diversification in small geographic areas. Facial size and shape of 9 osteological samples from central Patagonia (Argentina) were described using 2D landmarks and semilandmarks. Data on mean annual temperature, diet composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) and femoral head maximum breadth, used as a proxy of body mass, were obtained for each sample. We then tested the association of body mass and the ecological variables with facial morphology using spatial regression techniques and a model selection approach. Akaike Information Criterion produced disparate results for both components of facial morphology. The best model for facial size included temperature and body mass proxy, and accounted for more than 80% of variation in size. Lower temperatures were related to larger facial sizes. Body mass was negatively associated with facial size and showed no relationship with the temperature. This suggests a relatively independent variation of cranial traits and body mass at the spatial scale

* Corresponding author at: División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, La Plata 1900, Argentina. Tel.: +54 0221 4257744.

E-mail addresses: bernalv@fcnym.unlp.edu.ar, bernal.valeria@gmail.com (V. Bernal).

studied here. Facial shape was not associated with the temperature or diet composition, contrasting with the patterns observed at larger spatial scales. Our results point out that the effect of climatic variables on cranial traits might be a source of morphological differentiation not only at large scales but also in small geographic areas, and that size and shape display a differential preservation of environmental signals.

© 2013 Elsevier GmbH. All rights reserved.

Introduction

The morphological diversification of the southern South American aboriginal populations has been object of intensive research over the last century (Deniker, 1900; Perez et al., 2007; Pucciarelli et al., 2006; Rothhammer and Silva, 1990). As a result of these studies a clear pattern of variation at this geographic scale has emerged. Analyses of craniofacial morphology have shown that human populations from this region were characterized by exceptionally high levels of variation in size and shape compared to other areas of the world (Bernal et al., 2006; González-José et al., 2005; Perez et al., 2007; Sardi et al., 2005), which is thought to have originated in a relative short time, during the peopling of the region (Perez and Monteiro, 2009). Different ecological factors, such as temperature and diet, might have contributed to the patterns of craniofacial morphology in this region (Bernal et al., 2010a; González-José et al., 2005; Perez and Monteiro, 2009).

Accordingly, a strong association between temperature and cranial robusticity, with the most robust morphologies occurring at the highest latitudes, has been observed (Bernal et al., 2006; Gonzalez et al., 2010). In addition, remarkable differences in overall cranial size and shape have been documented between groups with different diets, with the agriculturalist groups possessing smaller crania and relatively shorter faces compared to the hunter-gatherers from the same region (Perez et al., 2011). Such differences have also been related to the direct influence of biomechanical stress produced by muscle forces during mastication (González-José et al., 2005; Sardi et al., 2006), which is supported by the well-established correlation between the degree of food hardness and muscle and bone development (Hanken and Hall, 1993; Herring, 1993; Pearson and Lieberman, 2004).

However, cranial features can also be under the influence of correlated responses to processes that target other characters, due to developmental and functional interactions among traits and pleiotropic effects during ontogeny (Frankino et al., 2005; Hendrikse et al., 2007; Jamniczky et al., 2010; Perez and Monteiro, 2009; Shingleton et al., 2007). In particular, a recent study suggests that a significant proportion of facial shape variation among South American populations might have resulted from allometric changes associated with variation in overall size (Gonzalez et al., 2011). This alternative is supported by data of body size, which shows a significant increase in size in hunter-gatherers compared to agriculturalists (Béguelin, 2011a). The proportion of carbohydrates and proteins consumed was proposed as an important factor of morphological diversification; the lower content of proteins of farmer's diets was related to a reduction in overall size, which in turn might have resulted in size-correlated shape changes in cranial traits (Perez et al., 2011).

Most of previous studies have emphasized the analysis of ecological factors at macro-regional scales, while their influence on morphological differentiation at local or micro-regional scales has been largely neglected. However, it is widely recognized in ecological and evolutionary studies that there is a strong dependence of patterns, processes, and their relationships on the spatial and temporal dimensions analysed (Levin, 1992; Wu et al., 2006). Consequently, studying the changes in patterns and their contributing factors across multiple scales is a necessary step towards understanding the role of ecological factors in driving the morphological evolution of recent human populations. The aim of this study is to evaluate whether the ecological factors with a known effect on the cranial variation at macro-regional scales also had an effect on population diversification at micro-regional scales. Particularly, we analyse the variation in size and shape of facial traits among the human groups that inhabited center of Patagonia during the late Holocene (ca. 2000–200 years B.P.) and test its association with variation in diet and temperature.

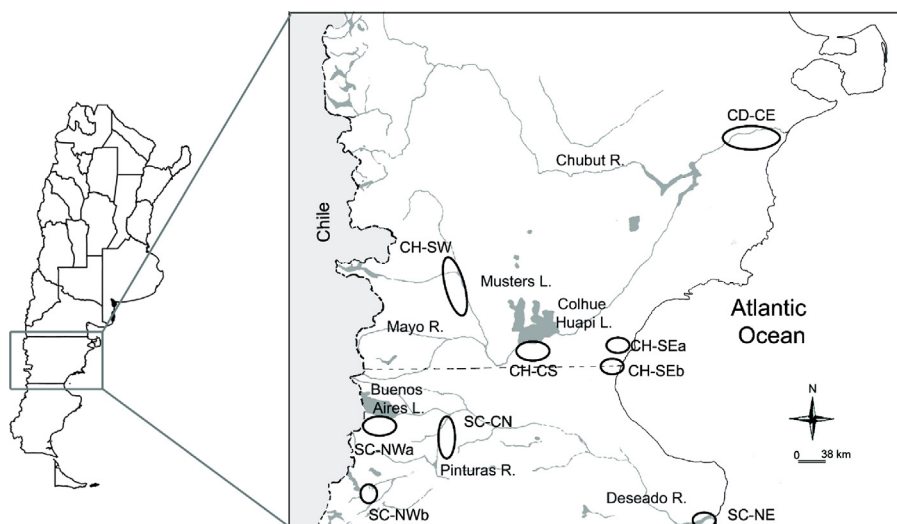


Fig. 1. Map showing the geographic location of the osteological samples analysed. Sample abbreviations are listed in [Table 1](#).

The region under study is relevant in the context of Amerindians due to the morphological singularity of the groups that inhabited this region. Particularly, the craniofacial morphology of late Holocene hunter-gatherers from Patagonia presents characteristics that depart from most of Amerindian samples and displays a broad range of variation ([González-José, 2003](#); [Lahr, 1995](#); [Lalueza et al., 1997](#); [Perez et al., 2007](#)). Several studies have focused on southernmost and northern groups, while the central portion of Patagonia remains scarcely studied. Therefore, this study attempts to contribute to fill this gap in the knowledge of South American populations.

To test the hypothesis that environmental factors influenced the morphological diversification of human populations in central Patagonia we used spatial regression techniques that take into account the spatial dependence of the samples, and a model selection approach to determine the variables that better fit craniofacial variation ([Diniz-Filho et al., 2009](#); [Johnson and Omland, 2004](#)). The ecological variables tested were mean annual temperature and diet composition. Because during the late Holocene all studied populations had similar food preparation techniques (e.g. use of grinding stone tools and pottery; [Bernal et al., 2010a](#)) the factor that is related to food hardness, and thus biomechanical stress, can be neglected as a source of variation of facial morphology in the region under study. Finally, the association between facial morphology and body size was also tested in order to evaluate whether a significant proportion of variation in facial size and shape among populations resulted mainly from changes associated with variation in body size; or alternatively, the ecological variables might have exerted a direct effect on facial size and shape.

