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An insight into the burial practices of the late pre-Hispanic Los Amarillos community (northwestern Argentina) through the study of ancient DNA

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ABSTRACT

A palaeogenetic analysis has been undertaken on the pre-Hispanic settlement of Los Amarillos (Regional Development Period, Jujuy Province, Argentina) to reconstruct kin relationship between individuals buried in two domestic areas. The aim of this study was first to genetically characterize the relationships between the individuals buried within the same funerary structure and, secondly, to correlate these genetic data with archaeo-anthropological data to discuss the burial practices and social organization of the Los Amarillos community. An analysis of both uniparental (mtDNA and Y-chromosome) and biparental (autosomal STRs) genetic markers was conducted on eighteen individuals recovered from three different burial structures. The very good DNA preservation contributed to characterize 13 mitochondrial haplotypes, 5 Y-chromosomal haplotypes and 11 complete autosomal STR profiles. The kinship analysis revealed that the domestic areas were used as family graves. Furthermore, they reveal that a maternal lineage is shared by a majority of the studied individuals from different sectors, suggesting matrilocal practices.

1. Introduction

Genetics provide powerful tools for studying the mortuary practices and the social organization of past societies when combined with archaeological and anthropological data. Only genetics can reveal reliably biological kinship ties between buried individuals. Mitochondrial DNA (mtDNA) is a powerful marker for studying population origin and divergence (Shriver and Kittles, 2004; Pakendorf and Stoneking, 2005; Underhill and Kivisild, 2007) but may also be useful for human identification. Mitochondrial DNA is particularly suitable for the analysis of low copy number (LCN) and/or highly degraded DNA (Budowle et al., 1999; Pääbo et al., 2004; Willerslev and Cooper, 2005). However, the analysis of the only mtDNA [mainly by a standard PCR-based sequencing of the mitochondrial hypervariable regions 1 and 2 (HVR-1, HVR-2)] can infer a lack of discriminating power for human identification (Butler and Levin, 1998). This disadvantage can be bypassed by the sequencing of complete mitochondrial genome (Paijmans et al., 2013; Templeton et al., 2013; Just et al., 2014), which provide a greater power of resolution. Despite the significant potential of such next-generation sequencing (NGS) approach, the fact remains that the strict uniparental inheritance of mtDNA provides only information about maternal lineages which may be insufficient to identify precise kinship relationship between individuals. The most effective method to identify human remains (Gill et al., 1994; Clayton et al., 1995; King et al., 2014) or to reconstruct close parentage relationships, within the same burial structure or the same necropolis (Gamba et al., 2011; Baca et al.,

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2012; Keyser-Tracqui et al., 2003; Deguilloux et al., 2014; Cui et al., 2015; Keyser et al., 2015), is the analysis of nuclear DNA (nuDNA), and more particularly the analysis of autosomal short tandem repeats (aSTRs). However, for ancient DNA analysis, access and exploitation of nuDNA can be very difficult, given the low number of genomes compared to mtDNA (Pääbo et al., 2004; Willerslev and Cooper, 2005). In addition, various factors can make the profiling of aSTRs difficult, such as contaminations, amplification failure (due to allele dropout or PCR inhibition for example), and too big amplicon sizes (often between 100 and 400 base pairs) (Alonso et al., 2003). To compensate and/or overcome these disadvantages, optimizations of DNA extraction protocols (Rohland and Hofreiter, 2007a, 2007b; Hervella et al., 2015), shorter amplicon commercial STR kits (mini-STRs) (Parsons et al., 2007; Senge et al., 2011; Oh et al., 2012), PCR conditions, capillary electrophoresis and statistical interpretation techniques were carried out, improving profiling methods.

