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An ontogenetic approach to facial variation in three Native American populations

J. Barbeito-Andrés*, H.M. Pucciarelli, M.L. Sardi

División Antropología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina

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ABSTRACT

Various explanations have been formulated regarding high levels of craniofacial variation among Native American populations but the contribution of developmental processes to the establishment of these patterns of variation remains unknown. In this study, we compare facial morphology in ontogenetic series of three Native South American populations, one hunter-gatherer group and two farmer groups, in order to test the null hypothesis that indicates that the pattern of facial differentiation between populations does not change during ontogeny. If diet-related factors contribute to outline facial morphology, it is likely to find greater differences between hunter-gatherer and both farmer groups than between two groups of farmers and this differentiation is expected to increase with age, especially in those structures that are influenced by the mechanical load of mastication. According to our results, hunter-gatherers clearly differ from the two groups of farmers. Non-heritable factors linked to diet, such as nutritional content of food, may increase differentiation across ontogeny in some cases. However, as hunter-gatherers were clearly separated from farmer populations during entire postnatal ontogeny, an important proportion of size variation may not necessarily reflect eco-sensitive changes. Consequently, the hypothesis cannot be completely rejected.

Resumen: Se han formulado diferentes explicaciones sobre los altos niveles de variabilidad craneofacial que existen entre las poblaciones nativas de América, sin embargo, aun no se conoce cuál es la contribución de los procesos de desarrollo en el establecimiento

* Corresponding author. Tel.: +54 221 425 7527x138.
E-mail address: barbeito@fcnym.unlp.edu.ar (J. Barbeito-Andrés).

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de estos patrones de variación. En este estudio, comparamos la morfología facial en series ontogénicas de tres poblaciones sudamericanas, una de cazadores-recolectores junto con dos grupos de agricultores, con el fin de poner a prueba la hipótesis según la cual los patrones de diferenciación entre poblaciones no cambian a lo largo de la ontogenia. Si los factores relacionados con la dieta contribuyen al establecimiento de la morfología facial, es esperable hallar una mayor diferenciación entre cazadores-recolectores y los otros dos grupos que entre los dos grupos de agricultores y esta variación debería profundizarse con la edad, especialmente en aquellas estructuras faciales influenciadas por las fuerzas masticatorias. De acuerdo con nuestros resultados, los cazadores-recolectores difieren claramente de los agricultores. Algunos factores no hereditarios asociados a la dieta, tales como el contenido nutricional de la misma, pueden llevar a un incremento de la diferenciación a lo largo de la ontogenia en algunos casos. Sin embargo, como los cazadores-recolectores están claramente separados desde etapas tempranas de la vida postnatal, una parte importante de la variación en tamaño no reflejaría cambios ecosensitivos. Consecuentemente, la hipótesis no puede ser rechazada en forma completa.

Introduction

Native South American populations are considered highly diverse in their craniofacial traits (Sardi et al., 2005; Pucciarelli et al., 2006a; Pérez et al., 2007). Whereas some authors have argued that the main cause of morphological variation among these populations was the contribution of different waves of migration (Imbelloni, 1938; Neves and Pucciarelli, 1989; Pucciarelli, 2004), in the few last years, several studies based on molecular data and quantitative genetic models, have suggested that South American populations share a common recent ancestry and the effect of genetic drift and phylogenetic divergence cannot explain the complex patterns of morphological variation found in this region (Moraga et al., 2000; García-Bour et al., 2004; Schurr, 2004; Bernal et al., 2006; Goebel et al., 2008; Pérez et al., 2009, 2011). In this context, the relevance of a developmental approach, highlighting some non-random factors that may be responsible for craniofacial variation, is revealed.

