

Functional-Cranial Approach to the Influence of Economic Strategy on Skull Morphology

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ABSTRACT Environmental factors are assumed to play an important role in the shaping of craniofacial morphology. Here we propose a statistical approach which can be of utility in estimating the magnitude and localization of a particular nongenetic factor upon the specific functional components of the skull. Our analysis is a combination of previous attempts of apportionment of variance and the application of craniofunctional theory. The effect of subsistence strategy on craniofacial functional components was studied on 18 populations of

hunter-gatherers and farmers from South America. Results demonstrate that the environmental factors studied likely influenced the masticatory component's size and shape. Even when this effect is not large enough to clearly differentiate among subsistence strategies (since whole craniofacial variation among populations remains greater), the method used here provides interesting clues to localize plastic or adaptive responses to external stimuli. *Am J Phys Anthropol* 126:000–000, 2005. © 2005 Wiley-Liss, Inc.

It is well-known that environmental factors account for a variable proportion of the phenotypic variability in craniofacial morphology. However, little effort has been made to detect which cranial regions are most sensitive to morphological changes due to nongenetic factors. For instance, estimates of the magnitude of environmental factors as potential sources of craniofacial variability are lacking. A possible explanation for this deficiency could be that most of the recent interpretations about the validity of craniometrics as indicators of among- and within-group genetic affinities fall into an extreme point of view associated with adaptationist models.

Adaptationism departs from the idea that, since craniometric traits are influenced in a certain (unknown) degree by environmental forces, they cannot be used as good estimators of genetic within- and among-groups variation. This point of view was early stressed by Boas (1912) after his classical study of change in the cranial index of European immigrants arriving to the US, and was formally stated by Cavalli-Sforza and Bodmer (1971, p. 704), who synthesized this vision in their observation that “All anthropometric characters are usually genetically complex and also subject to environmental influences. Even when heritability is relatively high... it is always dangerous to use the character for comparative observations between races, because there can be unsuspected environmental effects.”

Consequently, the majority of physical anthropologists gradually faced the study of the skull in a less genetic view, mainly devoting their efforts to the study of paleodemography, paleopathology, or lifestyle traits (Buikstra et al., 1990; Lahr and Foley, 1998). The problems of proportionality of additive genetic and phenotypic covariance matrices (e.g., Cheverud, 1988, 1996; Konigsberg and Ousley, 1995; Roff, 1996; González-José et al., 2004) and the heritability of craniofacial dimensions (Devor et al., 1986; Varela and Cocilovo, 1999; Sparks and Jantz, 2002) are points of more recent discussion. Although those approaches are important in understanding the apportionment of phenotypic variance components, little attention has been given to detection of the particular structures which are more sensitive to nongenetic factors.

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Environmental influence on skull morphology has been mainly associated with physical factors, such as altitude, climate (Guglielmino-Matessi et al., 1979; Rothhammer and Silva, 1990; Franciscus and Long, 1991; Hernández et al., 1997; Franciscus, 2003), and mechanical forces (Carlson and Van Gerven, 1977; Beecher et al., 1983; Hannam and Wood, 1989; van Spronsen et al., 1991; Varrela, 1990, 1992; Kiliaridis, 1995; Lahr and Wright, 1996; Ciochon et al., 1997; Bresin et al., 1999; Wood and Lieberman, 2001; Giesen et al., 2003; Sardi et al., 2004a). Mechanical loads on the skull have been widely studied in relation to masticatory forces. In particular, it was hypothesized that a reduction in the masticatory muscles' activity and a concomitant decrease in mechanical loading of the craniofacial skeleton induces a reduction in muscle size and their related structures. In this context, the technological changes related to the shift from hunting-gathering or foraging to food production and the consumption of softer foods are thought to be responsible for the reduced masticatory activity (Carlson and Van Gerven, 1977; Hannam and Wood, 1989; van Spronsen et al., 1991; Kiliaridis, 1995; Larsen, 1997).

Some experimental studies also showed that differences in the consistency of diet may contribute to modifications in cortical bone thickness and mandibular density (Bresin et al., 1999), the maxillary, mandible, and palate structures (Beecher et al., 1983; Giesen et al., 2003), and reduction of muscular size (Ciochon et al., 1997), among other changes. These experimental studies suggest that plastic response to differing levels of mechanical stress is mainly located in the masticatory and alveolar regions. To sum up, and as stated by Larsen (1997), skulls of animals fed soft foods tend to be smaller and less robust than animals fed hard foods.

Lieberman (1997) suggested that variables demonstrating a high degree of phenotypic plasticity due to epigenetic responses to mechanical stress are especially liable to provide misleading conclusions about intraspecific variation. Thus, if plastic responses to mechanical stressors are detected among a set of populations, then it is important to estimate the magnitude of among-group variation in both localized structures and global craniofacial shape. This addresses the problem of which methodology can be used to delimit particular regions of the skull in order to analyze them independently. In fact, any analysis testing for the effects of an environmental factor on craniofacial morphology must take into account that the skull is a complex of relatively but increasingly structured osseous components. Thus, individual bones can belong to different components, and conversely, different bones can make up a particular component (Pucciarelli et al., 1990). Furthermore, morphological integration accounts for covariation among single linear measurements, probably as a response to developmental and functional con-

straints (Lieberman et al., 2000a,b; González-José et al., 2004), turning the study of standard measurements into a not very efficient tool to study adaptation or plasticity. Therefore, analyses should be based on a methodology which explicitly delimits the skull structures associated with both a particular growth pattern and a specific functional requirement, such as the theory of functional craniology. This theory was first postulated by van der Klaauw (1948) for the analysis of cranial size and shape in vertebrates, and by Moss and Young (1960) and Moss (1973, 1997) for humans and nonhuman primates. Although functional components and classical variables provide very similar taxonomic classifications (Pucciarelli et al., 1990; Luis and Sardi, 2000; Sardi, 2002), classical macromorphological measurements, like the variables of Howells (1973), give no information about the biology of the variation. For instance, the variables of Howells (1973) encompass large regions of the skull, with dissimilar tissue composition, embryologic origin, growth pattern, and function. The use of such a theoretical and practical approach avoids illusory associations between a given macromorphological measurement, which does not necessarily reflect a genetic or functional unity of covariation, and the environmental variables under study.

Considering the experimental evidence cited above and departing from the advantages of the craniofunctional theory, a comparative study of human populations differing in their economic strategy can shed light on the problem of plasticity of the masticatory and alveolar structures. Here we present an analysis focused on testing the potential effect of an environmental factor (economic strategy intended here as hunting-gathering or farming) on the craniofacial variation of several South American groups. In particular, we test the null hypothesis that masticatory and/or alveolar regions contribute to discriminating better among economic strategies, thus masking actual genetic differences between local populations. This contribution will be estimated as the departure of a single component from the pattern of distances determined previously after the whole set of variables.

MATERIALS AND METHODS

Functional components were analyzed on 569 skulls belonging to 18 South American populations. Populations were classified according to their economic strategy in two categories: hunter-gatherers (HG) and farmers (F). The subsistence pattern is known or inferred through ethnographic and/or archaeological evidence. A complete list of references used to classify each sample as HG or F is presented in the Appendix.

The categories "hunter-gatherer" and "farmer" are diverse and not necessarily exclusive. In general terms, a farmer group is distinguished from a hunter-gatherer one by a semisedentary or sedentary settlement pattern and by the practice of agriculture

TABLE 1. Populations analyzed: codes, location, economic strategy, and sample sizes

Code	Location	Subsistence type	n (female)	n (male)	n (total)
FBL	Highlands of Bolivia	Farming	18	33	51
FCTM	Contumaza, Peru	Farming	0	12	12
HGCHA	Chaco, northeast Argentina	Hunting-gathering	5	22	27
HGCHU	Chubut, Argentinean Patagonia	Hunting-gathering	22	38	60
HGES	Espíritu Santo, Brazil	Hunting-gathering	7	4	11
HGGY	Guayaqui, Paraguay	Hunting-gathering	4	5	9
HGLS	Lagoa Santa, Brazil	Hunting-gathering	8	12	20
HGMG	Minas Gerais, Brazil	Hunting-gathering	7	13	20
FNCY	North of Cuyo, west central Argentina	Farming	13	7	20
FNCH	North of Chile	Farming	9	14	23
FNOA	Highlands of northwest Argentina	Farming	3	16	19
HGPAM	Coastal pampas, east central Argentina	Hunting-gathering	0	14	14
HGPD	Delta of Paraná river, central Argentina	Hunting-gathering	16	22	38
HGPTC	Paltacalo, Amazonas, Ecuador	Hunting-gathering	26	31	57
HGRN	Río Negro, Argentinean Patagonia	Hunting-gathering	31	41	72
HGSCY	South of Cuyo Region, west central Argentina	Hunting-gathering	18	31	49
HGTF	Fueguians, Tierra del Fuego	Hunting-gathering	9	21	30
FWP	Western Pampa, central Argentina	Farming	20	17	37
Total			216	353	569

(and pastoralism), at least by seasons. Even when some hunter-gatherers can practice the continued exploitation of wild species, we followed the criterion suggested by Harris (1989), who made an important qualitative distinction. According to this author, wild plant procurement and food production within a mixed economy (in which hunting and gathering still play a substantial role) are not enough to classify a group as full agriculturalist. Rather, Harris (1989) stated that true agricultural systems are based on domesticated crop production. Even when some degree of internal variation in these categories is expectable (e.g., hunter-gatherers can be further divided into marine and terrestrial HG), we opted for no further divisions in order to maintain acceptable sample sizes. Furthermore, hunting-gathering vs. farming is a good preliminary representation of diverging sources and levels of biomechanical stress. For instance, many technological innovations such as cooking, the invention of agriculture, and other food-processing techniques are thought to have caused a significant reduction in masticatory stress (Brace, 1979; Brace et al., 1987, 1991; Lieberman, 1993; Agrawal et al., 1997).

Information about the geographic location, sample size, and economic strategy assignation of samples is listed in Table 1.

Orthogonal lengths, widths, and heights were measured on two major components (neural and facial) and eight minor components (anteroneural, midneural, posteroneural, and otic, contributing to the neural major component; optic, respiratory, masticatory, and alveolar, localized in the facial major component).

Measurements and derived volumetric and morphometric indices are listed in Tables 2 and 3, respectively. Volumetric indices estimate size changes (sensu Jungers et al., 1995) and are expressed in arbitrary units; morphometric indices estimate shape changes in a major component in terms of relative size variations of their minor components.