Social anthropologists and ethnohistorians have argued strongly against generalizing particular models of kinship, descent, and post-marital residence in the Andes (Lambert, 1980; Arnold, 1998). Ethnographic data, for example, shows that even when patrilineal descent tends to prevail in the highlands of Peru and Bolivia, bilateral descent in which land, animals, and goods are inherited in both paternal and maternal lines, seems to be the norm in many cases (Lambert, 1980; Arnold, 1998). Moreover, based on the analysis of historical sources some authors believe that bilateral systems were predominant in prehispanic times (e.g., Zuidema, 1980) and that unilineal descent was only introduced after the Spanish conquest (Arnold, 1998). Post-marital residence also seems to vary; although virilocality seems to be the norm (e.g., Platt, 1976; Abercrombie, 1998) uxorilocal cases have also been reported (Spedding, 1998). Given this situation, rather than generalizing any particular model to prehistoric times, archeology and in particular paleogenetics should contribute to research on Andean kinship by documenting actual variability in relevant practices. Although a significant number of paleogenetic studies of South American populations was published during the last decades (Rothhammer et al., 2009; Sans et al., 2012; Baca et al., 2014; Dejean et al., 2014; Fehren-Schmitz et al., 2015; Gonçalves et al., 2014; Mendisco et al., 2014), very few contributed to discuss kinship relationships and mortuary practices. Still, two recent studies underline the patrilineal social organization of prehispanic communities from Peru (Baca et al., 2012, 2014).

In the present study, we analyzed complementary genetic markers with the aim of understanding and reconstructing the genetic relationships between the individuals buried at the Los Amarillos site. The archaeological site of Los Amarillos is located in Quebrada de Humahuaca, an arid valley in the Andes of Jujuy province, Northwestern Argentina (NWA, Fig. 1). It is a densely populated urban site of approximately 10 ha, among the largest known in the region (Nielsen, 2006). This complex settlement, which includes distinct public and residential areas, was first occupied in the early phase of the Regional Development Period (RDP, 900–1250 CE) and continued to grow mainly during the late phase of RDP (1250–1430 CE). The most common form of burial in Quebrada de Humahuaca and other regions of NWA during the periods considered in this work were pits or cists containing one or more individuals and placed in house floors. Funerary structures containing a variable number of individuals were discovered in most domestic areas excavated at the site, affording the opportunity of exploring the relationships among people buried in the same units. DNA provides a powerful line of evidence for undertaking such investigation.

A palaeogenetic study has already been carried out on some samples of Los Amarillos (Mendisco et al., 2014), demonstrating that DNA is well preserved at the site. While the previous study was designed to understand the evolutionary history of pre-Hispanic communities from the Humahuaca valley, we decided for this new study to focus on a very local scale. Our main objective was to decipher the relationships, particularly genetic links, between individuals inhumed on the same areas of the site, even in the same funerary structure. In this context, besides analyzing maternal (mtDNA HVR-1) and paternal (Y-STRs) lineages to identify potential kinship structures, autosomal STRs were examined to reconstruct more accurately the presumed close parentage relationships. Secondly, these genetic data can be correlated with archaeo-anthropological data to test common assumptions about mortuary practices in the region, and discuss the social organization of the late pre-hispanic groups of northwestern Argentina.

2. Materials and methods

2.1. Site and samples

Among the five sectors of Los Amarillos studied during successive excavations two are the object of this study: areas 320 and 400 (Fig. S1).

2.1.1. Area 320

In this area, located on the eastern part of the site, a rescue excavation was conducted in a burial structure, which contained at least sixteen individuals (10 adult individuals and 6 immature individuals). Since the remains lacked anatomical connections or burial goods, the context was interpreted as an ossuary (Seldes, 2012). Seven individuals of this burial structure were analyzed, i.e., samples LA-4, LA-5, LA-6, LA-7, LA-8, LA-9 and LA-20. Although the context was not dated, the chronological data available for this part of the site indicates that it was occupied during the late phase of the RDP (1250–1430 CE), exclusively. We can note that an osteological study carried out on cranial data allowed to highlight that half of the individuals analyzed have nutritional and/or metabolic stress linked to anemia or nutritional deficiencies during the childhood. In addition, more than half of the individuals (57.14%) have caries which is linked to the consumption of carbohydrate-rich foods, corn for example.

