informa
healthcare

FULL LENGTH RESEARCH PAPER

Mitochondrial origin of the matrilocal Mosuo people in China

YAN LU[1], CHUANCHAO WANG[1], ZHENDONG QIN[1], BO WEN[1], SARA E. FARINA[2],
LI JIN[1,2], & HUI LI[1,2], the Genographic Consortium[†]

[1]*MOE Key Laboratory of Contemporary Anthropology, School of Life Sciences, Fudan University, Shanghai 200433, People's Republic of China, and* [2]*Shanghai Society of Anthropology, Shanghai 200433, People's Republic of China*

Abstract
The Mosuo people are currently the only matrilocal population in China. The origins of the population and their matrilocal tradition remain unknown. To address these questions, we studied the mitochondrial DNA (mtDNA) diversity of the Mosuo. Lower mtDNA diversity is expected in matrilocal populations because the women remain with their families after marriage, and there is generally less movement of mtDNA genomes in matrilocal populations. However, the haplotype diversity of this population is not lower than the neighboring patrilocal populations, indicating that the Mosuo started practicing matrilocality at least after the Paleolithic Age. A previous haplogroup frequency clustering study indicated that the Mosuo are closest to the Naxi people, but the network analysis of individual sequence haplotypes presented herein shows that most Mosuo lineages cluster with Pumi lineages. Therefore, we concluded that the Mosuo people have the closest genetic relationship with the Pumi, and that they started to practice matrilocality several thousand years ago.

Keywords: *Molecular anthropology, maternal lineage, matrilocal populations, Southwest China*

Introduction

Human mitochondrial DNA (mtDNA) is passed onto the next generation through maternal lineages; therefore, it is the only genetic material available to trace the matrilineal history of individuals or populations. However, because most present-day populations have been practicing patrilocality (i.e. a practice in which females are exchanged frequently among populations) for many years, maternal lineages form very complex networks, making it difficult to trace the matrilineal history of these populations. Therefore, paternal genetic material (i.e. Y chromosome lineages) is much simpler and more helpful in understanding the population history in patriarchal populations (Su et al. 1999; Jin and Su 2000; Jobling and Tyler-Smith 2003). Nevertheless, there are still a few matrilocal populations in the world. MtDNA is therefore most useful in reconstructing the origins of these rare matrilocal populations. These populations also provide unique opportunities to study the population genetics of human mitochondria. In theory, there is less movement of mtDNA genomes in matrilocal populations because women tend to stay with their families after marriage. Here we examine a well-known matrilocal population in China, the Mosuo, to find an approach that could reveal their accurate maternal history.

