Archeological and mtDNA evidence for Tropical Lowland migrations during the Late Archaic / Formative in northern Chile

Evidencia arqueológica y de ADNmt para migraciones de Tierras Bajas Tropicales Durante el Arcaico Tardío/Formativo Temprano en el norte de Chile

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RESUMEN

La influencia de migraciones desde las tierras bajas tropicales en la emergencia de cambios culturales en los Andes Centrales, ha sido propuesta en términos generales desde comienzos de la última década (Tello 1929). Evidencia arqueológica y genético molecular reciente, particularmente la agricultura de cultígenos tropicales y la haplotipificacion de ADNmt antiguo, obtenida en el norte de Chile, sugieren una relación cronológicamente más acotada entre ambas regiones. Contrastamos en este artículo la hipótesis que el proceso de transformación cultural de las poblaciones prehistóricas costeras y vallunas del norte de Chile podría explicarse parcialmente por flujos migracionales originados en la vertiente oriental de los Andes y/o en las tierras bajas tropicales durante el periodo Arcaico Tardío / Formativo Temprano (ca. 3,500-2,000 A.P.).

Palabras clave: ADNmt antiguo, Andes Centrales, cambio cultural, foresta tropical, migración.

ABSTRACT

The influence of tropical lowland migrations on the emergence of cultural change in the Central Andes has been postulated in general terms since the beginning of last century (Tello 1929). Archeological and molecular genetic evidence, particularly agriculture of tropical cultigens and ancient mtDNA haplogroup typing in northern Chile, suggest a chronologically more precise relationship between both regions. We test in this article the hypothesis that the process of cultural transformation of prehistoric populations living on the coast and the desert valleys of northern Chile can be partially linked to gene flow from the eastern slopes of the Andes and/or from the tropical lowlands during the Late Archaic / Formative periods (ca. 3,500-2,000 B.P.).

Key words: ancient mtDNA, Central Andes, cultural change, tropical lowland migration.

INTRODUCTION

The influence of lowland migrations on the emergence of cultural complexity in the Central Andes was initially postulated in general terms by Tello (1929) and more specifically by Lathrap (1970). Conversely, Meggers et al. (1965) claimed that cultural elements of the South American Formative period would have spread toward the south across the Andes, starting from the Ecuadorian coastline. The axis of interpretations changed again after the publication of the archeological evidences of Wankarani and Chiripa, Formative sites located south of Lake Titicaca (Ponce Sanjinés, 1970), and the circum-Titicaca area came to be the nucleus from which novel cultural developments of this period emerged. Thus, it was assumed that highland political and ideological principles, became integrated into a cultural strata of millenary coastal traditions (Núñez 1972, 1994, 1999, Muñoz 1989, Santoro 1980).
In fact, during the fourth and third millennium B.P., important cultural changes in economic systems, political organization and ideological principles occurred, materialized in the installation of sedentary settlements within valleys or ravines in marshy or oasis-like environments close to the coast. Interestingly, settlements surrounded by graveyards and tumuli and early monumental ceremonial centers such as Chiripa (ca. B.P. 2,800-3,000) are also found in the circum-Titicaca area (Romero et al. 2004, Hastorf et al. 2001). Proposals for explaining sociocultural changes on the coast included highland migratory currents which had supposedly arrived in the valleys by means of vertically structured mechanisms of colonization, replacing the old hunting - gathering tradition (Rivera 1975, Rivera & Rothhammer 1986) and less invasive migratory fluxes derived from demographic pressures generated in the circum-Titicaca region (Chacama 2001, Muñoz 1989, Núñez 1989, Santoro 2000).

On the basis of bioanthropological, particularly genetic and cranimetrical, information available in the 1980s the cultural development of some archaic coastal populations had been linked by our group to the tropical forest (Rivera & Rothhammer 1986, Rothhammer & Silva 1989, Rivera & Rothhammer 1991, Rothhammer & Silva 1992). The application of novel methodological approaches to cranial morphological analysis and preliminary ancient mtDNA data, allowed us later to identify a chronologically more precise relation (Moraga et al. 2001, Varela & Cocilovo 2002, Rothhammer et al. 2002, Rothhammer et al. 2003, Varela et al. 2006).

The object of this article is to explore further this possible migrational link between coast and tropical lowlands, adding to the discussing recent bioarqueological evidence such as tropical agricultural products and molecular genetic data, particularly mtDNA.