Material and methods

Samples

We analysed the facial skeleton of nine samples of pooled male and female adults ($n=96$) from archaeological sites from Chubut and Santa Cruz (Patagonia, Argentina). The samples were chronologically assigned by radiocarbon dates to the later late Holocene (ca. 2000–200 years B.P.; [Arrigoni and Guichón, 2009](#); [Béguelin, 2011b](#); [Bernal and Aguerre, 2009](#); [García Guraieb et al., 2009](#); [Gómez Otero and Novellino, 2011](#); [Gradin and Aguerre, 1994](#); [Imbelloni, 1923](#); [Tessone et al., 2010](#); [Vignati, 1950](#)) ([Fig. 1](#) and [Table 1](#)). We limited our study to the facial skeleton because it was the cranial structure most well represented in the samples and because it has been frequently used in the study of South American populations due to the high frequency of cranial deformation in these groups. Previous

Table 1

Sample composition, with abbreviations used in the figures, sample sizes, predictor variables and facial data used in the analyses.

| Sample | Abbreviation | F | M | Predictor variables | | | | Facial data | | | |
|-------------------------|--------------|---|---|-----------------------|-----------------------|--------|-------|-------------|-------|--------|--------|
| | | | | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | Lat. | Temp. | FHMB | CS | RW1 | RW2 |
| Chubut Center East | CH-CE | 9 | 7 | -16.3 | 14.8 | -43.31 | 13.0 | 48.85 | 21.97 | 0.001 | -0.002 |
| Chubut Center South | CH-CS | 4 | 4 | -17.9* | 12.8* | -45.72 | 11.0 | 49.93 | 20.80 | -0.012 | -0.015 |
| Chubut South East a | CH-SEa | 2 | 7 | -17.0* | 13.9* | -45.92 | 12.0 | 50.04 | 20.81 | 0.011 | -0.009 |
| Chubut South East b | CH-SEb | 3 | 3 | -17.0* | 13.7* | -45.63 | 12.5 | 49.91 | 20.13 | 0.017 | 0.011 |
| Chubut South West | CH-SW | 7 | 8 | -18.4* | 12.7* | -45.36 | 9.0 | 49.93 | 21.95 | 0.008 | 0.003 |
| Santa Cruz Center North | SC-CN | 3 | 5 | -18.2* | 12.6* | -46.93 | 9.0 | 49.19 | 21.88 | 0.011 | 0.002 |
| Santa Cruz North East | SC-NE | 8 | 3 | -15.7 | 15.8 | -47.76 | 11.0 | 50.54 | 20.57 | -0.027 | 0.010 |
| Santa Cruz North West a | SC-NWa | 5 | 9 | -18.4 | 12.7 | -47.47 | 8.0 | 49.19 | 22.19 | -0.017 | 0.002 |
| Santa Cruz North West b | SC-NWb | 5 | 4 | -18.4 | 12.6 | -46.63 | 8.0 | 49.19 | 22.47 | 0.008 | -0.001 |

$\delta^{13}\text{C}$: delta carbon-13‰ based on bone collagen; $\delta^{15}\text{N}$: delta nitrogen-15‰ based on bone collagen; (*) values estimated by interpolation; Lat: Latitude; Temp: temperature; FHMB: femoral head anterior–posterior breadth maximum in mm; CS: centroid size; RW: relative warps.

studies have proved that the effect of artificial deformation on facial shape is negligible in samples from the studied area (Cocilovo, 1975; González-José, 2003; Perez, 2006).

Because some of the facial features used for sex estimation (Buikstra and Ubelaker, 1994) were included in morphometric analyses and no sex estimation independent from cranial morphology was available for most samples, males and females were pooled together for the comparisons. However, before comparing shapes among samples, the sex of each individual was estimated to evaluate whether the sex ratio was similar in all samples. Age estimation from the skull was based on suture closure, using the antero-lateral region, which is a more reliable predictor of chronological age than the vault region (Meindl and Lovejoy, 1985). Individuals were considered adults if their crania showed the basioccipital synchondrosis obliterated (Buikstra and Ubelaker, 1994).

The skeletal samples are housed in the División Antropología of the Museo de La Plata, the Museo Etnográfico “Juan B. Ambrossetti” (Universidad de Buenos Aires), the Museo Regional de Rada Tilly (Chubut), the Instituto de Ciencias Antropológicas (Universidad de Buenos Aires), and the Instituto Nacional de Antropología y Pensamiento Latinoamericano (Buenos Aires).

Morphometric analyses of facial traits

The facial skeleton was photographed with an Olympus SP 350 digital camera, positioning the skull in the Frankfurt plane, and the camera lens in the coronal plane. The images were taken at 250 mm from the prosthion point. Two-dimensional coordinates corresponding to 17 landmarks and 22 semilandmarks (Fig. 2) were obtained from the facial skeleton. Landmarks were located following the definitions of Buikstra and Ubelaker (1994) and Howells (1973). Although the reduction of three-dimensional structures to a 2D representation might bias the analyses, it is accepted that when the divergence among samples is low, a careful choice of two-dimensional landmarks allows a fairly accurate description of size and shape variation (Cardini and Thorington, 2006).

Both landmarks and semilandmarks were digitized by one of us (VC) using tpsDIG 2.12 software (Rohlf, 2008). To estimate the precision of the data collected, intraobserver error associated with the placement of landmarks coordinates, and with skull orientation in the Frankfurt horizontal plane was evaluated (Cobos et al., 2012). The results obtained show low levels of error in the placement of landmarks as well as in the skull orientation.

Size and shape variables were obtained from the two-dimensional coordinates of landmarks and semilandmarks. The effects of location, scaling, and orientation in landmark and semilandmark coordinates were removed using generalized Procrustes analysis (Bookstein, 1997; Rohlf and Slice, 1990). Centroid size (the square root of the summed squared distances from all landmarks and semilandmarks to the configuration centroid) was used as size measurement (Bookstein, 1991). Semilandmarks were aligned by means of perpendicular projection or minimum Procrustes distance criteria (Andresen et al., 2000; Bookstein et al., 2002; Perez et al., 2006; Sheets et al., 2004). This operation extends the

