Brief Communication: Restricted Geographic Distribution for Y-Q* Paragroup in South America

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ABSTRACT We analyzed 21 paragroup Q* Y chromosomes from South American aboriginal and urban populations. Our aims were to evaluate the phylogenetic status, geographic distribution, and genetic diversity in these groups of chromosomes and compare the degree of genetic variation in relation to Q1a3a haplotypes. All Q* chromosomes from our series and five samples from North American Q* presented the derivate state for M346, that is present upstream to M3, and determined Q1a3* paragroup. We found a restrictive geographic distribution and low frequency of Q1a3* in South America. We assumed that this low frequency could be reflecting extreme drift effects. However, several estimates of gene diversity do not support the existence of a severe bottleneck. The mean haplotype diversity expected was similar to that for South American Q1a3* and Q1a3a (0.478 and 0.501, respectively). The analysis of previous reports from other research groups and this study shows the highest frequencies of Q* for the West Corner and the Grand Chaco regions of South America. At present, there is no information on whether the phylogenetic status of Q* paragoup described in previous reports is similar to that of Q1a3* paragroup though our results support this possibility. Am J Phys Anthropol 140:578–582, 2009. © 2009 Wiley-Liss, Inc.

Seielstad et al. (2003) described the M242 Y-chromosome polymorphism defining the Q haplogroup (YCC, 2002), and proposed it as a founder for the Americas.

In relation to their geographic distribution, Q, similarly to C, is currently present in Eurasia, suggesting that they originated in Asia and then spread over Europe and America. Frequencies for Q were lower than 17% (5% average) for Asian populations (Seielstad et al., 2003), 18.8% for Siberia (Karafet et al., 2002), while for North America they were up to 47% (13.9% average) (Zegura et al., 2004; Bolnick et al., 2006). However, in most South American populations Q* is poorly represented (<6%) (Bortolini et al., 2003; this study). Findings from other authors make us presume that the divergence between Q and Q1a3a (YCC, 2002; Karafet et al., 2008) took place shortly before or during the Bering Strait crossing (Lell et al., 2002), while the origin of Q might have preceded the population expansion from Asia to the rest of the world (Bortolini et al., 2003; Seielstad et al., 2003).

Karafet et al. (2008) described an extensively revised Y-chromosome tree containing 311 distinct haplogroups and incorporating approximately 600 binary markers. They showed that Q haplogroup accumulated 17 mutations defining 14 haplogroups; they also described that all Q chromosomes from their series presented P36.2 downstream to M242, expecting that MEH2 could be a subset of Q-P36.2. In this scenario, we assumed that the presence of M346, downstream to MEH2 and upstream to M3, evidences the phylogenetic status of our Q* paragroup chromosomes (Karafet et al., 2008). Anyway, we still ignore the real status of Q* in America and Siberia (Bortolini et al., 2003; Bolnick et al., 2006; Karafet et al., 2002), though we could not discard that at least some haplotypes from that Q* paragroup also presented M346*G. Every sample from our series of Q* chromosomes presented M346, indicating that they belong to the Q1a3* paragroup.

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MATERIALS AND METHODS

We analyzed 759 samples from nonrelated males of 11 South American native populations (Lengua and Ayoreo from Paraguay; Huilliche and Pehuenche from Chile; Wichi, Toba, Chorote, Mocoví, Mapuche, Tehuelche, and Humahuaca from Argentina), and seven admixed urban populations (Jujuy, Catamarca, Tucumán, Salta, and Córdoba from Argentina; and La Paz and Tarija from Bolivia) (Table 1, Fig. 1). Because of Q* low frequency in native populations, we also analyzed urban populations considering that all Q* Y-chromosomes belong to Native American male ancestors. Bolivian samples increased the number of Andean samples in the series; Native American ancestry in all urban samples can be inferred from Q1a3a frequency (Table 1). These results contribute to certify the high proportion of Native American inheritance in urban populations.

All biological samples were collected with the informed consent of the donors, encoded, and sent to our laboratory in anonymity for DNA testing.