The Mosuo, the last living matrilocal population in Mainland China (Gottner-Abendroth 1999), have a population of around 53,000 (2010 census), mostly distributed around Lugu Lake, on the border of Yunnan and Sichuan provinces (Figure 1). The present language of the Mosuo belongs to Tangut-Qiang branch of the Sino-Tibetan language family. Ethnographic studies suggest that the Mosuo were believed to be descendants of the ancient Qiang tribes. The ancient Qiang group is believed to be the ancestor
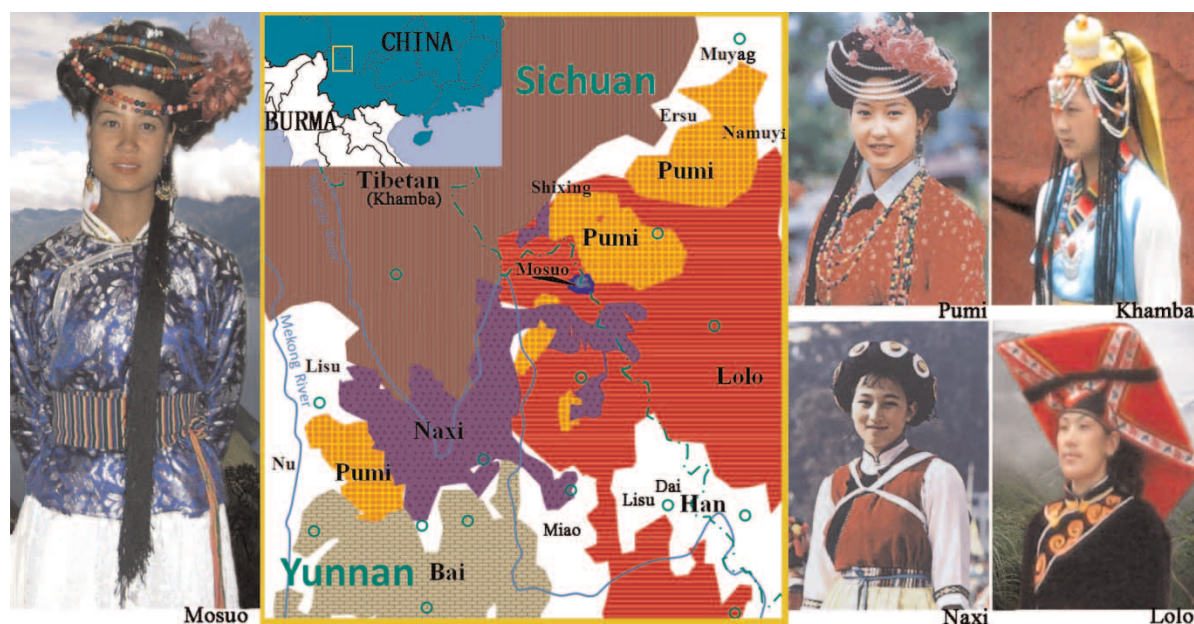
Figure 1.   Geographic location of the Mosuo people and the ethnic groups around.

of all Sino-Tibetan populations. They originally lived in Northwest China, and some migrated to Southwest China about 2700 years ago, where they diversified into several branches. Among these branches, the Tangut-Qiang is most similar to the ancient Qiang (He 1999; You 1997).

The origin of the Mosuo's matrilocality has been a controversial subject in Chinese anthropological literature. Some suggest that the Mosuo might have come from the ancient Qiang, and that matrilocality might have been practiced by all Sino-Tibetan populations, including Han Chinese (Zhong and Xiao 2008). Others think that the Mosuo are a recently admixed population, and the frequent mercantile travels of the men resulted in the matrilocality (Liu 2004, 2008). A study of the recent origin of the Mosuo might shed light on their adoption of matrilocality.

Although the Mosuo people are officially registered as the Naxi in Yunnan province and as Mongolian in Sichuan province, such official registrations have been contested for not reflecting the ethno-history of the population. The larger populations surrounding the Mosuo, including the Lolo, Naxi, Pumi, and Khamba Tibetan, have been considered as possibly contributing to the Musuo's origin and/or gene pools (Wen et al. 2004b; Figure 1). Cultural influences from neighboring populations on the Mosuo are evident (Xu 2004).

As there are few available historical records of the Mosuo, genetic studies could be helpful in reconstructing its origin. A study of Y-STR polymorphisms among five Chinese minorities shows that the Tibetan and Mosuo peoples are closest in paternal lineage (Yang et al. 2004). However, paternal origin may be inconsequential for a matrilocal population. Our

previous study of the Mosuo people suggests that they have various paternal origins, and therefore cannot identify a definitive source of genetic origin (Wen et al. 2004b). The maternal lineages of the Mosuo bear the strongest resemblance with those found in Naxi (Wen et al. 2004b). However, the results based on the haplogroup frequency comparison could be misleading due to the variability of the mtDNA lineage frequencies, since most mtDNA lineages are widely shared, and their frequencies among the population are changing quickly by positive selection or genetic drift (Yang et al. 2011). A network analysis of individual lineages will most likely offer a better means of investigating maternal relations among populations (Li et al. 2007; Qin et al. 2010).

