

Coastal, Valley, and Oasis Interaction: Impact on the Evolution of Ancient Populations in the South Central Andes

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ABSTRACT The existing biocultural links are analyzed among ancient inhabitants of the Cochabamba valleys (Bolivia) from the Formative and Tiwanaku periods, coastal and inland Azapa region (Chile) from the Late Archaic to the Late periods, and the Atacama Desert oases (Chile) from the Formative period to the time of European contact. Craniometric information obtained from a sample of 565 individuals from different sites of the studied regions was evaluated using methods derived from quantitative genetics and multivariate statistical analysis techniques. It is shown that during the Formative and Tiwanaku periods inhabitants of the Cochabamba valleys maintained contact with the population of northern Chile. This contact was more fluid with the people from the interior valley of Azapa than it

was with the settlers of San Pedro de Atacama (SPA). An important biological affinity in the Late Period between the inhabitants of the Azapa valley and the late SPA groups is also examined. The Late-Inca Catarpe SPA sample shows a broad genetic variability shared with the majority of the groups studied. The results reaffirm the differences between the coastal and interior Azapa valley groups and strengthen the hypothesis of two pathways to populating the south central Andean area. The divergence observed among subpopulations can be explained by the spatiotemporal dispersion between them, genetic drift dispersion compensated by the action of gene flow, and cultural norms that regulate within group mating. *Am J Phys Anthropol* 155:591–599, 2014. © 2014 Wiley Periodicals, Inc.

To understand the settlement and the evolution of the human groups who settled in the south central Andean area, it is necessary to evaluate the dispersion, interaction, and adaptation of the populations to the different spaces they explored and conquered. In northern Chile, distinct environments (coastal, valleys, foothills, and highlands) can be differentiated from the Pacific shore land inwards; areas that promoted the settlement and survival of human groups from as early as 10,000 BP (Núñez and Santoro, 2011) until the period of European contact. The valleys during prehistoric times were used as paths connecting the Pacific coast, the mountains, and the altiplano. In addition, the northern tip of Chile is related to other regions of the Andean region south central and northwest Argentina, the southern coast of Peru, the valleys of eastern Bolivia, and the Peruvian-Bolivian altiplano, the latter connected on the east with the Amazon basin.

The coast of Arica and the Azapa Valley in northern Chile were inhabited by fishing-gathering groups from 10,000 BP in the Archaic period which gradually transitioned into agriculture, beginning around 1,000 BC in the Formative period. For some authors, the changes in the latter period were accompanied by the entry of highland groups (Rivera, 1975, 1991). Others have emphasized the decisive participation of local archaic groups in the Archaic–Formative transition (Núñez and Santoro, 2011). Nevertheless, one position does not exclude the other, i.e., the formative population may be the result of a local genetic contribution and migration of individuals from another region (Varela et al., 2006).

The circumpuna region close to the San Pedro de Atacama oases would have been occupied by hunter-gatherers as early as 10,000 BP, but it was the late archaic groups, around 1,300 BC that established the first Formative Period societies in San Pedro de Atacama (Agüero, 2005; Núñez, 2005; Agüero and Uribe, 2011; Núñez and Santoro, 2011). Evidence has been found of a connection during this period between San Pedro de Atacama and the Bolivian Altiplano (Pimentel, 2008).

In the extreme north of Chile, the transition from the late Formative Period to the early Middle Period (500–1,290 AD) is characterized by local developments, and

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the arrival of groups from around the highland Lake Titicaca region (Berenguer and Dauelsberg, 1989; Rivera, 1991) and peripheral regions such as Moquegua and Cochabamba (Uribe and Agüero, 2001). This transition time is also marked by the influence in the region of the Tiwanaku culture, an increase in population and an increase of the interactions between different localities of northern Chile, northwestern Argentina, and southern Peru and Bolivia. However, when Tiwanaku's hegemony declines a period of the development of regional cultures emerge: Late Intermediate period or Regional Development (1,100–1,400 AD), that eventually culminates with the arrival of the Inca empire (Schiapacasse et al., 1989; Rivera, 1991).

Although the region of the eastern valleys of Cochabamba, Bolivia, was populated by hunter-gatherers from as early as 10,000 BC, it was during the Formative (1,500 BC–500 AD) that the first sedentary groups who started farming arise and began to produce ceramics. At this time, local cultures developed and interaction networks were established with locations from other valleys, from the altiplano, the tropical lowlands, and the Pacific coast (Pereira et al., 2000; O'Brien, 2003). During the influence of Tiwanaku (500–1,100 AD), the development of local cultures was also important; some pottery styles continued from the Formative and others are representative of the Late Tiwanaku period of Cochabamba. The collapse of Tiwanaku represents a transition toward the Regional Development period characterized by a variety of regional styles at least until the Inca expansion in 1,450 AD (Bennett, 1936; Oakland, 1986; O'Brien, 2003).

Previous research shows that ancient inhabitants of the Cochabamba valleys are more closely related biologically to groups in northwest Argentina and northern Chile than these two groups are related to each other (Varela et al., 2008; Cocilovo et al., 2009). It has also been found that the inhabitants of the Early Intermediate Period from the interior of the Azapa Valley of the extreme north of Chile increased their genetic variability as a result of gene flow with other regions, particularly with Cochabamba's eastern valleys (Varela et al., 2013).

The study of biological interactions between different locations in the south central Andes provides new information about the knowledge of inter-regional exchange networks; like those which permitted llama trade caravans to support the exchange of goods, ideas, and people between the different ecological environments (O'Brien, 2003). For this reason, in this article we propose to evaluate the biological relationships between groups from the Formative and Tiwanaku periods from the eastern Cochabamba valleys, the societies that inhabited the Atacama Desert Oases between 400 BC and 1,450 AD and Azapa (valley and coast) from the Late Archaic (3,500 BC) until the end of the Late Period (1,500 AD) in the far north of Chile. With this work, we hope to assess the magnitude of the interaction between these three regions in time and analyze the importance of evolutionary factors responsible for the observed morphological divergence.

POPULATION INTERACTION ACROSS THE STUDY AREA

As mentioned previously, the initial formative societies of northern Chile had their origins in local fishermen/gatherer groups between 3,500 and 2,400 BP (Núñez

and Santoro, 2011). However, there are archaeological and genetic lines of evidence that corroborate the suggestion that changes which occurred in these populations may be partially explained by migrations that originated from the eastern slope of the Andes or in the tropical lowlands (Rivera, 1975; Rothhammer et al., 2009). In addition, a genetic contribution from Archaic fishermen groups of Chinchorro to the Formative groups of Laucho on the Azapa coast has resulted in a gradual phenotypic change in the latter group over time; yet this does not rule out the possibility of gene flow coming from other regions of the south central Andes (Varela et al., 2004, 2006).

