

Research Article

Genetic affinity between the Kam-Sui speaking
Chadong and Mulam people

¹Qiong-Ying DENG^{*†} ²Chuan-Chao WANG[†] ¹Xiao-Qing WANG[†]
²Ling-Xiang WANG ²Zhong-Yan WANG ²Wen-Jun WU
²Hui LI^{*} the Genographic Consortium[‡]

¹(Department of Anatomy, Guangxi Medical University, Nanning 530021, China)

²(State Key Laboratory of Genetic Engineering and MOE Key Laboratory of Contemporary Anthropology, School of Life Sciences, Fudan University, Shanghai 200433, China)

Abstract The origins of Kam-Sui speaking Chadong and Mulam people have been controversial subjects in ethnic history studies and other related fields. Here, we studied Y chromosome (40 informative single nucleotide polymorphisms and 17 short tandem repeats in a non-recombining region) and mtDNA (hypervariable segment I and coding region single nucleotide polymorphisms) diversities in 50 Chadong and 93 Mulam individuals. The Y chromosome and mtDNA haplogroup components and network analyses indicated that both Chadong and Mulam originated from the admixture between surrounding populations and the indigenous Kam-Sui populations. The newly found Chadong is more closely related to Mulam than to Maonan, especially in the maternal lineages.

Key words East Asian population, genetic structure, mitochondrial DNA, Tai-Kadai, Y chromosome.

Chadong dialect is a newly discovered Kam-Sui language spoken by some 20 000 people, mainly in Chadong Township, Lingui County, northeastern Guangxi Zhuang Autonomous Region, China. According to inscriptions from the Ming dynasty, Chadong speakers originally came from Qingyuanfu, Nandan County, Guangxi, which is located to the west of the present Chadong region. They were originally sent to the Guilin Prefecture during the Yuan Dynasty to repress the rebellions of local Zhuang and Yao people. The most common surnames in Chadong, such as Xie, Lu, Meng, and Yao, are also frequent in the other Kam-Sui ethnic groups (Li, 2001; Anthony et al., 2008). Now, the Chadong people are mostly registered as Han Chinese. However, they themselves would prefer to identify with the Maonan official ethnicity because of the language similarity and historical records.

Preliminary comparative study shows that the Chadong language should be grouped into the Kam-Sui subfamily of the Daic family. Chadong dialect is closely related to the Maonan and Mulam languages. Maonan

and Mulam languages are both Kam-Sui languages spoken mainly in northern Guangxi by Maonan and Mulao people, respectively (Li, 2001; Anthony et al., 2008). The detailed relationships between the Chadong dialect and surrounding languages have not been systematically analyzed. Therefore, there is not enough evidence to define the ethnic affiliation of Chadong people. To define an ethnic population will be very difficult. Distinctive language may be one of the important criteria. As the Chadong dialect is closely related to the Maonan and Mulam languages, Chadong people may have two choices of an official ethnicity, Maonan or Mulam.

Mulam, with a population of approximately 200 000, is one of the 55 ethnic groups officially recognized by the Chinese government. Nearly 90% of the Mulam people live in Luocheng Mulao Autonomous County, Hechi Prefecture, Guangxi (Wang & Zheng, 1980). The origin of Mulam has been a controversial subject in linguistics and other related fields. Some researchers believed that the Mulam are the descendants of the ancient Ling and Liao tribes that inhabited the region during the time of the Eastern Jin Dynasty, and can be even traced back to *Baiyue* (Wen, 2010). Some researchers simply think that Mulam is a branch of Zhuang. Some genetic studies have also focused on the origin of Mulam. From the patrilineal side, the non-recombining portion of the Y chromosome (NRY) is

Received: 18 October 2012 Accepted: 14 January 2013

[†]These authors contributed equally to this work.

[‡]Members of the Genographic Consortium are listed in the Appendix.

