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South-Central Andean Area Settlement, Evolution, and Biocultural Interactions

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ABSTRACT. This article integrates a series of studies carried out with the aim to illustrate important aspects of the biology of the prehistoric human population that lived in the south-central Andean area, a key region of South America. These studies include (1) biological characterization of the local populations through analysis of a set of factors such as sex, age, and artificial deformation; (2) description of the structure of the populations at local and regional levels; (3) investigation of their genetic relationships; and (4) definition of the factors that determined their evolution. A synthesis of the cultural development of northern Chile and northwestern Argentina is also included to understand the natural and social historical circumstances associated with the colonization and occupation of the region.

RESUMEN. El presente trabajo integra una serie de experiencias realizadas con la finalidad conocer aspectos relevantes de la biología de la población humana prehistórica que habitó en el Área Andina Centro Meridional una región clave de América del Sur. Los trabajos citados incluyen (1) la caracterización biológica de las poblaciones locales mediante el análisis de un conjunto de factores como el sexo, la edad y la deformación artificial; (2) la descripción de la estructura de las poblaciones a nivel local y regional; (3) inferir sus relaciones genéticas; y (4) establecer los factores que determinaron su evolución. Además, se incluye una síntesis del desarrollo cultural del Norte de Chile y del Noroeste Argentino para permitir la comprensión de las circunstancias históricas sociales y naturales asociadas con la colonización y ocupación del territorio regional.

RESUMO. O presente trabalho integra uma série de experiências realizadas com a finalidade de conhecer aspectos relevantes da biologia da população humana pré-histórica que habitou na Área Andina Centro Meridional uma região chave de América do Sul. Os trabalhos citados incluem (1) a caracterização biológica das populações locais mediante a análise de um conjunto de fatores, tais como sexo, idade e deformação artificial; (2) a descrição da estrutura das populações a nível local e regional; (3) inferir suas relações genéticas; e (4) estabelecer os fatores que determinaram sua evolução. Ademais, incluíse uma síntese do desenvolvimento cultural do Norte de Chile e do Noroeste Argentino para permitir o entendimento das circunstâncias históricas, sociais e naturais associados à colonização e ocupação do território regional.

INTRODUCTION

Research carried out for the reconstruction of the biological history of the populations of northern Chile and northwest Argentina was based on information obtained about the local and regional phenotypic structure. Results of analysis for sexual dimorphism, age

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variation, artificial deformation, quality of life, and survival of populations from different sites are presented for the following regions: northern arid Chile (Arica, Pisagua, Caleta Huelén, San Pedro de Atacama), northern semiarid Chile (El Cerrito, Punta de Teatinos), and northwestern Argentina (Puna de Jujuy, Quebrada de Humahuaca, Valle Calchaquí and Pampa Grande). We mention experiences that allowed us to determine the environmental and genetic components of the phenotypic characters, as well as the reconstruction of several local models that helped to explain the regional evolutionary process and its relations with the other regions of the south-central Andean area.

NORTHERN CHILE

COMPOSITION AND STRUCTURE OF THE POPULATION

As of 1980, research has focused on studies of the structure of ancient populations, their biological relationships, and their evolution. This involved an important change from a theoretical, methodological, and technical point of view. From a theoretical perspective, change resulted from the unconditional adherence to the theory of evolution. From a methodological perspective, a key factor was the application of contrasting experimental designs based on explicit assumptions, consistent hypotheses, and appropriate evidence to support rational scientific knowledge. Technological advancement included application of protocols and analytical processes allowing researchers to obtain relevant information, as well as the use of statistical and numerical techniques to measure phenotypic and genetic information (Cocilovo, 1981; Cocilovo and Rothhammer, 1990; Cocilovo and Varela, 1999).

Reconstruction of the biological history of a population requires adequate information to be able to measure phenotypic differences in space and time without the influence of other effects associated with age, sex, and the artificial deformation of individuals. When research designs include heterogeneous samples from a wide territory, it is necessary to explore the magnitude of those effects, as they represent specific properties of the inhabitants of each locality. For this reason, determination of sex, age, and artificial deformation was a preliminary step in the studies of biological relationships among different groups. Having that information facilitated study of population structure at the local and regional levels, including the biocultural characteristics of each group. This included research carried out on materials dated between 3000 BC and AD 1450 from localities in or near Arica, Camarones 14, Pisagua, Caleta Huelén, San Pedro de Atacama, Punta de Teatinos, and El Cerrito, Chile (Figure 1; Cocilovo et al., 1982, 1999a; Varela et al., 1991, 1993; Cocilovo, 1994; Cocilovo and Costa-Junqueira, 2001; Quevedo et al., 2003; Manríquez et al., 2006; Rhode and Arriaza, 2006). These studies measured the magnitude of the effects of sexual dimorphism, age variation, and artificial deformation of the skull and estimated the paleodemographic parameters, ultimately

providing a synthesis of the distribution (Cocilovo and Varela, 2010) and effects of artificial cranial deformation at a regional level (Cocilovo et al., 2011a).

A set of environmental, cultural, economic, and social factors determined the quality of life and survival of the ancient population of Arica in northern Chile. For example, tuberculosis was endemic to the Andean region, affecting respiratory and skeletal systems (Arriaza et al., 1995; Lombardi and García Cáceres, 2000). From 9000 BC to AD 1800, Chagas disease affected a wide area that included southern Peru and northern Chile (Aufderheide et al., 2004, 2005; Arriaza et al., 2008). Nonvenereal Treponematoses (yaws) were detected both in the Azapa Valley and along the coast of Arica (Standen and Arriaza, 2000a). Diseases related to intestinal parasites were found in Arica and the Valley of Lluta (Arriaza, 1995; Reinhard and Urban, 2003; Santoro et al., 2003).