Archaeological data show a presence of the Archaic fishing-gathering tradition at the start of the Formative agricultural village tradition on the coast of Arica (Muñoz, 2011). Furthermore, morphological difference has been demonstrated between the inhabitants of the coast and the inland valley of Azapa. The first represents a more genetically isolated group, whereas those from the valley show greater gene flow and an obvious similarity with the eastern valleys groups of Cochabamba, Bolivia (Varela and Cocilovo, 2002; Varela et al., 2013).

Some archaeologists have interpreted the influence of the Tiwanaku culture (500–1,100 AD) in Azapa as a true productive colony, while San Pedro Atacama has been considered to be a Tiwanaku trading center (Berenguer and Dauelsberg, 1989; Berenguer, 2000). Other researchers say that the relation of these two regions of northern Chile with the center of Tiwanaku was more indirect, through peripheral centers such as Moquegua (southern Peru) and Cochabamba (Bolivia) that present a closer link with the highland center (Uribe and Agüero, 2001).

During the Middle and Late Formative periods (Tiwanaku) in the Azapa Valley two types of ceramics and textiles have been identified, one of highland tradition and the other linked to the western valleys of southern Peru (Uribe, 1995, 1999, 2004; Agüero, 2000). Two types of textiles from the Middle period have also been found in San Pedro Atacama. The first belongs to a Tiwanaku style and the second to an atacameña tradition linked to the Cochabamba-style textiles (Mojocoya and Omereque) of Bolivia (Uribe and Agüero, 2001).

Some studies show a close biological relationship between the core of Tiwanaku and groups from mid-valley Moquegua, Chen Chen (Blom et al., 1998). Whereas others have suggested the relationship of the highland center with the coastal inhabitants of this valley (Lozada et al., 2004) and the eastern valleys of Cochabamba to have been less important (O'Brien, 2003). As of the Late Archaic period, long-distance interactions between different nodes of the south central Andes occurred through a network of relationships in which the llama trade caravan was one of the many ways that ancient peoples had to interact and relate with one another (Núñez and Dillehay, 1979; Nielsen et al., 1999; Pimentel, 2008; Núñez and Nielsen, 2011; among others).

According to biological and archaeological background the following hypotheses are proposed: (1) Cochabamba valley population is more related to the Azapa valley than with San Pedro de Atacama, (2) an increase of gene flow between San Pedro de Atacama and Azapa Valley during the Late period, (3) phenotypic differentiation between the inhabitants of the coast and the valley Azapa.

TABLE 1. Sample description

Region	Group	Site	Date	N
Cochabamba	Formative/Tiwanaku (CO-FT)	Vinto/Quillacollo, Guillen, Cliza, Mojocoya, Pojo Amano, Incallaca, Omereque	0–1,100 AD	56
Azapa Coast	Late Intermediate/Late Coast (AZ-C-LA)	Camarones 8, Chacalluta, Playa Miller 3, 4	1,100–1,500 AD	46
	Formative Coast (AZ-C-FO)	Playa Miller 7	530 BC	47
	Archaic Late Coast (AZ-C-AR)	Morro 1, 1/6; Morro Uhle	3,500–1,700 BC	44
Azapa Valley	Late Intermediate Valley (AZ-V-LA)	AZ 115, 71, 79, 8–82; Llu 12, 13	990–1,145 AD	56
	Formative/Tiwanaku Valley (AZ-V-FT)	AZ 103, 115, 13, 14, 21–22, 3, 70	530 BC–1,270 AD	50
	Sub Total			243
San Pedro de Atacama	Late (SP-CA-LA)	Catarpe	1,470–1,535 AD	10
	Late Intermediate (SP-QU-LA)	Conde Duque; Quito 1, 9	950–1,200 AD	43
	Late Intermediate (SP-YA-LA)	Yaye 1, 2, 3, 4; Yaye Occidental	950–1,200 AD	50
	Tiwanaku (SP-CO-TI)	Coyo Oriental	700–1,000 AD	51
	Tiwanaku (SP-QU-TI)	Conde Duque bajo y norte; Quito 2, 5, 6	300–700 AD	52
	Tiwanaku (SP-SO-TI)	Solcor 3	400–700 AD	20
	Formative (SP-LA-FO)	Larrache	100–400 AD	15
	Formative (SP-QU-FO)	Quito 8	100–400 AD	12
	Formative (SP-TO-FO)	Toconao	300 BC–400 AD	13
		Sub total		
	Total			565

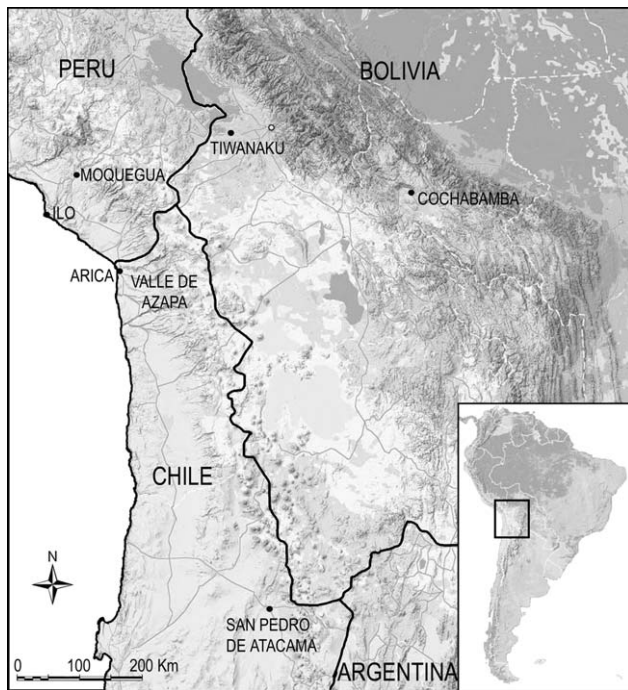


Fig. 1. Map of the south central Andes showing the location of the samples.

MATERIALS AND METHODS

The analysis includes a total of 565 adult skulls (297 males and 268 females), both undeformed (177) and artificially deformed (234 tabular and 154 circular), belonging to several cemeteries from the Atacama oases, Azapa coast and valley, and Cochabamba valleys (Table 1, Fig. 1). The determination of sex and age was performed using the methods suggested by Acsádi and Nemeskéri (1970), Bass (1981), Buikstra and Ubelaker (1994), Molnar (1971), and Lovejoy (1985). The identification of the type of artificial deformation was done using the method proposed by Dembo and Imbelloni (1938).