Methods

Populations and data

Peripheral blood samples from 47 Mosuo individuals, 14 Naxi individuals, and 18 Pumi individuals from various villages were collected for this study, with an approval from the Ethics Committee of the Fudan School of Life Sciences. Each subject was adequately informed and signed consent forms in either Chinese or Tibetan. For those who could not speak Chinese or Tibetan, the informed consent was translated into their respective languages. The subjects were all healthy and not related within five generations. Data (Table I) pertaining to neighboring populations were obtained from existing literature (Yao and Zhang 2002; Yao et al. 2002; Wen et al. 2004c). Data pertaining to the Naxi and Pumi were published in our

Table I. Information for populations examined.

Population	Language	Location	N	Reference
Mosuo	ST, TB, Tangut-Qiang	Ninglang, Yunnan	47	This study
Naxi	ST, TB, Loloish	Lijiang, Yunnan	44	Wen et al. (2004c)
Pumi	ST, TB, Tangut-Qiang	Ninglang, Yunnan	35	Wen et al. (2004c)
Hani	ST, TB, Loloish	Xishuanbanna, Yunnan	80	Wen et al. (2004c)
Bai	ST, TB, Bai	Dali, Yunnan	55	Wen et al. (2004c)
Dai	Daic	Jinghong, Yunnan	38	Yao and Zhang (2002)
Jino	ST, TB, Loloish	Xishuanbanna, Yunnan	18	Wen et al. (2004c)
Lisu	ST, TB, Loloish	Gongshan, Yunnan	37	Yao and Zhang (2002)
Lahu	ST, TB, Loloish	Xishuanbanna, Yunnan	15	Wen et al. (2004c)
Miao	HM, Hmongic	Wenshan, Yunnan	142	Wen et al. (2005)
Nu	ST, TB, Nu	Gongshan, Yunnan	30	Yao and Zhang (2002)
Lolo/Yi	ST, TB, Loloish	Shuangbai, Yunnan	87	Wen et al. (2004c) and Yao and Zhang (2002)
Tibetan	ST, TB, Himalayish	Zhongdian, Yunnan,	35	Wen et al. (2004c)
	ST, TB, Himalayish	Qinghai	56	Wen et al. (2004c)
	ST, TB, Himalayish	Deqin, Yunnan	40	Yao and Zhang (2002)
Tu	Altaic, Mongolic	Huzhu, Qinghai	35	Yao and Zhang (2002)
Tujia	ST, TB, Loloish	Western Hunan	96	Wen et al. (2004c)
Yao	HM, Mienic	Malipo, Yunnan	394	Wen et al. (2005)

Note: ST, Sino-Tibetan; TB, Tibeto-Burman; HM, Hmong-Mien. Haplogroup frequencies of the populations are in Table S1.

previous paper (Wen et al. 2004b), and the genotype data on Mosuo were generated in this study.

MtDNA HVS-1 region sequencing

The hypervariable segment 1 (HVS-1) region of mtDNA was amplified by the primers L15996 and H16401 (Lum et al. 1998). PCR products were purified by resin. The purified PCR product was sequenced using the Big-Dye Terminator Cycle Sequencing Kit and an ABI 3100 Genetic Analyzer (Wen et al. 2004a,c, 2005). Sequence Analysis 3.3 software (BigDye Terminator Cycle Sequencing Kit, AppliedBiosystems, Foster city, CA, USA; ABI 3100 Genetic Analyzer, Applied Biosystems, Foster City, CA, USA) was used to extract sequences.

The HVS-1 sequences were edited and aligned against the revised Cambridge reference sequence (CRS; Andrews et al. 1999) using DNASTAR software (DNASTAR, Madison, WI, USA). All the HVS-1 sequences of the Mosuo people in this study are included in GenBank (HM215521-67).

Data analysis

Haplotype diversity was calculated using Arlequin software (Version 3.11; Arlequin software, University of Bern, Bern, Swiss) (Excoffier et al. 2005). The mutation model used here was the Kimura two-parameter model with a gamma shape parameter (alpha) of 0.26 (Jin and Nei 1990). Networks of mtDNA HVS-1 motifs were constructed by the median-joining method (Bandelt et al. 1999) using Network version 4.5.1.0 (Fluxus-engineering.com). The time to the most recent common ancestor (TMRCA) and their standard error of the haplogroups

observed in Mosuo were both estimated by the methods developed by Forster et al. (1996) and Saillard et al. (2000), and calibrated using a mutation rate of one transition every 20,180 years.