Poor hygiene and health conditions as well as the prevalence of pulmonary diseases negatively impacted quality of life and infant mortality (Arriaza et al., 1988). Lobar pneumonia was identified by Fontana et al. (1983) in remains of the Early Intermediate and Middle periods in Arica and regions to the south (Aufderheide et al., 2008). Iron deficiency anemia was detected through porotic hyperostosis in groups of fishermen and agropastoralists (Arriaza, 1995; Costa-Junqueira et al., 2000). Analysis of trace elements in skeletal remains revealed information about the type of diet. For example, in Morro 1 (coastal Archaic) the preference was vegetal food, and in the Azapa valley (site AZ140) protein-rich animal food was prevalent (Razmilic et al., 1987).

Signs of forceful blows in the Chinchorro population (Acha 2–3, Maderas Enco, Morro 1, Morro 1/6, and Playa Miller 8 sites) evidenced a high frequency of trauma to the skull (25%) and upper limbs (9%) in adult individuals, which seemed to result from violent situations rather than everyday accidents (Standen and Arriaza, 2000b). In samples from Chinchorro, Uhle collection (calibrated radiocarbon dates: 3550 3300 BP, 3450 3200 BP, and 3520 3220 BP), the environmental impact was analyzed by growth and development factors, as well as by health, diet, daily activity, and demographic properties (Costa et al., 2000; Costa-Junqueira et al., 2000).

A topic of interest in evaluating conditions of life in ancient and modern populations is the expression of sexual dimorphism. Its variability may reflect conditions of a quality of life that determines the survival and persistence of the population. The cultural diversity of Arica over ten thousand years and the quality of available osteologic material found there have together provided an excellent opportunity to study variation of sexual dimorphism in space and time. Higher mean values were found in males than in females for most cranial measurements (average sexual dimorphism index [SDI], 5%). In general, the magnitude of sexual dimorphism is comparable with other pre-Hispanic groups, suggesting that this population, using the available technology at hand (hunting, fishing, grazing, and agriculture), was able to obtain sufficient food resources to ensure adequate growth and



FIGURE 1. Map of the south-central Andes region showing many localities where samples were obtained.

development according to the local way of life. However, this situation varies between the coast and the valley and, more remarkably, between cultural periods. Specifically, in the Middle and Late periods there were no gender differences, which indicates harsher conditions of life then (Cocilovo and Varela, 2014).

The town of San Pedro de Atacama in arid northern Chile is 2,430 m above mean sea level (AMSL) (Figure 1). North of the Salar de Atacama, the oasis area surrounding the town allows the practice of agriculture and llama breeding. This locality has long been exceptionally well situated in the south-central Andean area; archaeological evidence indicates it was an obligatory way station for caravan traffic and human groups that migrated from the neighboring regions of northern Chile, Peru, Bolivia, and Argentina. Studies of the area's began population biology in 1990 and were published by Varela et al. (1990a, 1995), Cocilovo et al. (1995), Varela and Cocilovo (1996), and Varela (1997). At the site of Coyo Oriente 3 (AD 910–960), biological and cultural indicators were studied to determine the style and quality of life (Costa and Llagostera, 1994). The cemetery of Coyo Oriental, 5 km south-southeast of San Pedro de Atacama, allowed the definition of a specific phase (AD 600–900) in which the Tiwanaku culture was more dominant (Berenguer et al., 1986; Berenguer and Dahuelsberg, 1989). This led to study of the biology of the Tiwanaku by Cocilovo et al. (1994, 2011b), Cocilovo and Zavattieri (1994), and Costa et al. (2008).

Quality of life in the prehistoric population of San Pedro de Atacama was assessed by analyses of pathologies, traumas, state of dentition, personal violence, and other bioanthropological aspects (Costa, 1988; Costa and Llagostera, 1994; Costa-Junqueira et al., 1999; Costa et al., 2004; Lessa, 1999; Torres-Rouff et al., 2005; Torres-Rouff and Costa Junqueira, 2006; Lessa and Mendonça de Souza, 2007; da-Gloria et al., 2011; Torres-Rouff, 2011; Hubbe et al., 2012; Nado et al., 2012). As in Arica, sexual dimorphism was studied as a possible indicator of the predominant quality of life in San Pedro de Atacama through analysis of 624 individuals and 35 craniometrical variables. Most measurements showed mean values higher in men than in women (average SDI, 4%). Sexual dimorphism did not vary through time. This would indicate that the reported changes in life condition throughout 60 generations with other markers (pathologies, trauma, and violence) did not have a substantial impact on the normal growth and development of the skull in both sexes (Cocilovo et al., 2014).

In the semi-arid north (of Chile), archaeological studies have established a series of Archaic period stages for the coastal sites of Complejo Huentelauquen, Guanaqueros and Punta Teatinos (Schiappacasse and Niemeyer, 1986). Relationships and biological affinities were investigated in materials from different stages of cultural development in this region (Quevedo et al., 1985), and the findings provide a primary explanation for the population structure and its ancestral relationships. Strange et al. (1991) added to the analyses in a similar study. Punta de Teatinos is an archaeological site located on Coquimbo Bay 12 km north of La Serena; the site is on a coastal terrace comprising a shell midden and an Archaic period burial ground. The cemetery there dates to

two periods: 4905 ± 100 BP and 4560 ± 95 BP (Quevedo, 1976; Schiappacasse and Niemeyer, 1986). The study of these materials represents the most complete biological anthropology research at a regional level (Quevedo, 1998). Dentition, pathology, chemical analysis of trace elements, population dynamics, and paleodemography were analyzed. This study also presents demographic statistics and their relationships with other sites in the region (Quevedo, 1998; Quevedo Kawasaki, 2000). A later review and update of available information focused on the numerical and genetic properties of the group buried in this locality (Quevedo et al., 2000).

Studies carried out at Punta de Teatinos provided a wealth of information about bone markers indicating nutritional and infectious diseases as well as physical activity of individuals (Quevedo, 1998; Quevedo Kawasaki, 2000; Quevedo et al., 2000). These findings established a certain profile that could be linked with variations of normal growth and development. Therefore, to obtain more information about quality of life and the adaptation process experienced by the population, investigation of bilateral asymmetry of the metric variables of the skull and postcranial skeleton was undertaken. Calculation of bilateral asymmetry allows for partition of the phenotypic variance into two components: (1) the so-called maximum genetic variance and (2) the special environmental variance. Although no significant variations of environmental variance were observed in the postcranial skeleton, variations of the skull were found (perhaps associated with plagiocephaly and artificial deformation) as well as in maximum and minimum width of the ascending ramus, which were linked to functional alterations of the masticatory apparatus (Cocilovo et al., 2006). A more complete analysis was performed by calculating the value of repeatability (r) and the special environmental variance (Varela et al., 2006).