Distances among groups and Fst values were computed separately, using both the total set of 24 measurements defining the minor components, and the three orthogonal measurements defining each component individually. Distances among groups and Fst values were obtained following Relethford and Blangero (1990) and Relethford et al. (1997). The 24 variables were used to establish the general pattern of distances, and those distances can be considered the starting point from which distances derived from single components were compared. The six variables covering the two major components were removed from this computation in order to avoid problems of colinearity between major and minor components' dimensions. Since the distance generated by the 24 variables represents the most multivariate approach to among-group differences, it can also be considered the most selectively neutral on average (Relethford, 1994, 2002; Sparks and Jantz, 2002; González-José et al., 2004). In consequence, deviations from this pattern of relationships between the different arrays of groups are likely to reflect selective pressures acting on the single component under analysis.

Computations of distance and Fst assume an additive polygenic model for the traits in which the expectation of environmental deviations is zero (Williams-Blangero and Blangero, 1989). The phenotypic variance, composed of genetic and environmental components ($\sigma_p^2 = \sigma_g^2 + \sigma_e^2$), must be greater than or equal to the genetic variance ($\sigma_p^2 \geq \sigma_g^2$). Those authors demonstrated that "D_p² represents a matrix containing the minimum genetic distances derived from the phenetic variation" (Williams-Blangero and Blangero, 1989, p. 5).

The resulting equation can be written as:

$$d_{ij}^2 = r_{ii} + r_{jj} - 2r_{ij}$$

where r_{ij} are the elements of an R matrix computed for each trait in populations i and j (Releth-

TABLE 2. Variables used in this study

Code	Variable	Description	Mode ¹
NL	Neurocranial length	Nasion-opisthocranium	Direct
NW	Neurocranial width	Eurion-eurion	Direct
NH	Neurocranial height	Basion-vertex	Projected
FL	Facial length	Inner prosthion-vomerobasilar	Projected
FW	Facial width	Zygion-zygion	Direct
FH	Facial height	Nasion-prosthion	Projected
ANL	Anteroneural length	Glabella-bregma	Projected
ANW	Anteroneural width	Pterion-pterion	Direct
ANH	Anteroneural height	Bregma-vomerobasilar	Direct
MNL	Midneural length	Bregma-lambda	Projected
MNW	Midneural width	Same as NW	Direct
MNH	Midneural height	Basion-bregma	Direct
PNL	Posteroneural length	Opistion-opisthocranium	Projected
PNW	Posteroneural width	Asterion-asterion	Direct
PNH	Posteroneural height	Lambda-opistion	Projected
OTL	Otic length	Timpanic bone posterior inferior end-midpoint of inner end of petrous bone	Direct
OTW	Otic width	External auditive width	Projected
OTH	Otic height	External auditive height	Projected
OL	Optic length	Dacrion-intersphenoidal foramen	Direct
OW	Optic width	Dacrion-ectocoquio	Projected
OH	Optic height	Mid-supraorbital point; mid-infraorbital point	Projected
RL	Respiratory length	Subnasal-posterior nasal espine	Direct
RW	Respiratory width	Maximum nasal width	Direct
RH	Respiratory height	Nasion-subnasal	Projected
ML	Masticatory length	Lower border zygomatic synchondrosis, posterior border of glenoid cavity	Projected
MW	Masticatory width	Anterior sulcus of sphenotemporal crest, lower point of zygotemporal synchondrosis	Projected
MH	Masticatory height	Lower border of zygotemporal synchondrosis, upper temporal line at coronal intersection	Projected
AL	Alveolar length	External prosthion-posterior alveolar border	Projected
AW	Alveolar width	From left to right, second-third molar width	Direct
AH	Alveolar height	Palatal deep at midsagittal/second-third molars width	Direct

¹ Projected measurements must be done in relation to auricular-infraorbital equalization (Frankfurt line). Correct anterior-posterior and vertical placement of skull must be done with, respectively, equalization of prosthion and inion points with respect to horizontal plane, and of palatal first molars perpendicular to this plane. Direct measurements may be made out of Frankfurt orientation.

TABLE 3. Volumetric and morphometric indices used in this study¹

Code	Formula	Description
Volumetric indices		
Major components		
NVI	$NVI = (NL * NW * NH)^{1/3}$	Neurocranial volumetric index
FVI	$FVI = (FL * FW * FH)^{1/3}$	Facial volumetric index
Minor components		
ANVI	$ANVI = (ANL * ANW * ANH)^{1/3}$	Anteroneural volumetric index
MNVI	$MNVI = (MNL * MNW * MNH)^{1/3}$	Midneural volumetric index
PNVI	$PNVI = (PNL * PNW * PNH)^{1/3}$	Posteroneural volumetric index
OTVI	$OTVI = (OTL * OTW * OTH)^{1/3}$	Otic volumetric index
OVI	$OVI = (OL * OW * OH)^{1/3}$	Optic volumetric index
RVI	$RVI = (RL * RW * RH)^{1/3}$	Respiratory volumetric index
MVI	$MVI = (ML * MW * MH)^{1/3}$	Masticatory volumetric index
AVI	$AVI = (AL * AW * AH)^{1/3}$	Alveolar volumetric index
Morphometric indices		
ANMI	$ANMI = 100 * ANVI / (ANVI + MNVI + PNVI + OTVI)$	Anteroneural morphometric index
MNMI	$MNMI = 100 * MNVI / (ANVI + MNVI + PNVI + OTVI)$	Midneural morphometric index
PNMI	$PNMI = 100 * PNVI / (ANVI + MNVI + PNVI + OTVI)$	Posteroneural morphometric index
OTMI	$OTMI = 100 * OTVI / (ANVI + MNVI + PNVI + OTVI)$	Otic morphometric index
OMI	$OMI = 100 * OVI / (OVI + RVI + MVI + AVI)$	Optic morphometric index
RMI	$RMI = 100 * RVI / (OVI + RVI + MVI + AVI)$	Respiratory morphometric index
MMI	$MMI = 100 * MVI / (OVI + RVI + MVI + AVI)$	Masticatory morphometric index
AMI	$AMI = 100 * AVI / (OVI + RVI + MVI + AVI)$	Alveolar morphometric index

¹ Size is estimated as geometric mean obtained from length, width, and height of each component. Shape is visualized as relative size of minor components in relation to major component's size. Variable codes are given in Table 2.

ford et al., 1997). The diagonal elements r_{ii} also give the genetic distance of each population to the group centroid, and the average diagonal element of the R matrix weighted by population size is equal to Wright's F_{st} , a measure of average genetic differentiation relative to the contemporary gene pool (Relethford, 1996).

Distances and F_{st} s were computed using the RMET 5.0 program, written by John Relethford. Heritability was set to a value of 0.55, on the basis of previous estimations of heritability for cranio-metric traits (Devor, 1987). Data used to obtain distances and F_{st} s were converted to standardized scores within each sex. This is a common method for removing sex-related size variation (Williams-Blangero and Blangero, 1989; Relethford, 1994; Relethford and Harpending, 1994).

As an additional test, univariate plots of each volumetric and morphometric index averaged for each local population were obtained, in order to visualize the dispersion of component's size and shape between and within each strategy.

Apportionment of quantitative variation

When the total observed variation is subjected to different apportionments of variation, computation of distances and F_{st} values for the different arrays can be of great utility in understanding microevolutionary mechanisms. For instance, Lewontin (1972), Relethford (2001, 2002), and González-José et al. (2001) opted for focus on variation on different geographical levels, comparing within- and between-group variation on a continental scale vs. local populations. Conversely, Steadman (2001) and Varela and Cocilovo (2002) studied apportionment of variation based on a diachronic partition of samples. Our approach here considers an apportionment of variance based on the economic strategy. In this context, we considered different categorizations and arrays of samples. Distances were computed 1) among all possible pairs of populations, regardless their economic strategy (denominated "global" level); 2) among pairs of populations sharing the same economic strategy (e.g., all pairs HG-HG and F-F); and 3) among pairs of populations not sharing economic strategy (all pairs HG-F). It is expected that if strategy mainly influences the morphology of a single component, then the average HG-HG and F-F distances will be lower than the average "global" distances, while the average HG-F distances will be greater than the average "global" distances.

Apportionment of variation to obtain F_{st} values was carried out considering different arrays of samples: 1) all populations, a figure called here "global" and coded as F_{st} ; 2) the two strategies as suprapopulation unities, an "among-strategy" value coded as $F_{st_{HG-F}}$ that results from classifying individuals according to their strategy and not considering their population assignment; 3) only the hunter-gatherer populations (coded as $F_{st_{HG}}$;

and 4) only the farmer populations (coded as F_{st_F}). Note that computation of F_{st} s after this apportionment of variation enables the detection of possible trends to the fixation of particular morphologies in each component. As already explained by Konigsberg (2000), the relationship between directional selection and evolution of a quantitative trait is quite straightforward. Since the immediate effect of directional selection is to eliminate the proportion of individuals which does not present the selected trait, a first consequence is the reduction of the additive genetic variance of the population, which also results in a reduction in phenotypic variation (Konigsberg, 2000).

To summarize, if the change in economic strategy has promoted selection (and consequent fixation) of a particular morphology, then $F_{st_{HG-F}}$ will be greater than the global F_{st} s, due to low differentiation among populations within a particular strategy and to high divergence among strategies. Moreover, these changes might be accompanied by a decrease of $F_{st_{HG}}$ and F_{st_F} , since populations within a strategy will tend to be more homogeneous.

Relethford (2001) demonstrated that geographic distribution of populations may inflate their F_{st} values. Since the subsample of hunter-gatherers used here covers a wider geographic area than the farmers' subsample, we weighted F_{st} s to adjust levels of differentiation to the spatial separation of subsamples. Following Relethford (2001) and according to the scheme of apportionment of variance explained above, F_{st} s were divided by the average geographic distance of local populations to the geographic center of 1) total populations, 2) hunter-gatherer populations, and 3) farmer populations. Thus, F_{st} s were obtained independent of the geographic dispersion of samples, which in the present case would tend to inflate diversity within hunter-gatherers (dispersed along the entire South American continent) in relation to farmers (mainly concentrated in the Andean zone).

RESULTS

Two different sets of analyses were performed: computation of distances among total and selected pairs of groups, and estimation of F_{st} values. Craniometric distances between pairs of populations are reported in Figure 1. All distances were large relative to their standard errors, indicating significant differentiation at each analysis' level.