For this study, we included samples corresponding to: Q* paragroup (their phylogenetic status was confirmed by the analysis of M9*G, M25*G, M120*T) (Underhill et al., 2001), P27*C (Karafet et al., 1999), M242*T (Seielstad et al., 2003), M3*C (Underhill et al., 1996)]. We sequenced M346 (Sengupta et al., 2006) in all Q* samples of our series and in two Sioux, one Navajo, and two Zuni from North American Q* (Bianchi et al., 1998), and identified haplotypes using seven Y chromosome STRs [DYS19, DYS389a, DYS389b, DYS390, DYS391, DYS392, and DYS393 (de Knijff et al., 1997; Kayser et al., 1997)]. From 21 samples characterized as Q*, only 17 could be analyzed for the seven specific microsatellites.

Lineage frequencies were calculated by direct counting. Microsatellite haplotype affinities were assessed through the Median Joining Network analysis (Bandelt et al., 1999) after the Star Contraction procedure (Forster et al., 2001), using the Network software (v 4.2.1.0, www.fluxusengineering.com). Data on Q* (Bortolini et al., 2003; Bolnick et al., 2006) and 129 Q1a3a haplotypes from the same populations included in this study were analyzed (Table 1) (Bianchi et al., 1998; present results).

To detect any possible differences in haplotype diversity between South and North American samples related to any bottleneck event, we computed several genetic diversity estimators (such as expected diversity, number of alleles, allelic size range, and Garza–Williamson index), using the Arlequin 3.1 software (Schneider et al., 2000).

Figure 2 and Table 2 show a total of 35 Q* paragroup haplotypes corresponding to 17 haplotypes from our South American series (identified with bold italic numbers in Table 2), and 19 North-American haplotypes reported by Bolnick et al. (2006) (identified with one asterisk preceding the population acronym in Table 2).

TABLE 1. Q1a3 and Q1a3a frequencies in South American populations*

Populations	Linguistic lineages[a]	N	Q1a3*	Q1a3a
Paraguay				
Lengua (tribal)	Mascoian	24	0.292	0.667
Ayoreo (tribal)	Zamucoan	9	0.222	0.556
Argentina				
Wichi (tribal)	Mataco	120	0.008	0.375
Toba (tribal)	Guaicuruan	12	0	0.833
Chorote (tribal)	Mataco	9	0	0.889
Mocoví (tribal)	Guicuruan	40	0.050	0.550
Mapuche (tribal)	Mapudungun	26	0.038	0.538
Tehuelche (tribal)	Chon	20	0	0.650
Humahuaca (urban)	Spanish	31	0	0.839
Jujuy (urban)	Spanish	46	0	0.360
Salta (urban)	Spanish	72	0.048	0.444
Catamarca (urban)	Spanish	98	0	0.112
Tucumán (urban)	Spanish	17	0	0.118
Córdoba (urban)	Spanish	156	0.006	0.147
Chile				
Huilliche (tribal)	Mupudungun	26	0.038	0.461
Pehuenche (tribal)	Mupudungun	18	0	0.833
Bolivia				
La Paz (urban)	Spanish	29	0.034	0.655
Tarija (urban)	Spanish	72	0.055	0.500
Total		759	0.029	0.427

Q1a3*, Q1a3a (YCC, 2002; Karafet et al., 2008).
[a] Ethnologue language database: http://www.ethnologue.com.

RESULTS

Of the 759 samples analyzed, we found 21 Q* chromosomes. Lengua and Ayoreo populations showed the highest Q* frequency in our series (7/24, 29.2%, and 2/9, 22.2%, respectively). Lower values were observed for Mocoví (2/40, 5%), Mapuche, Huilliche (1/26, 3.8%), and Wichi (1/120, 0.8%) (Table 1, Fig. 1). Q* Y-chromosome frequency for urban populations ranged from 0 for Catamarca, Jujuy, and Tucumán to 5.5% for Tarija; Salta, La Paz, and Córdoba showed 4.8, 3.4, and 0.6% intermediate frequencies, respectively (Table 1, Fig. 1).

To determine the phylogenetic status of this paragroup, we analyzed the M346 mutation that is positioned upstream to M3, accordingly with the phylogeny recently published by Karafet et al. (2008). We confirmed the presence of M346 G in all samples of our series, and in the Q* paragroup samples from North America: two Sioux, one Navajo, and two Zuni (data not shown, Bianchi et al., 1998). This evidences that probably most of the Q* chromosomes from North America (Bolnick et al., 2006) also present M346 G, this being the reason why we consider that all these samples belong to the Q1a3* paragroup, closely related with Q1a3a (Table 2, Fig. 2).