EVOLUTION OF THE POPULATION, LOCAL DIFFERENTIATION, AND REGIONAL RELATIONSHIPS

The discovery of changes to average phenotype of individuals in the same locality over time was a significant contribution to establishing a theory about settlement of the south-central Andean area. Experiments in Arica, Quebrada de Humahuaca, San Pedro de Atacama, and Pisagua revealed the existence of several microevolutionary models as well as the existence of a set of factors influencing composition and genetic structure of the population.

A series of studies in Arica established the existence of statistically significant phenotypic differences between the groups of the coast and of the Azapa Valley during different archaeological periods. These differences were evaluated by metric and nonmetric traits of the skull and showed a high correlation with chronological distances among groups of different periods (80%). An analysis of associated phenotypic and chronological distances through application of the method proposed by Relethford (1980) over a period of 6,500 years showed an increased kinship within groups and a decreased kinship over time both for males and females. From a population genetics point of view, for the first time in the south-central Andean area this analysis indicated the effect of a

microevolutionary process produced by a set of factors such as genetic drift and medium- and long-range migration (Rothhammer et al., 1982, 1984; Cocilovo and Rothhammer, 1996a, 1996b, 1999). A review of this model and explanation of the theory and methods were presented by Cocilovo and Varela (1999).

Subsequently, significant spatial and temporal differences between the coastal groups and those of the Azapa Valley were confirmed through analysis of a more complete database (245 individuals and 18 craniometric variables). The information was evaluated by means of multivariate statistical analysis (discriminant analysis, Mahalanobis D^2 distance, and cluster analysis). The results show that differences are greater among different periods on the coast than in the valley. This evidence can be explained by the existence of two major settlement events, one during the Archaic period by fishermen–hunter groups and another during the Early Intermediate or Formative period by shepherd–farmer groups. Both groups would have originated from an ancestral Andean population of individuals who were among the first settlers of the region. They would have differentiated gradually when they occupied specific niches suitable for their subsistence, due to the effect of various evolutionary (systematic and random) and cultural factors that continued to operate in the new scenario (Cocilovo et al., 2001a). Subsequently, a close relationship between the central plateau and the San Miguel and Alto Ramírez phases of the Azapa Valley was proposed, based on six craniometric variables (Rothhammer et al., 2002).

Whereas the phenotypic divergence of groups living in Arica has been increasingly demonstrated, other research offered contrary evidence suggesting uniformity of the population. This led to important debate about unity versus diversity of the ancient population of Arica and the Azapa Valley. Indeed, through use of nonmetric characters of the skull and dentition, deviating results were obtained by Sutter (2000) and Sutter and Mertz (2004) in samples from the valleys of Moquegua (Peru) and several sites on the coast and in the Azapa Valley (Chile). These authors found that the calculated distances (Mean Measure of Divergence or MMD) in the Azapa samples were not statistically significant. Thus, they concluded there would be a direct ancestor–descendant relationship between the Archaic period groups of the coast (Morro-1, Morro-5, Morro-6, and Plm-8) and the Formative period groups of the valley (Alto Ramírez: Az-71, Az-14, Az-70, and Az-115) and the coast of Arica (Laicho: Plm-7).

Controversy raised by the cited research about settlement of the Azapa coast and valley based on skeletal remains is most likely due to the use of different data (metric versus nonmetric traits) and samples of different sizes from various sites. The discrepancies prompted a note from Rothhammer et al. (2006) in response to the study of Sutter and Mertz (2004), a new response from Sutter (2006), and finally a complete evaluation of evidence presented by each opponent on the differentiation process that occurred in Arica (Rothhammer and Cocilovo, 2008).

Explanation of the evolution of northern Chilean groups saw significant progress through the application of key concepts of population genetics. Although understanding the evolutionary process in a region is dependent on analysis of chronological

variation, it is also necessary to adequately explain the variable gene frequencies that determine changes in the mean values as well as the variance of quantitative traits. To address this, models with estimations of the genetic divergence between groups or average within-group kinship (Wright's F_{ST}) were applied. This parameter can be calculated using the method proposed by Relethford and Blangero (1990).

A significant study in Arica was based on the theory of repeated measurements (Becker, 1975; Falconer and Mackay, 1996; Lynch and Walsh, 1998). Using bilateral craniometric variables, phenotypic variance was partitioned into genetic and general environmental variance, and into another special environmental variance. The repeatability (r) of a metric trait is the ratio between the genetic variance (plus environmental general variance) and phenotypic variance, and it is considered the upper limit of heritability ($h_m^2 \approx h^2$). It is calculated as the correlation between characters measured on both sides of a symmetrical structure. The special environmental component is obtained by the difference $1 - r$ (Varela and Cocilovo, 1999).

Also for Arica, the F_{ST} value was calculated by using r ($\approx h_m^2$) as an estimator of h^2 . This last parameter is involved in the model of Relethford and Blangero (1990) and Relethford and Harpending (1994). The F_{ST} value allows for deductions with regard to the population structure based on quantitative traits, as well as on evolutionary factors such as genetic drift and migration. Studies demonstrated that 82.5% of the total phenotypic variation is explained by the maximum genetic variance. In the Early Intermediate population of the valley an excess of extraregional gene flow was found. In addition, differentiation between coastal groups of Archaic and Early Intermediate periods was reduced. From the Middle period there is a substantial increase in genetic differences between both areas. These findings indicate that external gene flow was lower on the coast than in the valley, whereby the minimal F_{ST} estimated for the total population (coast and valley) amounted to 0.02, with $F_{ST} = 0.01$ for the coastal population and $F_{ST} = 0.006$ for the valley. The results are discussed by Varela and Cocilovo (2002) according to the ethnohistorical and archaeological evidence of the region, proposing a model explaining the genetic history of the population. Findings of genetic flow associated with low inbreeding in the Early Intermediate period of the valley (Alto Ramírez) indicated an increase of immigrants (Varela and Cocilovo, 2002). This could support the hypothesis of long-range migration across the highlands and tropical forest (Rivera and Rothhammer, 1986; Moraga et al., 2001; Rothhammer and Santoro, 2001; Rothhammer et al., 2002), but it does not discard the incorporation of genetic variability as a result of middle-range migration from other valleys and intermediate basins of northern Chile.