2.1.2. Area 400

This unit includes three interconnected enclosures that functioned as a domestic space in which both subsistence and artisanal tasks were conducted (Taboada, 2003; Taboada and Angiorama, 2004). This house was occupied during a relatively short period in which two small burial structures were constructed: cysts 1 and 3. Shortly after its abandonment, a third burial structure (cyst 2) was built (Taboada, 2003). In the burial structure 3 the remains of two adult individuals and two immature individuals were discovered. The cyst 2 was used as burial place for at least eighteen individuals, deposited during diverse burials events (Seldes, 2006, 2012). Abundant and varied grave goods were found in both sepulchers. Radiocarbon dating realized in this area (Angiorama, 2006) demonstrates that these burial structures were created and used during the late phase of the RDP. For the individuals of this area also evidences of nutritional and/or metabolic stress were revealed from cranial data, but with frequencies a little less important than for the area 320. One sample of cyst 3 (LA-13) and 10 samples of cyst 2 (samples LA-2, LA-3, LA-10, LA-11, LA-12, LA-14, LA-15, LA-22, LA-23, LA-24) were analyzed during this study.

The 18 individuals analyzed are of unknown sex. We favored the study of adult individuals, better results being often obtained for the adult individuals in comparison with the immature considering aDNA analysis. To avoid duplication and minimize contamination

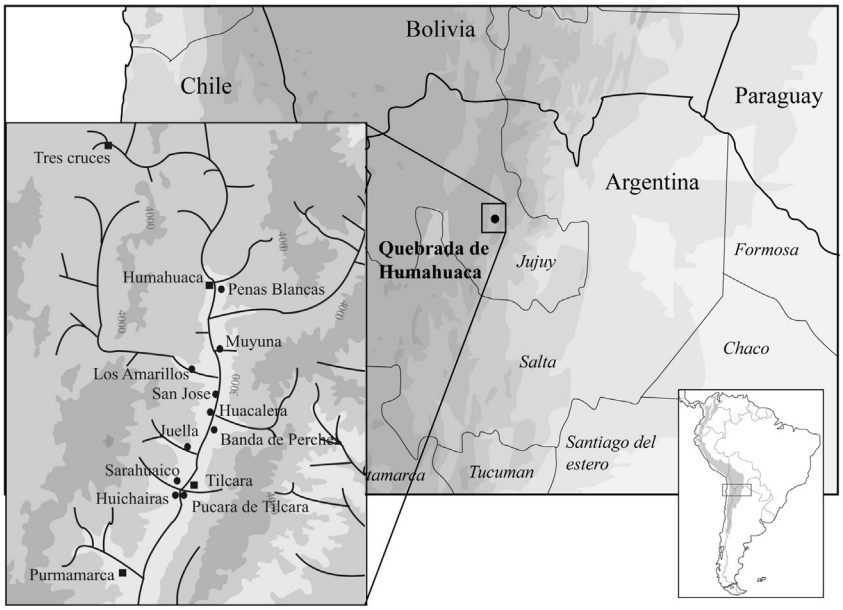

Fig. 1. Location of the Los Amarillos archaeological site in Quebrada de Humahuaca, Jujuy province, Argentina.

we chose to take for each individual two teeth intact and still in place in the mandible or maxilla.

2.2. Sample processing

All the investigations were performed in laboratories dedicated to the study of aDNA. The pre- and post-PCR steps were done in physically isolated areas. A set of precautions to avoid contamination of samples by the manipulators as well as crossed contaminations between samples were taken: (i) all the material used during the analysis was sterilized by autoclave and a long ultraviolet (UV) exposure, (ii) all the analyses were made by one manipulator, wearing an adapted equipment (face mask, sterile gloves), (iii) extraction and amplification blanks were used as negative controls during each step, (iv) all results were replicated at different times, from multiple extracts and amplifications of the same sample.

In order to remove possible surface contamination, each tooth was cleaned cautiously with bleach, rinsed with deionized water and, irradiated under UV light for 30 min on each face. Powder was generated by grinding the entire tooth under liquid nitrogen with a 6870 SamplePrep Freezer Mills (Fischer Bioblock, Illkirch, France). DNA extraction was done following a protocol previously described (Mendisco et al., 2011). At least two extracts per sample were obtained. Quantification of at least one DNA extract per sample was made using the Quantifiler Human DNA Quantification Kit (Applied Biosystems, Foster City, CA, USA), on an ABI PRISMs 7000 Sequence Detection System (Applied Biosystems, Courtaboeuf, France), following the recommended protocol of the company.