The material used consists of osteological samples from San Pedro Atacama and the Azapa Valley (coast and valley) in northern Chile and the eastern valleys of Cochabamba (Table 1, Fig 1), respectively curated in two Chilean museums: the RP Gustavo Le Paige Archaeological Museum in San Pedro de Atacama and the Archaeological Museum in San Miguel de Azapa Arica, and one in Cochabamba, Bolivia: the Archaeological Museum. The samples belonging to San Pedro de Atacama originate from different ayllu sites of Quito, Catarpe, Yaye, Larrache, Coyo Oriente, Toconao, and Solcor, correspond to the Formative or Early Intermediate, Tiwanaku or Middle, and Intermediate Late–Late periods (Le Paige, 1964, 1972–1973–1973; Berenguer et al., 1986; Bravo and Llagostera, 1986; Llagostera et al., 1988; Berenguer and Dauelsberg, 1989; Tarragó, 1989; Agüero, 2000, 2005; Costa et al., 2008).

The Azapa collection, obtained from sites located on the coast and the interior of the Azapa Valley, is associated with the Late Archaic, Formative or Early Intermediate, Tiwanaku or Middle, and Intermediate Late–Late periods (Focacci, 1974; Rivera, 1977, 1987, 1991; Allison et al., 1984; Hidalgo and Focacci, 1986; Focacci and Chacon, 1989; Standen, 1991; Espoueyes et al., 1995).

The samples from Cochabamba’s eastern valleys come from several regional archaeological sites from the Formative and Tiwanaku periods (Ibarra Grasso, 1965, 1967a,b; O’Brien, 2003).

For the present study, the following cranial metric characteristics were used: maximum cranial length, maximum cranial breadth, basion-bregma height, upper facial breadth, upper facial height, bizygomatic breadth, orbit height, basion-prosthion length, cranial base length, and nasal breadth. In order to work exclusively with the spatial and temporal variability among the groups analyzed, variation produced by sexual dimorphism and artificial deformation was eliminated using a linear regression model (Seber, 1984). That is, we work with the residuals of the regression between the dependent variable (phenotypic character) and independent variables (sexual dimorphism and artificial deformation). The difference between the observed value of the dependent variable and the predicted value is called the

TABLE 2. Mahalanobis distances (upper hemimatrix) and probabilities (lower hemi-matrix) between groups

	CO-TF	AZ-C-AR	AZ-C-FO	AZ-C-LA	AZ-V-FT	AZ-V-LA	SP-CA-LA	SP-QU-LA	SP-QU-LA	SP-QU-TI	SP-QU-FO	SP-YA-LA	SP-LA-LA	SP-CO-TI	SP-SO-TI	SP-TO-FO
CO-TF																
AZ-C-AR	0.000															
AZ-C-FO	0.000	0.002														
AZ-C-LA	0.000	0.077	0.000													
AZ-V-FT	0.089	0.001	0.000	0.000												
AZ-V-LA	0.002	0.000	0.000	0.000	0.000											
SP-CA-LA	0.350	0.051	0.001	0.104	0.193	0.403										
SP-QU-LA	0.000	0.000	0.000	0.000	0.000	0.002	0.826									
SP-QU-TI	0.000	0.000	0.000	0.000	0.000	0.000	0.490	0.000								
SP-QU-FO	0.002	0.190	0.001	0.026	0.032	0.000	0.126	0.000	0.004							
SP-YA-LA	0.000	0.000	0.000	0.000	0.000	0.000	0.683	0.001	0.000	0.000						
SP-LA-FO	0.014	0.049	0.000	0.019	0.001	0.001	0.308	0.000	0.953	0.105	0.128					
SP-CO-TI	0.000	0.000	0.000	0.000	0.000	0.000	0.265	0.000	0.174	0.000	0.001	0.435				
SP-SO-TI	0.001	0.000	0.000	0.001	0.000	0.000	0.199	0.000	0.897	0.015	0.005	0.978	0.640			
SP-TO-FO	0.000	0.000	0.000	0.002	0.000	0.000	0.119	0.000	0.027	0.076	0.010	0.260	0.032	0.348		
CO-TF																
AZ-C-AR	1.420															
AZ-C-FO	2.178	1.285														
AZ-C-LA	1.334	0.770	1.853													
AZ-V-FT	0.635	1.358	1.944	1.840												
AZ-V-LA	1.039	2.238	4.179	2.197	2.045											
SP-CA-LA	1.333	2.295	3.685	1.976	1.666	1.253										
SP-QU-LA	1.630	3.257	4.076	3.471	2.228	1.162	0.734									
SP-QU-TI	1.443	1.949	3.908	1.817	1.860	2.115	1.146	2.054								
SP-QU-FO	2.950	1.479	3.400	2.205	2.091	4.332	2.846	5.304	2.710							
SP-YA-LA	1.930	2.211	4.041	2.192	3.104	1.817	1.983	1.359	3.695	0.000						
SP-LA-LA	1.933	1.686	4.127	1.933	2.596	2.627	3.046	3.336	2.431	1.340	0.128					
SP-CO-TI	1.422	2.408	3.208	1.907	2.269	2.773	1.502	2.106	3.717	1.208	0.885	0.371				
SP-SO-TI	2.037	2.525	4.330	2.176	2.909	3.247	2.062	3.371	3.017	1.835	0.371	0.558				
SP-TO-FO	3.866	3.833	5.683	2.853	4.665	5.652	2.785	5.282	2.007	2.779	2.329	1.816	1.953			

residual. The independent variables are qualitative or attributes; artificial deformation has five categories (1 = Tabular Erect, 2 = Tabular Oblique, 3 = Annular Erect, 4 = Annular Oblique, 7 = Not Deformed) and sexual dimorphism two (1 = Male, 2 = Female).

Since the Tiwanaku samples from Coyo Oriental (SP-CO-TI) and Quito (SP-QU-TI) of San Pedro Atacama were of a larger size compared to the other groups, smaller subsamples were taken at random. This was done because we wanted the sample sizes to be roughly similar, to ensure more balanced results in the statistical analysis.

To assess the phenotypic relationships between the different groups that inhabited the Atacama oasis, the coast and the valley of Azapa and the eastern valleys of Cochabamba, Mahalanobis (D^2) multivariate biological distances were estimated, and from them a dendrogram was produced using the Neighbor-Joining method (Saitou and Nei, 1987).