Subsequently, Rothhammer et al. (2009) reaffirmed the relationships between northern Chile, the highlands, and the rainforest by using a broad register of ancient and modern mtDNA from the Azapa Valley, Amazonas, Tiwanaku, Quechua, Aymara, and Atacameños samples. An F_{ST} value of 0.157 ($p = 0.002$) was obtained, which indicated a significant process of genetic divergence beyond the connections and relationships implied by the

discovery of tropical products in a local framework with nonsignificant genetic distances between Amazonia and Azapa Valley group samples.

Another important step allowed for establishment of the nature of early settlement based on divergence of Archaic human groups of the northern Chilean coast: Arica (Morro 1, Morro 1/6, and Morro Uhle) and semiarid north (El Cerrito and Punta Teatinos). The study was conducted using 29 metric (177 nondeformed individuals) and 25 nonmetric traits (288 individuals). Analyses of D^2 distances for the first study and MMD for the second study indicated significant differences among the four groups. This evidence is significant with regard to the process in which an ancient coastal population differentiated itself while migrating southward, causing spatial segregation of four different phenotypes due to evolutionary forces such as migration, drift, and reproductive isolation (Cocilovo et al., 2004). Later, evidence of a north–south coastal Archaic settlement was enhanced with incorporation of the Caleta Huelén-42 sample for analysis of their relationships with the Archaic groups mentioned above. Evaluation of the differences (D^2) showed they were significant among localities. However, distances between Arica and Caleta-Huelén were lower than between the latter group and the semiarid north, confirming the existence of a dispersive process regulated by migration. It is possible that the inhabitants of Caleta Huelén 42 share a proportion of genetic variation derived from an ancestral population, with the migratory contribution of other regions, possibly from intermediate basins (Cocilovo et al., 2005).

A key issue was also the explanation of genetic relationships between Archaic and Formative groups of Arica, both along the coast and in the valley. Materials from the sites Morro-Uhle, Morro 1, and Morro 1/6 (coast Archaic), Playa Miller-7 (coast Formative), and Alto Ramírez (Azapa Valley Formative) were analyzed. The total sample included 181 individuals and 29 metric variables, excluding effects of sex, age, and artificial deformation. The four subsamples showed significant differences. The most divergent group was Alto Ramírez, whereas Morro 1 and Morro1/6 appeared to show the least differentiation. A gradual phenotypic change on the coast was observed, proving the genetic contribution of the Archaic fishermen to the Formative group of Playa Miller-7 and their differentiation from the Alto Ramírez group of the valley. The F_{ST} value of 0.04 reflects the effect of a dispersive process regulated by a large or medium-range migration (Varela et al., 2006), which differs from the biological homogeneity proposed by Sutter (2000) and Sutter and Mertz (2004).

In Pisagua in northern Chile, however, the process was different. The results indicated that for the duration of 48 generations, genetic composition of the population fluctuated through increased local kinship and less interaction with bordering areas. This conclusion is based on analysis of the nonlinear correlation between the D^2 chronological values and the distances between cemeteries explained by a kinship bioassay model (Morton et al., 1971; Morton, 1977; Relethford, 1980). Indeed, phenotypic changes correspond to a population with an effective size of 200 individuals per generation, a migration

rate of 2.2%, and a kinship average of 5.4% (Cocilovo, 1994; Cocilovo et al., 1999a).

In the population of San Pedro de Atacama, chronological differentiation was also studied from a sample of 120 individuals and 32 metric variables of the skull, excluding the effects of sex, age and artificial deformation. Analysis of 11 variables demonstrated significant differences among the chronological phases, covering approximately 70 generations (Cocilovo and Varela, 2002). This study resulted in the proposal of a local evolutionary model (Varela, 1997, Varela and Cocilovo, 2000) together with the studies of Arica (Rothhammer et al., 1982, Cocilovo et al., 2001a), Pisagua (Cocilovo, 1994), Semiarid North, and Central Chile (Cocilovo and Quevedo, 1998). Thus, the reconstruction of local biochronological sequences allowed an advanced knowledge of the settlements in northern Chile and their relationship with other regions of the central-southern Andes.

The results in San Pedro de Atacama encouraged the idea of assessing variability over time in the same community, or ayllu, with a larger sample. In the Quito cemetery, the phenotypic difference between the Formative period (300 BC–AD 400), Tiwanaku period (AD 400–1000), and Regional Development period (AD 1000–1470;) was studied with data obtained from 326 individuals and 37 metric characters; temporal differentiation was evaluated by means of univariate and multivariate statistical analyses. Average estimated kinship (F_{ST}) for this ayllu was 0.046 ($h^2 = 0.55$), and it was higher in women than in men. According to this value, inhabitants of Quito lived in greater isolation than did the Azapa Valley agricultural groups ($F_{ST} = 0.013$). Also in the Middle Horizon period (Tiwanaku), a moderate increase of phenotypic variance was observed caused by a greater gene flow from neighboring regions (Varela and Cocilovo, 2009).