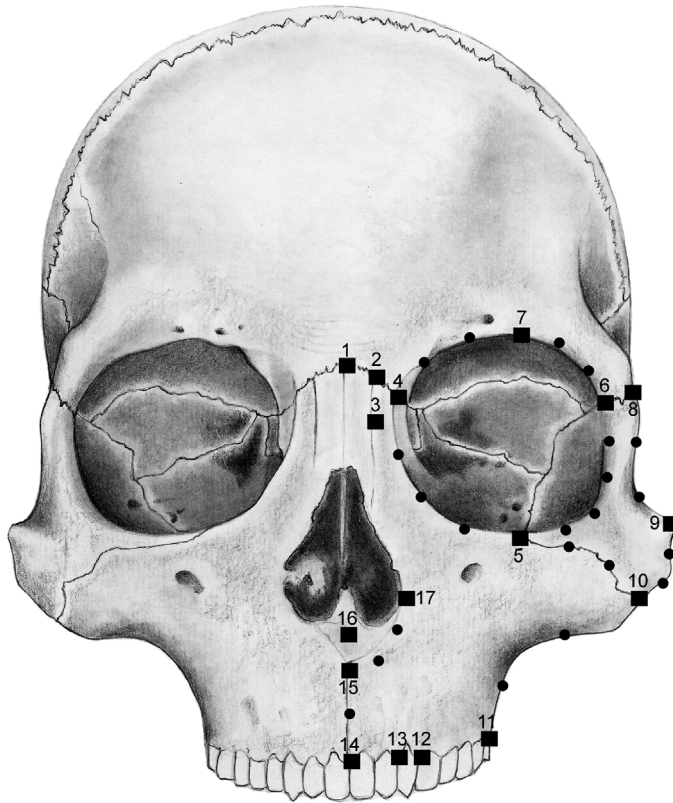


Fig. 2. Points measured on facial view. Landmarks are represented as squares (■) and semilandmarks as circles (●).

generalized least-squares Procrustes superimposition (Rohlf and Slice, 1990); in addition to optimally translating, scaling, and rotating landmarks, the semilandmarks are slid along the outline curve to minimize the Procrustes distance between the subject and the reference specimen until they match as much as possible the positions of corresponding points along the outline of a reference specimen (Adams et al., 2004; Perez et al., 2006).

The coordinates obtained after generalized Procrustes analysis (i.e. Procrustes coordinates) are suitable for statistical analyses. However, because these coordinates are highly correlated, we used a principal components (PC) analysis to calculate independent scores that describe major trends in shape variation (called relative warps in geometric morphometrics; Bookstein, 1991; Rohlf, 1993). These scores were the variables effectively used in the statistical analyses. The principal component analysis was conducted based on the consensus shapes of each sample. PCs calculated with mean values of shape variables give a robust description of shape differences among samples because the small sample sizes and heterogeneous covariance structures between samples have little influence on this analysis (Polly, 2003). Previous studies have shown that morphometric means treated this way, based on at least five individuals are accurate for intraspecific comparisons (Perez, 2006; Polly, 2003, 2005).

Body mass, space and ecological variables estimation

The size of long bones is highly and positively correlated with overall body size, and thus, is frequently used to estimate body size in prehistoric populations (Auerbach and Ruff, 2004; Raxter et al., 2006). Femoral head is particularly valuable in this regard because it is frequently preserved in human

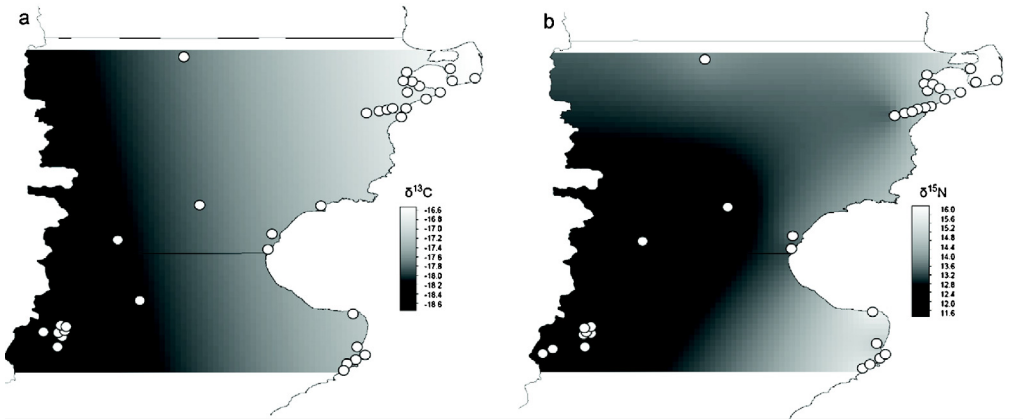


Fig. 3. Geographic patterns of values of stable isotopes of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b). The interpolation maps were created using the ordinary kriging function in SAGA software, freely available at <http://www.saga-gis.org/en/about/software.html>.

archaeological samples, and its breadth is an easily taken and highly reproducible measurement. In addition, several studies of modern humans with known body masses have proved that femoral head breadth produces reliable body mass estimation formulae (McHenry, 1992; Ruff et al., 1991).

Here, we used the femoral head maximum breadth as a proxy of body mass. The use of the raw variables as proxies of body size has two main advantages, it increases the sample size and overcomes the errors associated with estimation methods (Béguelin, 2011b; Stock, 2002). Measurements on left side were taken by one of us (M.B.) with a digital calliper 0.01 mm, following the method of Martin and Saller (1957) and recommendations of Buikstra and Ubelaker (1994). Only individuals with fully fused epiphyses were included in this study. When the left femur was missing or the femoral head was damaged, the right side was measured instead. A total of 110 male adult individuals from the same samples are used for the craniofacial analysis were measured. Females were excluded due to the small sample sizes for this sex.

Data on diet and temperature for each sample were collected to be used as estimators of ecological variation in the region. Variation in diet was measured using 95 values of $\delta^{13}\text{C}$ and 90 values of $\delta^{15}\text{N}$ isotopes for adult individuals taken from archaeological literature sources (Ambrústolo, 2011; Arrigoni and Guichón, 2009; Béguelin, 2011b; Bernal and Aguerre, 2009; Cassiodoro and García Guraieb, 2009; Castro et al., 2009; Fernández and Panarello, 1994; García Guraieb et al., 2009; Gómez Otero and Novellino, 2011; Gómez Otero et al., 2000; Goñi et al., 2000–2002; Moreno et al., 2011; Tessone et al., 2010). For most of the samples there was only one value for the type of isotope. When more than one value was available for the same geographic location, an average was used for the spatial analyses. The values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysed here show a strong spatial structure, with values corresponding to marine and mixed diets in sites near the coast and values consistent with terrestrial resources in the inland sites (Fig. 3). This is consistent with recent studies showing that human populations from this region mainly consumed meat of *Lama guanicoe*, although in areas near the coast they also incorporated some marine resources to the diet (Tessone et al., 2010). Because data on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were only available for 4 from the 9 osteological samples studied here, the unknown values were predicted by spatial interpolation using the observations available for neighbouring areas (data summarized in Fig. 3). Specifically, these methods work under the assumption that the interpolated values are likely to resemble known values of the same area, and therefore the values of known points are used to calculate the unknown ones in the proximity (Legendre and Legendre, 1998). We applied the kriging method and used semivariograms to model the autocorrelation in the empirical data, which was then used to predict the values for 5 human samples. Gaussian and exponential functions were used to model the empirical semivariograms for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, in SAGA 2.0.8 (Böhner et al., 2006).

Table 2

Pearson's r correlation coefficients among the original predictor variables. The correlation greater than 0.8 is shown in bold. Values in the lower half show the r values, while the corresponding p values are shown in the upper half of the table.

| | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | Latitude | Temperature | FHMB |
|-----------------------|-----------------------|-----------------------|----------|-------------|-------|
| $\delta^{13}\text{C}$ | – | <0.001 | 0.611 | 0.012 | 0.299 |
| $\delta^{15}\text{N}$ | 0.980 | – | 0.767 | 0.050 | 0.297 |
| Latitude | 0.197 | 0.116 | – | 0.087 | 0.392 |
| Temperature | 0.788 | 0.667 | 0.600 | – | 0.490 |
| FHMB | 0.391 | 0.392 | –0.326 | 0.266 | – |

$\delta^{13}\text{C}$: delta carbon-13‰ based on bone collagen; $\delta^{15}\text{N}$: delta nitrogen-15‰ based on bone collagen; FBMH: femoral head anterior-posterior breadth maximum in mm.