2.3. mtDNA analysis

Mitochondrial DNA analyses were performed on the first hypervariable segment of the control region (16,024–16,383 bp) divided in two overlapping sub-regions. The used primers and PCR conditions are described in a previous study (Carnese et al., 2010). All PCR products were analyzed on an ABI Prism 3500 automated DNA sequencer (Applied Biosystems). Mitochondrial sequence analysis was performed using the Sequencher 4.8 software (GeneCodes), and mutations determined by comparison with the revised Cambridge Reference Sequence (rCRS) (Anderson et al., 1981; Andrews et al., 1999). For each ancient sample, mitochondrial consensus HVR-1 sequences were determined from the analysis of various PCR products (at least four). To confirm the mitochondrial haplogroup deduced from the sequencing of HVR-1, several coding region mitochondrial SNPs (mt-SNPs) [characterizing founding Native American haplogroups A2, B2, C1b, C1c, C1d, and D1 (Tamm et al., 2007; Achilli et al., 2008)] were typed by MALDI-ToF (Matrix Assisted Laser Desorption/Ionisation - Time of Flight) mass spectrometry using the iPLEX® technology (Sequenom Inc. San Diego, CA, USA), as described in Mendisco et al. (2011).

2.4. Autosomal marker amplification

Analysis of autosomal STRs (aSTRs) was performed with the *AmpFlSTR*® Identifiler™ kit (Applied Biosystems) which allows to amplify simultaneously 15 autosomal loci (D2S1338, D3S1358, vWA, FGA, D5S818, D7S820, D8S1179, D13S317, D16S539, D18S51, D19S433, D21S11, TH01, CSFPO, TPOX) and the sex determination amelogenin locus. To confirm and complete these profiles, mini-STRs were amplified thanks to the *AmpFlSTR*® MiniFiler™ kit (Applied Biosystems) which allows simultaneous amplification of nine markers (D3S1358, vWA, FGA, D5S818, D7S820, D8S1179, D13S317, D18S51, D21S11) and the amelogenin locus. PCRs were performed according to the manufacturer's protocol except that 34 cycles instead of 28 were used for the Identifiler™ kit in a final reaction volume of 12.5 μL. Consensus genotypes presented derived from the analysis of multiple PCR products (at least four).

2.5. Y-chromosome analysis

For the ancient male individuals 17 Y-chromosomal STR loci (DYS19, DYS385a/b, DYS389I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635 and Y GATA H4) included in the *AmpFlSTR*® Y-filer™ Kit (Applied Biosystems) were analyzed. The experimental conditions were those recommended by the manufacturer, except that 34 PCR cycles were used instead 30. The amplified Y-chromosomal STR products were

analyzed on an ABI Prism 3500 Genetic Analyzer (Applied Biosystems) using the GeneMapper software, version 4.1 (Applied Biosystems). Consensus haplotypes were determined from several amplifications (at least four amplifications) by preserving the alleles having been typed at least twice. To determine the Y-haplogroups several Y-chromosomal SNPs (Q-M242, Q-M346, Q-M3, Q-M19, Q-M194, Q-M199, Q-SA01, and C-M217) (Jota et al., 2011; Seielstad et al., 2003; Tarazona-Santos et al., 2001; Underhill et al., 1996) were typed by MALDI-ToF mass spectrometry thanks to the iPLEX® Gold technology (Sequenom Inc. San Diego, CA, USA), as described in Mendisco et al. (2011).

2.6. Kinship determination

To estimate the probability of putative genetic relationship between individuals, we calculated the likelihood ratio (LR) thanks to the Familias v.2.0 software (Egeland et al., 2000). To calculate these probabilities we generated a personal database collecting allele frequencies of ancient and contemporary Andean populations (Albeza et al., 2002; Berardi et al., 2003; Toscanini et al., 2003, 2007; Marino et al., 2006a, 2006b, 2006c; Crossetti et al., 2008; Borosky et al., 2009, 2014; Carnese et al., 2010; Sala et al., 2010; Vullo et al., 2010; Callegari-Jacques et al., 2011; Baca et al., 2012, 2014; Muñoz et al., 2012; Parolin et al., 2014; Fehren-Schmitz et al., 2015), since there is not enough data on allele frequencies of autosomal STRs from ancient Amerindian populations.