* Authors for correspondence. E-mail: lhca@fudan.edu.cn. Tel.: 86-21-55664574. Fax: 86-21-55664885 (LI). E-mail: yingzideng@sina.com. Tel.: 86-771-5358854. Fax: 86-771-5355801 (DENG).

strictly inherited paternally, and the small effective population size, low mutation rate, sufficient markers, and population-specific haplotype distribution, make it one of the best materials to trace the patrilineal lineage of the population (Jobling & Tyler-Smith, 1995; Underhill et al., 2000). Liu et al. (2006) reported 24 Y chromosomes of Mulam in Xuanwei Township, Majiang County of Guizhou Province, and the frequencies of haplogroup O3*-M122, O3a2c1*-M134, O2a1*-M95 and O2a1a-M88 were 22.2%, 37%, 7.4%, and 25.9%, respectively. The principal component analysis (PCA) suggested this Mulam was closely related to Di-Qiang people (Liu et al., 2006). However, the Guizhou Mulam is actually Mollao of the Kadai subfamily in Tai-Kadai, different from the Guangxi Mulam. Li et al. (2008) reported that the frequencies of haplogroup O1a*-M119, O1a2-M110, and O2a1*-M95 in 40 Y chromosomes of Mulam in Luocheng County, Guangxi were 5%, 25%, and 30%, respectively. The high frequencies of haplogroup O1 and O2a suggested a clear Daic genetic background of Mulam (Li et al., 2008).

Other genetic evidence might also help to resolve these disputes. Similar to NRYs, the maternally inherited mtDNA also lacks recombination and the high mutation rate makes it more likely to generate population-specific mtDNA polymorphisms, which helps to trace the human population maternal lineages in ethnic recognition (Pakendorf & Stoneking, 2005). In this paper, we typed the relevant Y chromosome and mtDNA markers of Chadong and Mulam population samples and gained a better understanding of genetic structures of Chadong and Mulam.

1 Material and methods

1.1 Population samples

Peripheral blood samples of 50 Chadong individuals from Lingui County and 93 Mulam individuals from Luocheng County in Guangxi, China, were collected for this study, with approval from the Ethics Committee of the Fudan School of Life Sciences (Fudan University, Shanghai, China). All subjects were adequately informed and signed consent forms. The subjects were all healthy and not related within three generations.

1.2 Y chromosome markers

The samples were typed through 40 single nucleotide polymorphisms (SNPs) as listed in the latest Y chromosome phylogenetic tree (Karafet et al., 2008; Yan et al., 2011).

Core set: M130, P256, M1, M231, LLY22g, M168, M174, M45, M89, M272, M258, M242, M207,

M217, M9, M96, P125, M304, M201, and M306; haplogroup O: M175, M119, P203, M110, M268, P31, M95, M88, M176, M122, M324, M121, P201, M7, M134, M117, 002611, P164, L127 (rs17269396), and KL1 (rs17276338).

Those binary markers were hierarchically genotyped by SNaPshot (SNaPshot Multiplex Kit; Applied Biosystems, Carlsbad, CA, USA) and fluorescent allele-specific polymerase chain reaction (PCR). The PCR products were also electrophoresed on a 3730xl Genetic Analyzer (Applied Biosystems).

Seventeen Y chromosome short tandem repeats (STRs) (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385a, DYS385b, DYS438, DYS439, DYS437, DYS448, DYS456, DYS458, DYS635, and YGATAH4) were amplified using the AmpFISTR Yfiler PCR Amplification kit (Applied Biosystems). Amplified products were separated and detected using the ABI 3730xl Genetic Analyzer (Applied Biosystems) according to the manufacturer's recommended protocol. The data were analyzed using GeneMapper ID version 3.2 (Applied Biosystems).

1.3 Mitochondrial DNA markers

The hypervariable segment I (HVS-I) region of mtDNA was amplified by the primers L15974 and R16488 (Yao et al., 2002). The PCR products were purified by Shrimp Alkali Enzyme and ExonI (Roche Diagnostics, Shanghai, China). The purified PCR product was sequenced using the Big-Dye Terminator Cycle Sequencing Kit and an ABI 3730xl Genetic Analyzer (both Applied Biosystems). Sequence Analysis 3.3 software was used to extract sequences. The HVS-I sequences were edited and aligned against the revised Cambridge reference sequence (Andrews et al., 1999; van Oven & Kayser, 2009) using DNASTAR software (DNASTAR, Madison, WI, USA). A further 22 polymorphisms in the coding regions of mtDNA (3010, 7598, 663, 10 400, 10 310, 4216, 4491, 12 308, 10 646, 11 719, 4715, 4833, 8271, 5301, 70 287, 13 263, 14 569, 5417, 5178, 12 705, 15 607, and 9824) were also hierarchically genotyped by SNaPshot (Applied Biosystems) as described in our previous published report (Qin et al., 2010). The PCR products were also electrophoresed on the 3730xl Genetic Analyzer. Haplogroup affiliation of each mtDNA sequence was inferred by combined use of the HVS-I motif and diagnostic polymorphisms in the coding regions (Kivisild et al., 2002; Kong et al., 2003).