Mean annual temperature was used as an indirect estimator of climate, and data were obtained for each of the 9 samples from climatic databases (SMN, 1961–1990). Values of mean annual temperature recorded for the sampling areas ranged between 13° and 8° (Table 1). If temperature had an effect in the cranial differentiation among these populations, we would expect a significant correlation between these two variables.

Finally, the genetic relationships among populations need to be taken into account. While genetic data on the same archaeological samples analysed here are not publicly available, previous studies on extant as well as prehistoric populations from Patagonia provide valuable information about the patterns of genetic markers. mtDNA data show that genetic distances between samples from Patagonia are clearly associated with geographical distances in a North–South gradient (Moraga et al., 2000; Schurr, 2004). Morphometric studies on dental variation also supported a latitudinal gradient concordant with the direction of peopling (Bernal et al., 2010b). Consequently, it is expected that facial size and shape similarity among populations decreases as the difference in latitude between them increases. To account for this geographical structure we incorporated latitude as a predictor variable in the statistical analyses.

Statistical methods

The correspondence of facial size and shape (represented by the centroid size and the scores of first RWs for consensus shapes) with body mass, latitude, temperature and diet was tested by a multivariate multiple regression approach. Firstly, we tested for the presence of multicollinearity among the predictor variables summarized above using Pearson's correlations. Because some of the variables used to generate the models measure similar dimensions of the population niche (e.g. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), they might be highly correlated, affecting the estimation of the regression coefficients (Graham, 2003; Terribile et al., 2009).

Secondly, the models were investigated by using ordinary least squares multiple regressions (OLS), in which facial size and shape variables were regressed against the predictors. Particularly, we used the spatial eigenvector mapping (SEVM; for details, see Diniz-Filho et al., 2008; Perez et al., 2010) model to take into account the spatial structure in the dataset. Then, we used an Akaike's-based approach (Akaike information criteria; AIC) for model selection (Burnham and Anderson, 2004; Diniz-Filho et al., 2008). Specifically, we calculated the Akaike information criteria of each model corrected by sample size (AICc; Burnham and Anderson, 2004). The statistical analyses were performed using R 2.13.0 (R Development CoreTeam, 2011) and SAM 4.0 (Rangel et al., 2006).

Results

The results of relative warp analysis for facial shape indicated low levels of differentiation among samples (Fig. 4). Fig. 4 displays the first two relative warps calculated from facial landmarks and semi-landmarks, which account for 64.6% of total shape variation among sample means. The first relative warp explains 48.48% of total variance, and summarizes variation in shape of the zygomatic bone. Facial size, as represented by centroid size, is shown in Table 2. The two samples from NW Santa Cruz

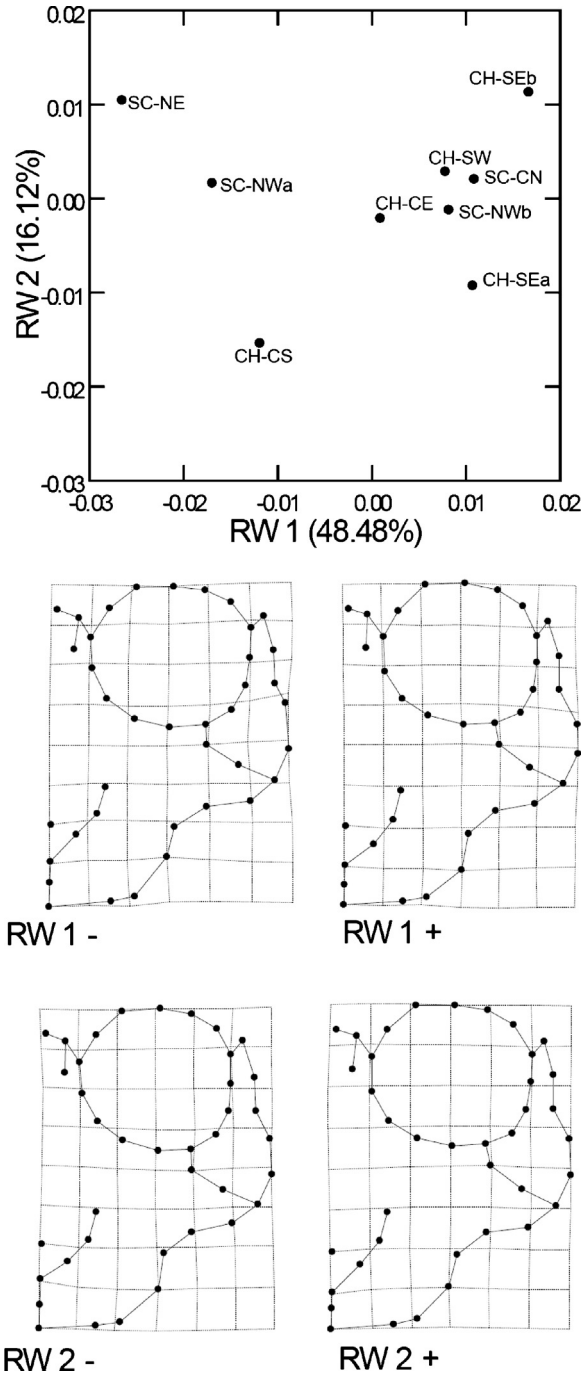


Fig. 4. Relative warps (RW) of the face calculated with sample means, and deformation grids depicting shape variation along the first RW. Sample abbreviations are listed in [Table 1](#).

Table 3

Results for the ordinary least squares model selection procedure, sorted by Akaike information criterion (AICc).

| Response variable | Model | % Predicted | AICc |
|-------------------|-----------------------|-------------|---------|
| CS | Temperature, FHMB | 83.6 | 23.055 |
| | FHMB | 58.7 | 24.159 |
| | Temperature, Latitude | 79.5 | 25.052 |
| | Temperature | 46.9 | 26.427 |
| RW1 | Latitude | 18.0 | -42.232 |
| | $\delta^{13}\text{C}$ | 8.3 | -41.234 |
| | FHMB | 7.4 | -41.138 |
| | Temperature | 1.3 | -40.568 |
| RW2 | Latitude | 8.5 | -51.281 |
| | $\delta^{13}\text{C}$ | 7.5 | -51.186 |
| | FHMB | 2.2 | -50.682 |
| | Temperature | 0.3 | -50.509 |
| RW1 and RW2(*) | Latitude | 26.5 | 10.697 |
| | $\delta^{13}\text{C}$ | 15.9 | 11.909 |
| | FHMB | 9.6 | 12.560 |
| | Temperature | 1.6 | 13.318 |

FHMB: femoral head maximum breadth in mm; CS: centroid size; RW: relative warps. Only the models with the lowest AICc values are shown, ranked from the most to the least important variable according to their respective regression coefficients. % Predicted represents the models' coefficients of determination (R^2) for univariate models and Pillai trace value for the multivariate model (*).

display the highest values, while the samples from SE Chubut and NE Santa Cruz have the smallest faces.