Results

We detected 35 mtDNA HVS-1 motifs within 11 haplogroups from the 47 Mosuo individuals (Table II). Lower mtDNA diversity is usually expected in the matrilocal populations with long histories. However, we found that the mtDNA HVS-1 haplotype diversity of Mosuo (0.9843) is not always lower than those of surrounding patriarchal populations, but even higher than those of the Naxi and Pumi (Table III). Meanwhile, this pattern is less clearly reflected in the haplotype mutation-drift statistic (θ_k), segregating sites mutation-drift statistic (θ_S), or the mean number of pairwise differences (π). θ is the expected level of diversity in a population in terms of the mutation rate and drift. Different estimators of θ should give the same value in a neutrally evolving population. However, in the presence of natural selection or other evolution processes, these estimators might vary greatly. For instance, π is a sample size independent measurement of nucleotide diversity, and θ_S is clearly dependent on the length and the number of sequences analyzed. Taking into account all of these diversity estimators, the Mosuo are considered intermediate among comparative populations.

There may be three mechanisms for a matrilocal population that would result in a population not exhibiting low mtDNA diversity: large population size, frequent admixture with other populations, and short matrilocality history (i.e. only several hundred or thousand years). Large population size may result

in high diversity; however, the Mosuo is a very small population and, aside from matrilocality, does not display a lifestyle different from neighboring populations. Therefore, it is unlikely that the maternal population size of the Mosuo is larger than that of neighboring populations. Admixture between Mosuo and neighboring populations is frequent but only in paternal lineages (Mu 1990; Liu 2004, 2008). Social studies have proven that maternal lineages of matrilocal populations are seldom exchanged with other populations (Gottner-Abendroth 1999), which also proves to be true in our later analyses. The last possible explanation for this pattern is that the Mosuo might have switched from patrilocality to matrilocality

very recently, and that their matrilocal society has not yet left visible effects on their genetic structure. We tried to estimate the time of coalescence for the Mosuo lineage clusters; however, present methods can only give very rough estimates and are not helpful in realizing TMRCA of the Mosuo. In Figure 2, ages of some clusters had extremely large standard errors and were therefore unreliable. The others with moderate standard errors included 5045 ± 2912 years (Clade 2), 7338 ± 2427 years (Clade 4), 8072 ± 5708 years (Clade 5), and 8649 ± 3223 years (Clade 6), mostly during the Neolithic Age, indicating that the Mosuo may not be a population that has existed since Paleolithic Age, as previously suggested. The short

Table II.　MtDNA HVS-1 motifs of the Mosuo people.

Haplogroup	HVS-1 motif (16,000 +)	Frequency	Sample	GenBank accession no.
A	129 223 239A 290 319 362	1	MOS36	HM215537
B4	187 189 217 264	1	MOS4	HM215540
	69 189 197 217 223 311 362 380	1	MOS14	HM215523
	187 189 217	2	MOS3	HM215532
			MOS46	HM215545
	189 217 311 362	2	MOS34	HM215558
			MOS40	HM215541
B5a	140 189 266A 270	1	MOS5	HM215546
	38C 85 140 189 228G 266A	1	MOS7	HM215547
	42C 91T 140 189 225A 266A 270	1	MOS31	HM215534
	46 140 189 266A	1	MOS11	HM215549
	140 189 266A	3	MOS18	HM215552
			MOS26	HM215530
			MOS50	HM215564
C	189 223 293 298 357	1	MOS49	HM215563
	111 189 223 293 298 349 357	1	MOS23	HM215528
	223 298 311 327 354 357	1	MOS37	HM215538
	92 129 223 298 311 327 357	4	MOS1	HM215521
			MOS2	HM215525
			MOS17	HM215551
			MOS42	HM215542
D⋆	158 223 234 274 362	1	MOS10	HM215548
	158 223 234 362	1	MOS43	HM215561
	223 232 362	1	MOS15	HM215524
	86 223 271 338C 362	1	MOS20	HM215554
	223 362	2	MOS21	HM215526
			MOS39	HM215539
	86 223 362	2	MOS44	HM215543
			MOS45	HM215544
D5	42C 163 189 223 242 296 300 362 380	1	MOS27	HM215531
D5a	92 111 129 164 189 223 266 362	1	MOS33	HM215557
	92 111 129 164 179 189 223 266 362	3	MOS29	HM215556
			MOS32	HM215535
			MOS38	HM215559
F1b	189 212 232A 249 304 362	1	MOS6	HM215565
	189 232A 249 304 311 343C	1	MOS12	HM215522
	189 232A 249 304 311 376	1	MOS35	HM215536
	189 304	1	MOS30	HM215533
	189 304 351	1	MOS9	HM215567
	189 232A 249 304 311	2	MOS19	HM215553
			MOS41	HM215560
F2a	185 266G 291 304	1	MOS8	HM215566
	185 266G 291 304 362	1	MOS48	HM215562
F⋆	86 167 304 318	1	MOS24	HM215529
M13	145 148 188 189 223	1	MOS13	HM215550
	145 148 223 381	1	MOS22	HM215527
	145 148 223	1	MOS25	HM215555