METHODS

Ancient and extant mtDNA samples

Ancient mtDNA was extracted from skeletal remains exhumed in the archeological sites of Morro 1 and 1-6D, located at the outlet of the Azapa Valley and dated with \(^{14}\)C between 4,300 and 3,600 B.P. (Arriaza 2003). Furthermore, samples from the following archeological sites: Pircas-2, Caserones Sur, Tarapacá-40A and Tarapacá-0 (Tarapacá Valley) dated with \(^{14}\)C between 3,790 and 1,350 B.P. were also analyzed (Moraga et al. 2005, Núñez 1982). The sites of Morro 1 and Morro 1-6 D belong to the Chinchorro Culture and are Late Archaic (Standen & Santoro 2004, Moraga et al. 2005), whereas the sites located in the Tarapacá Valley, are Formative (Núñez 1982).

As known, the mtDNA from 95 % of contemporary Amerindians falls within four maternal groups stemming from related lineages. These so called haplogroups are defined by a specific mtDNA marker. Haplogroup A is defined by the gain of a restriction site for the enzyme Hae III in the position 663, haplogroup B, by the deletion of 9 bp in the intergenic region COII/tRNALys, haplogroup C, by the loss of a site for the enzyme Hinc II in the position 13,259 and, finally, haplogroup D by the loss of a site for the enzyme Alu I in the position 5,176 (Schurr et al. 1990, Torroni et al. 1992, Wallace & Torroni 1992). Other founding lineages have been postulated in extant and prehistoric aboriginal populations (Baillet et al. 1994, Easton et al. 1996, Stone & Stoneking 1993; 1998, Ribeiro-dos-Santos et al. 1996).

DNA extraction and contamination precautions are described in Moraga et al. (2005). For comparative purposes we incorporated published mtDNA haplogroup frequencies from the archeological site of Tiwanaku, Bolivia dated at 1,400 B.P. (Rothhammer et al. 2003), the tropical forest, dated 4,000-500 B.P. (Ribeiro-Dos-Santos et al. 1996), the Lluta, Azapa and Camarones Valleys dated 1,650-500 B.P. (Moraga et al. 2005) and extant samples from Aymara, Atacameño and Quechua populations inhabiting the Central Andean region (Moraga 2001) (Table 1).

Population genetic analyses

Correspondence factor analysis was performed on the haplogroup contingency table using Genetix software (Belkhir et al. 2001) and employed as an exploratory tool to evaluate the genetic similarity/dissimilarity among samples.
EVIDENCE FOR TRANSANDEAN PREHISTORIC MIGRATIONS

An unrooted neighbor-joining tree was constructed from a matrix of pairwise FST (coancestry distances) with the GDA software (Lewis & Zaykin 2001). In order to estimate and compare haplotype frequencies among samples the Arlequin 3.11 program (Excoffier et al. 2005) was utilized. Random distribution hypotheses of the 4 haplogroups among pairwise samples were tested using permutation tests on Weir & Cockerham (1984) pairwise $F_{ST}$. A two-level hierarchical analysis of molecular variance (AMOVA) was conducted on 4 groups determined by FCA analysis: [Chinchorro, Tiwanaku (Tiwan), Quechua], [Alto Ramirez (AltoR), Amazonia (Amazo)], [Cabuza-Maitas (CabMai), Late Alto Ramírez (LAltoR)] and [Atacameño (Ataca), Aymara, Gentilar-Inca (GenInc)]. Total genetic variance was partitioned in among group, among populations within groups and within population components. $F$-statistics based on haplogroup frequency differences were calculated among all samples ($F_{st}$), among samples within groups ($F_{sc}$) and among groups ($F_{ct}$). A non-parametric permutation procedure was used to test whether statistics were significantly different from zero as implemented in Arlequin software.

RESULTS

Examination of haplogroup distribution of the skeletal material included in the analysis indicates that B and C haplogroups are the most frequent, followed by A and, at a much lower frequency, D (Table 1). Factorial correspondence analysis on haplogroup frequencies (Fig. 1) revealed four distinct clusters, namely [Chinchorro, Tiwan, Quechua], [AltoR, Amazo], [CabMai, LAltoR] and [Ataca, Aymara, GenInc]. First factorial component (61% of the total genetic variation) clearly separated [AltoR, Amazo] and [Ataca, Aymara, GenInc] from the other samples. Among them, the second factorial component (29% of the total genetic variation) separated [Chinchorro, Tiwan, Quechua] and [CabMai, LAltoR].