3. Results

3.1. MtDNA analysis

As shown in Table 1, reproducible HVI sequences were obtained for 13 of the 18 individuals of Los Amarillos tested. The mitochondrial sequences are classified into three different haplotypes. Thanks to the typing of the mt-SNPs, the haplogroups inferred by HV1 sequencing were confirmed and maternal lineages of two samples (LA-2 and LA-6), for which HV1 sequences were not reproducibly obtained, were determined. Although this is not the most common mitochondrial lineage among contemporary populations of the region (Rodriguez-Delfin et al., 2001; Fuselli et al., 2003; Alvarez-Iglesias et al., 2007; Afonso Costa et al., 2010; Carnese et al., 2010; Barbieri et al., 2011; Fehren-Schmitz et al., 2011; Gaya-Vidal et al., 2011; Baca et al., 2012, 2014), 11 samples share the same maternal lineage A2. The two other samples belong to the D1 maternal lineage.

Table 1
Mitochondrial HVRI sequences and mitochondrial SNPs obtained from the Los Amarillos human remains.

Sample	Mitochondrial haplotypes	Mt-SNP	Hg
Los Amarillos - domestic area 320			
LA-4	16223T 16325C 16362C	2092T	D1
LA-6	n.d.	12007A–64T	A2
LA-7	16111T 16125A 16223T 16290T 16319A 16362C	12007A	A2
LA-8	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-9	16223T 16325C 16362C	2092T	D1
LA-20	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
Los Amarillos - domestic area 400			
LA-2	n.d.	12007A–64T	A2
LA-3	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-10	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-12	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-13	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-14	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-22	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-23	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2
LA-24	16111T 16223T 16290T 16319A 16362C	12007A–64T	A2

3.2. Nuclear DNA amplifications

As presented in Table 2, estimation of the nuclear DNA concentration for the samples studied varies from below the detection capability of the kit to 1430 pg/μL (with an average of 1167 pg/μL). The combination of different kits used (*AmpFlSTR*® Identifiler™ and MiniFiler™) as well as the good preservation of DNA allowed to obtain complete aSTR profiles for 11 of the 18 Los Amarillos samples, what is exceptional for ancient DNA studies. Partial autosomal profiles were obtained for 4 samples. The amplification of the amelogenin locus reveals that the Los Amarillos sample is composed of 9 male individuals, 5 female individuals, and 4 individuals of unknown sex.

Y chromosome haplotypes and haplogroups obtained for the 9 male individuals of Los Amarillos are shown in Table 3. Eight of these male individuals share the paternal lineage Q-M346 (currently called Q1a2a1a1), which is the most common Y-haplogroup in contemporary Amerindian populations (Zegura et al., 2004; Battaglia et al., 2013; Roewer et al., 2013; Geppert et al., 2015). The last one belongs to the haplogroup Q-M3 (today corresponding to the Q1a2 haplogroup).

3.3. Investigation of kinship relationships

As a first step, mitochondrial and Y-chromosomal data can reveal some genetic relationships between individuals sharing the same paternal and/or maternal lineages. These supposed relationships were statistically tested by comparing the corresponding STRs profiles. We investigated possible relationships between individuals buried in the same burial structure.

For the burial structure excavated in the unit 320 we revealed close genetic relationships between two couples of samples. Samples LA-4 and LA-8 have relatively close genetic profiles, including a shared allele for each of the 15 aSTRs amplified. This result is consistent with a parent/offspring (PO) relationship. Both individuals having a different mitochondrial haplotypes it seems likely that LA-4 (male individual) is the father of LA-8 (female individual), as supported by a high LR value (LR = 10,969947 corresponding to a PO probability of 0,999999909) (Table 4). Within the same funerary structure, two other samples share a close genetic relationship. Individuals LA-9 and LA-20, both male, have exactly the same Y haplotype but a different mitochondrial haplotype, suggesting a PO relationship. This relationship seems very likely, as confirmed by the analysis of genetic profiles (LR = 28,803, P = 0,999965) (Table 4).