Traditionally, the assessment of between-population variation has been carried out with adult individuals, but little is known about how craniofacial morphology of Native Americans was outlined across ontogeny. When primate (Mitteroecker et al., 2004) and hominid (Bastir et al., 2007) species were compared, it has been observed that some proportion of morphological differentiation among adults is established throughout postnatal growth, whereas some other studies (Ponce de León and Zollikofer, 2001; Ackermann and Krovitz, 2002) suggested that adult differentiation is already present in early ontogenetic stages. Few works have undertaken a developmental perspective on human craniofacial variation. Strand Vidarsdottir et al. (2002) studied facial variation in 10 modern human populations and concluded that the major aspects of population-specific morphology arise in the early stages of postnatal growth, even during prenatal life. Similarly, González et al. (2010) found that the pattern of variation of robust traits among subadults is similar to that observed among adults, suggesting that the differences are established early.

When considering the ontogenetic basis of variation, genetic factors may intervene but it is important to take into account environmental factors, such as diet, which influence facial morphogenesis (Pérez and Monteiro, 2009; Pérez et al., 2011). It is generally accepted that the transition from foraging to food production led to craniofacial gracilisation probably due to lesser muscular loading because of the softer consistency of the food consumed in several world regions (Wiercinska, 1989; Carlson and Van Gerven, 1977; Larsen, 1995; Sardi et al., 2004; González-José et al., 2005; González et al., 2010). The adoption of agriculture in the Andean region would also have contributed to morphological diver-

Table 1
Sample composition.

	Pt	PG	SP	Total
Adult (*N*)	32 (17 F; 15 M)	18 (11 F; 7 M)	114 (55 F; 59 M)	163
Subadult (*N*)	27	16	37	
Total (*N*)	59	34	151	244
Min. age subadults (years)	5	3	2	
Max. age subadults (years)	15	12	15	

F = female; M = male.

sification among Native South Americans, since the characteristics of diets were modified with the introduction of crops and new techniques of food preparation (Sardi et al., 2006; Bernal et al., 2007). Other populations, such as some Patagonian groups based their subsistence on the hunting of wild camelids and had a nomadic way of life until historical times.

At the southernmost frontier of Andean agriculture, cranial morphology of farmers is characterised by smaller size and relative reduction of structures that support masticatory and neck muscles (Sardi et al., 2006; Sardi and Béguelin, 2010). It has been suggested that when Native populations adopted agriculture in different world regions, diets became poorer in nutritional content (Larsen, 1995; Temple, 2010). When food becomes limited or there are deficiencies of some nutrients, as in low-protein diets, one of the consequences is growth retardation and reduction of adult size (Tanner, 1988). Experimental studies indicate that undernutrition produces a reduction in cranial size (Pucciarelli, 1981; Pucciarelli and Goya, 1983; Pucciarelli et al., 1990; Reichling and German, 2000).

This study aims to assess facial diversity among three Native South American populations with different subsistence systems and to compare their trajectories of facial growth (size changes according to age) in order to evaluate the role of ontogeny in shaping craniofacial morphology. Considering previous ontogenetic studies, the null hypothesis to be tested is that the pattern of facial differentiation between populations does not change during ontogeny. If diet-related factors contribute to facial variation, morphological changes associated to biomechanical and nutritional factors may be found. Consequently, it is likely that: (a) greater differentiation will be observed between hunter-gatherer and both farmer groups than among farmers, (b) if food consistency affects morphology, greater cumulative effects will be found among adults than among subadults and the structures more affected throughout postnatal growth will be those that are influenced by the mechanical loads of mastication, and (c) an overall size reduction among farmers will be observed if nutritional content of food affects cranial growth.

Materials and methods

Samples

We studied the ontogenetic series of three populations from South America, represented by samples of well-preserved skulls (Table 1, Fig. 1). Age assessment in subadults was carried out according to the standards based on tooth eruption described by Buikstra and Ubelaker (1994). Since sex assessment among subadults was not possible, both sexes were pooled in those comparisons that included subadults. Among adults, sex was assessed with methods found in Buikstra and Ubelaker (1994).