Unrooted neighbour-joining dendrogram (Fig. 2) also strongly grouped Ataca, Aymara, GenInc samples, as well as AltoR with Amazo. Furthermore, the first cluster of the dendrogram included, beside Alto Ramírez (Tarapacá Valley Formative) and Amazonia, also Tiwanaku, whereas the second cluster the Chinchorro fishermen (Late Archaic), most Azapa Valley prehistoric groups and extant Atacameño and Aymara samples from the Central Andes. The Quechua constitute a separate group. It is noteworthy that populations included in cluster I exhibit on the average higher frequencies of B, whereas cluster II groups, higher frequencies of haplogroups A and D.

Most of pairwise exact tests were not statistically significant, probably because of small sample sizes. Only comparisons including Aymara ($n = 172$) or Atacameño ($n = 77$) populations exhibited deviations from a random distribution of haplogroups. However, and despite the large sample size of both contemporary samples, Aymara and Atacameño populations did not exhibit statistically or

TABLE 1

Amerindian haplogroup relative frequencies for ten populations included in the analysis.

<table>
<thead>
<tr>
<th>Locus</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.3333</td>
<td>0.4286</td>
<td>0.2857</td>
<td>0.3333</td>
<td>0.2000</td>
<td>0.4545</td>
<td>0.1111</td>
<td>0.2632</td>
<td>0.1558</td>
<td>0.0698</td>
</tr>
<tr>
<td>B</td>
<td>0.3333</td>
<td>0.1429</td>
<td>0.4286</td>
<td>0.4167</td>
<td>0.5333</td>
<td>0.0909</td>
<td>0.2222</td>
<td>0.3684</td>
<td>0.6883</td>
<td>0.6802</td>
</tr>
<tr>
<td>C</td>
<td>0.0667</td>
<td>0.2857</td>
<td>0.2857</td>
<td>0.2500</td>
<td>0.2000</td>
<td>0.3636</td>
<td>0.3333</td>
<td>0.0526</td>
<td>0.1169</td>
<td>0.1221</td>
</tr>
<tr>
<td>D</td>
<td>0.2667</td>
<td>0.1429</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0667</td>
<td>0.0909</td>
<td>0.3333</td>
<td>0.3158</td>
<td>0.0390</td>
<td>0.1279</td>
</tr>
</tbody>
</table>

Nota: (1) Chinchorro; (2) AltoR; (3) LAltoR; (4) CabMai; (5) GenInc; (6) Amazo; (7) Tiwan; (8) Quechua; (9) Ataca; (10) Aymara.
Fig. 1: Factorial Correspondence Analysis (FCA) plot.
Trazado del análisis factorial de correspondencia.

Fig. 2: Neighbor-joining unrooted tree constructed using pairwise F.
Árbol sin raíz construido a partir del método de unión de pares de valores F vecinos.
marginaly statistically significant genetic
difference between them, nor with GenInc and
LAaltoR. On the contrary, and despite small
sample size of ancient DNA samples,
significant genetic differences were found with
Amazonian samples and GenInc, as well as
Quechua samples. AMOVA (Table 3) revealed
that although most of the genetic diversity was
attributable to differences among individuals
within populations (85.03 %), there was still a
high level of variation among groups (15.66
%). On the contrary, no significant difference
was found among populations within groups.

DISCUSSION

Archeologists have advocated the view that
local populations of the coast and valleys of
northern Chile, and possibly southern Peru,
maintained a long cultural maritime tradition
that was gradually changed, along with the
emergence of a new way of life characterized
by ideological principles associated to a mixed
economy that combined coastal resources and
agriculture. Population movements from the
eastern slopes of the Andes and/or the tropical
lowlands could have been responsible for the
introduction of tropical agricultural products
found on the Pacific coastline in Late Archaic
and Early Formative sites (ca. 3,500-2,000 BP).
We note that this was a period of cultural
changes at a continental level, which implied
population movements associated with an
improvement in the conditions of humidity in
relation to the Middle Holocene, characterized
by long periods of drought. Prehistoric groups
in this region handled the complementary
cultivation of edible roots, such as cassava or
yuca (Manihot esculenta Crantz) and sweet

TABLE 3

Molecular variance analysis for the partitioning among groups and among populations
within groups. (***, P < 0.001).