Regarding the burial structures excavated in the unit 400 of Los Amarillos, we were able to demonstrate that the eight individuals, for whom we obtained repeatable results, share the same mitochondrial haplotype. Thus, all these individuals share a maternal genetic relationship. Besides an identical mitochondrial haplotype, both male individual LA-3 and LA-10 have an identical Y-haplotype, suggesting a relationship such as PO or sibling. Considering the absence of common alleles for both D21S11 and CSF1PO markers, the hypothesis of paternity was unlikely. Thus, according to their genetic profiles it seems that these individuals were two brothers (LR = 5,463167; P = 0,99999982). Regarding the rest of the individuals buried within the unit 400, two PO relationships were highlighted, on the one hand between individuals LA-12 and LA-13 (LR = 550 731; P = 0,99999818) and on the other hand between LA-14 and LA-23 (LR = 4 775 234; P = 0,99999979).

Table 2
Autosomal STR profiles obtained from Los Amarillos human remain.

	AMEL	D8S1179	D21S11	D7S820	CSF1PO	D3S1358	THO1	D13S317	D16S539	D2S1338	D19S433	vWA	TPOX	D18S51	D5S818	FGA	nuDNA quantity (pg/μL)
Los Amarillos - domestic area 320																	
LA-4	XY	12/13	31,2/34,2	10/11	11/14	15/17	7/7	9/11	9/9	17/22	14/15	17/19	8/12	13/17	7/13	23/26	56,3
LA-6	XX	–	–	–	10/12	–	–	10/10	–	19/19	–	–	–	13/13	–	–	3,4
LA-7	XY	13/15	–	–	–	15/15	7/7	10/14	9/9	–	14/15	16/18	8/8	–	11/12	25/25	17
LA-8	XX	12/15	30/31,2	10/11	10/14	15/17	7/7	11/13	9/9	22/23	12,2/15	17/19	8/8	13/13	11/13	25/26	55,7
LA-9	XY	12/15	30/31,2	11/12	10/12	15/15	7/7	13/13	9/10	22/23	13/13	16/16	8/8	12/13	11/13	19/25	80,9
LA-20	XY	12/14	30/32,2	11/12	10/12	15/17	7/9,3	13/13	9/9	19/23	13/15	16/18	8/11	12/13	12/13	25/26	69,8
Los Amarillos - domestic area 400																	
LA-2	–	–	28/28	–	–	–	–	–	–	20/20	–	–	–	13/13	–	23/23	n.d.
LA-3	XY	13/13	30/30	10/12	12/12	15/16	7/7	12/13	11/12	17/19	12,2/15	17/21	8/11	13/16	11/11	19/26	151
LA-10	XY	13/13	31,2/31,2	10/10	10/11	15/16	7/7	12/13	10/12	19/20	12,2/15	17/21	8/8	13/16	11/13	19/21	13,3
LA-12	XY	13/14	31,2/31,2	10/11	11/11	15/15	7/7	12/13	9/10	17/17	13,2/15	15/18	8/8	16/16	7/11	19/24	31,7
LA-13	XX	13/14	29/31,2	10/10	11/12	14/15	7/7	8/12	9/10	17/21	13,2/14	15/18	8/11	16/17	11/11	19/24	1430
LA-14	XX	11/13	31,2/32,2	10/11	10/11	15/15	7/7	13/13	11/12	17/20	12,2/12,2	16/17	11/11	13/14	9/13	25/25	43,1
LA-22	XY	13/14	30/30	–	12/12	15/15	7/7	–	–	19/22	12,2/15	16/16	–	13/13	9/11	26/26	n.d.
LA-23	XX	13/13	31,2/31,2	10/12	10/11	15/15	6/7	12/13	9/12	17/19	12,2/13	16/17	11/11	13/16	9/11	25/26	140
LA-24	XY	13/14	31,2/32,2	10/12	10/11	15/15	6/7	9/12	9/9	19/20	13/14	16/16	8/8	13/16	9/11	24/25	10

Table 3
Y chromosome STR profiles obtained for the 9 male individuals from Los Amarillos.