First sample examined was a sample from Patagonia (Pt), which includes individuals from the Chubut River valley dated to the final late Holocene (ca. 1500–200 years BP) (Pérez et al., 2009). Their subsistence was based on hunting guanaco (*Lama guanicoe*) and other animals as well as gathering some wild plants (Bernal et al., 2007). As a consequence, this group was characterised by the intake of a great amount of protein and low amounts of carbohydrates, as suggest some bioarchaeological indicators (Bernal et al., 2007). This population, as well as other hunter-gatherers from the region, show craniofacial robusticity due to their large size and pronounced development of structures such as supraorbital and superciliary regions (Lahr and Wright, 1996; Hernández et al., 1997; Bernal et al., 2006; Pérez et al., 2007; Baab et al., 2010; González et al.,

Fig. 1. Geographic location of the samples.

2010). It has been revealed that Patagonians are morphologically related to neighbouring populations and they exhibit similar robusticity to other hunter-gatherer and farmer groups (Bernal et al., 2006).

The Pampa Grande sample (PG) comes from archaeological sites located in the hills of Las Pirgüas, in northwestern Argentina (Carnese et al., 2010; González et al., 2010). The sites were dated to around 1500 BP according to the archaeological objects associated with them (Baldini et al., 2003; Carnese et al., 2010). Domesticated and wild plants were the main resources of their subsistence (Baldini et al., 1998). According to bioarchaeological studies, this population was under a remarkable nutritional

Table 2
Facial components, measurements and volumetric indices.

Skeletal component	Abbreviation	Measurement
Optic	OL	Length: dacryon-optic foramen
	OB	Breadth: dacryon-ectoconchion
	OH	Height: supraorbitary-infraorbitary
Respiratory	RL	Length: subspinale-posterior nasal spine
	RB	Breadth: widest extension of anterior nasal aperture
	RH	Height: nasion-subspinale
Masticatory	ML	Length: zygomaxillare-posterior border of glenoid cavity
	MB	Breadth: anterior sulcus of sphenotemporal crest-lower point of zygotemporal suture
	MH	Height: lower border of zygotemporal suture-upper temporal line at coronal intersection
Alveolar	AL	Length: external prosthion-posterior alveolar border
	AB	Breadth: from left to right alveolar borders, at unions between second and third molars
	AH	Height: intermaxillary synchondrosis-alveolar border, at unions between second and third molars
Volumetric index	VI	$\sqrt[3]{(\text{length. breadth. height})}$

stress due to the high content of carbohydrates as well as iron deficiency, in their diet (Baffi et al., 1996).

Finally, the third ontogenetic series is the San Pedro de Atacama (SP) sample, derived from northern Chile, a geographical region characterised by high aridity and very irregular and rough terrain (Neves et al., 1997). Subsistence was based on domesticated camelid meat, cultivation of corn, potatoes, among other plants, and on gathering wild plants (Nuñez Atencio, 2007; Neves et al., 1997; Torres-Rouff and Costa-Junqueira, 2006). These individuals can be dated approximately, to between 1750 and 950 BP (Costa-Junqueira et al., 1998).

Craniometric method

The craniometric method applied in this study was developed elsewhere (Pucciarelli, 1981; Sardi, 2002; Pucciarelli et al., 2006b; Sardi and Ramírez-Rozzi, 2007), and is based on the Functional Matrix Hypothesis. According to this model, craniofacial form has to be understood in relation to the functions of the related tissues. Each functional component comprises the functional matrix – i.e. all soft tissues, organs and cavities necessary to carry on a function – as well as an associated skeletal unit. The functional matrix hypothesis states that bone does not regulate its growth by its own genetic control but it is epigenetically controlled by the growth of its associated functional matrix (Moss and Young, 1960; Atchley and Hall, 1991; Moss, 1997; Sardi et al., 2006).

The morphological assessment of facial variation was carried out by considering four facial functional components: optic, respiratory, masticatory and alveolar. Length, breadth, and height were measured for each component. Volumetric indices, represented by the geometric mean of three dimensions, were calculated (Sardi and Ramírez-Rozzi, 2005; Pucciarelli et al., 2006b; Table 2). These three orthogonal variables ensure that no component is over- or underestimated and that three-dimensional changes can be assessed. As measurements do not overlap among them, redundancy is avoided.