The first plot reflects differentiation among groups after using 24 orthogonal variables covering all regions of the skull. An inspection of the first group of distances reflects that, despite their strategy, distances between all populations were almost equal to those computed among groups with different strategies (HG-F). Conversely, differentiation within hunter-gatherer groups was greater than in the global analysis, whereas differentiation within agriculturalists was lower than all the

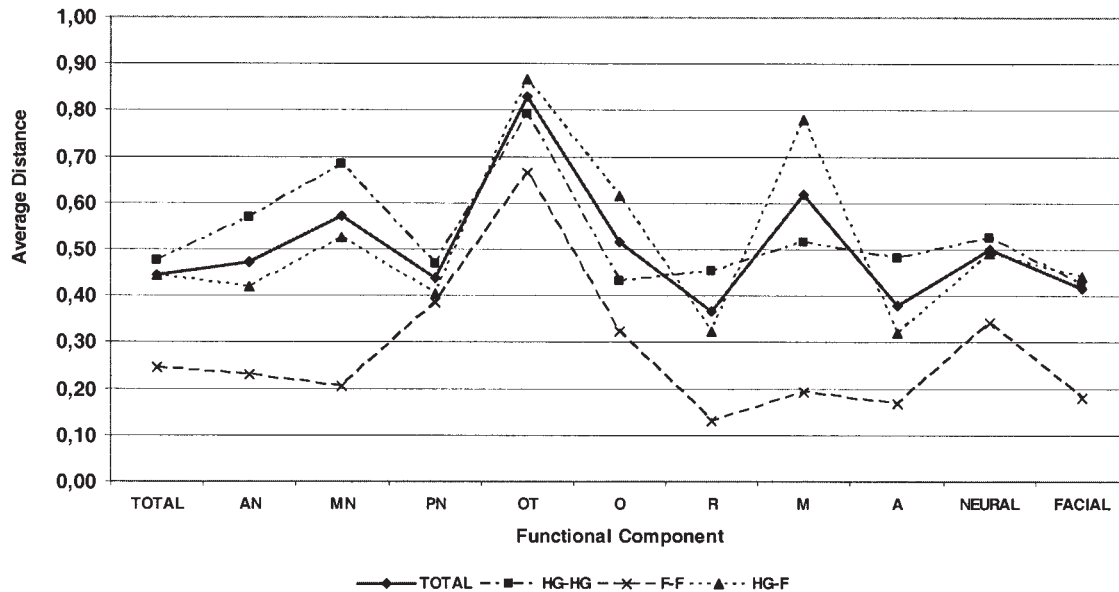


Fig. 1. Average pairwise distances between different arrays of samples calculated after total set of variables and particular functional components. Solid line with diamonds, global comparisons among all populations; dashed-dotted line with squares, distances among pairs of hunting-gathering populations; dashed line with crosses, distances among pairs of farmer populations; dotted line with triangles, distances between pairs of populations with different strategies.

remaining distances. This is an expected result, since the geographic separation between hunter-gatherers is wider than between farmers. Furthermore, since most farmer groups occupy the Andean region, strong similarities based on common ancestry and gene flow are expected. Nevertheless, this initial pattern is uninformative with respect to the problem of differences among strategies. The most important point here is the deviation of this initial pattern obtained after analyzing single components.

In the same way, comparisons across different regions of the skull within a strategy are limited because estimations of heritability for each component are not available. However, potential plastic effects can be indirectly estimated by comparing variation within components among strategies. Note that these comparisons are independent of differential heritability among components. If all heritabilities are set to a constant value for all components, then those components that are likely to respond to plastic effects are expected to provide higher F_{st} s (Williams-Blangero and Blangero, 1989).

As reflected in Figure 1, the anteroneural, midneural, and posteroneural components tend to reflect the same pattern of diversification as the total set of variables, i.e., global differentiation at the same level as HG-F comparisons, HG-HG distances being the highest, and F-F distances being the lowest. A strong differentiation at the posterior neurocranium is observable within farmers. The major source of differentiation is clearly concentrated in the otic component, where distances reach the highest levels in all arrays of samples. How-

ever, note that the pattern of relative differences between arrays remains very similar to the total variable analysis. Two out of four facial minor components show interesting deviations from the global pattern: the optic and the masticatory components. In these two components, differentiation among groups with a different strategy increases and surpasses the average distance of the global array. Related to this trend, differentiation within hunter-gatherers diminishes in relation to the global sample in both components. As expected, the final configuration of distances observed in the facial major component is largely driven by the particular trend detected in the optic and masticatory component.

Estimates of F_{st} s for the different levels of analysis are presented in Figure 2. The first result is quite clear: phenotypic differentiation at the local population level (F_{st}) is one order of magnitude greater than differentiation based on strategy ($F_{st_{HG-F}}$). The global F_{st} , computed after 24 variables, is similar to previous estimations of craniometric (González-José et al., 2001; Sardi, 2002) and molecular differentiation for South America (Mesa et al., 2000).

No major deviations in the pattern of variation are observed in the four minor components of the neurocranium, with the exception of high differentiation in the posterior neurocranium within the farmer group. The increase of differentiation at the otic component is coincident with the previous distance analysis.

An inspection of the optic component reveals that even when the average distance between hunter-gatherers and farmers was greater than global

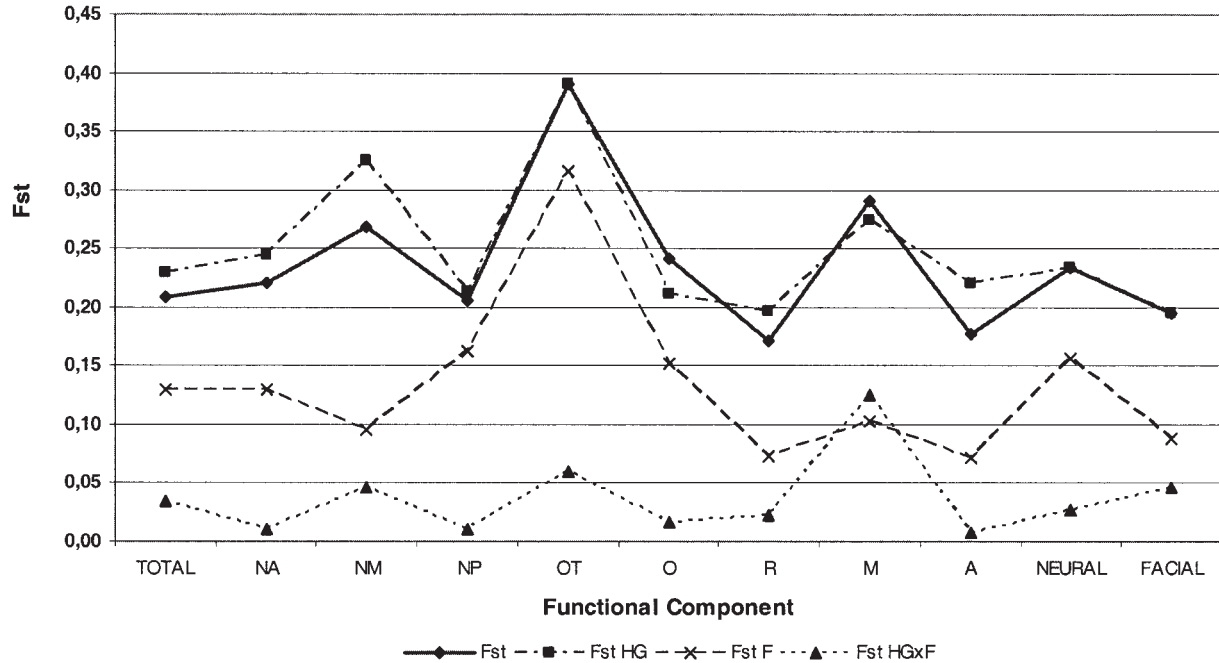


Fig. 2. Fst values for different arrays of samples, calculated after total set of variables and particular functional components. Solid line with diamonds, global Fst; dashed-dotted line with squares, Fst_{HG} obtained using only populations within hunting-gathering strategy; dashed line with crosses, Fst_F obtained using only populations within farming strategy; dotted line with triangles, Fst_{HG-F} considering strategy as unit of analysis.

distances, the Fst values remained low and reflected the same pattern as the total variable estimations. This indicates not only that groups of different strategies display divergent centroid values for this component, but also that intrastratagem variation is very important.

A different behavior is observed at the masticatory component, which not only showed a greater than global average distance, but also resulted in an increase of Fst_{HG-F} values in relation to the global figure. This implies that separation of centroids at the strategic level is accompanied by a reduction of within-strategy diversity, which causes an increase in Fst_{HG-F}. In particular, the craniofacial morphology of farmers is characterized by a reduction of the masticatory component both in absolute and relative size. Even when the masticatory component showed the best performance to differentiate between strategies, note that interpopulation differentiation (Fst) remained greater than economic strategy differentiation (Fst_{HG-F}). To further explore deviations from the total-variable pattern of distances when the masticatory component is analyzed, we plotted both distance matrices by means of a principal coordinate (PC) plot (Fig. 3). As expected, when analyzing the masticatory component, farmers tend to cluster together, confined to the positive values of PC1 and the negative values of PC2, and clearly separated from hunter-gatherer populations. Note that a considerable dispersion is observable among the hunting-gathering strategy group.