Sample	Amel	DYS456	DYS389I	DYS390	DYS389II	DYS458	DYS19	DYS385	DYS393	DYS391	DYS439	DYS635	DYS392	GA-H4TA	DYS437	DYS438	DYS448	Hg
Los Amarillos - domestic area 320																		
LA-4	XY	15	13	25	30	20	13	14/14	13	10	12	22	14	13	14	11	20	Q-M3
LA-7	XY	16	14	25	33	18	–	14/18	13	10	11	–	14	11	14	–	–	Q-M3
LA-9	XY	15	14	24	32	17	13	15/16	13	11	11	22	14	12	14	11	20	Q-M3
LA-20	XY	15	14	24	32	17	13	15/16	13	11	11	22	14	12	14	11	20	Q-M3
Los Amarillos - domestic area 400																		
LA-3	XY	15	14	23	32	15	13	13/18	13	9	11	22	14	12	14	11	20	Q-M3
LA-10	XY	15	14	23	32	15	13	13/18	13	9	11	22	14	12	14	11	20	Q-M3
LA-12	XY	15	13	25	–	20	–	14/14	13	10	–	22	–	13	14	11	–	Q-M3
LA-22	XY	16	13	–	–	–	–	13/18	13	10	–	–	–	12	13	–	–	Q-M3
LA-24	XY	17	13	23	30	16	13	14/16	13	10	11	–	14	12	14	11	20	Q-M3

Table 4
Detail of the probability of kinship for some pairs of samples from Los Amarillos.

	Putative kinship	Mt-Ht	Y-Ht	aSTRs	LR	P (%)
Los Amarillos - domestic area 320						
LA-4/LA-8	parental/offspring	different	/	15/15	10 969 947	0,999999909
LA-9/LA-20	parental/offspring	different	identical	15/15	28 803	0,999 965
Los Amarillos - domestic area 400						
LA-3/LA-10	sibling	identical	identical	13/15	5 463 167	0,99999982
LA-12/LA-13	parental/offspring	identical	/	15/15	550 731	0,99999818
LA-14/LA-23	parental/offspring	identical	/	15/15	4 775 234	0,99999979

4. Discussion

The analytical development strategy, combining rigorous precautions and the analysis of various genetic markers thanks to different techniques, was extremely valuable to assess the results. The results obtained are considered with confidence as authentic because of different criteria: (i) mitochondrial haplogroups determined are consistent with the studied area; (ii) genetic profiles obtained are all unique and different from the profiles of all the people who handled the samples; (iii) negative controls used confirm that there were no exogenous or crossed contaminations; (iv) results obtained from different markers are all consistent. Moreover, it is interesting to note the exceptional preservation of nuDNA, which facilitated an accurate study of kinship relations between the ancient samples and allowed to answer the objectives of the study. During the last years, other studies managed to obtain nuDNA data for Andean pre-Colombian individuals (Carnese et al., 2010; Fehren-Schmitz et al., 2011; Baca et al., 2012, 2014; Russo et al., 2016), confirming that the environmental conditions of the region contribute to the good preservation of ancient DNA molecules.

The individuals buried in these two particular areas exhibit a very high frequency of mitochondrial haplogroup A2 (13 individuals, 76.5%), and a lower frequency of haplogroup D1 (2 individuals). It is interesting to note the total absence of haplogroup B2 which is nevertheless characteristic of numerous ancient (Carnese et al., 2010; Fehren-Schmitz et al., 2011; Baca et al., 2012, 2014) and contemporary Andean communities (Rodriguez-Delfin et al., 2001; Fuselli et al., 2003; Lewis et al., 2005, 2007; Alvarez-Iglesias et al., 2007; Corella et al., 2007; Afonso Costa et al., 2010; Barbieri et al., 2011; Gaya-Vidal et al., 2011). A very low haplotypic diversity was detected with only three different mitochondrial haplotypes for 13 samples out of the 18 tested. Unfortunately, these haplotypes do not allow to specify a potential origin of the individuals, as they are actually widespread throughout South America. It is important to keep in mind that the diversity existing in the population of the site can be biased by the fact that all the samples come from only two areas. So, the real diversity of the whole community of Los Amarillos could be very different from that detected in the studied areas. Additional samples, from other areas of the site showed the presence of the same haplotype A2 for additional two individuals, one individual with a B2 haplotype and one individual with a C1b haplotype (Mendisco et al., 2014). For the nine male individuals tested, we could identify eight different haplotypes belonging to two sub-haplogroups (Q-M3 and Q-M346) that are currently the most common haplogroups among Native American populations (Zegura et al., 2004; Battaglia et al., 2013; Roewer et al., 2013; Geppert et al., 2015).