Statistical treatment

Firstly, adults were compared. Differences between sample means of volumetric indices were evaluated separately for each sex through an analysis of variance (ANOVA) and a *post hoc* Tukey test. This comparison enabled us to assess the pattern of variation among adults once facial growth has finished.

To describe the differentiation among subadults and to estimate growth trajectories up to adulthood in the three samples, volumetric indices were adjusted to chronological age using the non-

Table 3
ANOVA on facial volumetric indices for between-groups differentiation.

	F-ratios	
	Female	Male
Masticatory VI	26.31**	20.94**
Respiratory VI	20.01**	28.34**
Optic VI	9.72**	5.58**
Alveolar VI	2.44	4.38*

* $p < 0.05$.
** $p < 0.01$.

parametric smoothing spline. This test consists of dividing the range of the *x* variable into segments and then the *y* values were adjusted through a parametric regression within each segment. The smoothing spline requires the establishment of a smoothing parameter (λ) that represents a balance between smoothness and variance. A small parameter produces low smoothness and high variance while a high λ produces better smoothness with lower variance. After the evaluation of different smoothing parameters, we chose $\lambda = 100$. The graphical inspection of this non-parametric adjustment allowed us to establish the degree of advance in different ontogenic stages and whether the pattern of variation is set up early (Sardi and Ramírez-Rozzi, 2005).

Finally, a principal components analysis was performed in order to describe facial growth multivariately and to identify those sets of craniometric traits that had greater influence on the differentiation. In this case, subadults and adults were pooled together to evaluate how these axes of variation are associated with age and to ascertain whether some facial traits are population-specific and whether they are influenced by postnatal ontogeny.

Results

Tables 3 and 4 summarise the results of ANOVA and *post hoc* Tukey test carried out among adults. All the volumetric indices, except the alveolar index in females, present highly significant differences. In all cases, Pt showed larger size than the other groups, while in those components where differences between PG and SP were found, PG was smaller.

Table 4
Matrix of pairwise means differences between pairs of samples according to Tukey test.

	Female			Male		
	Pt	PG	SP	Pt	PG	SP
Masticatory VI						
Pt	0			0		
PG	−5.791**	0		−6.663**	0	
SP	−3.109**	2.682**	0	−2.239**	4.424**	0
Pt	0			0		
Respiratory VI						
PG	−3.100**	0		−5.058**	0	
SP	−3.227**	−0.128	0	−2.992**	2.066**	0
Pt	0			0		
Optic VI						
PG	−1.854**	0		−1.668**	0	
SP	−0.729*	1.125**	0	−0.671	0.998	0
Pt	0			0		
Alveolar VI						
PG	1.126	0		−3.103*	0	
SP	−1.447	−1.573	0	−1.428	1.675	0

* $p < 0.05$.
** $p < 0.01$.