The Pearson's correlations (r) performed across the predictor variables revealed a value higher than 0.8 between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data (Table 2). Even though the two isotopic values reflect distinct dietary categories, in the region under study both are highly correlated and thus for statistical purposes either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ can be used as a continuous variable summarizing diet composition. To avoid the effect of multicollinearity, we only included one of the highly correlated variables for each regression model. As a result, four predictors were used for the OLS models: mean annual temperature, $\delta^{13}\text{C}$ values, latitude and body mass.

The OLS model selection procedure, sorted by Akaike information criterion (AICc), yielded disparate results for the size and shape of the face. The model that included CS as a response variable and the four predictor variables (mean annual temperature, $\delta^{13}\text{C}$ values, body mass and latitude) was significant ($F = 31.617$, $P = 0.003$; r^2 adj = 0.951), indicating that the global model provides a reasonable fit to the data and accounts for 95% of variation in size among samples. Then, the analysis proceeded by fitting each of the models in the candidate set to the observed data. According to the AIC values the best model for facial size included the temperature and the body mass proxy (Table 3). This model not only had the best support but also explained more than 80% of facial size variation in the region under study. The next model with high support comprised only the variable used as a proxy of body mass (Table 3). This single variable explains almost 60% of centroid size. The diet did not seem to be an important factor in shaping the variation of facial size since the models including $\delta^{13}\text{C}$ as an explanatory variable had the lowest support.

Because two of the samples were not completely sex balanced, we repeated the previous analyses using the males only. The global model including male centroid size as independent variable was also significant ($F = 11.623$; $P = 0.018$) and explained more than 80% of size variation ($r^2 = 0.873$). The results for the model selection procedure were similar to those based on pooled sexes. Models including temperature and body size had the lowest AIC values and accounted for a large percentage of variation in facial size (from 30% to 70%).

Conversely, none of the models tested explained an important percentage of variation in facial shape (Table 3). The best model for the RW1, as indicated by its AICc value included the variable latitude, but it only explained 18% of the shape variation summarized by this component. The second

best model included $\delta^{13}\text{C}$, which explained 8.3% of shape variation in RW1. In addition, the global model fit to the RW1 was not statistically significant ($F=0.715$; $P=0.623$; $r^2 \text{ adj}=0.067$). Similar results were obtained for the RW2, for which the first two models included latitude and $\delta^{13}\text{C}$ (Table 3). When the RW1 and RW2 were analysed together, the best models for facial shape also included latitude and $\delta^{13}\text{C}$ (Table 3). However, the low percentages of shape variation explained by these models, indicate that both environmental variables and body mass are poorly associated with facial shape in Central Patagonian populations.

Discussion

One interesting finding of this study was the significant association between temperature and facial size variation among populations, particularly given the small range of variation in temperature across the region. We found a negative association between temperature and facial size at the micro-regional spatial scale analysed. Previous studies of size-related metrics of craniofacial traits in South American as well as worldwide samples have detected signatures of significant associations between morphology and climate. For example, strong correlations with climate were found for facial breadth, dimensions of the orbits, nasal aperture, zygomatic height, facial robusticity and some dimensions of the cranial vault (Bernal et al., 2006; Betti et al., 2010; Franciscus and Long, 1991; Harvati and Weaver, 2006a,b; Hubbe et al., 2009; Roseman, 2004). Even though the magnitude of these correlations decreases when populations from extremely cold regions are excluded from the analyses, the correlations between some facial traits and temperature are still similar to those obtained with geographic or genetic distances. This suggests that both neutral processes and climate adaptation contributed to the pattern of cranial morphological variation observed in modern humans. It must be noted though, that most of these studies have not explicitly incorporated the effect of diet into the analyses due to the lack of information about the items consumed and the techniques of food preparation used. Consequently, the effects of food composition and hardness, which are known to affect craniofacial morphology (Lieberman et al., 2004), cannot be separated from the effect of temperature.

Here, we explicitly evaluated the effect of diet composition by incorporating the proportion of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ obtained from human remains into the models. Because these isotopes inform about the type and proportion of items consumed, the lack of association between these variables and cranial size suggests that diet composition can be ruled out as a significant factor in Central Patagonia. While the available evidence suggests that diet played an important role in the diversification of South American populations (Perez et al., 2011) it does not seem to have contributed to facial variation in the area under study. Overall, our results point out that climatic variables might be an important source of cranial size differentiation in small geographic areas. Independent evidence coming from technological, bioarchaeological and radiocarbon studies, as well as stable isotope (^{13}C and ^{15}N) analyses, suggests that Central Patagonia was inhabited by relatively mobile and low-density hunter-gatherer groups, whose home ranges were not very large (Borrero and Barberena, 2006; Gómez Otero and Novellino, 2011; Tessone et al., 2010). The mobility of these groups was spatially restricted to small areas, for instance, the maximum dispersion of individuals with a marine dietary component was 90 km away from the coast, which suggests that individuals lived in a rather constant environment throughout their lives. Whether the observed association between temperature and cranial size resulted from adaptive responses via natural selection or from developmental plasticity cannot be determined based solely on the analysis of morphological traits (Losos, 2000; Perez and Monteiro, 2009).

It has been previously hypothesized that variation in cranial size among South American populations might have resulted from correlated responses to changes in overall body size (Gonzalez et al., 2011; Perez and Monteiro, 2009). Accordingly, a positive association was expected between body mass and facial centroid size. The results obtained here contrast with such expectation, since we found a negative relationship between these two variables, larger-bodied populations were characterized by smaller faces compared to those with smaller bodies. Moreover, no association was found between body mass, estimated by femoral head size, and temperature. In contrast, a North–South gradient was documented for femoral size among terrestrial hunter-gatherers from Pampa and Patagonia, between 33° and 54°S (Béguelin, 2011b,c). Larger body sizes were found at higher latitudes, associated with

a reduction in the mean annual temperature. That pattern fits a model of body size increase with the consequent reduction in the heat loss due to a decrease in the surface area/volume ratio (Ruff, 1994; Ruff et al., 1997). Consequently, divergence in body size at such macro-regional scale has been explained as the result of directional selection associated with cold temperatures. In contrast, variation in mean annual temperature does not seem to have had a significant effect on body size at the geographical scale studied here. These results suggest a relative independence of cranial and postcranial traits, which can be under the influence of different factors. To the best of our knowledge though, no study has evaluated the variation in the cranial and postcranial skeleton in the same set of populations, limiting the discussion of whether the results obtained are particular of the populations under study.

The geometric morphometric techniques used here allowed us to evaluate the influence of ecological variables on facial shape independently from size. Contrary to size, the best model adjusted to the first RW included the variable latitude, while neither the environmental variables nor the body mass estimation were associated with facial shape. Although latitude explained less than 20% of the shape variation summarized by the first RW, our results suggest that variation in facial shape among Central Patagonian populations might have resulted from neutral processes related to the North–South direction of the peopling of this region. In a previous study we also showed that facial shape variation among populations belonging to Chaco, Pampa, and Patagonia regions was congruent with the pattern found using mtDNA from the same populations and thus, we concluded that evolutionary neutral factors might account for a large amount of the inter-population variation (Perez et al., 2007). In a comparable study in terms of the geometric morphometric methods used, Harvati and Weaver (2006a,b) analysed populations for which both morphological and genetic data were available. They found that facial shape was only weakly associated with neutral genetics and was instead related to climatic variables, as were vault and temporal bone size. One of the likely causes of such discrepancies is the spatial scale sampled; while the studies on small regions found an association between facial shape and genetic or geographic distances, those including populations from different continents found a stronger climatic signature.