Table III. Diversity indices of the 16 populations, based on 360-bp-length sequences (from neighboring populations 16,024–16,383) of HVS-1 region.

Population	$n^{\star}$	$H^{\dagger}$ (SE)	$K^{\ddagger}$	$S^{\P}$	$\Pi^{\S}$ (SE)	θ_k (95% CI)	θ_{π} (SE)	θ_S (SE)
Lahu	15	1.0000 (0.0243)	15	36	8.010 (3.943)	NA	8.010 (4.421)	11.072 (4.343)
Bai	55	0.9960 (0.0046)	50	78	7.343 (3.489)	261.24 (120.82–614.98)	7.343 (3.870)	17.048 (4.941)
Lolo	87	0.9952 (0.0026)	71	91	8.057 (3.778)	178.02 (107.65–303.32)	8.058 (4.185)	18.065 (4.807)
Dai	38	0.9943 (0.0082)	35	59	8.283 (3.924)	209.67 (82.10–597.94)	8.283 (4.360)	14.042 (4.429)
Tujia	96	0.9936 (0.0028)	74	75	7.202 (3.405)	146.21 (93.04–234.45)	7.202 (3.771)	14.602 (3.888)
Hani	80	0.9905 (0.0048)	64	80	7.318 (3.461)	146.38 (87.93–250.76)	7.318 (3.835)	16.151 (4.397)
Tibetan	132	0.9874 (0.0029)	79	79	6.423 (3.061)	82.10 (57.78–117.00)	6.423 (3.389)	14.479 (3.667)
Yao	394	0.9866 (0.0021)	190	117	6.767 (3.196)	143.72 (116.72–176.80)	6.767 (3.535)	17.856 (3.791)
Mosuo	47	0.9843 (0.0083)	35	61	8.047 (3.805)	60.52 (32.95–114.43)	8.047 (4.223)	13.811 (4.188)
Tu	35	0.9832 (0.0112)	27	56	7.538 (3.605)	52.32 (25.74–110.99)	7.538 (4.008)	13.598 (4.370)
Miao	142	0.9832 (0.0048)	97	87	6.482 (3.085)	133.61 (94.15–191.04)	6.482 (3.415)	15.734 (3.910)
Naxi	44	0.9810 (0.0102)	33	61	8.534 (4.021)	58.31 (31.10–112.88)	8.534 (4.465)	14.023 (4.300)
Pumi	35	0.9798 (0.0159)	29	50	7.555 (3.612)	76.87 (35.81–175.48)	7.555 (4.016)	12.141 (3.939)
Jino	18	0.9739 (0.0293)	15	34	7.111 (3.500)	39.68 (14.47–118.30)	7.111 (3.914)	9.885 (3.755)
Lisu	37	0.9520 (0.0171)	20	45	8.413 (3.983)	17.01 (9.03–32.05)	8.413 (4.427)	10.780 (3.498)
Nu	30	0.8483 (0.0363)	8	27	7.120 (3.436)	3.226 (1.409–7.040)	7.120 (3.823)	6.815 (2.426)

$\star$ Sample size; † Haplotype diversity; ‡ Number of different haplotypes; ¶ Number of segregating sites; § Average number of pairwise differences.

history of the Mosuo's matrilocality is also supported by several anthropological studies (Mu 1990; Liu 2004, 2008).