We succeeded in characterizing the full set of seven microsatellites (DYS 19, 389 I, 389 II, 390, 391, 392, and 393) in 17 of the 21 Q* chromosomes; each one of the 17 fully tested chromosomes exhibited a private single haplotype (Table 2, Fig. 2). Haplotypes 1 and 2 were found in two Lengua, and haplotype 3 was exhibited by one Creek individual. Similar haplotypes were described in one Guaraní, three Ingano, and one Wayuu (Haplotype 2; Bortolini et al., 2003) (Table 2, Fig. 2). Haplotype 1 was also found in the Q1a3a haplogroup proposed as the haplotype from which M3 originated (Bortolini et al., 2003).

Figure 2 shows the network of South and North American Q* haplotypes, in which the South American haplotypes occupy a central position. Because it was not possible to compare them with Siberian Q* haplotypes, we cannot assert further conclusions about their phylogenetic status.

The mean number of alleles were 3.00, 3.43, and 5.00 for North American Q*, South American Q1a3* and Q1a3a, respectively. The range of allele size was 2.14, 2.71, and 4.00, respectively. Expected diversity was 0.482 for North American and 0.478 for South American

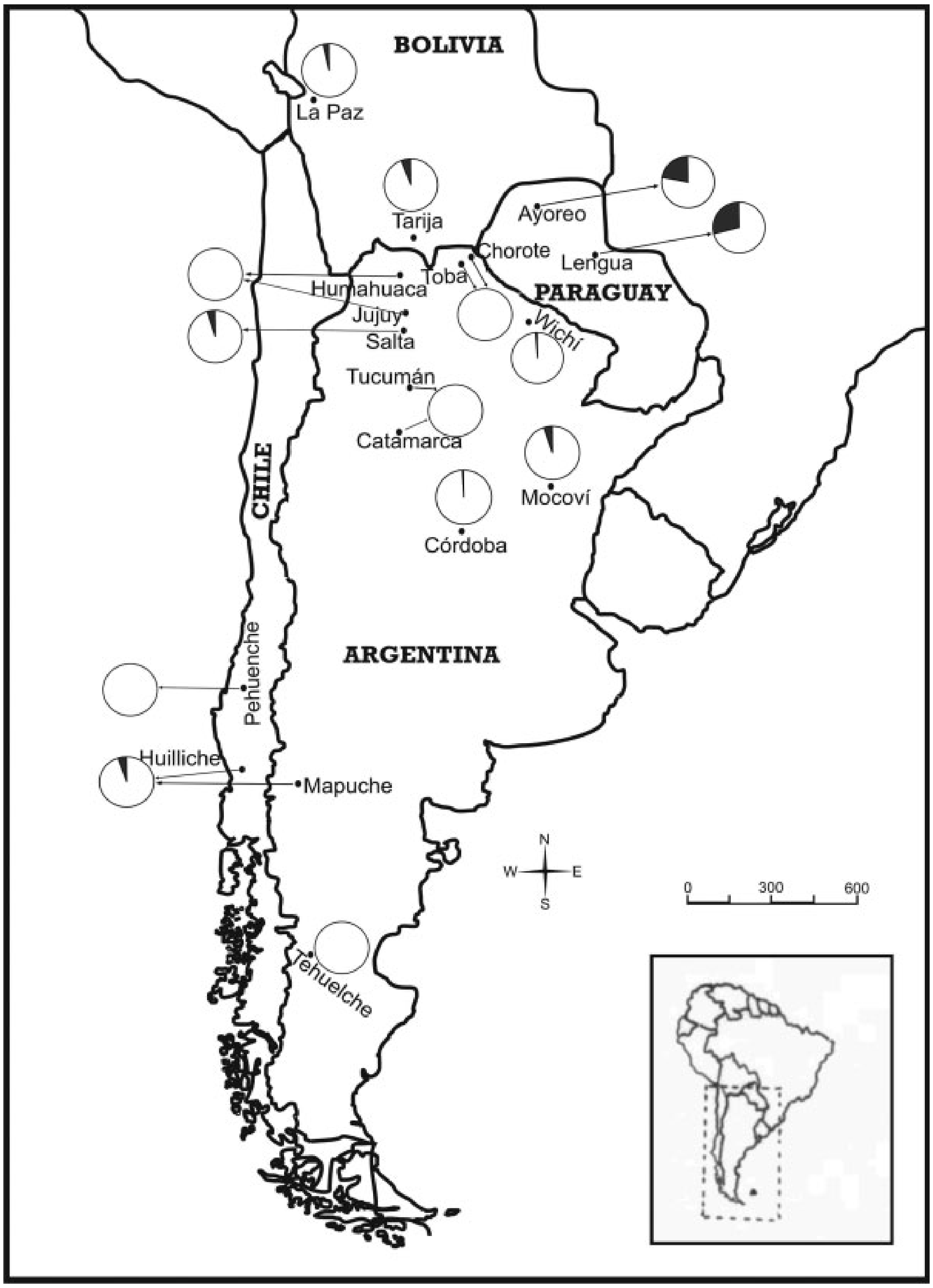

Fig. 1. Map of South American sampling localities were Q* paragroup is represented by circles, with an area proportional to frequency. See Table 1 for names, size, and language of populations samples.

Q1a3* lineages, and 0.501 for South American Q1a3a haplotypes. Distance assessed by the addition of square size differences (RST) was 0.0196, not significant (P = 0.144) between North American Q* and South American Q1a3* haplotypes. Meanwhile, distances between Q1a3a haplotypes and North and South American Q* were 0.0796 and 0.614, respectively, both statistically significant ($P < 0.001$). Fixation index for the three groups was 0.069 ($P = 0.001$). Finally, the Garza–Williamson index (the number of alleles divided by the allelic range, expected to be low in bottlenecked populations and close to one in stationary populations) was >0.96.

DISCUSSION