In order to test if geographic dispersion is affecting general differentiation patterns, we reanalyzed data by computing the Fsts weighted by the average spatial separation of the samples. These results (Fig. 4) show that when geographic distances are included in the computation of parameters, the Fsts obtained considering all variables are rather equal for the different arrays (global, Fst = 0.121; hunter-gatherers, Fst_{HG} = 0.114; farmers, Fst_F = 0.113), but still remain one order of magnitude lower in the among-strategies comparison (Fst_{HG-F} = 0.022). Disruption of the pattern of Fsts, considering individual functional components rather than total variables, shows a pattern similar to that observed in Figure 2: the masticatory component dramatically increases the among-strategies Fst, indicating that its morphology constitutes a powerful variable to discriminate among subsistence strategies. Univariate analysis of average volumetric and morphometric indices is shown in Figure 5. A first important observation is that all farmers fall well within the range of variation of hunting-gathering groups. Overlapping of ranges of variation may be produced by the greater dispersion and consequent diversification of hunter-gatherers in relation to farmers. However, it is interesting to note that a trend toward a reduced absolute and relative size is detected in the masticatory component among farmers, despite some strict hunter-gatherers groups like those from Espiritu Santo, Chaco, Pampa, or Paraná's Delta (data not shown) presenting relative masticatory sizes very similar to the

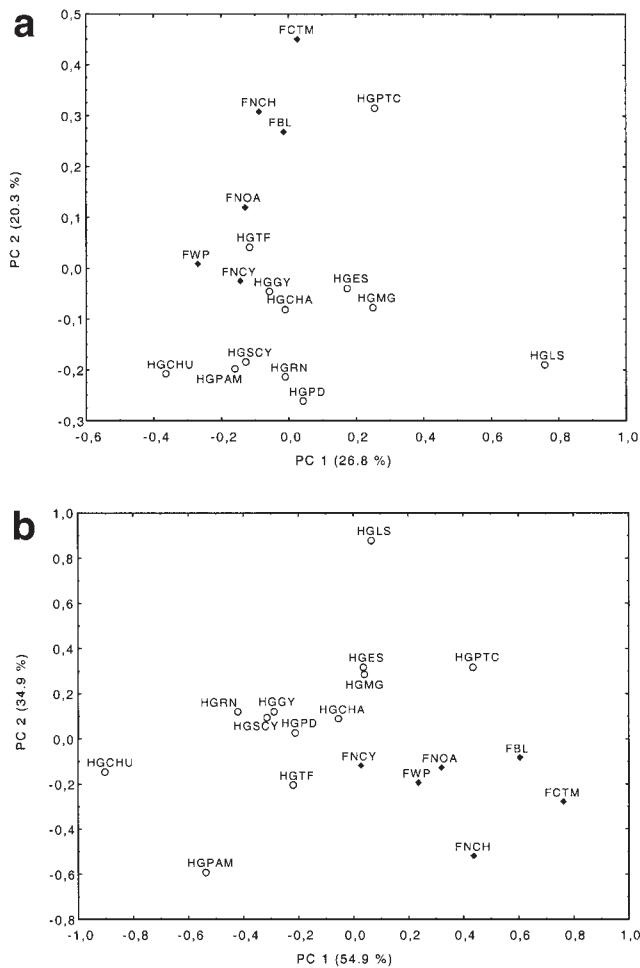


Fig. 3. Principal coordinate plots reflecting distances computed after total set of variables (**a**: 47.1% of variance explained) and variables related to masticatory component (**b**: 89.8% variance explained). Solid diamonds, farmers; open circles, hunter-gatherers.

farmer's masticatory sizes. Variation in alveolar absolute size (AVI) seems to be very restricted among farmers, who however, do not diverge in terms of their relative size (AMI).

DISCUSSION

This study sheds light on two important points concerning the influence of nongenetic factors on morphological differentiation at the craniofacial level: the magnitude of variation accounted for by a particular environmental force (the subsistence strategy of populations), and the localization of structures which are most likely affected by this particular factor.

On the one hand, a craniofunctional standpoint enables the study of specific regions of the skull on a functional and developmental basis. On the other hand, an apportionment of variance taking into account the "problem" factor is a valid approach to estimate its effect on biological variation, since

powerful parameters such as distances and F_{st} values enable direct comparisons between levels of variability.

Distance values among the global set of local populations were systematically greater than distances computed exclusively between pairs of groups of different subsistence strategies. In parallel, F_{st} values computed on the global set were also greater than the F_{st} obtained after considering subsistence strategy as the unit of study. Thus, differentiation at the craniofacial level is stronger among local populations than among groups of populations sharing a subsistence strategy. This pattern remains observable, even when geographic dispersion of the samples considered is taken into account in the computation of F_{st} s. Figure 3 shows that this is a consistent view: hunter-gatherers from Lagoa Santa present an outlier position, probably due to their plesiomorphic characteristics and their differentiation from the Amerindians (Neves and Pucciarelli, 1991; Lahr, 1995). Moreover, some Andean groups (FBL, FCTM, FNCH, and HGPTC; see Appendix for expansion of abbreviations) form a cluster differentiated from a separate aggregation of groups which comprises Patagonian (HGTF, HGCHU, and HGRN), central Argentinean (FWP, HGPAM, FNCY, and HGSCY), and Amazonian/Chaco (HGES, HGMG, HGCHA, HGGY, and HGPD) groups. Within this second cluster, a clear geographical pattern showing a Patagonia-central Argentina-Chaco-Amazonia cline can be observed along principal coordinate 1.

As is evident in Figure 3, when the total set of variables is considered, hunter-gatherers and agriculturalists are not consistently differentiated in their overall shape. In fact, some clusters are formed both by agriculturalists and by hunter-gatherers. This result contradicts some previous studies, which concluded that reduction in robusticity and an increase of brachycephally are ubiquitous and mainly associated with masticatory, dietary, and technological changes characterizing the Neolithic transition. In a complete review of this issue and in agreement with the statement by Carlson and Van Gerven (1977), Larsen (1997) found that earlier hunter-gatherers tend to have dolichocephalic and robust skulls, and later agriculturalists tend to have more brachycephalic and gracile crania. Nevertheless, the results in Figure 5 show an important overlap between farmers and hunters for almost all volumetric and morphometric indices, and also give evidence that the range of morphological variation within hunter-gatherers is important enough to reduce their morphology to an overall form like "robust" or "dolichocephalic." Similarly, Sardi et al. (2004a) found that post-Mesolithic groups of Europe and North Africa showed a smaller size than Paleolithic and Mesolithic ones, and also showed more narrow crania, associated with a reduction in the masticatory component.

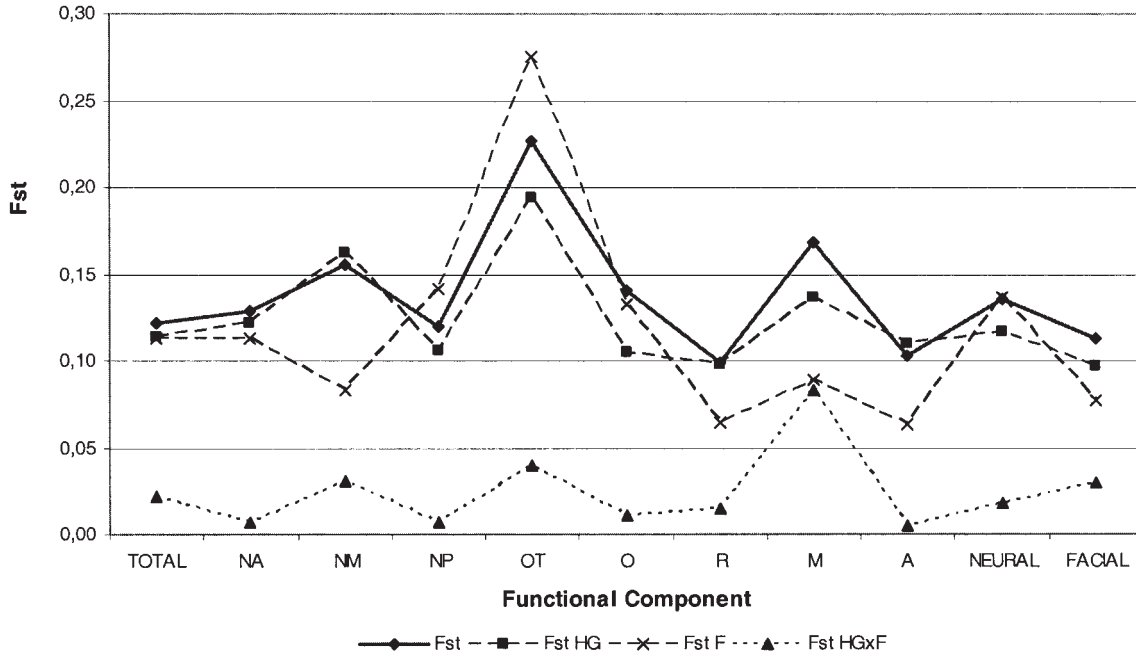


Fig. 4. Geographically standardized F_{st} values for different arrays of samples, calculated after total set of variables and particular functional components. Raw F_{st} s were divided by average distance to geographic centroid of each array of samples, and multiplied by 1,000. Solid line with diamonds, global F_{st} ; dashed line with squares, $F_{st_{HG}}$ obtained using only populations within hunting-gathering strategy; dashed line with crosses, F_{st_F} obtained using only populations within farming strategy, dotted line with triangles, $F_{st_{HG-F}}$ considering strategy as unit of analysis.

In contrast, our results are in agreement with the conclusions of Lahr and Wright (1996), who failed to detect an unambiguous reduction of craniofacial size and robusticity associated with technological shifts (see below).

The levels of differentiation observed here are consistent with a scenario in which craniofacial divergence arose mainly as a result of disruption in the history and structure of populations, rather than as a consequence of adaptation to particular selective pressures. This observation is also congruent with some previous analyses on the apportionment of cranial measurements' variance, which concluded that, from a multivariate perspective, selective neutrality seems to be the rule rather than the exception (Relethford, 2002; Sparks and Jantz, 2002).

However, the craniofunctional approach goes further in the discrimination of genetic and nongenetic putative causes of variation, because it enables us to detect morphological changes in particular localized structures. These structures are not arbitrary constructs or simple linear measurements between landmarks, but units of functional and developmental covariance. The method also has a twofold advantage, according to the analysis' requirements. For instance, one can use the method in a more "eco-resistant" way, considering many variables equally and geometrically distributed along the entire skull, and then obtaining levels of variation which would better reflect the unknown genetic background of the population. Alternatively, one can concentrate the analysis on

the modification in particular components after a specific apportionment of variation based on the environmental forces under study, thus regarding more efficiently the nongenetic (plastic) causes of variation in that component. Both approaches were depicted here. Unfortunately, estimations of heritability for each component are unavailable, and it is important to note that heritabilities might differ between traits and across populations (Konigsberg, 2000) and are also expected to vary in differing environments. However, some predictions concerning heritability of single components can be stated after observation of our results. For instance, if we assume that among-group genetic differences are better depicted by the total set of measurements, then deviations from this pattern in localized components can be viewed as variation due to environmental differences, and hence this particular component is expected to present low heritability. If environmental factors mainly influence the morphology of components showing greater differentiation among hunters and farmers, then low values of heritability are an expectable result for these structures. Variation of heritability in differing environmental conditions was discussed in great detail in the IQ literature (e.g., Turkheimer et al., 2003), and models applied can be of great utility in future works to estimate which proportion of each functional component is attributable to either genes or environment.