The phenotypic distance matrix was correlated with geographic and chronological distances matrices by partial Mantel test (Smouse et al., 1986). This method allows to evaluate how much of the morphological differences between groups can be explained by geographical or temporal distances. Geographic distance was estimated as the linear distance between sites, the temporal distance was calculated as the difference in years between the maximum values of chronologic intervals of each sample (see Table 1).

The genetic divergence between the populations was analyzed by applying the model developed by Relethford and Blangero (1990) for quantitative characteristics that strikes a balance between genetic drift and migration [$E(V_{P_i}) = V_{P_W} (1 - r_{ii}) / (1 - F_{ST})$]. This model expresses that the expected mean phenotypic variance of the population i ($E(V_{P_i})$) is a function of the pooled average within-group phenotypic variance (V_{P_W}), of the genetic distance of population i to the centroid (r_{ii}), and of the average genetic distance to the centroid (F_{ST}), which is estimated as the mean for the r_{ii} for all populations. A heritability (h^2) of 0.55 was used since it is the value most often used in the specific literature and thus allows comparisons with results reported in other studies.

According to this model if a group receives greater gene flow than average, it will display a greater-than-expected variance, and if it receives gene flow less than average, it will display a less-than-expected variance.

RESULTS

The upper hemimatrix of Table 2 displays the between-group distances and the lower hemimatrix shows the probability values. The majority of the distances are statistically significant. However, there was no statistically significant differences between the following groups pairs: Cochabamba (CO-FT) and the Azapa Valley Formative/Tiwanaku group (AZ-V-FT); San Pedro Catarpe Late group (SP-CA-LA) in regards to all of the groups except the Archaic and Formative samples from the Azapa coast (AZ-C-AR, AZ-C-FO); and the Late Archaic from the Azapa coast (AZ-C-AR) and Formative Quito from San Pedro Atacama (SP-QU-FO).

Within San Pedro Atacama (Table 2), there is no differences statistically significant between Catarpe (SP-CA-LA) and the rest of the samples; between Quito Tiwanaku (SP-QU-TI) and Coyo Tiwanaku (SP-CO-TI), Solcor Tiwanaku (SP-SO-TI) and Larrache Formative

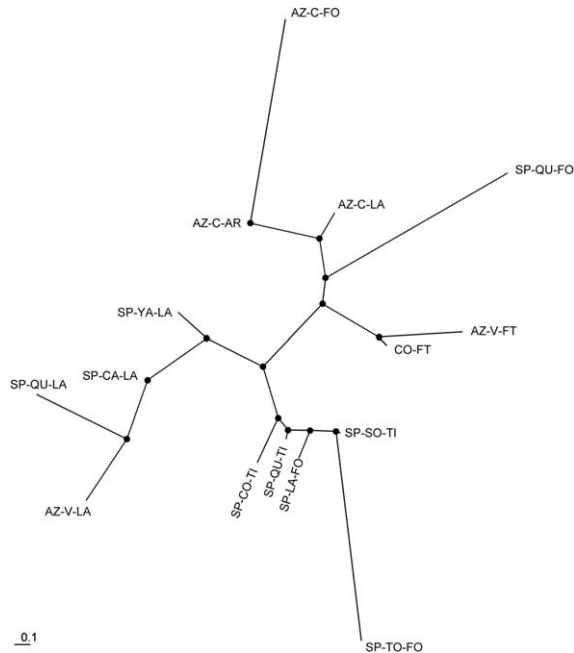


Fig. 2. Neighbor-joining tree obtained from a pair-wise Mahalanobis distance.

(SP-LA-FO); between Quitor Formative (SP-QU-FO) and Larrache and Toconao Formative (SP-LA-FO and SP-TO-FO); between Larrache Formative (SP-LA-FO) and Toconao Formative (SP-TO-FO), Solcor Tiwanaku (SP-SO-TI) and Coyo Tiwanaku (SP-CO-TI); between these last two groups, and between Solcor Tiwanaku and Toconao Formative (SP-SO-TI and SP-TO-FO). Within the Azapa samples it was not possible to demonstrate differences between the coastal Archaic (AZ-C-AR) and the coastal Late (AZ-C-LA).

The dendrogram (Fig. 2) clearly shows a conglomerate formed by San Pedro Atacama groups, which comprises two subgroups, one consisting of samples from the Formative and Tiwanaku (SP-CO-TI, SP-QU-TI, SP-LA-FO, SP-SO-TI, SP-TO-FO) and the other subgroup consists of groups from the Late Period (SP-YA-LA, SP-CA-LA, SP-QU-LA). A clustering between samples from the Late Archaic, Formative and Late groups from the Azapa coast (AZ-C-AR, AZ-C-FO, AZ-C-LA) is also visible.

It is interesting to highlight the following three associations (Fig. 2): (1) Formative Quitor San Pedro Atacama (SP-QU-FO) with samples from the Azapa coast (AZ-C-AR, AZ-C-FO, AZ-C-LA), (2) Formative-Tiwanaku of Cochabamba (CO-FT) with the Azapa valley sample from the same periods (AZ-V-FT), and (3) the late groups from the Atacama Oases (SP-YA-LA, SP-CA-LA, SP-QU-LA) with the Late sample from the Azapa valley (AZ-V-LA).

The partial Mantel test results indicate that there is a significant correlation of 0.24 ($P = 0.034$) between morphological and geographical distances while controlling effect for chronological distances. In addition, this test shows that the correlation between phenotypic and chronological distances is not significantly different from zero ($r = 0.009$; $P = 0.354$), independently from geographical distances.

Table 3 and Figure 3 show the results achieved from the application of the equilibrium model between genetic

TABLE 3. Variance (observed, expected, residual) and distance to the centroid (r_{ii})

Population	r_{ii}	Variance		
		Observed	Expected	Residual ^a
CO-FT	0.041	1.001	0.942	0.058
AZ-C-AR	0.059	0.923	0.925	-0.002
AZ-C-FO	0.163	0.939	0.822	0.117
AZ-C-LA	0.056	0.828	0.927	-0.099
AZ-V-FT	0.075	1.109	0.909	0.200
AZ-V-LA	0.104	0.949	0.881	0.068
SP-CA-LA	0.003	1.075	0.980	0.096
SP-QU-LA	0.117	0.881	0.868	0.013
SP-QU-TI	0.032	0.815	0.951	-0.137
SP-QU-FO	0.114	0.789	0.870	-0.081
SP-YA-LA	0.062	0.814	0.922	-0.108
SP-LA-FO	0.024	0.907	0.959	-0.051
SP-CO-TI	0.050	0.878	0.933	-0.055
SP-SO-TI	0.053	1.083	0.931	0.152
SP-TO-FO	0.132	0.685	0.853	-0.169
$F_{ST}=0.07$				

^a Difference between observed and expected variance.

drift and gene flow for quantitative traits. It is noticeable that there are groups that had an observed variance substantially greater than the expected variance (AZ-C-FO, AZ-V-FT, SP-CA-LA, SP-SO-TI), suggesting an excess of gene flow from other regions. In addition, there are groups with an observed variance significantly lower than expected by the model (AZ-C-LA, SP-QU-TI, SP-YA-LA, SP-TO-FO), suggesting a lower gene flow than the expected due to a balance between migration and genetic drift. The average divergence between groups was 7% ($F_{ST} = 0.07$), the group farthest from the average of the total population was the Formative Toconao group (SP-TO-FO) with a $r_{ii} = 0.132$ and group with the least distance was the Late Catarpe sample (SP-CA-LA) with a r_{ii} value of 0.003.