To analyze the phyletic origin of the Q* lineages in our series, we confirmed the status of Q1a3* by the presence of M346, upstream to M3. Even when there are no specific mutations that define Q1a3* by itself, this finding confirms the close phylogenetic relationship between Q1a3* and Q1a3a. In this case, Q1a3* would have entered Siberia from Asia (Gonzales-José et al., 2008). As complementary evidence of its Asian origin, M 346 has been previously described in India and Pakistan as Q4 (Sengupta et al., 2006). Furthermore, Q is exclusively distributed in North Western and North Eastern Siberia,

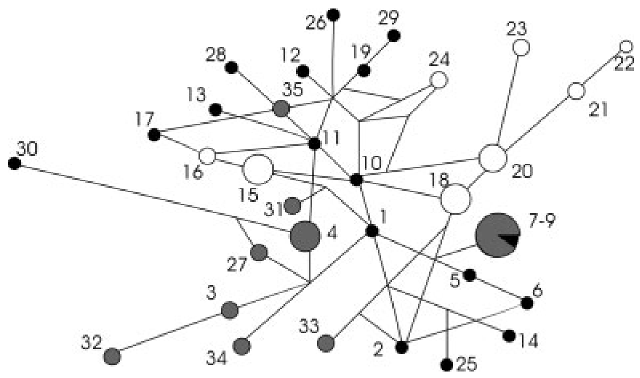

Fig. 2. Microsatellite network for North and South American Q* paragroup haplotypes represented in Table 2. Black circles, South American haplotypes (this study); gray circles, South East North American haplotypes; white circles, North East North American haplotypes (Boltnick et al., 2006). Circle size is proportional to frequency.

all these Q presented P36 derivated allele (Karafet et al., 2002). The analysis of M346 in the Siberian Q haplogroup would help to draw further conclusions about the complexity of populations that were the source of current American populations (Karafet et al., 2002; Bortolini et al., 2003).

The genetic diversity of Q* (Bolnick et al., 2006) and Q1a3* (this study) was similar, and they showed the same genetic distance from Q1a3a. Even when Q* and Q1a3* seem to be a little less diverse than Q1a3a, we cannot confirm any bottleneck effect. These analyses, and the presence of M346 G in Q* North American samples (data not shown), make us presume that most North American Q* might also be Q1a3*.

When our data were pooled with those from Bortolini et al. (2003), a particular geographic distribution of Q* chromosomes was observed in South American populations: the highest concentration was shown by the Northwest border (67% Ingano, 48% Zenu, and 21% Wayuu) (Bortolini et al., 2003), followed by the Gran Chaco region (29% Lengua, 22% Ayoreo) (this study), whereas the remaining populations showed frequencies below 6%.