In this study, we tested the association of mean annual temperature, diet composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and body mass with facial morphology at a micro-regional scale. Our results showed that temperature and body mass were significantly associated with facial size variation, while facial shape was not associated neither with the temperature nor with diet composition. Such results contrast with the patterns observed at larger spatial scales in South America where craniofacial variation is mainly related to differences in diet among populations. From an ecological point of view a reduction in scale extent may lead to lower variation in ecological variables due to averaging or smoothing effects, while an increase in extent may lead to higher variation due to the inclusion of more diverse ecological conditions. Consequently, analysis of a single scale can often result in generalizations and biased results, such as concluding that temperature had no influence on cranial traits based on the patterns observed at macro-regional scales, and prevent us from making accurate interpretations as the pattern of variation will be conditional on the scale of description. Overall, this study highlights the importance of studying patterns, processes and their relationships at multiple spatial and temporal scales in order to better understand the process of morphological diversification in human populations. Future studies that explicitly incorporate the dependence on the scale in their models will result in fruitful ways to better understand the processes of diversification in humans.

Acknowledgements

We are grateful to Héctor M. Pucciarelli (División Antropología, Facultad de Ciencias Naturales y Museo, La Plata, Argentina), Inés Baffi and Leandro Luna (Museo Etnográfico “J.B. Ambrosetti,” Buenos Aires, Argentina), Rafael Goñi (Instituto Nacional de Antropología y Pensamiento Latinoamericano, Buenos Aires, Argentina), Gloria Arrigoni and Marcos Andrieu (Museo Regional de Rada Tilly, Chubut, Argentina), Ana M. Aguerre (Instituto de Ciencias Antropológicas, UBA) for providing access to the human skeletal collections in their care. This work was supported by the Consejo Nacional de

Investigaciones Científicas y Técnicas (00829-2007) and Agencia Nacional de Promoción Científica y Tecnológica (PICT 1527-2007).

References

- Adams, D., Rohlf, F., Slice, D., 2004. Geometric morphometrics: ten years of progress following the “revolution”. *Ital. J. Zool.* 71, 5–16.
- Ambrústolo, P., 2011. Estudio de las Estrategias de Aprovisionamiento y Utilización de los Recursos Líticos por Grupos Cazadores-Recolectores en la Costa Norte de Santa Cruz, Patagonia Argentina. Ph.D. dissertation. Universidad Nacional de La Plata, La Plata, Argentina.
- Andresen, P.R., Bookstein, F.L., Couradsen, K., Ersboll, B.K., Marsh, J.L., Kreiborg, S., 2000. Surface-bounded growth modeling applied to human mandibles. *IEEE Trans. Med. Imaging* 19, 1053–1063.
- Arrigoni, G., Guichón, R., 2009. Resultados de Análisis Isotópicos en la Costa Central del Golfo San Jorge, Provincia de Chubut. V Taller de Arqueología de la Costa, Puerto Santa Cruz.
- Auerbach, B.M., Ruff, C.B., 2004. Human body mass estimation: a comparison of “morphometric” and “mechanical” methods. *Am. J. Phys. Anthropol.* 125, 331–342.
- Béguelin, M., 2011a. Variación ecológica y diversificación morfológica poscraneal en el sur de Sudamérica. In: Libro de Resúmenes de las X Jornadas Nacionales de Antropología Biológica. Asociación de Antropología Biológica de Argentina, La Plata, pp. 97.
- Béguelin, M., 2011b. Variación geográfica en la morfología del esqueleto postcraneal de las poblaciones humanas de Pampa y Patagonia durante el Holoceno tardío. Una aproximación morfométrica. In: Izeta, A. (Ed.), *South American Archaeology Series No. 12*. BAR S2253. Archaeopress, Oxford, p. 87.
- Béguelin, M., 2011c. Stature estimation in a central Patagonian prehispanic population: development of new models considering specific body proportions. *Int. J. Osteoarchaeol.* 21, 150–158.
- Bernal, V., Aguerre, A.M., 2009. Investigaciones bioarqueológicas en Río Mayo (So de la Prov. de Chubut). In: Pérez de Micou, C., Burry, S.L., Trivi, M. (Eds.), *Huellas del hombre en el sudoeste de Chubut*. Fundación Félix Azára, Buenos Aires, pp. 43–60.
- Bernal, V., Perez, S.I., Gonzalez, P.N., 2006. Variation and causal factors of craniofacial robusticity in Patagonian hunter-gatherers from the late Holocene. *Am. J. Hum. Biol.* 18, 748–765.
- Bernal, V., Perez, S.I., Gonzalez, P.N., Diniz-Filho, J.A.F., 2010a. Ecological and evolutionary factors in dental morphological diversification among modern human populations from southern South America. *Proc. R. Soc. Lond. B: Biol. Sci.* 277, 1107–1112.
- Bernal, V., Perez, S.I., Gonzalez, P.N., Sardi, M.L., Pucciarelli, H.M., 2010b. Spatial patterns and evolutionary processes in southern South America: a study of dental morphometric variation. *Am. J. Phys. Anthropol.* 142, 95–104.
- Betti, L., Balloux, F., Hanihara, T., Manica, A., 2010. The relative role of drift and selection in shaping the human skull. *Am. J. Phys. Anthropol.* 141, 76–82.
- Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data. Geometry and Biology*. Cambridge University Press, Cambridge.
- Bookstein, F.L., 1997. Landmark methods for forms without landmarks: localizing group differences in outline shape. *Med. Image Anal.* 1, 225–243.
- Bookstein, F.L., Streissguth, A.P., Sampson, P.D., Connor, P.D., Barr, H.M., 2002. Corpus callosum shape and neuropsychological deficits in adult males with heavy fetal alcohol exposure. *Neuroimage* 15, 233–251.
- Böhner, J., McCloy, K.R., Strobl, J. (Eds.), 2006. *SAGA – Analysis and Modelling Applications*, vol. 115. Göttinger Geographische Abhandlungen, Göttingen.
- Borrero, L.A., Barberena, R., 2006. Hunter-gatherer home ranges and marine resources. *Curr. Anthropol.* 47, 855–868.
- Buikstra, J., Ubelaker, D., 1994. *Standards for Data Collection from Human Skeletal Remains*. Arkansas Archaeological Survey, Research Series 44, Fayetteville.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304.
- Cardini, A., Thorington Jr., R.W., 2006. Post-natal ontogeny of the marmot (*Rodentia, Sciuridae*) cranium: allometric trajectories and species divergence. *J. Mammal.* 87, 201–216.
- Cassiodoro, G., García Guraieb, S., 2009. Análisis del registro tecnológico y osteológico de los entierros humanos del Holoceno tardío del lago Salitroso (Santa Cruz): un aporte al estudio del comportamiento mortuario de cazadores recolectores. In: Salemme, M., Santiago, F., Alvarez, M., Piana, E., Vázquez, M., Mansur, E. (Eds.), *Arqueología de Patagonia: una mirada desde el último confin*. Editorial Utopías, Ushuaia, pp. 613–628.
- Castro, A., Salceda, S., Plischuk, M., Desántolo, B., 2009. Bioarqueología de rescate: Sitio Carsa (Costa Norte de Santa Cruz, Argentina). In: Salemme, M., Santiago, F., Alvarez, M., Piana, E., Vázquez, M., Mansur, E. (Eds.), *Arqueología de Patagonia: una mirada desde el último confin*. Editorial Utopías, Ushuaia, pp. 629–638.
- Cobos, V., Della Negra, C., Bernal, V., 2012. Patrones de variación morfométrica craneofacial en poblaciones humanas del noroeste de Patagonia durante el Holoceno tardío. *Rev. Arg. Antrop. Biol.* 14, 5–16.
- Cocilovo, J.A., 1975. Estudio de dos factores que influyen la morfología craneana en una colección andina: el sexo y la deformación artificial. *Rev. Inst. Antropol.* 3, 197–212.
- Deniker, J., 1900. *Races et peuples de la Terre*. Paris.
- Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bini, L.M., 2008. Model selection and information theory in geographical ecology. *Global Ecol. Biogeogr.* 17, 479–488.
- Diniz-Filho, J.A.F., Nabout, J.C., Campos Telles, M.P., Soares, T.N., Rangel, T.F.L.V.B., 2009. A review of techniques for spatial modeling in geographical, conservation and landscape genetics. *Genet. Mol. Biol.* 32, 203–211.
- Fernández, J., Panarello, H.O., 1994. Estimaciones paleodietéticas y ambientales: esqueletos 1 y 2 Puesto El Rodeo. In: Gradín, C., Aguerre, A.M. (Eds.), *Contribución a la Arqueología del Río Pinturas. Búsqueda del Ayllu, Concepción del Uruguay*.
- Franciscus, R.G., Long, J.C., 1991. Variation in human nasal height and breadth. *Am. J. Phys. Anthropol.* 85, 419–427.
- Frankino, W.A., Zwaan, B.J., Stern, D.L., Brakefield, P.M., 2005. Natural selection and developmental constraints in the evolution of allometries. *Science* 307, 718–720.