Despite the low power of subsistence strategy as a source of total craniometric variation, the analy-

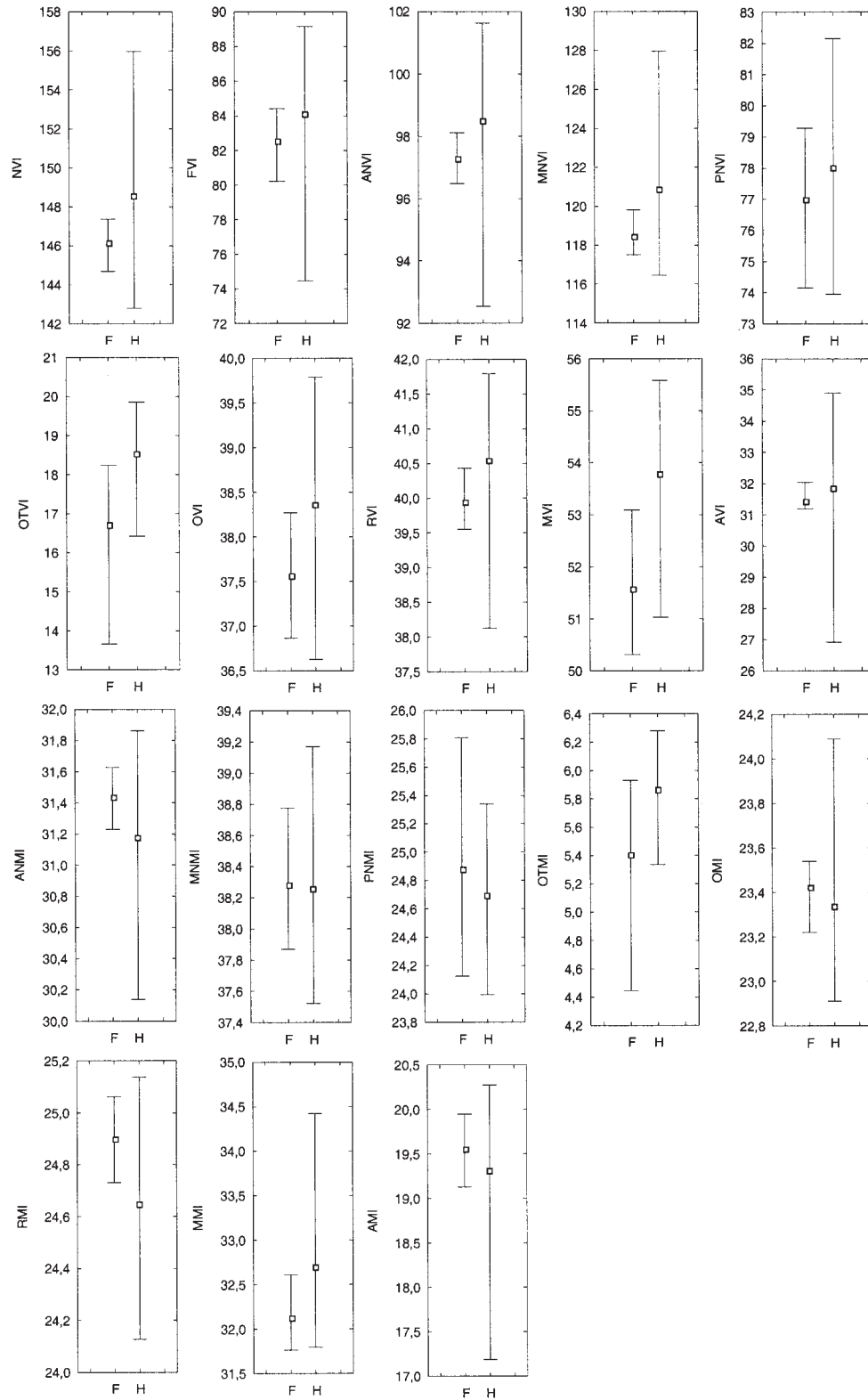


Fig. 5. Mean (square) and range (whisker) depicting variation between and among strategies along volumetric and morphometric indices. F, farmers; H, hunter-gatherers.

sis of single functional components reveals interesting differences in the behavior of particular structures. The most interesting deviation from the

pattern depicted by the total-set-of-variables analysis is exhibited by the masticatory component. Both parameters computed here, distances and

Fst, seem to reflect that a proportion of variation in the morphology of the masticatory component is probably driven by either a selective process or plastic responses during ontogeny, leading to large relative masticatory sizes prior to the transition to food production, and a relaxation and consequent decrease of masticatory size after the adoption of farming. This view is supported by the combined facts that distances among hunter-gatherer/farmer pairs are greater than total pairwise averaged distances, and that an $F_{st_{HG-F}}$ increase is accompanied by a slight decrease of F_{st_F} and $F_{st_{HG}}$ (Fig. 2). As expected, distances computed after the three masticatory orthogonal measurements (Fig. 4) tend to form two clear clusters, corresponding to farmers on one side and hunter-gatherers on the other. This pattern of interpopulation clustering is mainly based on economic strategy and is probably caused by a reduction of mechanical stress, the farmers displaying lower absolute and relative masticatory sizes.

The consumption of a softer diet, because of the farmers' food sources and/or processing techniques, may have yielded reduced loadings on the masticatory structure. In this context, independent evidence supports the contention that the farmers' diet consists of softer food, and can be found independently in dental microwear analyses and molecular genetics studies of crop plants. Differences in food availability, stone tool technology, and food-processing techniques seem to be responsible for a decrease in microwear through time (Pérez-Pérez et al., 2003). Microwear features tend to be more abundant in groups whose diet was abrasive than those who ate soft foods (Romero et al., 2004). Research on dental microwear documented a significant shift in microwear patterns from hunting-gathering to subsistence farming, showing that embracing an agricultural lifestyle results in a significantly softer diet (Teaford and Tylenda, 1991; Teaford and Lytle, 1996; Romero et al., 2004). Further support for this contention is provided by analyses of allelic selection in crop plants. Such studies performed on maize demonstrated that starch properties were one of the key targets of a strong process of artificial selection tending toward softer crops (Whitt et al., 2002; Jaenicke-Després et al., 2003). This is relevant in the context of our analysis, since starch (unlike protein) is often lacking in hunter-gatherer diets in the tropics and subtropics (Piperno and Pearsall, 1998; Whitt et al., 2002). Thus it would be reasonable that early cultivators of maize focused on improving the yield of softer starch, thus diminishing the mechanical pressure on the masticatory apparatus. In summary, several independent, nonskeletal data point to a reduction of masticatory stress after the adoption of an agriculturalist/farming lifestyle.

Meanwhile, plastic changes rather than adaptive mechanisms are also suspected of causing the pattern observed in the masticatory structures (see

below). Strains (deformations) generated by mastication of different kinds of diet are widely thought to be responsible for major shape changes during the ontogeny of cranial regions around the teeth (mandibular and maxillary arches) as well as near the origin and insertion of the major muscles of mastication (Hylander, 1988; Herring and Mucci, 1991; Herring, 1993). During the evolution of modern humans, many technological innovations such as the Neolithic transition are thought to have caused a significant reduction in masticatory stress (Brace, 1979; Brace et al., 1987, 1991; Lieberman, 1993; Agrawal et al., 1997; Sardi et al., 2004a). For instance, previous studies on nonhuman primates demonstrated that specific regions of the face are differentially affected by masticatory strains, the effect being higher in the lower face (occlusal plane) and lower in the middle and upper face (Hylander et al., 1991; Hylander and Johnson, 1992).

In their research on cranial size, shape, and robusticity in modern humans, Lahr and Wright (1996) deduced that a reduction in masticatory size and robusticity could be the final result of either phylogenetic or functional processes. If reduction in masticatory size is associated with transition to food production and technological advance, then one must observe this reduction in all populations that underwent these processes. However, the authors detected a wide range of masticatory size and robusticity variation among hunter-gatherer groups. Lahr and Wright (1996) concluded that the lack of association between the masticatory robusticity of a population and their level of technological development indicates that mechanisms other than selective pressures acted upon the gracilization of the modern human skull. Despite the trend showed by the masticatory component, our results are highly congruent with the deduction of Lahr and Wright (1996): the levels of differentiation among subsistence strategies never surpassed the level of interpopulation differentiation. Even when other components also showed greater among-subsistence than global average distances, this trend seemed to be the effect of plastic changes rather than adaptive ones. Plastic changes can in fact generate changes in craniofacial morphology, but they are not fixed in the population genetic pool. In consequence, Fsts tend to remain unaltered after plastic changes, in contrast to adaptive ones, which inflate Fst as a response to diminution of internal variability caused by directional selection. This difference could be viewed as a plausible explanation for the pattern observed in the optic component. Unfortunately, our results cannot solve which plastic mechanisms are suspicious enough to be involved in changes at the optic component.

Experimental studies on nonhuman primates clearly reflect the influence of some extreme environmental forces, such as malnutrition or protein-deficient nutrition. In this field, Pucciarelli et al. (1990, 2000) and Dressino and Pucciarelli (1997)

combined the advantages of functional craniology with those of experimentation in biological anthropology, in order to study alterations by nutritional factors in the growth of skull components of non-human primates. Those analyses showed that malnutrition delayed growth in size and altered the normal shape changes. Even though the results of Pucciarelli et al. (1990, 2000) and Dressino and Pucciarelli (1997) provide strong evidence supporting a large effect of nongenetic agents, it should be taken into account that in those analyses, the environmental effect was forced to an extreme.

Our results do not mean that selective or plastic pressures do not play a role in the expression of morphological traits. Rather, they demonstrate that these effects did exist and can be reasonably localized by studying specific components after an apportionment of variation based on the distribution of the nongenetic factor under consideration. Despite the finding that economic strategy mainly influences the size and shape of the masticatory component, quantification of its effect in terms of within- vs. between-group differences points to a low effect upon cranio-metric distances when compared with simple, inter-population differences, thus contradicting pure adaptationism as a mechanism determining morphological variation at the craniofacial level.

CONCLUSIONS

Our approach, based on the craniofunctional theory combined with statistical tools (apportionment of variance and computation of intra- and inter-group variability), allows us to accept the null hypothesis that masticatory and/or alveolar regions contribute to discriminate better among economic strategies rather than between local populations. In particular, there is a clear plasticity of the masticatory complex, reflecting the environmental influence of diet and mechanical loading of the face. However, differences between levels of diversity obtained after analyzing subsistence-based aggregates vs. local populations suggest that craniometrics should not be disregarded as a source of data for the genetics of population models. When the total craniofacial shape is considered, variation is more clearly patterned by structural-historical aspects of the population than by some important nongenetic differences, such as subsistence type, thus giving null support to adaptationist arguments. Future work must be focused on the exploration of further environmental factors, their impact on the growth of specific regions of the skull, and departures from more complex models of variation apportionment.

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APPENDIX

Superscript letters below indicate the following: A, archaeological reference; E, ethnographic reference; I, isotopic reference; P, paleopathological reference.