DISCUSSION AND CONCLUSION

While a geographical structuring is seen of the Azapa population on one side and San Pedro Atacama on the other, it is also evident that some spatially distanced groups reveal an important morphological affinity and others that are very close geographically are differentiated biologically. These assertions, under the assumption of selective neutrality, would support the idea that biological differentiation between subpopulations due to isolation through distance can be moderated by the effect of gene flow and certain mating patterns. That is to say, that the genetic differences between populations decrease when the migration rate is high and they increase through the action of genetic drift in small populations and with the establishment of a reproductive system that promotes more frequent mating within groups.

The Mahalanobis distances (Table 2) shown in Figure 2 demonstrate a spatial and temporal organization of the Azapa and San Pedro Atacama groups, establishing the role played by geographical distance, approximately 550 km, and the chronological difference of the human groups that inhabited this region. This is consistent with the archaeological and bioanthropological works that have studied and characterized both regions of northern Chile (Rothhammer et al., 1982; Berenguer and Dauelsberg, 1989; Llagostera, 1989; Muñoz, 1989;

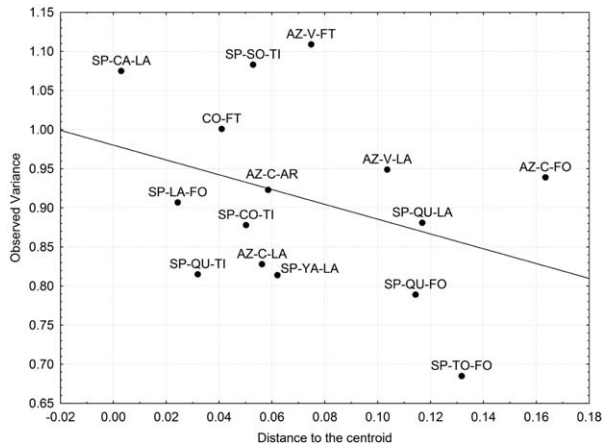


Fig. 3. Plot of observed mean phenotypic variance (V_{Pw}) versus genetic distance from the centroid (r_{ii}) for south central Andes groups.

Núñez, 1989; Schiappacasse et al., 1989; Cocilovo and Rothhammer, 1990; Uribe, 1999; Agüero, 2000; Cocilovo et al., 2001; Uribe and Agüero, 2001; Varela and Cocilovo, 2002, 2011; Agüero and Uribe, 2011, among others).

The genetic proximity between the Cochabamba peoples (CO-FT) and the farmers from Azapa Valley Formative and Tiwanaku periods (AZ-V-FT), previously observed by Varela et al. (2013) indicates a genetic interaction between these two populations, despite the geographical barriers and nearly the 600 km that separates them. These results are consistent with the existence of two traditions of ceramics and textiles in the Late Formative and Tiwanaku in Azapa, one linked to the western valleys of southern Peru and the other related to the eastern valleys of southern Bolivia, Cochabamba: Omerque and Mojocoya (Espoueyes et al., 1995; Uribe, 1995, 1999, 2004; Agüero, 2000). Our results are related to the first archaeological and genetic evidences that postulated a link between the populations of the north coast of Chile, and the Amazon basin (Rivera, 1975; Rivera and Rothhammer, 1986). As well as with some evidence of ancient mtDNA from the Azapa valley populations that show genetic affinity with an amazonic sample, belonging to eighth tribes of four different linguistic groups, distributed over a vast area of the Amazon Region, northern Brazil (Moraga et al., 2001; Rothhammer et al., 2009).

The relation of Cochabamba with San Pedro Atacama was clearly less intense than with the Azapa valley. With the exception of Catarpe which is discussed below, the distance values of less magnitude, yet statistically significant, occurred during the Formative and Tiwanaku periods, in particular with the peoples of Quitor and Coyo Oriental ayllus of the Tiwanaku period (SP-QU-TI, SP-CO-TI). Archaeological studies have also observed two types of textiles in San Pedro Atacama; one with a Tiwanaku tradition and the other with an atacameña tradition associated with the Mojocoya and Omerque textiles (Uribe and Agüero, 2001).

Phenotypic proximity (Fig. 2) between the Late inhabitants of the Azapa valley (AZ-V-LA) and the San Pedro Atacama societies from the same period (SP-YA-LA, SP-CA-LA, SP-QU-LA) suggests a greater biocultural exchange between the two regions of northern Chile dur-

ing the Late period. These results are supported by the archaeological record allowing the deduction that during this period the Desert Tradition groups interacted with populations from the Pacific Coast and other regions (Schiappacasse et al., 1989).

The biological closeness of the Early period group from the Quitor ayllu of San Pedro (SP-QU-FO) in relation to the fishermen/gatherers from the Azapa coast (Fig. 2), in particular the archaic group (AZ-C-AR, see Table 2), is probably expressing common ancestral genetic information of the early groups that occupied the Valles and Oasis of northern Chile. In a similar vein, Cocilovo and Rothhammer (1990) observed biological proximity between the early sample from San Pedro (San Pedro 1-2) and the late archaic samples from Morro de Arica and Punta Teatinos.

It is also important to emphasize the morphological difference between the costal groups with respect to those from the interior of the Azapa Valley, separated by a small distance (about 40 km), suggesting the action of genetic drift and the existence of cultural patterns that contributed to more frequent mating within the coast or within the valley than between the two regions. These results confirm the previously proposed conclusions (Varela and Cocilovo, 2002; Varela et al., 2013) and are linked to the hypothesis of economic and social differences between the costal and valley groups (Rostworowsky 1981, 1986; Schiappacasse and Niemeyer, 1989). Moreover, this evidence is consistent with the existence of two ceramic and textile traditions, one associated with the Pacific Coast and the other with highland and Cochabamba valley groups (Espoueyes et al., 1995; Uribe, 1995, 1999, 2004; Agüero, 2000).