- García Guraieb, S., Bernal, V., González, P., Bosio, L.A., Aguerre, A.M., 2009. Nuevos estudios del esqueleto del sitio Cerro Yanquenao (Colhué Huapi, Chubut): veintiocho años después. *Magallania* 37, 165–175.
- Gómez Otero, J., Belardi, J.B., Tykot, R., Grammer, S., 2000. Dieta y poblaciones humanas en la costa norte del Chubut (Patagonia argentina). In: Belardi, J.B., Carballo Marina, F., Espinosa, S. (Eds.), *Desde el País de los Gigantes. Perspectivas arqueológicas en Patagonia*. Universidad Nacional de la Patagonia Austral, Río Gallegos, p. 109.
- Gómez Otero, J., Novellino, P., 2011. Diet, nutritional status and oral health in hunter-gatherers from the central-northern coast of Patagonia and the Chubut River lower valley, Argentina. *Int. J. Osteoarchaeol.* 21, 643–659.
- Goñi, R.A., Barrientos, G., Cassiodoro, G.E., 2000–2002. Condiciones previas a la extinción de las poblaciones humanas del sur de Patagonia: una discusión a partir del análisis del registro arqueológico de la cuenca del lago Salitroso. *Cuadernos del Instituto Nacional de Antropología y Pensamiento Latinoamericano* 19, 249–266.
- Gonzalez, P.N., Perez, S.I., Bernal, V., 2010. Ontogeny of robusticity of craniofacial traits in modern humans: a study of South American populations. *Am. J. Phys. Anthropol.* 142, 367–379.
- Gonzalez, P.N., Perez, S.I., Bernal, V., 2011. Ontogenetic allometry and cranial shape diversification among human populations from South America. *Anat. Rec. Part A* 294, 1864–1874.
- González-José, R., Ramírez-Rozzi, F., Sardi, M., Martínez- Abadías, N., Hernández, M., Pucciarelli, H.M., 2005. Functional-cranial approach to the influence of economic strategy on skull morphology. *Am. J. Phys. Anthropol.* 128, 757–771.
- González-José, R., 2003. El poblamiento humano de la Patagonia: análisis de la variación craneofacial en el contexto del poblamiento de América. Ph.D. dissertation. Universidad de Barcelona, Barcelona.
- Gradin, C.J., Aguerre, A.M., 1994. Contribución a la arqueología del Río Pinturas. Provincia de Santa Cruz. Ediciones Búsqueda de Ayllu, Concepción del Uruguay.
- Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815.
- Hanken, J., Hall, B.K., 1993. *The Skull. Functional and Evolutionary Mechanisms*. University of Chicago Press, Chicago.
- Harvati, K., Weaver, T.D., 2006a. Reliability of cranial morphology in reconstructing Neanderthal phylogeny. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, New York, pp. 239–254.
- Harvati, K., Weaver, T.D., 2006b. Human cranial anatomy and the differential preservation of population history and climate signatures. *Anat. Rec. Part A* 288A, 1225–1233.
- Hendrikse, J.L., Parsons, T.E., Hallgrímsson, B., 2007. Evolvability as the proper focus of evolutionary developmental biology. *Evol. Dev.* 9, 393–401.
- Herring, S.W., 1993. Epigenetic and functional influences on skull growth. In: Hanken, J., Hall, B.K. (Eds.), *The Vertebrate Skull*, vol. 1. Development. University of Chicago Press, Chicago, pp. 153–206.
- Howells, W.W., 1973. *Cranial Variation in Man: A Study by Multivariate Analysis of Patterns of difference among Recent Human Populations*. Papers of the Peabody Museum No. 67. Harvard University Press, Cambridge, MA.
- Hubbe, M., Hanihara, T., Harvati, K., 2009. Climate signatures in the morphological differentiation of worldwide modern human populations. *Anat. Rec.* 292, 1720–1733.
- Imbelloni, J., 1923. *Habitantes neolíticos del Lago Buenos Aires*. Documentos para la antropología física de la Patagonia Austral. *Rev. Mus. La Plata* 27, 85–160.
- Jamniczky, H.A., Boughner, J.C., Gonzalez, P.N., Powell, C.D., Rolian, C., Schmidt, E.J., Parsons, T.E., Bookstein, F.L., Hallgrímsson, B., 2010. Mapping the epigenetic landscape: rediscovering Waddington in the post-genomic age. *Bioessays* 32, 1–6.
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108.
- Lahr, M.M., 1995. Patterns of modern human diversification: Implications for Amerindian origins. *Am. J. Phys. Anthropol.* 38, 163–198.
- Lalueza, C., Pérez-Pérez, A., Prats, E., Cornudella, L., Turbón, D., 1997. Lack of founding Amerindian mitochondrial DNA lineages in extinct aborigines from Tierra del Fuego-Patagonia. *Hum. Mol. Genet.* 6, 41–46.
- Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73, 1943–1967.
- Lieberman, D.E., Krovitz, G.E., Yates, F.W., Devlin, M., Claire, St.M., 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J. Hum. Evol.* 46, 655–677.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, 3rd ed. Elsevier, Amsterdam.
- Losos, J.B., 2000. Ecological character displacement and the study of adaptation. *Proc. Natl. Acad. Sci. USA* 97, 5693–5695.
- Martin, R., Saller, K., 1957. *Lehrbuch der Anthropologie*, band 1. Gustav Fischer Verlag, Stuttgart.
- McHenry, H.M., 1992. Body size and proportions in early Hominids. *Am. J. Phys. Anthropol.* 87, 407–431.
- Meindl, R.S., Lovejoy, C.O., 1985. Ectocranial suture closure: a revised method for the determination of skeletal age at death based on the lateral-anterior sutures. *Am. J. Phys. Anthropol.* 68, 57–66.
- Moraga, M.L., Rocco, P., Miquel, J.F., Nervi, F., Llop, E., Chakraborty, R., Rothhammer, F., Carvallo, P., 2000. Mitochondrial DNA polymorphisms in Chilean aboriginal populations: implications for the peopling of the southern cone of the continent. *Am. J. Phys. Anthropol.* 113, 19–29.
- Moreno, E., Zangrando, F.A., Tessone, A., Castro, A., Panarello, H., 2011. Isótopos estables, fauna y tecnología en el estudio de los cazadores-recolectores de la costa norte de Santa Cruz. *Magallania* 39, 265–276.
- Pearson, O.M., Lieberman, D.E., 2004. The aging of “Wolff’s law”: ontogeny and responses to mechanical loading in cortical bone. *Yearbk Phys. Anthropol.* 47, 63–99.
- Perez, S.I., Monteiro, L.R., 2009. Nonrandom factors in modern human morphological diversification: a study of craniofacial variation in southern South American populations. *Evolution* 63, 978–993.
- Perez, S.I., 2006. El poblamiento holocénico del sudeste de la Región Pampeana: Un estudio de morfometría geométrica craneofacial. Ph.D. dissertation. Universidad Nacional de La Plata, La Plata, Argentina.
- Perez, S.I., Bernal, V., Gonzalez, P.N., 2006. Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. *J. Anat.* 208, 769–784.
- Perez, S.I., Bernal, V., Gonzalez, P.N., 2007. Morphological differentiation of aboriginal human populations from Tierra del Fuego (Patagonia): implications for South American peopling. *Am. J. Phys. Anthropol.* 133, 1067–1079.
- Perez, S.I., Diniz-Filho, J.A.F., Bernal, V., Gonzalez, P.N., 2010. Spatial regression techniques for inter-population data: studying the relationships between morphological and environmental variation. *J. Evol. Biol.* 23, 237–248.