Different sources of evidence support the hypothesis of a coastal colonization route into South America (Fuselli et al., 2003; Wang et al., 2007), thus explaining Q* high frequency in the Northwest border. Furthermore, South American inland population has been proposed to derive from the subsampling of western towards eastern populations (Fuselli et al., 2003; Wang et al., 2007). This pattern could explain the absence of Q* in most Eastern populations due to genetic drift, while similarities among different populations mismatching geographic distribution are attributed to founder effects. However, this cannot explain the high frequency and the ancestral status of lineages from the Gran Chaco area. Interestingly, this population shows the highest diversity level in South America (Demarchi et al., 2001; Cabana et al., 2006; Crossetti et al., 2008).

The low frequency of the Q1a3* paragroup observed in South America suggests that it is probably being lost by an eventual bottleneck or genetic drift, especially when we consider its small effective population size among South American hunting-gathering groups. However, several estimators show a similar degree of diversity for North and South American samples. These values were similar to those found for Q1a3a lineages from South America and allow to rule out the possible existence of a bottleneck event explaining the low representation of the Q1a3* paragroup in South America.

TABLE 2. Q haplotypes in North and South America*

Haplotypes[a]	19	389a	389b	390	391	392	393	Populations[b] (cases[c])
1	13	13	30	24	10	14	13	L (1)
2	13	12	32	24	10	14	13	L (1)
3	13	12	29	24	10	14	13	*CRK (1)
4	13	13	29	24	10	14	14	*SC (1), *OC (1), *SC (1)
5	13	13	30	23	10	13	13	Map (1)
6	13	13	31	23	10	13	13	Mo (1)
7	13	13	29	23	10	15	13	L (1), *CHO (3)
8	13	12	28	23	10	15	13	*SC (1)
9	13	14	30	23	10	15	13	*CHO (1)
10	14	13	30	24	10	14	13	A (1)
11	14	13	29	24	10	14	13	B (1)
12	14	15	29	24	10	14	13	L (1)
13	14	13	27	24	10	14	13	L (1)
14	14	14	32	24	10	14	13	B (1)
15	14	13	30	24	10	14	12	*CA(1), *SIO (1), *WC (3)
16	14	13	29	24	10	14	12	*MC (1)
17	14	14	29	24	10	14	12	B (1)
18	14	13	30	23	10	14	13	*SIO (2), *OC (1)
19	14	14	29	23	10	14	13	B (1)
20	14	13	30	23	10	14	14	*CA (2), *MC (2)
21	14	12	28	23	10	14	14	*SIO (1)
22	14	12	28	25	10	14	14	*SIO (1)
23	14	13	30	23	10	14	14	*WC (1)
24	15	14	30	24	10	14	14	*SHA (1)
25	14	13	32	24	10	13	13	Mo (1)
26	14	14	29	24	10	15	13	A (1)
27	13	13	29	25	10	14	13	*CRK (1)
28	14	13	29	24	11	13	13	Cor (1)
29	15	14	29	23	10	14	13	L (1)
30	13	16	26	25	10	14	14	Sal (1)
31	13	13	30	24	9	14	12	*OC (1)
32	16	10	29	24	10	14	14	*OC (1)
33	13	14	32	23	10	14	13	*OC (1)
34	13	13	29	24	10	12	13	*SC (1)
35	14	13	29	24	11	14	13	*OC (1)

[a] South American populations (bold).
[b] South American populations: A, Ayoreo; L, Lengua; B, Bolivia; Cor, Córdoba; Map, Mapuche; Mo, Mocoví; Sal, Salta. (*) North American haplotypes from Bolnick et al. (2006): CA, Cheyenne Arapaho; CHIC, Chickasaw; CHO, Choctaw; CRK, Creek; KIC, Kickapoo; MC, Minnesota Chippewa; MIC, Micmac; OC, Oklahoma Red Cross Cherokee; SC, Stillwell Cherokee; SEM, Seminole; SHA, Shawnee; SIO, Sisseton Wahpeton Sioux; TMC, Turtle Mountain Chippewa; WC, Wisconsin Chippewa.
[c] Number of cases in parenthesis.

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