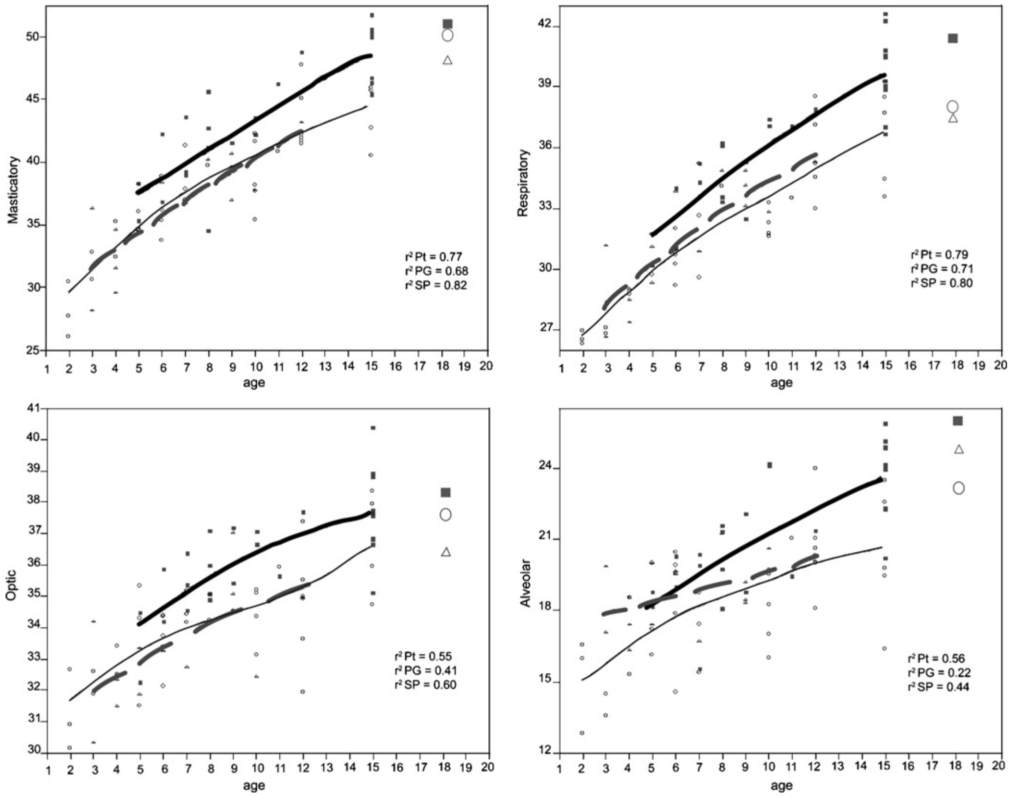

Fig. 2. Smoothing spline on volumetric indices against age. Grey square = Pt; triangle = PG; circle = SP. Black thick solid lines: Pt; grey dashed lines: PG; black thin solid lines: SP. The mean for adults by sample is indicated on charts at the age of 18 years.

Fig. 2 shows the results of the smoothing spline adjustment, which represent facial growth trajectories. Greater adjustments were obtained for the masticatory and respiratory components than for the optic and alveolar components. Despite minor variation in the shape of growth trajectories, the main result indicates that size differentiation between Pt and the other two groups was similar across postnatal life. In general, Pt had greater size than farmer samples along the whole ontogeny. On the other hand, the differentiation between PG and SP subadults was not the same when compared with the pattern of differentiation among adults. The respiratory component, for instance, was greater in PG than in SP among subadults, whereas the inverse differentiation occurred among adults.

After data reduction, a first principal component (PC1) that explains 63.41% and a second component (PC2) that accounts for 10.56% of the total variance were obtained. PC1 presented all eigenvectors with positive values, indicating that it comprised mostly variation in size and, thus, growth. The facial variables better correlated with PC1 were respiratory height, optic breadth, alveolar length, masticatory breadth and respiratory length (Table 5) and these were the dimensions with greater growth rates across postnatal ontogeny. Despite some overlapping, Pt faces present greater values on PC1 along all ontogeny, while the distributions of PG and SP overlap among them and have lowest values (Fig. 3).

PC2 is plotted against PC1 in Fig. 4. It describes purely shape variation and it leads to a clear differentiation among the three samples. According to Table 5, PC2 describes morphology in which optic, alveolar and respiratory heights are negatively associated with optic, respiratory and alveolar lengths. Pt and PG samples, which occupy high negative values in PC2, are characterised by longer, in antero-posterior sense, and shorter midfaces than the SP individuals.

Table 5
PC1 and PC2 eigenvectors.

Variable	Principal component	
	1	2
ML	0.814	0.334
MB	0.880	−0.083
MH	0.822	−0.083
RL	0.834	−0.349
RB	0.816	0.101
RH	0.926	0.147
OL	0.662	−0.514
OB	0.889	0.231
OH	0.575	0.626
AL	0.885	−0.279
AB	0.793	−0.288
AH	0.563	0.343