- Perez, S.I., Lema, V., Diniz-Filho, J.A.F., Bernal, V., Gonzalez, P.N., Gobbo, D., Pucciarelli, H.M., 2011. The role of diet and temperature in shaping cranial diversification of South American human populations: an approach based on spatial regression and divergence rate tests. *J. Biogeogr.* 38, 148–163.
- Polly, P.D., 2003. Paleophylogeography of *Sorex araneus*: molar shape as a morphological marker for fossil shrews. *Mammalia* 68, 233–243.
- Polly, P.D., 2005. Development, geography, and sample size in P matrix evolution: molar-shape change in island populations of *Sorex araneus*. *Evol. Dev.* 7, 29–41.
- Pucciarelli, H.M., Neves, W.A., González-José, R., Sardi, M.L., Rozzi, F.R., Struck, A., Bonilla, M.Y., 2006. East–West cranial differentiation in pre-Columbian human populations of South America. *Homo – J. Comp. Hum. Biol.* 57, 133–150.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F., Bini, L.M., 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecol. Biogeogr.* 15, 321–327.
- Raxter, M.H., Auerbach, B.M., Ruff, C.B., 2006. Revision of the fully technique for estimating statures. *Am. J. Phys. Anthropol.* 130, 374–384.
- R Development CoreTeam, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at <http://www.R-project.org>
- Rohlf, F.J., 1993. Relative warp analysis and an example of its application to mosquito wings. In: Marcus, L.F., Bello, E., Garcia Valdecasas, A. (Eds.), *Contributions to Morphometrics*. Museo Nacional de Ciencias Naturales (CSIC), Madrid, p. 131.
- Rohlf, F.J., 2008. TPS series software, Available at <http://www.life.bio.sunysb.edu/morph/>
- Rohlf, F.J., Slice, D., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Biol.* 39, 40–59.
- Roseman, C.C., 2004. Detecting interregionally diversifying natural selection and morphometric data. *Proc. Natl. Acad. Sci. USA* 101, 12824–12829.
- Rothhammer, F., Silva, C., 1990. Craniometrical variation among South American prehistoric populations: climatic, altitudinal, chronological, and geographic contributions. *Am. J. Phys. Anthropol.* 82, 9–17.
- Ruff, C.B., 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbk Phys. Anthropol.* 37, 65–107.
- Ruff, C.B., Scott, W.W., Liu, A.Y., 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am. J. Phys. Anthropol.* 86, 397–413.
- Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387, 173–176.
- Sardi, M.L., Rozzi, F.R., González-José, R., Pucciarelli, H.M., 2005. South Amerindian craniofacial morphology: diversity and implications for Amerindian evolution. *Am. J. Phys. Anthropol.* 128, 747–756.
- Sardi, M.L., Novellino, P.S., Pucciarelli, H.M., 2006. Craniofacial morphology in the Argentine center-west: consequences of the transition to food production. *Am. J. Phys. Anthropol.* 130, 333–343.
- Schurr, T.G., 2004. The peopling of the new world: perspectives from molecular anthropology. *Annu. Rev. Anthropol.* 33, 551–583.
- Sheets, H.D., Kim, K., Mitchell, C.E., 2004. A combined landmark and outline-based approach to ontogenetic shape change in the Ordovician trilobite *Triarthrus becki*. In: Elewa, A.M.T. (Ed.), *Morphometrics: Applications in Biology and Paleontology*. Springer, New York, pp. 67–82.
- Shingleton, A.W., Frankino, W.A., Flatt, T., Nijhout, H.F., Emlen, D.J., 2007. Size and shape: the developmental regulation of static allometry in insects. *Bioessays* 29, 536–548.
- SMN, 1961–1990. Climatic Database of Servicio Meteorológico Nacional, Available at <http://www.smn.gov.ar/>
- Stock, J.T., 2002. Climatic and behavioural influences on postcranial robusticity among Holocene foragers. Ph.D. dissertation. University of Toronto, Toronto, Canada.
- Terribile, L.C., Olalla-Tárraga, M.Á., Diniz-Filho, J.A.F., Rodríguez, M.Á., 2009. Ecological and evolutionary components of body size: geographic variation of venomous snakes at the global scale. *Biol. J. Linn. Soc.* 98, 94–109.
- Tessone, A., Zangrando, F.A., Barrientos, G., Goñi, R., Panarello, H., Cagnoni, M., 2010. Stable isotope studies in the Salitroso Lake Basin (Southern Patagonia, Argentina): assessing diet of Late Holocene hunter-gatherers. *Int. J. Osteoarchaeol.* 19, 297–308.
- Vignati, M.A., 1950. Estudios antropológicos en la zona militar de Comodoro Rivadavia. In: *Anales del Museo de La Plata, NS, Sección Antropología* 1. Museo de La Plata.
- Wu, J., Jones, K.B., Li, H., Loucks, O.L. (Eds.), 2006. *Scaling and Uncertainty Analysis in Ecology: Methods and Applications*. Springer, Dordrecht, the Netherlands.