The existence of chronological variation established for this locality, and in particular for the site of Quito (Varela and Cocilovo, 1996; Cocilovo and Varela, 2002; Varela and Cocilovo, 2009), gave rise to a new study testing chronological differentiation with a larger sample of different cemeteries (Varela and Cocilovo, 2011). A group of 622 individuals from seven ayllus dating to the Early Intermediate, Middle Horizon, and Late Intermediate periods was studied. Differences were tested using 37 craniometrical traits excluding effects of sex, age, and artificial deformation. Multivariate analysis of variance, canonical discriminant analysis, and Mahalanobis D^2 distance was applied. Genetic divergence was measured using F_{ST} statistics according to Relethford and Blangero (1990) for the total population and for each period. Significant differences among samples, including spatial and temporal variation, were verified. The average F_{ST} of 0.05 showed a process of genetic divergence that explains the differences between the mean values of all groups with respect to the regional average. Statistics F_{ST} for the Early Intermediate period of 0.11, for the Middle Horizon period of 0.005, and the Late Intermediate period of 0.03, revealed an interesting variation of the differentiation process in time (Varela and Cocilovo, 2011), which had already been noted in the ayllu of Quito (Varela and Cocilovo, 2009).

The F_{ST} values per cultural period provide a higher resolution and a more appropriate explanation of settlement in the Atacama oasis. During the Early period, an F_{ST} of 11.4% is explained by a strong divergence among groups (Quitor 8, Larrache, and Toco-nao) due to the small population size and a greater reproductive isolation. During the Middle period, the value of 5 % indicates a considerable growth of the local population and an increased gene flow (medium- and long-range), and these factors contribute to greater homogeneity in the physical aspects of individuals. In the Late period, the situation is partially reversed by the 3% divergence between Quitor (Q1 and Q9) and Yaye, indicating a reduced population and a higher isolation of groups. Temporal and spatial variation was produced by factors that influenced the bio-social history of the population. These factors include the origin of the founding groups, effective size, mating patterns, kinship, genetic drift, and migration. Also, economic relations and the exchange of products through medium- and long-range networks (along the coast, valleys, and highlands, including more distant regions such as Bolivia and northwestern Argentina) played an important role (Varela and Cocilovo, 2011).

NORTHWEST ARGENTINA

Northwestern Argentina includes several geographical subregions which were inhabited beginning approximately 8000 BC (Fernández Distel, 1975; Aschero, 1984, 2011) by hunter-gatherers, who were carriers of lanceolate and triangular points. In layer 6 of the Pintoscayoc-1 site located north of Quebrada de Humahuaca, periods dating between 10,889 and 8176 BC were delineated. In the Inca Cueva and the caves of Huachichocana located along the lateral ravines of Quebrada de Humahuaca, the dates range between 6720 and 7670 BC (Ruiz, 1995–1996; Aschero, 2011). At around 2500 BC there is evidence of specialized gathering and handling of plant species in Cave III in Huachichocana. The presence of pottery, monticular structures, circular housing distributed among crops fields, and other clusters in villages characterizes the Early Formative period. In Jujuy, dates between 2042 and 1505 BC are obtained for El Alero Unquillar, 1500 BC for Abra de los Morteros, 1008 BC for Cueva de Cristóbal, between 1300 and 230 BC for Alero de Tomayoc, 950 BC for Inca Cueva (Alero I), and 440 BC for Estancia Grande. This period is present in Tafi (Tucumán), in the Sajuil valley and Alamito sites (Catamarca), in Campo Colorado (Valle Calchaquí, Salta), in the sites of La Cuevas and Cerro El Dique, and in Quebrada del Toro dating to between 600 and 400 BC (Ruiz, 1995–1996; Yacobaccio et al., 2000). The cultures of Candelaria (Las Pirguas, east and south of Salta and northern Tucuman), Ciénaga (Valle Calchaquí, Catamarca, La Rioja, and northern San Juan), and Condorhuasi (Catamarca and northern La Rioja) characterize the Formative period.

During the Middle Horizon period (AD 650–1000), the Aguada culture was developed in the valley of Catamarca, La Rioja, and north of San Juan. The relationship between this culture and the Tiwanaku culture as well as the possible Tiwanaku

influence on the Isla culture of Jujuy is highlighted. Isla pottery with Tiwanaku elements was found in San Pedro de Atacama, northern Chile (Ruiz, 1995–1996).

The beginning of the Late Intermediate period (AD 1100) is related to decline of the Tiwanaku in the south-central Andes, disappearance of the Aguada culture, robust local entities, population growth, and differentiation of ethnic groups with territorial autonomy. The presence of pukará would be associated with a new stressful situation and the organized exchange of routes. During this period the cultures of Santa Maria, Humahuaca, and “Complex Puna” in the Valliserrana, Humahuaca, and Puna subregions were identified, respectively. The end of the Late Intermediate period occurs around AD 1470 and is associated with arrival of the Incas in the region (González and Pérez, 1987; Ruiz, 1995–1996).

PUNA DE JUJUY

This subregion is a high plateau with elevations that range between approximately 3,500 and 4,500 m AMSL in the north and west of Jujuy province (Figure 1). It is characterized by large depressions and sedimentary basins of endorheic drainage and surrounded by hills and salt flats or significant lagoons, such as in Pozuelos, Vilama, and Guayatayoc.

Analysis of sexual dimorphism with 31 craniometrical variables indicated sex differentiation. Only nose width and orbit height did not differ between men and women. The latter feature is shared with other populations of the south-central Andean area, such as San Pedro de Atacama (Varela, 1997), Pisagua (Cocilovo, 1994), Morro de Arica (Cocilovo et al., 1982), Las Pirguas (Baffi and Cocilovo, 1989), and Cochabamba (Cocilovo et al., 2013), and it may be related to similar growth in the regions of olfactory and visual systems in both sexes. Correct assignment was 86% for observations of either sex by discriminant function.

Analysis of age variation of the population in this subregion showed that metric variables vary significantly among age groups (infant, juvenile, adult, mature, senile). Age classes that contributed most to this variation were infant and juvenile, which differed from postreproductive ages. Furthermore, the characters that involved the alveolus, such as maxillo-alveolar width, showed a decrease in average values in mature and senile ages as a result of tooth loss and alveolar resorption. These results are consistent with other studies in prehistoric populations (Varela et al., 1990a; Cocilovo et al., 1994; Varela et al., 1995; Varela, 1997; Quevedo, 1998).