The very low mitochondrial diversity observed can be explained by a specific recruitment within both domestic areas. Indeed, close relatives (parent/offspring or sibling) are found in both domestic areas. Part of the genealogies for each of the areas studied could be reconstructed. However, it was not possible for us to complete them because some samples were too degraded and we do not have access to all the individuals buried in each structure. In the case of the domestic area 400, all individuals share the same mitochondrial haplotype, suggesting that these individuals were kindred. In addition, it is interesting to note that the sample LA13, buried during the occupation of this house, is most likely the mother of the sample LA12 who was buried in the larger funerary structure 2, built after the abandonment of the area as habitation. In this larger structure, other close relatives were found between the remains deposited during successive burial events. Thus, there is continuity in the burial recruitment, with the grouping over time of close relatives in the place they had probably inhabited. Since unit 320 was a funeral ossuary grouping human remains buried secondarily, the recruitment may have been totally different. Even if a more important maternal genetic diversity was discovered within this structure, there are also close relatives buried together (for example, LA-4/LA-8 and LA-9/LA-20 who are most likely parent/offspring). Despite the very different types of burial structures studied, in both cases we found high levels of genetic kin relationship among the individuals buried in the same area. The burial of the dead within domestic areas is a common feature in pre-Hispanic communities from Northwestern Argentina (Nielsen, 2001; Seldes, 2014). In this case, the genetic data confirm the hypothesis that the individuals buried in the same grave were close relatives. It is interesting to note that no link of very close genetic kinship was discovered between individuals buried in different sectors of the site. Although, as already noted, the same maternal lineage is shared by the majority of the individuals buried in different areas of the site. This very low mitochondrial haplotypic diversity compared to the Y-chromosomal haplotypic diversity could be an argument in favor of a matrilocal post-marital residential pattern in the community of Los Amarillos. However, it should be kept in mind that we analyzed only two areas of a very extensive site, so this hypothesis should be verified through the analysis of additional samples. A previous study also showed high levels of kinship relationships among individuals buried in one residential structure of Muyuna, another archaeological site from the early phase of the RDP in Quebrada de Humahuaca (Russo et al., 2016). Although all individuals had the same mitochondrial lineage, males shared the same Y-chromosome haplotype and a possible patrilocal organization was inferred through similar analyzes to those performed in this study. However more studies are needed and for this reason Russo et al. (2016) proposed taking the results with caution until we can count on more samples in the same region. Whatever, considering these two studies, it seems that the burial of highly related individuals in domestic areas could be a common practice of pre-Hispanic communities from Quebrada de Humahuaca, at least during the Regional Development Period.

The value of the present study rests on proving that collective burials gathered close relatives. On the other hand, this research shows that the majority of the people buried in Los Amarillos was relatives on the maternal side, while in other Andean groups from Perú a patrilineal organization was demonstrated (Baca et al., 2012,

2014). This apparent variability supports Arnold's proposal about taking distance from the classic studies of kinship and their static typologies (Arnold, 1998).

5. Conclusion

The discovery of collective burials in domestic areas of one of the most important site of the late pre-Hispanic period of northwestern Argentina was a unique opportunity to test the influence of the social organization of the communities on the mortuary practices. The genetic kinship analysis revealed that close relatives were deposited and grouped in the same domestic area, demonstrating that the degree of relationship was considered for mortuary practices. This aDNA analysis also allowed identifying a maternal lineage shared by the majority of the individuals, indicating that the Los Amarillos community was probably organized around a matrilineal residence pattern. This study provides an example of the importance of multidisciplinary studies combining archeology, anthropology, and ancient DNA studies for understanding the history of Andean kinship systems.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jas.2018.01.005.

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