A similar situation was noted in an analysis of mtDNA in prehistoric populations of southern Peru, it has been observed that the groups of the high valleys of the Middle Horizon and Late Intermediate Period differ significantly from the coastal towns of the Early Horizon and the Early Intermediate Period, including when geographic distance is only 50 km (Fehren-Schmitz et al., 2010, 2011). There are also some morphological tests using discrete traits of the skull that show differences between inhabitants of the coast and the middle valley of Moquegua in southern Peru (Lozada et al., 2004). According to the evidence presented above, the observed differences between the populations of the Pacific coast and valleys-highlands seem to represent two distinct genetic components associated with the highland and costal settlement currents proposed by Rothhammer and Dillehay (2009).

The Late Catarpe sample in San Pedro Atacama (SP-CA-LA) does not differ morphologically from the majority of the groups analyzed (Table 2), with the exception of the Late Archaic and Formative groups from the Azapa coast (AZ-C-AR, AZ-C-FO). This indicates that it contains an important genetic variability that it shares with other groups, and therefore has a very low morphological distance from the average of the total population ($r_{ii} = 0.003$, see Table 4). This genetic similarity of the sample from the Catarpe Inca period with the majority of the groups may be a consequence of the significant movement of people that occurred during this empire's influence in the region.

The Mantel test showed an association between phenotypic and geographic distances ($r = 0.24$, $r^2 = 0.06$), indicating that 6% of the existing morphological variability between groups is explained by geographic distance.

This result suggests that there are other factors involved in the explanation of biological variability observed in the population.

The analysis of the results derived from the model of equilibrium between drift and migration provides the ability to understand the structuring of the biological variability observed in the population. The application of this method (Table 3; Fig. 3) allows the identification of groups with a genetic variability that is reduced and isolated from the rest (SP-TO-FO, SP-QU-FO), indicating gene flow lower than expected and a greater effect from genetic drift, and others with significant phenotypic variability (SP-CA-LA, SP-SO-TI, AZ-V-FT), suggesting gene flow greater than expected. The average genetic divergence between populations (F_{ST}) is 7%, comparable to those obtained for northern Chile (6%): San Pedro Atacama 5%, and Azapa 3% and 4% for the Valley and the Coast, respectively. In the case of the Argentine Northwest, the divergence is significantly higher ($F_{ST} = 0.14$) (Varela et al., 2008; Varela and Cocilovo, 2009, 2011).

The caravan model explains the movement of goods, animals and people, and provides a means of connection and complementarity between varied regions of the south central Andes (Pacific Coast, western valleys, mid-basin, altiplano and eastern valleys). Few individuals participated in these caravans and their frequency was more significant during the Middle and Late periods (Núñez and Dillehay, 1979; Nielsen et al., 1999; Pimentel, 2008; Núñez and Nielsen, 2011). This movement of people must have played an important role in gene flow between different regions, which is evident in the genetic proximity observed between the societies that inhabited the valleys of Cochabamba and the Azapa valley, between the Quito Formative San Pedro Atacama ayllu and the Azapa coast, and between the Azapa valley Late period population and Late period groups from the Atacama oases.

In summary, this study provides important results for a better understanding of the evolutionary process of the human groups who inhabited the south central Andean region. It was shown that during the Formative and Tiwanaku periods the inhabitants of the eastern valleys of Cochabamba maintained contact with the populations of northern Chile; although greater with the interior Azapa valley than with the inhabitants of the San Pedro Atacama oasis. An important genetic affinity in the Late period between the inhabitants of the Azapa valley and Late groups from Yaye, Quito and Catarpe de San Pedro Atacama was also found. In addition, the results reinforce the differences between coastal and inland groups of the Azapa Valley. The biological divergence observed among the subpopulations, assuming selective neutrality of the metric skull characters, can be explained by their spatial dispersion, genetic drift, migration, and social rules regulating within group mating. Finally, these statements are consistent with the archaeological and genetic evidences previously discussed, and they strengthen the hypothesis of two paths to the settlement of the south central Andean area.

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LITERATURE CITED

- Acsádi G, Nemeskéri J. 1970. History of human life span and mortality. Budapest: Akadémiai Kiadó.
- Agüero C. 2000. Las tradiciones de Tierras Altas y de Valles Occidentales en la textilera arqueológica del valle de Azapa. *Chungara* 32:217–225.
- Agüero C. 2005. Aproximación al asentamiento humano temprano en los oasis de San Pedro de Atacama. *Estudios Atacameños* 30:29–60.
- Agüero C, Uribe M. 2011. Las sociedades Formativas de San Pedro de Atacama: Asentamiento, cronología y proceso. *Estudios Atacameños* 42:53–78.
- Allison M, Focacci G, Arriaza B, Standen V, Rivera M, Lowenstein J. 1984. Chinchorro. Momias de preparación complicada: métodos de momificación. *Chungara* 13:155–174.
- Bass WM. 1981. Human osteology: a laboratory and field manual of the human skeleton. Springfield: University of Missouri.
- Bennett WC. 1936. Excavations in Bolivia. *Anthropol Pap Am Mus Natl Hist* 35:327–507.
- Berenguer J. 2000. Tiwanaku: Señores del Lago Sagrado. Santiago, Chile: Museo Chileno de Arte Precolombino.
- Berenguer J, Dauelsberg P. 1989. El Norte Grande en la órbita de Tiwanaku (400 a 1.200 d.C.). In: Hidalgo J, Schiappacasse V, Niemeyer H, Aldunate C, Solimano I, editors. *Culturas de Chile. Prehistoria. Desde sus orígenes hasta los albores de la conquista*. Santiago: Editorial Andrés Bello. p 129–180.
- Berenguer J, Deza A, Román A, Llagostera A. 1986. La secuencia de Myriam Tarragó para San Pedro de Atacama: Un test por termoluminiscencia. *Rev Chil Antropol* 5:17–54. Santiago, Chile.
- Bravo L, Llagostera A. 1986. Solcor 3: Un aporte al conocimiento de la Cultura San Pedro. Período 500 al 900 DC. *Chungara* 16–17:323–332.
- Blom DE, Hallgrímsson B, Keng L, Lozada CMC, Buikstra JE. 1998. Tiwanaku “colonization”: Bioarchaeological implications for migration in the Moquegua valley, Peru. *World Arch* 30: 238–261.
- Buikstra JE, Ubelaker D. 1994. Standards for data collection from human skeletal remains. Research series no. 44. Fayetteville: Arkansas Archaeological Survey.
- Cocilovo JA, Rothhammer F. 1990. Paleopopulation biology of the southern Andes: craniofacial chronological and geographical differentiation. *Homo* 41:16–31.
- Cocilovo JA, Varela HH, O'Brien TG. 2009. La divergencia genética entre poblaciones del Área Andina Centro Meridional evaluada mediante rasgos no métricos del cráneo. *Rev Arg Antrop Biol* 11:43–59.
- Cocilovo JA, Varela HH, Espouey O, Standen V. 2001. El proceso microevolutivo de la población nativa antigua de Arica. *Chungara* 33:13–20.
- Costa MA, Llagostera A, Cocilovo JA. 2008. La deformación craneana en la población prehistórica de Coyo Oriente, San Pedro de Atacama. *Estudios Atacameños* 36:29–41.
- Dembo A, Imbelloni J. 1938. Deformaciones intencionales del cuerpo humano. *Humanior*. Sección A3. Buenos Aires: Imprenta Luis L. Gotelli.
- Espouey E, Uribe M, Roman A, Deza A. 1995. Nuevos fechados por termoluminiscencia para la cerámica del Período Medio del Valle de Azapa (Primera parte). In *Actas del XIII Congreso Nacional de Arqueología*. Antofagasta: Sociedad Chilena de Arqueología/Instituto Investigaciones Antropológicas. p 31–54.
- Fehren-Schmitz L, Reindel M, Tomasto Cagigao E, Hummel S, Herrmann B. 2010. Pre-Columbian population dynamics in