The most frequent artificial deformation in this subregion was found to be the oblique tabular (68.7%), and less common were the erect tabular (4.5%), oblique circular (1.9%), and erect circular (0.2%). Furthermore, nondeformed skulls were represented by 24.6%. The effect of artificial cranial deformation occurred with greater magnitude in the vault and base and with less influence with regard to the facial region (Cocilovo and Varela, 2010).

In a preliminary study, Mendonça et al. (1990) observed no differences in skull morphology among different sites in the Puna de Jujuy. In an exhaustive study by Fuchs (2014), biological

relationships between groups of this subregion were evaluated by increasing the sample size and the amount of skull metric traits and then using discriminant and cluster analysis. The results showed phenotypic differences between Agua Caliente and Casabindo, between Agua Caliente and Doncellas, and between Agua Caliente and Queta; among Casabindo, Doncellas, and Queta; and between Sorcuayo and Queta. The other comparisons did not reveal any differences between sites; in particular, Río Negro was morphologically similar to the other five samples studied.

Queta and Sorcuayo represented the most isolated groups; in these, the phenotypic variance was lower than expected for a balanced model between genetic drift and gene flow, indicating less migration than expected. In Agua Caliente, a higher variance than expected was observed, indicating a higher than expected average gene flow. Genetic divergence (F_{ST}) represents 2.5% of the total genetic variation, using quantitative characters and an average heritability of 0.55 (Fuchs, 2014). Similar estimates were obtained for San Pedro de Atacama and Azapa Valley in northern Chile (Varela and Cocilovo, 2002, 2011).

A bioarchaeological study of groups that inhabited the Puna de Jujuy has been developed by Fuchs (2014) with samples from different archaeological sites. The combined collections in the Juan B. Ambrosetti Ethnographic Museum (University of Buenos Aires) and La Plata Museum (National University of La Plata) contain 371 skulls. With radiocarbon dates determined from teeth, the combined sample was identified as from the Late Intermediate period (AD 1029–1497; Fuchs and Varela, 2013), which coincided with results of other archaeological studies (Alfaro and Suetta, 1970; Alfaro, 1988; Ruiz and Albeck, 1997; Albeck and Zarbulín, 2008).

As demonstrated by sexual dimorphism, low values of developmental instability evaluated in the bilateral characters of the skull, and low frequency of diseases of the metabolic and masticatory system (Miranda de Zela and Fuchs, 2014), this population was not exposed to extreme environmental conditions that affected normal growth and development of individuals. Furthermore, $\delta^{13}C$ and $\delta^{15}N$ values showed that the inhabitants of Puna de Jujuy maintained a mixed diet with an important meat component in the composition (Fuchs, 2014). These latest results were in accordance with those obtained by Perez and Killian Galván (2011) and Killian Galván et al. (2012).

QUEBRADA DE HUMAHUACA

The deep and narrow valley of Quebrada de Humahuaca in the province of Jujuy (Figure 1) is 2000–3500 m AMSL, runs in a north–south direction, and is crossed by the Río Grande; it is approximately 150 km long and is associated with side ravines connecting with the adjacent areas.

According to Nielsen (2001), for each site of the Quebrada de Humahuaca it is possible to establish highly probable ranges of occupation. For El Alfarcito, from the Late Formative (Early Horizon) period to the Middle Horizon period; for La Isla, to the Middle Horizon period; for Juella, to the Late Intermediate

period; for Los Amarillos, Yacoraite, Campo Morado, La Huerta, Pukara de Tilcara, Peñas Blancas, El Volcán, and Angosto Chico, from the Middle Horizon period to the Inca (Late Horizon); and for Ciénega Grande, from the Late Intermediate period to the Inca (Late Horizon).

Ranges of occupation for additional sites were determined by several other researchers. El Volcán's range of occupation falls in the period between AD 1168 and 1533 (Cremonte and Garay de Fumigalli, 1997). Occupation ranges for other sites are as follows: Pucara de Tilcara, AD 1100–1530 (Zaburlín, 2009); Los Amarillos, AD 1000–1600 (Nielsen, 1996; Rivolta, 2007); Juella, AD 1284–1442 (Nielsen, 1996); and La Huerta, AD 800–1470 (Rivolta, 2007).

In an initial study using characters of the skull, differences between Pukará de Tilcara and the Isla groups were observed by Dillenius (1913). According to artificial deformation, a certain affinity between the Isla groups and groups of the northern region of Humahuaca was suggested, while Pukará de Tilcara is more similar to Valle Calchaquí (Dillenius, 1913).

For better insight into the bioanthropological profile of the Quebrada de Humahuaca population, existing phenotypic variation within and between sites was evaluated (Cocilovo et al., 1999b, 1999c, 2001b) using 416 skulls from the Ambrosetti Ethnographic Museum. The material belongs to several sites (Peñas Blancas, Yacoraite, Campo Morado, Los Amarillos, Angosto Chico, La Huerta, Juella, La Isla, El Alfarcito, Pukara de Tilcara, Ciénega Grande, and El Volcán) associated with the Early, Middle, Late, Inca, and Hispanic cultural periods. The type of artificial cranial deformation is differentially distributed among sites. A predominance of skulls show oblique and erect tabular deformation, whereas the circulars and nondeformed are less frequent (Cocilovo et al., 2001b). Similar results were obtained in a sample of 153 skulls from the Yacoraite, Los Amarillos, and La Huerta sites (Seldes and Botta, 2014). The predominance of oblique tabular deformation in this subregion agrees with findings obtained in the Puna (Cocilovo and Varela, 2010; Fuchs, 2014).