<table>
<thead>
<tr>
<th>Groups</th>
<th>df</th>
<th>Variance components</th>
<th>% Total variance</th>
<th>Fixation Indices (P values)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among groups</td>
<td>3</td>
<td>0.05167</td>
<td>15.66</td>
<td>F_{CT} = 0.157 (P = 0.002)</td>
</tr>
<tr>
<td>Among populations / Within groups</td>
<td>6</td>
<td>-0.00229</td>
<td>-0.70</td>
<td>F_{SC} = -0.70^{NS} (P = 0.843)</td>
</tr>
</tbody>
</table>
potato (*Ipomoea batatas* Linn. Poir.) among others (Table 4). Although the origin and time of introduction of these crops into the region is still under debate, indirect evidence shows that cassava was a basic food crop in the Amazonian lowlands toward the year 3,000 B.P. (Meggers 1973). Sweet potato, of South American origin, is cultivated in the Amazon basin, the eastern plains of Bolivia, the warm (yungas) and mesothermal Andean valleys at a height of 2,400 m. Cassava and achira (*Canna edulis* Ker) are typical plants of the tropical zone of South America. The first competes with corn and potatoes as a main food, while the roots of achira are used as potato substitutes (Cárdenas 1989).

Interestingly, the vegetable strata which compose the ceremonial tumuli which typically characterize a late stage of the Formative of the western valleys, present precisely these plants of origin (Focacci & Erices 1972-73). Local wild weeds are added, such as pitcher plant (*Tessaria absinthioides* Hook. & Arn. DC.), and cortadera (*Cortaderia atacamensis* Ph l.) (Niemeyer & Schiappacasse 1963). Furthermore, recent excavations in Tumulus 8 of San Miguel (Late Formative) located in the Azapa Valley, show the presence of cultivated plants such as achira, yuca, pallar (*Phaseolus lunatus* L.), bean (*Phaseolus vulgaris* L.), cotton (*Gossypium barbadense* L.) and pumpkin (*Cucurbita pepo* L.) in one of the vegetable layers that conform the tumulus (CV4). Also, sites, such as Camarones 15 (ca. 1,100 B.C.) exhibit evidence of *Mucuna elliptica* (Ruiz Lopez & Pavon. DC) seeds and cassava together with other diagnostic elements such as feathers of tropical lowland birds (Fig. 3), and components of the hallucinogen complex (Romero et al. 2004).

As has been mentioned earlier, links between Chinchorro and the tropical forest, in the terms stated initially by Rivera (1975) were basically backed up by the early genetic and craniometrical data obtained in the 1980s. Also, the cultural traits presented as evidence for a relation between Chinchorro and the tropical forest, corresponded to elements linked to the Late Chinchorro in transition toward the Early Formative (Standen & Santoro 2004). Consequently, cultural traits tend to prove that links with the lowlands are much more evident during the initial farming period.

The unrooted neighbour-joining dendrogram (Fig. 2) reveals (see Results) that cluster one (C1) includes the Alto Ramírez (Quebrada de Tarapacá Formative), Amazonia and Tiwanaku samples. The Chinchorro fishermen (Late

### Table 4

<table>
<thead>
<tr>
<th>Site</th>
<th>Lab number</th>
<th>Radiocarbon date B.P.</th>
<th>Calibrated dating (95.4 % probability) B.P.</th>
<th>Tropical cultigen</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Capilla 1</td>
<td>I-11642</td>
<td>3,450 ± 90</td>
<td>3,930-3,470</td>
<td>Manioc</td>
<td>Muñoz &amp; Chacama 1982</td>
</tr>
<tr>
<td>Camarones 15</td>
<td>GaK 5813</td>
<td>3,060 ± 100</td>
<td>3,500-2,950</td>
<td><em>Mucuma elliptica</em> seeds</td>
<td>Rivera et al. 1974</td>
</tr>
<tr>
<td>Azapa 71</td>
<td>I-10,856</td>
<td>2,855 ± 85</td>
<td>3,220-2,770</td>
<td><em>Mucuma elliptica</em> seeds</td>
<td>Santoro 1980</td>
</tr>
<tr>
<td>Azapa 71</td>
<td>I-10,859</td>
<td>2,685 ± 85</td>
<td>3,050-2,450</td>
<td>Manioc</td>
<td>Santoro 1980</td>
</tr>
<tr>
<td>Azapa 71</td>
<td>-</td>
<td>ca. 3,000-2,500</td>
<td></td>
<td><em>Achira</em></td>
<td>Santoro 1980</td>
</tr>
<tr>
<td>PML 7</td>
<td>GaK 5812</td>
<td>2,480 ± 100</td>
<td>2,760-2,340</td>
<td><em>Mucuma elliptica</em> seeds</td>
<td>Focacci 1974</td>
</tr>
<tr>
<td>Azapa 14</td>
<td>GaK 5815</td>
<td>2,360 ± 90</td>
<td>2,750-2,150</td>
<td>Manioc</td>
<td>Santoro 1980</td>
</tr>
<tr>
<td>AZ-12</td>
<td>-</td>
<td>ca. 2,500-1,900</td>
<td></td>
<td>Sweet potatoes</td>
<td>Erices 1975</td>
</tr>
</tbody>
</table>