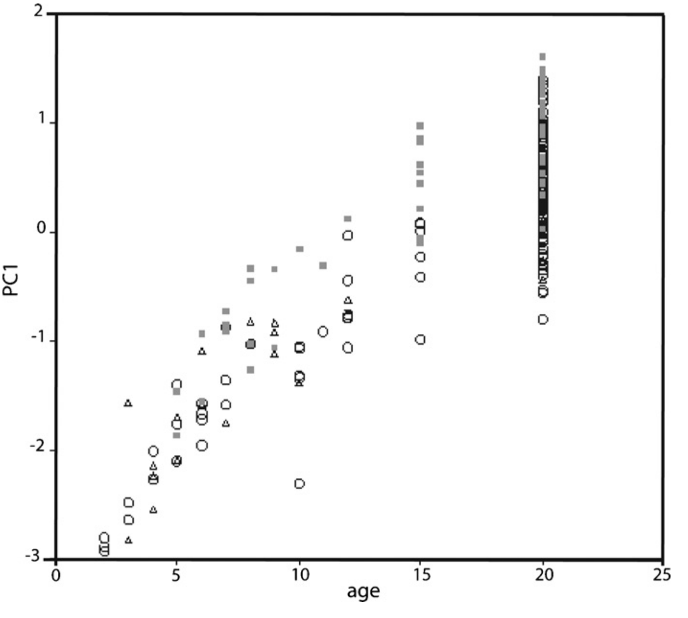

Fig. 3. PC1 against age. Grey square = Pt; triangle = PG; circle = SP.

Discussion and conclusion

The findings of this study allow us to discuss some processes that could be responsible for facial differentiation among Native South Americans. According to our results, there is a remarkable size difference between Patagonian hunter-gatherers and the other two samples of farmers, especially in the masticatory and respiratory structures.

This pattern of variation is in agreement with previous studies that have characterised Patagonian groups by their cranial robusticity given by large size and well-developed muscular insertions (Lahr and Wright, 1996; Hernández et al., 1997; Bernal et al., 2006; Baab et al., 2010). Some authors have related this morphology to biomechanical factors since this population was under large masticatory stress caused by the hardness of their food and the use of dentition for paramasticatory purposes (Lahr and Wright, 1996; Hernández et al., 1997), which are important causes of the high level of dental wear observed elsewhere (Bernal et al., 2007).

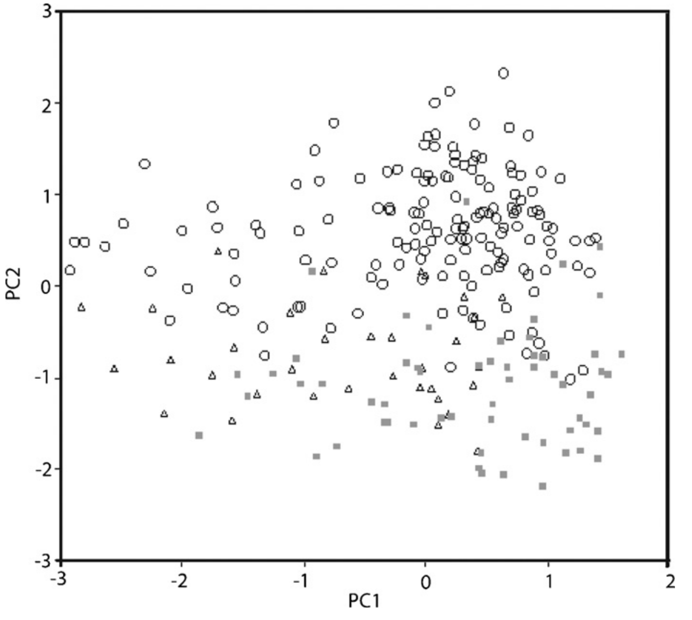

Fig. 4. Distribution of the individuals based on the first two principal components. Grey square = Pt; triangle = PG; circle = SP.

Food consistency has been emphasised as one of the most important diet-related factors responsible for cranial morphological differentiation. For instance, Sardi et al. (2006) studied craniofacial changes associated with transition to agriculture in centre-west Argentina, and they suggested that differences in food consistency might have accounted for an important part of variation between populations with different subsistences. Food production and cooking with the incorporation of pottery, led to the consumption of softer diets (Larsen, 1995), and a reduction of masticatory workloads (Sardi et al., 2006). Results of some experimental studies have demonstrated that smaller and less active muscles apply weaker forces on the bone, promoting little ossification in immature animals (Beecher and Corruccini, 1981; Mavropoulos et al., 2004).