FBL: highlands of Bolivia; FNCH: north of Chile

Ecological setting: Highlands (altiplano) between 2,000–4,000 m, a rolling high plain delimited on the East and West by mountains that occasionally exceed 6,000 m.

Economy: Primarily peasant pastoralists deriving their livelihood from herds of alpaca and llama, or subsistence agriculturalists, the former in the altiplano and the latter in the sierras (between 2,000–3,000 m). Generally, potatoes were the staple crop, although quinoa was the most important grain. Pastoralism was important not for food, but for transport and for the use of wool to make clothes.

Settlement pattern: More or less autonomous villages or hamlets within which some social hierarchical levels occurred.

References: Chervin (1908),^E Berenguer and Daulsberg (1989),^A Núñez (1989),^E Barton et al. (1990),^E Schull (1990),^E Olivera and Yacobaccio (1999).^I

FCTM: Contumaza, Peru

Ecological setting: Andean mountains of northern Peru, between 2,000–4,000 m in elevation.

Economy: The chief crop was maize, although cotton, potatoes, quinoa, and an edible tuber called oca were also cultivated. Traditional Inca agriculture had very cleverly combined irrigation and soil conservation techniques, with a great diversity of species and varieties of perennial and annual crops.

Settlement pattern: More or less autonomous villages or hamlets within which some social hierarchical levels occurred.

References: Salomon (1986),^I Burguer and Van der Merwe (1990),^I Smith (1995),^{A,I} Piperno and Pearsall (1998).^{A,I}

HGCHA: Chaco, northeast Argentina

Ecological setting: Marshlands formed by the mid-

dle course of the Pilcomayo River, in southern Paraguay, and northeastern Argentina.

Economy: Fishing is the most important subsistence activity, reaching its peak between May–July, when large schools migrate upstream. The gathering of wild fruits by women is a very important source of nutrition during the ripening season, especially between November–March.

Settlement pattern: Groups of related families reside in long communal houses, which are merely a series of individual huts linked together end to end, without internal partitions.

References: Métraux (1946a),^E Hernández (1992),^E Gordillo (1999).^E

HGCHU: Chubut, Argentinean Patagonia; HGRN: Río Negro, Argentinean Patagonia; HGPAM: coastal pampas, east-central Argentina

Ecological settings: Steppe grassland plain extending from central Argentina to the southern coast of continental Patagonia, with a temperate climate characterized by a warm period between November–March.

Economy: Mainly based on the hunting of guanaco, which was intensively exploited until nearly historic times. As alternative game, they also hunted armadillo, and pampean and swamp deer.

Settlement pattern: Territory strictly parceled into a number of areas where each family group had exclusive rights for hunting and gathering. Each group moved freely within its own territory throughout the year, only crossing into another territory when circumstances demanded.

References: Cooper (1946b),^E Politis and Salemme (1990),^E Borrero (1990, ;1997),^{E,A} Fernández and Pannarello (1991),^I Martinic (1995),^E Gómez Otero et al. (2000).^A

HGGY: Guayaqui, Paraguay

Ecological settings: Neotropical forest interrupted by small patches of grassland, cerrado, swamp, and coatinga.

Economy: Hunting mammals (nine-banded armadillo, capuchin monkey, white-lipped peccary, paca, coatí, brocket deer, collared peccary) represents 78% of their economic activity; 14% is devoted to gathering palm starch, palm heart, insect larvae, and fruits.

Settlement pattern: Family group camps. Nomads.

References: Métraux and Baldus (1946),^E Roosevelt (1994),^{E,A} Hill and Hurtado (1999).^E

HGLS: Lagoa Santa, Brazil

Ecological settings: The region is dominated by cerrado vegetation, and gallery forest along watercourses. The climate is warm and seasonally dry in the winter, and moist and warm in the summer.

Economy: Paleopathological studies suggest that the main subsistence economy consisted of hunting (not necessarily big-game hunting, as generally suggested for Paleoindians) and gathering plant resources rich in carbohydrates.

Settlement pattern: Unknown.

References: Neves and Cornero (1997),^P Cornero et al. (1999),^P Neves et al. (2003).^{A,P}

HGMG: Minas Gerais, Brazil; HGES: Espírito Santo, Brazil

Ecological setting: Eastern Amazonian rain forest.

Economy: The economy rested essentially on hunting, fishing, and collecting fruits and insect larvae.

Settlement pattern: Hunting bands of from 50–200 individuals were led by men considered most powerful in terms of the supernatural realm.

References: Métraux (;1946b),^E Olson (1991),^E Roosevelt (1994).^{E,A}

FNCY: north of Cuyo, west-central Argentina, FNOA: highlands of northwest Argentina

Ecological settings: Northern area of the western subregion of Cuyo, comprising the territory of San Juan and Mendoza provinces up to the Diamante River and limited by the meridional Andean region. Farmer groups of Cuyo (FNCY), called Huarpes, lived north of the Diamante and Atuel Rivers. Farmers from north Argentina (FNOA) inhabited the Calchaquí valleys, in the Argentinean provinces of Catamarca and Jujuy.

Economy: Around 4400 years BP, the first evidence of agriculture appeared. The adoption of agriculture and domesticated animals was a gradual process, first as a complementary resource to hunting and gathering. By 1500 years BP, agriculture was the main subsistence activity, although hunting and gathering were never abandoned and continued to be developed during the winter season. Some of the cultivated species were potato, manioc, beans, and maize. Pastoralism was important not for food, but for transport and for the use of wool to make clothes.

Settlement pattern: Sedentary way of life at permanent or semipermanent villages.

References: Bárcena (1985),^A Canals Frau (1946),^E Gambier (1993),^A Lagiglia (2002),^A Novellino (2002),^A Sardi et al. (unpublished findings).^A

HGPD: Paraná River Delta, central Argentina

Ecological settings: Large floodplain composed of an intricate system of streams and minor waterways; islands and marshlands of the Paraná Delta.

Economy: Remains associated with the “Cultura Entrerriana” or “Básica del Litoral,” which is

characterized by a subsistence based on hunting and fishing.

Settlement pattern: Probably divided into small hunting groups based on kinship.

References: Torres (1911),^A Lothrop (1946),^E Caggiano (1984).^A

HGPTC: Paltacalo, Amazonas, Ecuador

Ecological setting: Amazonian rainforest.

Economy: Hunted almost exclusively monkeys (especially woolly monkey, howler monkey, and spider monkey), birds, and white-lipped peccaries. Gathered fruits form an important part of daily food intake (peach palm, ungurahua, and morete).

Settlement pattern: High residential mobility, confined to particular areas. Dispersed networks of intermarrying longhouses separated by vast stretches of unoccupied forest.

References: Rival (1999),^E Mena et al. (2000).^E

HGSCY: south of Cuyo Region, west-central Argentina

Ecological settings: Southern area of the western sub-region of Cuyo, located between the Diamante River and the Patagonian and Pampean regions.

Economy: Subsistence was mainly based on the hunting of guanaco and ñandú, as well as the gathering of some fruits and roots, through seasonal movements from lowlands to highlands. Palaeodietary reconstructions by stable isotope analysis show a small proportion of cultivable plants' consumption.

Settlement pattern: Dispersed groups with high mobility, not showing prolonged occupations. Their way of life, characterized by mobile and seasonal hunting-gathering, was maintained up to historical times.

References: Lagiglia (2002),^A Novellino (2002),^A Gil (2003),^A Sardi et al. (unpublished findings).^A

HGTF: Fueguians, Tierra del Fuego

Ecological setting: Channels, fiords, and rugged islands from the southern coast of Tierra del Fuego (marine hunter gatherers); shrub-grassland of the Patagonian steppe from northern Tierra del Fuego (terrestrial hunter gatherers).

Economy: Archaeological, ethnographic, and isotopic data suggest that hunting of guanaco and sea lions played the leading subsistence role. Collecting shellfish on the shoreline and fishing were also important sources of food intake. Marine hunter-gatherers were predominantly hunters of seals, whereas terrestrial hunter-gatherers hunted guanacos.

Settlement pattern: Nuclear families usually moved carrying their belongings. Multifamily

settlements only occurred for socializing and collective ceremonies.

References: Gusinde (1937),^E Cooper (1946a,b,c),^E Yesner et al. (1991),^I García-Moro et al. (1997),^E Vidal (1999).^E

FWP: Western Pampa, central Argentina

Ecological settings: Grassplains of the Western Pampa region in central Argentina.

Economy: In the mid-18th century, the staple food of this group was horse meat. They must have acquired horses somewhere around the early 18th century. This economic change toward an extensive use of horse was called "complejo ecuestre" by Casamiquela (1990).

Settlement pattern: This group appears to have been broken up into relatively small bands, each with its own headman.

References: Zeballos (1960),^E Casamiquela (1970, 1985, 1990),^E Fernández and Pannarello (1991).^I

LITERATURE CITED

- Agrawal KR, Lucas PW, Prinz JF, Bruce IC. 1997. Mechanical properties of foods responsible for resisting food breakdown in the human mouth. *Arch Oral Biol* 42:1-9.
- Bárcena R. 1985. Agricultores y alfareros tempranos del noroeste de Mendoza según la excavación arqueológica de varios abrigos rocosos. *Mendoza: Resúmenes IX Jornadas de Investigación de la UNC*. p 154.
- Barton SA, Castro Williams N, Barja I, Murillo F. 1990. Nutritional characteristics of the Aymara of northern Chile. In: Schull WJ, Rothhammer F, editors. *The Aymara strategies in human adaptation to a rigorous environment*. Dordrecht: Kluwer Academic Publishers. p 63-74.
- Beecher RM, Corruccini RS, Freeman M. 1983. Craniofacial correlates of dietary consistency in a nonhuman primate. *J Craniofac Genet Dev Biol* 3:193-202.
- Berenguer J, Daulsberg P. 1989. El Norte Grande en la órbita de Tiwanaku. In: Hidalgo JL, Schiappacasse F, Niemeyer HF, Aldunate C, Solimano I, editors. *Culturas de Chile, prehistoria*. Santiago de Chile: Andrés Bello. p 129-180.
- Boas F. 1912. Changes in the bodily form of descendants of immigrants. *Am Anthropol* 14:530-562.
- Borrero LA. 1990. Fuego-Patagonian bone assemblages and the problem of communal guanaco hunting. In: Davis LB, Reeves BOK, editors. *Hunters of the recent past*. London: Unwin Hyman. p 373-399.
- Borrero LA. 1997. The origins of ethnographic subsistence patterns in Fuego-Patagonia. In: Mc Ewan C, Borrero LA, Prieto A, editors. *Patagonia. Natural history, prehistory, and ethnography at the uttermost end of the earth*. London: British Museum Press. p 60-81.
- Brace CL. 1979. Krapina "classic" Neanderthals, and the evolution of European face. *J Hum Evol* 8:527-550.
- Brace CL, Rosenberg K, Hunt KD. 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. *Evolution* 41:705-720.
- Brace CL, Smith SL, Hunt KD. 1991. What big teeth you had, grandma! Human tooth size, past and present. In: Kelley MA, Larsen CS, editors. *Advances in dental anthropology*. New York: Wiley-Liss. p 33-57.
- Bresin A, Kiliaridis S, Strid KG. 1999. Effect of masticatory function on the internal bone structure in the mandible of the growing rat. *Eur J Oral Sci* 107:35-44.
- Buikstra JE, Frankenberg SR, Konigsberg LW. 1990. Skeletal