In Quebrada de Humahuaca, a high proportion of skull metric traits vary among the different localities. Distances between groups in multivariate analysis showed a biological heterogeneity greater than was expected for a limited geographic region (Bordach and Cocilovo, 1991; Cocilovo et al., 1999d). In addition, a cluster analysis proposed a first cluster associated with the northern sector of Quebrada de Humahuaca (Peñas Blancas, Yacoraite, Campo Morado, Los Amarillos, Angosto Chico, and La Huerta) and two additional clusters associated with the southern sector (Pukará de Tilcara and Ciénega Grande; Juella and El Volcán). El Alfarcito and La Isla may be the earliest samples of the system in which the tabular erect deformation is predominant. Materials that were excavated in the Til-20 site by Mendonça et al. (1991) show the exclusive use of the tabular erect deformation in earlier times.

The magnitude of phenotypic differentiation observed in ancient inhabitants of Quebrada de Humahuaca represents a microevolutionary process that determined a strong structuring of the local population, with a significant migratory contribution of other differentiated human groups in neighboring regions.

The biological structure generally obtained for this population is in accordance with the settlement systems during the Late Intermediate and Inca (Late Horizon) periods studied by Nielsen (1989). The Los Amarillos site, west of Quebrada de Humahuaca in the Quebrada de Yacoraite, was a complex polynuclear center with an estimated population of 2,000 people. It is located in the central sector and was associated with other sites called mononuclear complexes (400–1000 inhabitants), such as Yacoraite, Campo Morado, La Huerta, and a set of simple settlements, all integrating a Maximum Subsistence Unit. Los Amarillos was an important point for the exchange of products between Puna (via the Quebrada de Yacoraite) and the eastern valleys. Analysis of phenotypic distances effectively established this relationship (Cocilovo et al. 2001b). Furthermore, in Los Amarillos, Yacoraite, Peñas Blancas, Juella, Ciénega Grande, and El Volcán, the oblique tabular deformation is more frequent than the erect tabular deformation (Cocilovo et al., 1999b).

The Pucara de Tilcara was another complex polynuclear site located south of Quebrada representing an enclave of exchange with Puna and the eastern valleys. Ciénega Grande and El Volcán, located further south, constituted key connection points with Puna and with the Yunga and the eastern valleys, respectively (Nielsen, 1989). The phenotypic cluster analysis (Cocilovo et al., 2001b) demonstrated the integration of Ciénega Grande and El Volcán with components the origin of different from the previous system controlled by Los Amarillos. The analysis of the quality of life and health status of the inhabitants of the Quebrada de Humahuaca was initially studied using 30 skeletons from the Late Intermediate period of the Pukará Tilcara. The observation of traits associated with nutritional, functional, infectious, and traumatic pathologies demonstrated that this population would represent a functionally adapted community (Mendonça et al., 1993).

In a first approximate finding, using individuals of the sites of the Late Formative (500–900 A.D.) (TIL20 and Flores-1), Regional Development I periods (900–1250 A.D.) (Muyuna), and the Regional Development II period (1250–1430 A.D.) (Los Amarillos and Hornillos), there is no evidence of nutritional stress. Additionally, significant evidence of increased occupational stress was found in the Regional Development period, as well as a high presence of caries, due to a diet rich in carbohydrates and sugars, and significant incidence of tooth wear (Seldes, 2006). Later, a high frequency of interpersonal violence related with trauma was determined at three Regional Development sites (Los Amarillos, La Huerta, and Yacoraite) of the Quebrada de Humahuaca (Seldes and Botta, 2014). In a larger Late Intermediate sample of the Valle Calchaquí and the Quebrada de Humahuaca (ca. AD 1000–1432), 14% of individuals showed traumatic injuries, with a higher frequency found in individuals from Quebrada de Humahuaca (Gheggi and Seldes, 2012).

VALLE CALCHAQUÍ

The Valliserrana region includes a group of valleys and ravines at 1,500–3,000 m AMSL in the provinces of Catamarca,

La Rioja, northern San Juan, western Tucuman, and western Salta, including the Valle Calchaquí (Gonzalez, 1977; Baffi and Cocilovo, 1989–1990).

The first research specifically dedicated to study of ancient inhabitants of the Valle Calchaquí was performed by Ten Kate (1896), and subsequent studies followed by Thibon (1907), Dillenius (1910), and Marelli (1915), among others. Constanzó (1942) analyzed bone material and classified it as *ándidos* following the criteria established by Imbelloni (1938), using racial morphological characters. This genetic homogeneity *ándida* was questioned by Cocilovo (1981).

The site of Santa Rosa de Tastil is located in northwest Salta at more than 3,000 m AMSL (Cigliano, 1973). Marcellino and Ringuet (1973) performed morphological descriptions of the individuals collected from this site. The sample of 39 skulls included 19 individuals with oblique tabular deformation and 9 with erect tabular deformation; in other individuals the type of deformation could not be established due to the poor state of conservation. These researchers also carried out an osteological analysis of the postcranial skeletons.

Cocilovo and Baffi (1985) examined local phenotypic variability at La Paya, a locality of Valle Calchaquí, as well as relationships with neighboring populations, by studying a sample of 55 skulls from the Ambrosetti Ethnographic Museum and using 41 metric characters. The erect tabular artificial deformation was most common, and a smaller proportion of skulls exhibited oblique tabular deformation, which agreed with findings by Constanzó (1942).

In the Valle Calchaquí population comprising the sites of Fuerte Alto, Payogasta, La Poma, La Paya, Tacuil, Luracatao, and Cachi, 87% of skull metric characters varied between sexes. Variables that did not change with sex are the orbit, nose, and palate areas. A predominance of skulls exhibited erect tabular deformation. The results showed that only 10 traits differed between adult and mature ages. A significant loss of teeth and alveolar resorption was observed, likely the result of diet and prevalent infectious diseases in this population (Baffi, 1992).

To assess phenotypic unity or diversity in various groups of the Valliserrana region using quantitative traits of the skull, an estimate was made of the biological distances between groups located in Valle Calchaquí and elsewhere in the same region (e.g., Santa Rosa de Tastil and Belén; Baffi and Cocilovo, 1989–1990). The results showed a biological unity in the Valle Calchaquí during the Late period, coinciding with the cultural homogeneity proposed by archeological research. There is also a morphological differentiation between groups from Belén and Santa Rosa de Tastil and between these two sites and Valle Calchaquí (Cocilovo and Baffi, 1985; Baffi and Cocilovo, 1989–1990).