- coastal southern Peru: a diachronic investigation of mtDNA patterns in the Palpa region by ancient DNA analysis. *Am J Phys Anthropol* 141:208–221.
- Fehren-Schmitz L, Warnberg O, Reindel M, Seidenberg V, Tomasto-Cagigao E, Isla-Cuadrado J, Hummel S, Herrmann B. 2011. Diachronic investigations of mitochondrial and Y-chromosomal genetic markers in pre-Columbian Andean highlanders from South Peru. *Ann Hum Gen* 75:266–283.
- Focacci G. 1974. Excavaciones en el cementerio Playa Miller 7, Arica. *Chungara* 3:23–74.
- Focacci G, Chacón S. 1989. Excavaciones arqueológicas en los faldeos del Morro de Arica, sitios 1/6 y 2/2. *Chungara* 22:15–62.
- Hidalgo J, Focacci G. 1986. Multietnicidad en Arica. S.XVI. Evidencias etnohistóricas y arqueológicas. *Chungara* 16–17:137–147.
- Ibarra Grasso DE. 1965. Prehistoria de Bolivia. La Paz: Empresa Industrial Grafica.
- Ibarra Grasso DE. 1967a. Argentina Indígena y Prehistoria Americana. Buenos Aires: Tipo Grafico Editorio Americana.
- Ibarra Grasso DE. 1967b. Introducción a la Americanista Crítica y Teorista. Cochabamba: Editorial Universitaria.
- Lovejoy CO. 1985. Dental wear in the Libben population: its functional pattern and role in the determination of adult skeletal age and death. *Am J Phys Anthropol* 68:47–56.
- Llagostera A. 1989. Caza y pesca marítima (9000 a 1000 a.C.). In: Hidalgo J, Schiappacasse V, Niemeyer H, Aldunate C, Solimano I, editors. *Culturas de Chile. Prehistoria. Desde sus orígenes hasta los albores de la conquista*. Santiago: Editorial Andrés Bello. p 57–79.
- Llagostera A, Torres CM, Costa MA. 1988. El complejo psicotrópico en Solcor-3 (San Pedro de Atacama). *Estudios Atacameños* 9:61–98.
- Le Paige G. 1964. El precerámico en la cordillera de atacameña y los cementerios del periodo agroalfarero de San Pedro de Atacama. *Anales de la Universidad del Norte* 3.
- Le Paige G. 1972–1973. Tres cementerios indígenas de San Pedro de Atacama y Toconao. *Actas del VI Congreso de Arqueología Chilena*, Santiago. p 163–187.
- Lozada MC, Blom DE, Hallgrímsson B, Buikstra JE. 2004. Las relaciones biológicas y culturales entre Tiwanaku y Chiribaya en la cuenca del Osmore, extremo sur de Perú. In: Rivera M, Kolata AL, editors. *Tiwanaku: Aproximaciones a sus contextos históricos y sociales*. Santiago: Editorial Universidad Bolivariana. p 179–190.
- Molnar S. 1971. Human tooth wear: tooth function and cultural variability. *Am J Phys Anthropol* 34:175–189.
- Moraga M, Aspillaga E, Santoro MC, Standen GV, Carvallo P, Rothhammer F. 2001. Análisis de ADN mitocondrial en momias del norte de Chile avala hipótesis de origen amazónico de poblaciones andinas. *Rev Chil Hist Nat* 74:719–726.
- Muñoz I. 1989. El periodo Formativo en el Norte Grande (1000 a.C. a 500 d.C.). In: Hidalgo J, Schiappacasse V, Niemeyer H, Aldunate C, Solimano I, editors. *Culturas de Chile. Prehistoria. Desde sus orígenes hasta los albores de la conquista*. Santiago: Editorial Andrés Bello. p 107–128.
- Muñoz I. 2011. Persistencia de la tradición pescadora recolectora en la costa de Arica: Identificación de rasgos culturales y discusión sobre su alcance en el contexto de las poblaciones agrícolas tempranas. *Chungara* 43:469–485.
- Nielsen AE, Vázquez MM, Avalas JC, Angiorama CI. 1999. Prospecciones arqueológicas en la reserva “Eduardo Avaroa” (Sud Lipez, Dpto. Potosí, Bolivia). *Relac Soc Argent Antropol* 24:95–124.
- Núñez L. 1989. Hacia la producción de alimentos y la vida sedentaria (5.000 a.C a 500 d.C.). In: Hidalgo J, Schiappacasse V, Niemeyer H, Aldunate C, Solimano I, editors. *Culturas de Chile. Prehistoria. Desde sus orígenes hasta los albores de la conquista*. Santiago: Editorial Andrés Bello. p 81–105.
- Núñez L. 2005. La naturaleza de la expansión aldeana durante el Formativo Tardío en la cuenca de Atacama. *Chungara* 37: 165–193.
- Núñez L, Dillehay T. 1979. Movilidad Giratoria, Armonía Social y Desarrollo en los Andes Meridionales: Patrones de Tráfico e Interacción Económica. Antofagasta: Universidad Católica del Norte.
- Núñez L, Nielsen AE, editors. 2011. *En ruta. Arqueología, historia y etnografía del tráfico sur andino*. Córdoba, Argentina: Editorial Brujas.
- Núñez L, Santoro CM. 2011. El tránsito arcaico-formativo en la circumpuna y valles occidentales del centro sur andino: hacia los cambios “neolíticos”. *Chungara* 43:487–530.
- Oakland AS. 1986. Tiwanaku textile style from the South Central Andes, Bolivia and North Chile. Unpublished PhD Dissertation, University of Texas at Austin, TX.
- O’Brien TG. 2003. Cranial microvariation in prehistoric south central andean populations: an assessment of morphology in the Cochabamba collection, Bolivia. Ph.D. Dissertation, Binghamton University, State University of New York.
- Pereira DM, Brockington DL, Sanzeteña R. 2000. Arqueología del periodo Formativo en Cochabamba y Bolivia. *Boletín del Instituto de Investigaciones Antropológicas, Museo Arqueológico, serie arqueológica Boliviana N° 13*, Universidad Mayor de San Simón.
- Pimentel G. 2008. Evidencias formativas en una vía interregional entre San Pedro de Atacama y el Altiplano de Lipez. *Estudios Atacameños* 35:7–33.
- Relethford JH, Blangero J. 1990. Detection of differential gene flow patterns of quantitative variation. *Hum Biol* 62:5–25.
- Rivera M. 1975. Una hipótesis sobre los movimientos poblacionales altiplánicos y transaltiplánicos a las costas del norte de Chile. *Chungara* 5:7–31.
- Rivera M. 1977. Prehistoric chronology of northern Chile. Ph.D. Dissertation, University of Wisconsin at Madison.
- Rivera M. 1987. Tres fechados radiométricos de Pampa de Alto Ramirez. Norte de Chile. *Chungara* 18:7–13.
- Rivera M. 1991. The prehistory of northern Chile: a synthesis. *J World Prehist* 5:1–47.
- Rivera M, Rothhammer F. 1986. Evaluación biológica cultural de las poblaciones Chinchorro: nuevos elementos para la hipótesis de contactos transaltiplánicos, cuenca Amazonas-Costa Pacífico. *Chungara* 16/17:295–306.
- Rostworowsky M. 1981. Recursos naturales renovables y pesca. Siglo XVI y XVII. Lima: Instituto de Estudios Peruanos.
- Rostworowsky M. 1986. La region del Colesuyu. *Chungara* 16–17:127–135.
- Rothhammer F, Dillehay TD. 2009. The Late Pleistocene Colonization of South America: An Interdisciplinary Perspective. *Ann Hum Genet* 73:540–549.
- Rothhammer F, Cocilovo JA, Quevedo S, Llop E. 1982. Microevolution in prehistoric Andean populations. I Chronologic craniometric variation. *Am J Phys Anthropol* 58: 391–396.
- Rothhammer F, Santoro C, Poulin E, Moraga M, Standen VG. 2009. Archeological and mtDNA evidence for tropical lowland migrations and cultural change during the Late Archaic/Formativo in northern Chile. *Rev Chil Hist Nat* 82: 543–552.
- Saitou N, Nei M. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4: 406–425.
- Schiappacasse V, Niemeyer H. 1989. Avances y sugerencias para el conocimiento de la prehistoria tardía en la desembocadura del Valle de Camarones. *Chungara* 22:63–84.
- Schiappacasse V, Castro V, Niemeyer H. 1989. Los desarrollos regionales en el Norte Grande (1000 a 1400 d.C.). In: Hidalgo J, Schiappacasse V, Niemeyer H, Aldunate C, Solimano I, editors. *Culturas de Chile. Prehistoria. Desde sus orígenes hasta los albores de la conquista*. Santiago: Editorial Andrés Bello. p 181–220.
- Seber AF. 1984. *Multivariate observation*. New York: Wiley.
- Smouse PE, Long JC, Sokal RR. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zool* 35:727–732.
- Standen VG. 1991. El cementerio Morro 1: nuevas evidencias de la tradición funeraria Chinchorro (Periodo Arcaico, norte de Chile). Tesis de Maestría. Lima: Universidad Católica de Lima.