- biological distance studies in American physical anthropology: recent trends. *Am J Phys Anthropol* 82:1–7.
- Burguer RL, Van der Merwe J. 1990. Maize and the origin of highland Chavín civilization: an isotopic perspective. *Am Anthropol* 92:85–95.
- Caggiano MA. 1984. Prehistoria del Noreste Argentino. Sus vinculaciones con la República Oriental del Uruguay y Sur de Brasil. *Pesquisas* 38:5–109.
- Canals Frau S. 1946. The Huarpe. In: Steward J, editor. *Handbook of South American Indians*. Washington Smithsonian Institution. p 169–175.
- Carlson DS, Van Gerven DP. 1977. Masticatory function and post-Pleistocene evolution in Nubia. *Am J Phys Anthropol* 46:495–506.
- Casamiquela RM. 1970. La realidad arqueológica de la Patagonia Austral a la luz del panorama etnohistórico. *Rel Soc Argent Antropol* 5:105–115.
- Casamiquela RM. 1985. Bosquejo de una etnología de la provincia de Río Negro. *Viedma: Ministerio de Educación y Cultura de la Provincia de Río Negro, Fundación Ameghino*.
- Casamiquela RM. 1990. Los pueblos indígenas de la Patagonia. *Cienc Hoy* 2:18–28.
- Cavalli-Sforza LL, Bodmer WF. 1971. *The genetics of human populations*. San Francisco: W.H. Freeman.
- Chervin A. 1908. *Anthropologie bolivienne. Tome I: Ethnologie, démographie, photographie métrique*. Paris: Imprimerie Nationale.
- Cheverud JM. 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42:958–968.
- Cheverud JM. 1996. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddleback (*S. fuscicollis*) tamarins. *J Evol Biol* 9:5–42.
- Ciochon RL, Nisbett RA, Corruccini RS. 1997. Dietary consistency and craniofacial development related to masticatory function in minipigs. *J Craniofac Genet Dev Biol* 17:96–102.
- Cooper JM. 1946a. The Ona. In: Steward J, editor. *Handbook of South American Indians*. Washington Smithsonian Institution. p 107–126.
- Cooper JM. 1946b. The Patagonian and Pampean hunters. In: Steward J, editor. *Handbook of South American Indians*. Washington Smithsonian Institution. p 127–168.
- Cooper JM. 1946c. The Yaghan. In: Steward J, editor. *Handbook of South American Indians*. p 81–106.
- Cornero S, Neves W, Prous A. 1999. Prevalencia de caries en una muestra de la población de Santana do Riacho I, o el mito del paleoindio cazador. *Rev Argent Antropol Biol* 2:301–306.
- Devor EJ. 1987. Transmission of human craniofacial dimensions. *J Craniofac Genet Dev Biol* 7:95–106.
- Devor EJ, McGue M, Crawford MH, Lin PM. 1986. Transmissible and nontransmissible components of anthropometric variation in the Alexanderwohl Mennonites: II. Resolution by path analysis. *Am J Phys Anthropol* 69:83–92.
- Dressino V, Pucciarelli HM. 1997. Cranial growth in *Saimiri sciureus* (Cebidae) and its alteration by nutritional factors: a longitudinal study. *Am J Phys Anthropol* 102:545–554.
- Fernández J, Pannarello HO. 1991. Isótopos estables del carbono y paleodieta. *Shincal* 3:149–161.
- Franciscus RG. 2003. Internal nasal floor configuration in *Homo* with special reference to the evolution of Neandertal facial form. *J Hum Evol* 44:701–729.
- Franciscus RG, Long JC. 1991. Variation in human nasal height and breadth. *Am J Phys Anthropol* 85:419–427.
- Gambier M. 1993. *Prehistoria de San Juan*. San Juan: Editorial Universidad Nacional de San Juan.
- García-Moro C, Hernández M, Lalueza C. 1997. Estimation of the optimum density of the Selk'nam from Tierra del Fuego: inferences about human dynamics in extreme environments. *Am J Hum Biol* 9:699–708.
- Giesen EB, Ding M, Dalstra M, van Eijden TM. 2003. Reduced mechanical load decreases the density, stiffness, strength of cancellous bone of the mandibular condyle. *Clin Biomech* 18:358–363.
- Gil A. 2003. *Zea mays* on the South American periphery: chronology and dietary importance. *Curr Anthropol* 44:295–300.
- Gómez Otero J, Belardi JB, Tykot R, Grammer S. 2000. Dieta y poblaciones humanas en la costa norte del Chubut (Patagonia, Argentina). In: Desde el país de los gigantes. *Perspectivas arqueológicas en Patagonia*. Río Gallegos: Universidad Nacional de la Patagonia Austral. p 109–122.
- González-José R, Dahinten S, Luis M, Hernández M, Pucciarelli HM. 2001. Craniometric variation and the settlement of the Americas: testing hypotheses by means of R matrix and matrix permutation tests. *Am J Phys Anthropol* 116:154–166.
- González-José R, Van der Molen S, González-Pérez E, Hernández M. 2004. Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. *Am J Phys Anthropol* 123:69–77.
- Gordillo G. 1999. The Toba of the Argentine Chaco. In: Lee RB, Daly H, editors. *The Cambridge encyclopedia of hunter-gatherers*. Cambridge: Cambridge University Press. p 110–113.
- Guglielmino-Matessi CR, Gluckman P, Cavalli-Sforza LL. 1979. Climate and evolution of skull metrics in man. *Am J Phys Anthropol* 50:549–564.
- Gusinde M. 1937. *Die Feuerland Indianer*. Vienna: Verlag St. Gabriel.
- Hannam AG, Wood WW. 1989. Relationships between the size and spatial morphology of human masseter and medial pterygoid muscles, the craniofacial skeleton, and jaw biomechanics. *Am J Phys Anthropol* 80:429–445.
- Harris D. 1989. An evolutionary continuum of people-plant interaction. In: Harris D, Hillman G, editors. *Foraging and farming: the evolution of plant exploitation*. London: Unwin Hyman. p 11–26.
- Hernández I. 1992. *Los Indios de Argentina*. Buenos Aires: Fundación Mapfre.
- Hernández M, Lalueza C, García-Moro C. 1997. Fuegian cranial morphology: the adaptation to a cold, harsh environment. *Am J Phys Anthropol* 103:103–117.
- Herring SW. 1993. Epigenetic and functional influences on skull growth. In: Hanken J, Hall B, editors. *The skull*, volume 1. Chicago: University of Chicago Press. p 153–206.
- Herring SW, Mucci RJ. 1991. In vivo strain in cranial sutures: the zygomatic arch. *J Classif* 207:225–239.
- Hill K, Hurtado AM. 1999. The Aché of Paraguay. In: Lee RB, Daly H, editors. *The Cambridge encyclopedia of hunter-gatherers*. Cambridge: Cambridge University Press. p 92–96.
- Howells WW. 1973. *Cranial variation in man*. Papers of the Peabody Museum of Archaeology and Ethnology. Cambridge, MA: Harvard University.
- Hylander WL. 1988. Implications of in vivo experiments for interpreting the functional significance of “robust” australopithecine jaws. In: Grine FL, editor. *Evolutionary history of the “robust” australopithecines*. Chicago: Aldine. p 55–80.
- Hylander WL, Johnson KR. 1992. Strain gradients in the craniofacial region of primates. In: Davidovitch Z, editor. *The biological mechanisms of tooth movement and craniofacial adaptation*. Columbus: Ohio State University College of Dentistry. p 559–569.
- Hylander WL, Picq PG, Johnson KR. 1991. Masticatory-stress hypotheses and the supraorbital region of primates. *Am J Phys Anthropol* 86:1–36.
- Jaenicke-Després V, Buckler ES, Smith BD, Gilbert MT, Cooper A, Doebley J, Pääbo S. 2003. Early allelic selection in maize as revealed by ancient DNA. *Science* 302:1206–1208.
- Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. *Yrbk Phys Anthropol* 38:137–161.
- Kiliaridis S. 1995. Masticatory muscle influence on craniofacial growth. *Acta Odontol Scand* 53:196–202.
- Konigsberg LW. 2000. Quantitative variation and genetics. In: Stinson S, Bogin B, Huss-Ashmore R, O'Rourke D, editors. *Human biology. An evolutionary and biocultural perspective*. New York: Wiley Liss. p 135–162.
- Konigsberg LW, Ousley SD. 1995. Multivariate quantitative genetics of anthropometric traits from the Boas data. *Hum Biol* 67:481–498.
- Lagiglia H. 2002. Arqueología prehistórica del sur mendocino y sus relaciones con el centro oeste argentino. In: Gil A, Neme G, editors. *Entre montañas y desiertos: arqueología del Sur*