In addition, the noteworthy differentiation of the masticatory component fits in well with the fact that masticatory structures have a long growth period and consequently, their morphologies may be susceptible to environmental factors (Sardi and Ramírez-Rozzi, 2005). Following Martínez-Abadías et al. (2009), masticatory dimensions have the lowest heritabilities when compared with other facial regions.

If masticatory loadings promoted facial differentiation as a result of phenotypic plasticity, greater variation would be found among adults than among subadults. However, we have showed that adult variation between Patagonian hunter-gatherers and the other two samples is similar to subadult variation, indicating that there is not a linear cumulative effect of some diet-related factors. Previous studies have observed that population-specific aspects of facial morphology develop prenatally or early postnatally (Ackermann and Krovitz, 2002; Strand Vidarsdottir et al., 2002; González et al., 2010). In other words, facial differentiation may not necessarily reflect eco-sensitive changes and there might be heritable morphological patterns of development involved, which regulate growth and establish facial characteristics. Our results suggest that Patagonian individuals around 4–6 years old are clearly separated from other groups of similar age; at about these ages the permanent dentition has not been completely erupted and an adult diet is not yet consumed. Thus, the differentiation of Patagonians was not promoted exclusively as a plastic response to biomechanical factors. Further studies may be useful to assess whether these diet-related variables are involved in processes of directional selection that lead to morphological differentiation (Pérez et al., 2009).

Besides the biomechanical effects of food consistency, some diet-related factors have to be taken into account when discussing craniofacial differentiation. For instance, the nutritional content of diet exerts a systemic influence on craniofacial growth. Cordain (2000) stated that most worldwide hunter-gatherers obtain more than 50% of their diet from animal foods, and the most important percentage of their energy derives from proteins. As reported in many groups, with the adoption of agriculture, the dependence on carbohydrates increased and the importance of proteins was reduced (Larsen, 1995). With regard to the amount of protein intake, some experimental studies have demonstrated that low-protein diets lead to a significant reduction in size (Pucciarelli, 1980, 1981; Pucciarelli and Goya, 1983; Pucciarelli et al., 1990; Miller and German, 1999).

Previous bioarchaeological studies demonstrated that the Pampa Grande sample was under severe nutritional stress (Baffi et al., 1996; Baldini et al., 1998). In this sense, we found that adult Pampa Grande individuals had smaller sizes in all components in which they differed. These results are in agreement with the findings of Paschetta et al. (2010) when comparing the size of the face of adults from Pampa Grande with other hunter-gatherers and farmers. However, this pattern of differentiation is not the same in early stages of ontogeny, suggesting that part of the variation in this population has been established during growth, and that the overall size reduction in Pampa Grande was probably related to the nutritional content of the diet.

Apart from size variation, the PCA provided a second component that expresses pure shape variation and indicates that Patagonian hunter-gatherers and Pampa Grande farmers are closely related and San Pedro farmers are distant with respect to the former (Fig. 4). Several studies have proposed that cranial shape is related to neutral genetic variation while size differentiation is more associated with environmental factors (Roseman and Weaver, 2004; Smith et al., 2007). Pérez et al. (2011) have found that diet has a significant effect on the patterns of size variation among populations but the contribution of this factor to shape variation is less relevant.

San Pedro de Atacama was separated from Patagonia and Pampa Grande by the Andes, which acted as a geographic barrier. The similarity between Pampa Grande and Patagonian samples might be the result of genetic relatedness among them as suggested by Pucciarelli et al. (2006a) and Varela et al. (2008).

Summarising, the hypothesis that facial differentiation between populations does not change during postnatal life cannot be completely rejected. Even if the pattern of variation between populations was similar in all facial components, the masticatory component was the most important to show differentiation, with the hunter-gatherer sample the most distanced from other groups in every component. Since this pattern emerges early across ontogeny and it may be heritable, other non-heritable factors linked to diet (i.e. hard consistency of food and high protein intake) may increase differentiation among adults.

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