Our previous analyses based on the haplogroup frequency data (Table S1) suggest that Mosuo are most similar to the Naxi, a neighbor in the south. However, that does not mean that the Mosuo share a common maternal ancestor. A detailed mtDNA sequence comparison among populations will be more reliable for population relationship evaluation. We used the Network program for an HVS-1 sequence comparison.

The six major mtDNA haplogroups (B4, B5a, C, D*, D5a, and F1b) encompass over 80% of the Mosuo samples. The origins of these haplogroups may reflect the origins of the founders of the population. A network of these six haplogroups was reconstructed for populations from the region (Figure 2). The branch length between each of the two haplotypes in the network is proportional to the number of mutations (or nucleotide differences) between the individuals with relevant haplotypes. Most populations are scattered all over the network, indicating high diversity in maternal lineages as well as an ancient common ancestors for Sino-Tibetan populations. If the Mosuo (M) was closest to the Naxi (X), as we previously showed, or shared or connected haplotypes are expected between the two populations in Figure 2, we would expect them to share a recent common ancestor. However, no such relationship was seen in the network, strongly arguing against the assumption that the Mosuo and Naxi share a recent common ancestor in their maternal lineages. (NB: A few haplotypes connect the two populations, e.g. B5a, D*, but such connections are indirect or connected to the ancestral haplotype and are therefore not informative). However, most Mosuo haplotypes are shared or connected to Pumi haplotypes (Clades 1–3 in Figure 2). Some are also close to Mien (Clade 4) or Lolo (Clade 5), or found in unique clades (Clades 6 and 7). This provides strong evidence for the affinity between the Mosuo and Pumi in the maternal lineages.
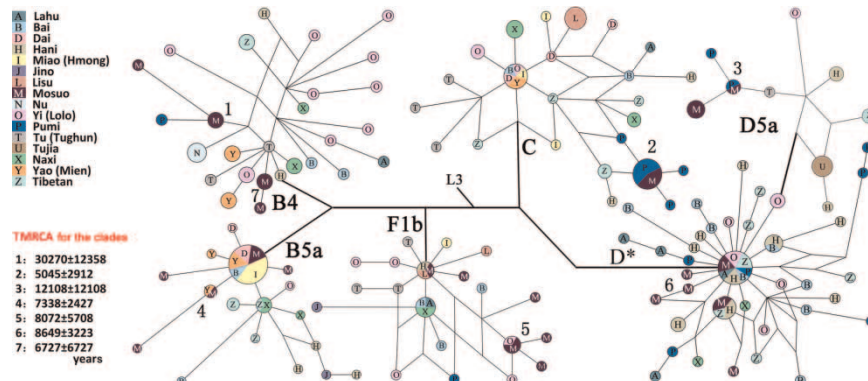

Figure 2. An mtDNA HVS-1 haplotype network of the populations in Southwest China. Note: A, Lahu; B, Bai; D, Dai; H, Hani; I, Miao (Hmong); J, Jino; L, Lisu; M, Mosuo; N, Nu; O, Yi (Lolo); P, Pumi; T, Tu (Tughun); U, Tujia; X, Naxi; Y, Yao (Mien); Z, Tibetan.