- Tarragó MN. 1989. Contribución al conocimiento arqueológico de las poblaciones de los oasis de San Pedro de Atacama en relación con los otros pueblos puneños, en especial, el sector septentrional del Valle Calchaquí. Ph.D. dissertation, Facultad de Humanidades y Artes, Universidad Nacional de Rosario, Argentina.
- Uribe M. 1995. Cerámicas arqueológicas de Arica (Extremo norte de Chile): Primera etapa de una revaluación tipológica. In *Actas del XII Congreso Nacional de Arqueología Chilena, Hombre y Desierto 9 (TII)*, Antofagasta. p 81–96.
- Uribe M. 1999. La cerámica de Arica 40 años después de Dauelsberg. *Chungara* 31:189–228.
- Uribe M. 2004. De la colección al poder: reflexiones en torno al impacto Tiwanaku sobre la cerámica de Arica (Extremo norte de Chile). *Boletín de la Sociedad Chilena de Arqueología* 37: 25–35.
- Uribe M, Agüero C. 2001. Alfarería, Textiles y la integración del Norte Grande de Chile a Tiwanaku. *Boletín de Arqueología PUCP, Perú*. 5:397–426.
- 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.
- Varela HH, Cocilovo JA. 2009. Microevolución en San Pedro de Atacama (Norte de Chile): El cementerio de Quito. *Lat Am Antiq* 20:333–342.
- Varela HH, Cocilovo JA. 2011. Divergencia fenotípica en los Oasis de San Pedro de Atacama, Norte de Chile. *Estudios Atacameños* 4:101–112.
- Varela HH, O'Brien TG, Cocilovo JA. 2008. The genetic divergence of prehistoric populations of the South-central Andes as established by means of craniometric traits. *Am J Phys Anthropol* 137:274–282.
- Varela HH, Cocilovo JA, O'Brien TG. 2013. Valley to valley: the biological connection between prehispanic residents of Cochabamba, Bolivia, and Azapa, Chile. *Adv Anthropol* 3: 210–215.
- Varela HH, Cocilovo JA, Quevedo S, Costa M. 2004. La estructura de la población de pescadores del período Arcaico Tardío y Formativo de Arica. *Boletín del Museo Nacional de Historia Natural, Chile* 53:149–160.
- Varela HH, Cocilovo JA, Santoro C, Rothhammer F. 2006. Microevolution of human archaic groups of Arica, northern Chile, and its genetic contribution to populations from the Formative Period. *Rev Chil Hist Nat* 79:185–193.