List of dated tropical cultigens identified in archaeological sites of northern Chile.
Archaic) and Azapa Valley prehistoric groups cluster together with Atacameño and Aymara samples from the Central Andes (see cluster 2 (C2)). Prehistoric populations of C1 are characterized by relatively higher frequencies of haplogroups A and by lower frequencies of haplogroup B, which exhibits very high frequencies among the Aymara and Atacameño (C2). Archaeological evidence indicates that during the Formative, Quebrada de Tarapacá was peopled by small bands of immigrants from the southern highlands of Bolivia, close to Lake Poopo, as judged by the presence of ceramic fragments and other cultural traits linked to Wankarani, a culture which established itself in that region around 3,000 B.P. (Ponce Sanjinés 1970). Interestingly, Wankarani predates Tiwanaku and has been related to Tropical Lowland sites. (Ponce-Sanjínés 1970, Núñez 1982)

The origin of the Tiwanaku population, hypothesized previously on the basis of ethnohistorical information, was explored by our group using ancient mtDNA extracted from skeletal remains from the archaeological sites of Akapana, Chiji, Jawira, Mollo Kontu and Putuni kindly provided by Dr. Alan Kolata and collaborators (Kolata 1993, 2003). Eighteen samples were analyzed, of which 13 could be typed for Amerindian haplogroups. The frequency distribution of haplogroups (A: 8 %, B: 15 %, C: 23 %, D: 23 % and others 31 %) relates in our analysis the remains from Tiwanaku genetically to extant Amazonian populations. Although the number of analyzed Tiwanaku individuals is very small, we note that their B haplogroup frequency is significantly lower than the frequency that characterizes the Aymara (P = 0.0156) (Rothhammer et al. 2003) (see also Table 1). Although the decline of Tiwanaku, around 900 B.P. has been attributed to climatic changes (Albarracín-Jordan 1996, Kolata 1993, Kolata et al. 1997), we note that ethnohistoric data point to a military conquest of the circunmiticaca region by the Aymara during the same time (Gisbert et al. 1987, see also Torero 2003).

Recently, we presented a detailed analysis of chronologic mtDNA variation in the desert valleys of northern Chile, with the object of reconstructing the microevolutionary history of prehistoric groups in the context of their interaction with socially more complex highland populations including Tiwanaku (Moraga et al. 2005). We obtained the following haplogroup distribution (A through D) for 19 individuals belonging to the Middle Period: 0.316, 0.421, 0.263 and 0.0. Lewis et al. (2007), addressing hypothesis concerning the origin of the Moquegua Valley Chen Chen site (A. D. 785-1,000), a Tiwanaku settlement

Fig. 3: Tropical feather headdress from Camarones 15 archeological site (Museo Arqueológico Universidad de Tarapacá San Miguel de Azapa, photo courtesy of Fernando Maldonado).

Tocado de plumas de aves tropicales sitio arqueológico Camarones 15 (Museo Arqueológico Universidad de Tarapacá, San Miguel de Azapa, foto cortesía de Fernando Maldonado).
located close to the Chilean Azapa Valley in southern Peru, examined 27 informative skeletal samples obtaining the following mt DNA haplogroup frequency distribution (A through D): 0.391, 0.391, 0.741 and 0.043. These frequencies are similar to our Azapa Valley samples for the same archaeological period. Apart from the methodological implication of this finding, it suggests a genetic link between the prehistoric populations of both valleys. No doubt, the process of change of coastal societies also included technologies linked to the exploitation of maritime resources from the southern coast of Peru which endured until late stages of regional prehistory.

Haplogroup B increases its frequencies progressively from the Middle Period (ca. 1,000 B.P.) to the Late Period in the Azapa Valley. In the case that this frequency change is not the result of stochastic microevolutionary phenomena, it could be interpreted as backing up archaeological evidence suggesting the arrival in Azapa Valley of the Aymara during the Middle Period.

Concluding, the simultaneous analysis of archaeological and mtDNA data revealed results, whose interpretation may contribute to a better understanding of the prehistoric population movements which had a bearing on the cultural changes that took place during the fourth and third millennium before present in northern Chile, the Bolivian Highands and southern Peru.

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