Discussion

Inferring origin(s) of a population from modern genetic data is a considerable challenge. In this study, the great distance between the Mosuo and Naxi in the network is inconsistent with similar haplogroup frequencies of the two populations. This indicates that simply comparing haplogroup frequencies among populations is not sufficient in mtDNA data analyses and sometime even results in large bias. A network analysis can offer more details and higher resolution about population relationships. In this case, the close relationship between the Mosuo and Pumi revealed by the network analysis is a more reliable finding. Small sample sizes could underestimate haplogroup percentages, diversity indexes, and TMRCA for a population growing at a constant rate, in theory, because some deep phylogeny branches might be missing. However, the probability of capturing both sides of the basal split in a sample of n lineages is estimated as $(n - 1)/(n + 1)$ (Saunders et al. 1984; Henn et al. 2009). This would mean that there is an 87.5% chance of observing the deepest branching divergence from our smallest sample of the Lahu (15 samples).

The genetic resemblance of the Mosuo and Pumi is supported by other evidence; for example, the two ethnic groups have much in common in terms of culture, language, and clothing (Guo and He 1994). These similarities can be explained as legacies from the common ancestor of the Mosuo and Pumi people. According to our results, most Mosuo maternal lineages share a recent common origin with the Pumi, and share some common origins with other neighbors such as the Lolo. However, the matrilocality of the Mosuo is probably not a legacy from their common ancestor with the Pumi or Lolo, because neither the Pumi nor Lolo have evinced practicing matrilocality recently. It is certainly possible that matrilocality could have been practiced by their common ancestors; however, to explain why only the Mosuo have kept this tradition is difficult under this assumption. The Mosuo are not really isolated from the Pumi or the Lolo, but rather they are quite possibly a part of Pumi. Therefore, the most probable explanation is that Mosuo started matrilocality not long ago, and a possible reason for abandoning patrilocality is the frequent mercantile travels of their men.

Acknowledgements

University, Madurai, Tamil Nadu, India), Pedro Paulo Vieira (Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil), R. Spencer Wells (National Geographic Society, Washington, DC, USA), Janet S. Ziegle (Applied Biosystems, Foster City, CA, USA).

Declaration of interest: The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

References

Andrews RM, Kubacka I, Chinnery PF, Lightowlers RN, Turnbull DM, Howell N. 1999. Reanalysis and revision of the Cambridge reference sequence for human mitochondrial DNA. Nat Genet 23:147.

Bandelt HJ, Forster P, Rohl A. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16:37–48.

Excoffier L, Laval G, Schneider S. 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evol Bioinform Online 1:47–50.

Forster P, Harding R, Torroni A, Bandelt HJ. 1996. Origin and evolution of Native American mtDNA variation: A reappraisal. Am J Hum Genet 59:935–945.

Gottner-Abendroth H. 1999. The structure of matriarchal societies. Revision 21:31–35.

Guo D, He ZW. 1994. The History of Naxi Ethnic Group. Chengdu: Sichuan Minzu Press. 51–56.

He J. 1999. A brief discussion on the essence and existing value of Mosuo culture. Xue Shu Tan Suo [in Chinese] 5(5):60–62.

Henn BM, Gignoux CR, Feldman MW, Mountain JL. 2009. Characterizing the time dependency of human mitochondrial DNA mutation rate estimates. Mol Biol Evol 26(1):217–230.

Jin L, Nei M. 1990. Limitations of the evolutionary parsimony method of phylogenetic analysis. Mol Biol Evol 7:82–102.

Jin L, Su B. 2000. Natives or immigrants: Modern human origin in east Asia. Nat Rev Genet 1:126–133.

Jobling M, Tyler-Smith C. 2003. The human Y chromosome: An evolutionary marker comes of age. Nat Rev Genet 4:598–612.

Li H, Cai XY, Winograd-Cort ER, Wen B, Cheng X, Qin ZD, Liu W, Liu Y, Pan S, Qian J, Tan CC, Jin L. 2007. Mitochondrial DNA diversity and population differentiation in southern East Asia. Am J Phys Anthropol 134:481–488.

Liu SH. 2004. The matriarchy and marriage of Muosuo people. J Southwest Univ Nationalities 25:40–43.

Liu F. 2008. An anthropological interpretation of the family and marriage system of the Mosuo people. J Yunnan Nationalities Univ 25:20–23.

Lum JK, Cann RL, Martinson JJ, Jorde LB. 1998. Mitochondrial and nuclear genetic relationships among Pacific Island and Asian populations. Am J Hum Genet 63:613–624.