- de Mendoza. Buenos Aires: Sociedad Argentina de Antropología. p 43–64.
- Lahr MM. 1995. Patterns of modern human diversification: implications for Amerindian origins. *Yrbk Phys Anthropol* 38:163–198.
- Lahr MM, Foley R. 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yrbk Phys Anthropol* 41:137–176.
- Lahr MM, Wright RVS. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *J Hum Evol* 31:157–191.
- Larsen CL. 1997. Bioarchaeology: interpreting behavior from the human skeleton. Cambridge: Cambridge University Press.
- Lewontin RC. 1972. The apportionment of human diversity. *Evol Biol* 6:381–398.
- Lieberman DE. 1993. Life history variables preserved in dental cementum microstructure. *Science* 261:1162–1164.
- Lieberman DE. 1997. Making behavioural and phylogenetic inferences from fossils: considering the developmental influence of mechanical forces. *Annu Rev Anthropol* 26:185–210.
- Lieberman DE, Ross CR, Ravosa M. 2000a. The primate cranial base: ontogeny, function, and integration. *Yrbk Phys Anthropol* 43:117–169.
- Lieberman DE, Mowbray KM, Pearson OM. 2000b. Basicranial influences on overall cranial shape. *J Hum Evol* 38:291–315.
- Lothrop SK. 1946. Indians of the Paraná Delta and La Plata littoral. In: Steward J, editor. *Handbook of South American Indians*. Washington Smithsonian Institution. p 177–190.
- Luis MA, Sardi ML. 2000. Comparaciones entre las técnicas craneofuncional y howelliana para explicar una prueba de diferenciación poblacional. In: VI Cong Asoc Latinoamericano Antrop Biol. p 74.
- Martinić M. 1995. Los Aonikenk. Historia y cultura. Punta Arenas: Universidad de Magallanes.
- Mena PV, Stallings JR, Regalado JB, Cueva RL. 2000. The sustainability of current hunting practices by the Huaorani. In: Robinson JG, Bennet EL, editors. *Hunting for sustainability in tropical forests*. New York: Columbia University Press. p 57–78.
- Mesa N, Mondragón MC, Soto ID, Parra MV, Duque C, Ortiz Barrientos D, García LF, Vélez ID, Bravo ML, Múnera JG, Bedoya G, Bortolini MC, Ruiz-Linares A. 2000. Autosomal, mtDNA, and Y-chromosome diversity in Amerinds: pre- and post-Columbian patterns of gene flow in South America. *Am J Hum Genet* 67:1277–1286.
- Métraux A. 1946a. Indians of the Gran Chaco. Ethnography of the Chaco. In: Steward J, editor. *Handbook of South American Indians*. p 197–370.
- Métraux A. 1946b. The Botocudo. In: Steward J, editor. *Handbook of South American Indians*. p 531–540.
- Métraux A, Baldus H. 1946. The Guayakí. In: Steward J, editor. *Handbook of South American Indians*. Washington Smithsonian Institution. p 435–444.
- Moss ML. 1973. A functional cranial analysis of primate craniofacial growth. In: Zingesser M, editor. *Basel: Karger. Symp IVth Int Congr Primatol* 3:191–208.
- Moss ML. 1997. The functional matrix hypothesis revisited. 4. The epigenetic antithesis and the resolving synthesis. *Am J Orthod Dentofacial Orthop* 112:410–417.
- Moss ML, Young RW. 1960. A functional approach to craniology. *Am J Phys Anthropol* 18:281–291.
- Neves W, Cornero S. 1997. What did South American Paleoindians eat? *Curr Res Pleist* 14:93–96.
- Neves WA, Pucciarelli HM. 1991. Morphological affinities of the first Americans: an exploratory analysis based on early South American human remains. *J Hum Evol* 21:261–273.
- Neves WA, Prous A, González-José R, Kipnis R, Powell J. 2003. Early Holocene human skeletal remains from Santana do Riacho, Brazil: implications for the settlement of the New World. *J Hum Evol* 45:759–782.
- Novellino PS. 2002. Bioarqueología del Sur de Mendoza. In: Gil A, Neme G, editors. *Entre montañas y desiertos: arqueología del Sur de Mendoza*. Buenos Aires: Sociedad Argentina de Antropología. p 119–139.
- Núñez L. 1989. Hacia la producción de alimentos y la vida sedentaria. In: Hidalgo JL, Schiappacasse F, Niemeyer HF, Aldunate C, Solimano I, editors. *Culturas de Chile, Prehistoria*. Santiago de Chile: Andrés Bello. p 81–105.
- Olivera DE, Yacobaccio HD. 1999. Estudios de paleodieta en poblaciones humanas de los Andes del Sur a través de isótopos estables. In: Sánchez Sánchez A, editor. *Actas del V Congreso Nacional de Paleopatología*. Alcalá la Real: Asociación Española de Paleopatología. p 190–211.
- Olson JS. 1991. *The Indians of Central and South America: an ethnohistorical dictionary*. Westport, CT: Greenwood Press.
- Pérez-Pérez A, Espurz V, Bermúdez de Castro JM, de Lumley MA, Turbon D. 2003. Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. *J Hum Evol* 44:497–513.
- Piperno DR, Pearsall DM. 1998. *The origins of agriculture in the lowland neotropics*. San Diego: Academic Press.
- Politis GG, Salemme MC. 1990. Prehispanic mammal exploitation in Argentina. In: Davis LB, Reeves BOK, editors. *Hunter of the recent past*. London: Unwin Hyman. p 352–365.
- Pucciarelli HM, Dressino V, Niveiro M. 1990. Changes in skull components of the squirrel monkey evoked by growth and nutrition: an experimental study. *Am J Phys Anthropol* 81:535–543.
- Pucciarelli HM, Muñe MC, Oyhenart EE, Orden AB, Villanueva ME, Rodriguez RE, Pons ER. 2000. Growth of skeletal components in the young squirrel monkey (*Saimiri sciureus boliviensis*): a longitudinal experiment. *Am J Phys Anthropol* 112:57–68.
- Relethford JH. 1994. Craniometric variation among modern human populations. *Am J Phys Anthropol* 95:53–62.
- Relethford JH. 1996. Genetic drift can obscure population history: problem and solution. *Hum Biol* 68:29–44.
- Relethford JH. 2001. Global analysis of regional differences in craniometric diversity and population substructure. *Hum Biol* 73:629–636.
- Relethford JH. 2002. Apportionment of global human genetic diversity based on craniometrics and skin color. *Am J Phys Anthropol* 118:393–398.
- Relethford JH, Blangero J. 1990. Detection of differential gene flow from patterns of quantitative variation. *Hum Biol* 62:5–25.
- Relethford JH, Harpending HC. 1994. Craniometric variation, genetic theory and modern human origins. *Am J Phys Anthropol* 95:249–270.
- Relethford JH, Crawford MH, Blangero J. 1997. Genetic drift and gene-flow in post famine Ireland. *Hum Biol* 69:443–465.
- Rival LM. 1999. The Huaorani. In: Lee RB, Daly H, editors. *The Cambridge encyclopedia of hunter-gatherers*. Cambridge: Cambridge University Press. p 101–14.
- Roff DA. 1996. The evolution of genetic correlations: an analysis of patterns. *Evolution* 50:1392–1403.
- Romero A, Martínez-Ruiz N, De Juan J. 2004. Non-occlusal dental microwear in a Bronze-Age human sample from East Spain. *Anthropologie* 42:65–70.
- Roosevelt A. 1994. *Amazonian Indians: from prehistory to the present, anthropological perspectives*. Tucson: University of Arizona Press.
- 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.
- Salomon FA. 1986. *Native lords of Quito in the age of the Incas: the political economy of North Andean chiefdoms*. Cambridge: Cambridge University Press.
- Sardi ML. 2002. *Diferenciación craneofacial en aborígenes de la Patagonia y su relación con grupos americanos y extra-americanos*. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Argentina.
- Sardi ML, Ramírez-Rozzi F, Pucciarelli HM. 2004. The Neolithic transition in Europe and North Africa. The functional craneology contribution. *Anthropol Anz* 62:120–145.
- Schull WJ. 1990. Introduction: the place and the study. In: Schull WJ, Rothhammer F, editors. *The Aymara: strategies in human adaptation to a rigorous environment*. Dordrecht: Kluwer Academic Publishers. p 1–18.

- Smith DD. 1995. The emergence of agriculture. New York: Scientific American Library.
- Sparks CS, Jantz RL. 2002. A reassessment of human cranial plasticity: Boas revisited. *Proc Natl Acad Sci USA* 99:14636–14639.
- Steadman DW. 2001. Mississippians in motion? A population genetic analysis of interregional gene flow in west-central Illinois. *Am J Phys Anthropol* 114:61–73.
- Teaford MF, Lytle JD. 1996. Brief communication: diet-induced changes in rates of human tooth microwear: a case involving stone-ground maize. *Am J Phys Anthropol* 100:143–147.
- Teaford MF, Tylenda CA. 1991. A new approach to the study of tooth wear. *J Dent Res* 70:204–207.
- Torres LM. 1911. Los primitivos habitantes del Delta del Paraná. La Plata: Universidad Nacional de La Plata.
- Turkheimer E, Haley A, Waldron M, D'Onofrio B, Gottesman II. 2003. Socioeconomic status modifies heritability of IQ in young children. *Psychol Sci* 14:623.
- van der Klaauw CJ. 1948. Size and position of the functional components of the skull. *Arch Neerl Zool* 9:1–559.
- Van Spronsen PH, Weijs WA, Valk J, Prah-Andersen B, van Ginkel FC. 1991. Relationships between jaw muscle cross-sections and craniofacial morphology in normal adults, studied with magnetic resonance imaging. *Eur J Orthod* 13:351–361.
- Varela HH, Cocilovo JA. 1999. Evaluation of the environmental component of the phenotypic variance in prehistoric populations. *Homo* 20:46–53.
- Varela HH, Cocilovo JA. 2002. Genetic drift and gene flow in a prehistoric population of the Azapa valley and coast, Chile. *Am J Phys Anthropol* 118:259–267.
- Varrela J. 1990. Effects of attritive diet on craniofacial morphology: a cephalometric analysis of a Finnish skull sample. *Eur J Orthod* 12:219–223.
- Varrela J. 1992. Dimensional variation of craniofacial structures in relation to changing masticatory-functional demands. *Eur J Orthod* 14:31–36.
- Vidal HJ. 1999. The Yamana of Tierra del Fuego. In: Lee RB, Daly H, editors. *The Cambridge encyclopedia of hunter-gatherers*. Cambridge: Cambridge University Press. p 114–118.
- Whitt SR, Wilson LM, Tenailon MI, Gaut BS, Buckler ES IV. 2002. Genetic diversity and selection in the maize starch pathway. *Proc Natl Acad Sci USA* 99:12959–12962.
- Williams-Blangero S, Blangero J. 1989. Anthropometric variation and the genetic structure of the Jirels of Nepal. *Hum Biol* 61:1–12.
- Wood B, Lieberman DE. 2001. Craniodental variation in *Paranthropus boisei*: a developmental and functional perspective. *Am J Phys Anthropol* 116:13–25.
- Yesner DR, Figuerero Torres MJ, Guichón R, Borrero LA. 1991. Análisis de isótopos estables en esqueletos humanos: confirmación de patrones de subsistencia etnográficos para Tierra del Fuego. *Shincal* 3:182–191.
- Zeballos E. 1960. Viaje al país de los Araucanos. Buenos Aires: Hachette.