PAMPA GRANDE (LAS PIRGUAS)

Las Pirguas is located at the boundary between Valliserrana and the *selvas occidentales* (western forests) regions. It is situated in the area known as Pampa Grande, Guachipas department, Salta province. The first archaeological and

bioanthropological studies in this area are from Ambrosetti (1906), Aparicio (1941), and Constanzó (1941). Thanks to later excavations carried out by Rex González from 1969 to 1971 in the mountain caves of Las Pirguas, an exceptional archaeological collection was obtained and is now housed at La Plata Museum. The Las Pirguas site corresponds to the Candelaria culture of the Early period in northwestern Argentina (Baffi and Cocilovo, 1989) and dates back to BP 1310 ± 40 (Carnese et al., 2010). Two new dates, BP 1327 ± 44 and BP 1501 ± 41, were determined for materials from Las Pirguas (University of Arizona's Accelerator Mass Spectrometry Laboratory, 2012/07/11, personal communication).

The Las Pirguas sample is composed of 80 individuals (55 adults and 25 subadults); 45 present erect tabular deformation, 2 present oblique tabular deformation, 29 are nondeformed, and 4 are undetermined. Analysis of 31 nonmetric traits revealed that none of the variables changed between sexes, one varied with artificial deformation, and three varied with age (Baffi et al., 1996).

Studies using 38 metric variables of the skull showed little sexual dimorphism—only 17 of them varied between sexes. For this group there is evidence of a low life expectancy at birth (22 years). Numerous pathologic features (porotic hyperostosis, cribra orbitalia, sinking of the maxillary bone) and a high proportion of indicators of aggression (rupture and healing of nasal bones, blows to parietal and other sectors of the vault) were observed (Baffi and Cocilovo, 1989; Baffi et al., 1996). Additionally, higher values of developmental instability were estimated for this group as compared with those calculated for other ancient populations in northern Chile (Varela and Cocilovo, 1999; Varela and Cocilovo, 2002; Cocilovo et al., 2006; Varela et al., 2006) and Puna de Jujuy (Fuchs et al. 2014). This was evaluated from the proportion of the special environmental component (26%) using bilateral metric variables of the skull. This information suggests that the inhabitants of Las Pirguas lived in an environment of great social tension, with prolonged and severe nutritional stress, and in conditions that influenced the complex processes that regulated a stable development (Baffi and Cocilovo, 1989; Baffi, 1992; Baffi et al., 1996; Medeot et al., 2008).

EVOLUTION OF THE POPULATION, LOCAL DIFFERENTIATION, AND REGIONAL RELATIONSHIPS

In a comparative analysis of samples from a wide region covering southern Peru to Tierra del Fuego, the formation of three groups was demonstrated by using metric traits of the splanchnocranium as well as discriminant and cluster analyses: one Andean group was integrated into the samples of Peru, Bolivia, northern Chile, and northwestern Argentina; a second group was of Fluvial Litoral and Patagonia; and a third insular group in Tierra del Fuego. The Andean group consists of two clusters—the first formed by Peru, Bolivia, and Quebrada de Humahuaca, and the second formed by Valle Calchaquí, Santa Rosa de Tastil,

and San Pedro de Atacama (northern Chile). Thus, this model represents the first hypothesis about spatial structure and kinship relationships in the studied prehistoric groups (Cocilovo, 1981). Subsequently, settlement of northwestern and northern Chile was investigated through the study of biological relationships among different samples of the south-central and southern Andean area (Cocilovo and Di Rienzo, 1984–1985; Rothhammer et al., 1984; Cocilovo and Rothhammer, 1990).

Assuming that the metric and nonmetric traits are selectively neutral with a random distribution of the nongenetic (environmental) effects, we can see that the observed phenotypic variability in the subregions of northwest Argentina is the result of evolutionary factors such as genetic drift and particular mating patterns within subpopulations, moderated by medium and long-range migration.

In a sample of 961 individuals and different statistical analyses, a marked morphological difference was demonstrated among the four subregions of northwest Argentina (Puna de Jujuy, Quebrada de Humahuaca, Valles Calchaquíes (Vallieserrana), and Las Pirguas (Selvas Occidentales)). The Puna is the most representative group of the total population because it is closest to the regional average. The formation of two clusters is observed, one associated with the Puna de Jujuy and Quebrada de Humahuaca and the other related to Las Pirguas and Vallieserrana (Varela, et al., 2004a; Paschetta, 2005).

This same pattern of geographic variation among the four subregions was obtained in the analysis of 27 nonmetric traits of the skull in 673 individuals. Furthermore, a detailed analysis of the relationship of each trait was performed according to sexual dimorphism, age, and artificial cranial deformation (González, 2004; Varela et al., 2004b). These results are consistent with previous findings (Cocilovo, 1981; Rothhammer, et al., 1984; Cocilovo and Rothhammer, 1990). There were differences between the Valle Calchaquí (Vallieserrana) and the groups of Quebrada de Humahuaca (La Isla and Pukará de Tilcara). The relationship between Puna and Quebrada de Humahuaca and a greater differentiation for Vallieserrana had been observed by Varela et al. (1999) and Cocilovo et al. (2001b). On the basis of Relethford and Blangero's (1990) model for quantitative traits, a high phenotypic divergence ($F_{ST} = 0.14$) was found between the four subregions of northwest Argentina (Varela et al., 2008).

According to the results obtained, the ancient population that inhabited the Argentine northwest would have originated from the same ancestral population of Andean origin, with subdivision into smaller groups that settled in different environments (Varela et al., 1999). Over the course of time and due to influence from biological and cultural evolutionary factors, the subpopulations were differentiated until they obtained the configuration that is observed in the Late period. This explanation does not exclude their possible participation in the genetic composition of groups coming from other neighboring regions such as northern Chile (medium-range migration) or from more distant regions such as the Bolivian highlands and the tropical forests (long-range migration).

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