Mu Q. 1990. The association of Naxi matrilocal family in Yongning with feudal society. Si Xiang Zhan Xian 5:71–78.

Qin Z, Yang Y, Kang L, Yan S, Cho K, Cai X, Lu Y, Zheng H, Zhu D, Fei D, Li S, Jin L, Li H, Genographic Consortium. 2010. A mitochondrial revelation of early human migrations to the Tibetan Plateau before and after the last glacial maximum. Am J Phys Anthropol 143(4):555–569.

Saillard J, Forster P, Lynnerup N, Bandelt HJ, Norby SS. 2000. MtDNA variation among Greenland Eskimos: The edge of the Beringian expansion. Am J Hum Genet 67:718–726.

Saunders IW, Tavare S, Watterson GA. 1984. On the genealogy of nested subsamples from a haploid population. Adv Appl Probab 16:471–491.

Su B, Xiao J, Underhill P, Deka R, Zhang W, Akey J, Huang W, Shen D, Lu D, Luo J, Chu J, Tan J, Shen P, Davis R, Cavalli-Sforza L, Chakraborty R, Xiong M, Du R, Oefner P, Chen Z, Jin L. 1999. Y-chromosome evidence for a northward migration of modern humans into Eastern Asia during the last Ice Age. Am J Hum Genet 65:1718–1724.

Wen B, Li H, Gao S, Mao X, Gao Y, Li F, Zhang F, He Y, Dong Y, Zhang Y, Huang W, Jin J, Xiao C, Lu D, Chakraborty R, Su B, Deka R, Jin L. 2005. Genetic structure of Hmong-Mien speaking populations in East Asia as revealed by mtDNA lineages. Mol Biol Evol 22:725–734.

Wen B, Li H, Lu D, Song X, Zhang F, He Y, Li F, Gao Y, Mao X, Zhang L, Qian J, Tan J, Jin J, Huang W, Deka R, Su B, Chakraborty R, Jin L. 2004a. Genetic evidence supports demic diffusion of Han culture. Nature 431:302–305.

Wen B, Shi H, Ren L, Xi HF, Li KY, Zhang WY, Su B, Si SH, Jin L, Xiao CJ. 2004b. The origin of Mosuo people as revealed by mtDNA and Y chromosome variation. Sci China C Life Sci 47:1–10.

Wen B, Xie X, Gao S, Li H, Shi H, Song X, Qian T, Xiao C, Jin J, Su B, Lu D, Chakraborty R, Jin L. 2004c. Analyses of genetic structure of Tibeto-Burman populations reveals sex-biased admixture in southern Tibeto-Burmans. Am J Hum Genet 74:856–865.

Xu JS. 2004. The history of Han Chinese folklore (in Chinese). Shanghai: Xue Lin Press.

Yang X, Yang Z, Shi H, Dong Y, Yang J, Zeng W, Gao L, Xiao C. 2004. Y-STR polymorphisms among five Chinese minorities, Mosuo, Mongolian, Naxi, Pumi and Tibetan, in Yunnan Province, PR China. Ann Hum Biol 31:103–111.

Yang K, Zheng HX, Qin ZD, Lu Y, Farina SE, Li SL, Jin L, Li DN, Li H, Genographic Consortium. 2011. Positive selection on mitochondrial M7 lineages among the Gelong people in Hainan. J Hum Genet 56:253–256.

Yao YG, Nie L, Harpending H, Fu YX, Yuan ZG, Zhang YP. 2002. Genetic relationship of Chinese ethnic populations revealed by mtDNA sequence diversity. Am J Phys Anthropol 118:63–76.

Yao YG, Zhang YP. 2002. Phylogeographic analysis of mtDNA variation in four ethnic populations from Yunnan Province: New data and a reappraisal. J Hum Genet 47:311–318.

You Z. 1997. The history of nationalities in Yunnan (in Chinese). Kunming, Yunnan: Yunnan University Press.

Zhong JW, Xiao F. 2008. The history of Chinese folklore (in Chinese). Beijing: People's Press.