1.4 Statistical analyses

Networks of Y chromosome STRs and mtDNA HVS-I motifs were constructed by the median-joining

method (Bandelt et al., 1999) using Network version 4.5.1.0 (www.fluxus-engineering.com). Genotype data on Chadong and Mulam were generated in this study. Data pertaining to neighboring populations were obtained from existing published reports (Yao et al., 2002; Yao & Zhang, 2002; Wen et al., 2004a, 2004b). Arlequin 3.11 was used to calculate the Y-STR R_{st} genetic distances (Excoffier et al., 2005). Both PCA and multidimensional scaling (MDS) were carried out using SPSS 18.0 software (SPSS, Chicago, IL, USA).

2 Results and Discussion

2.1 Y chromosomes

According to the nomenclature of Y Chromosome Consortium (Karafet et al., 2008; Yan et al., 2011), 13 SNP haplogroups were determined from the 21 Chadong and 51 Mulam individual samples (Table S1). Although most of the Chadong people are now temporarily registered under the Han ethnicity, their genetic structure is not similar to other Han Chinese populations, with high frequencies of haplogroup O2 and its subhaplogroup O2a1 (Table 1). The dominant haplogroups of Han Chinese, O3a1c-002611, O3a2c1*-M134, and O3a2c1a-M117 (Yan et al., 2011; Wang et al., 2013), only make up relatively small percentages in Chadong (23.8%) and Mulam (11.8%) populations. However, these proportions were probably induced from the recent gene flow from the neighboring Han migrants. The dominant Y chromosome haplogroups of Chadong are C-M130, O2*-P31, and O2a1*-M95, comprising 23.8%, 19%, and 19%, respectively. O1a1-P203 is also a dominant group (up to 29.5%) beside O2a1*-M95 (27.5%) among Mulam samples, and haplogroup O1a is the major haplogroup among the Daic and Western Austronesian populations (Li et al., 2008). Maonan contains an even higher frequency of O2a1*-M95 (56%), but no O1a1-P203. It is noteworthy that haplogroup O1a2-M110, which occurs predominantly among Austronesian peoples of Taiwan, the Philippines, Indonesia, Melanesia, Micronesia, and Near Oceania (Loo et al., 2011; van Oven et al., 2011), was also detected at a moderate frequency in Mulam. Haplogroup C-M130 is distributed widely across East Asia with a low frequency in most

populations except in North Asian Altaic populations (Su et al., 2000). D1 is common in Tibet and neighboring areas, but is very rare in Southeast Asia (Shi et al., 2008). The high frequency of haplogroup C in Chadong and the moderate frequencies of haplogroup D1 among the Chadong and Mulam may result from the genetic drift of certain ancestral contributors to the two populations.

The patrilineal genetic relationships among Chadong, Mulam, and other East Asian populations were discerned with the aid of additional published Y chromosome datasets. We used an MDS analysis based on the R_{st} genetic distance of six common Y-STRs (DYS19, DYS389I, DYS390, DYS391, DYS392, and DYS393) to show the overall clustering pattern of the 21 populations (Fig. 1). The MDS associated Mulam with southern populations, and Chadong also showed a close affinity to some southern populations, especially the Kam-Sui populations. To discern the detailed relationship between the Y-STR haplogroups in Chadong, Mulam, and Maonan, a median-joining network was constructed based on 6-STR haplotypes of O2a1*-M95 individuals in those ethnic groups (Fig. 2). Most Maonan samples are scattered through the network, indicating high diversity in the O2a1* lineage of Maonan. This lineage in Maonan was most likely introduced by recent gene flow from surrounding populations. However, some Mulam haplotypes are in a clade that is connected with the main haplotype of Dong (Kam), and others clustered with Zhuang, Sui, or Pinghua Han. The same pattern was found in the Chadong samples. Some of the Chadong haplotypes are shared with or connected to Dong and Sui haplotypes, and others are close to Zhuang and Mulam. The detailed structure of haplogroup O2a1* also suggests the Chadong is closely related to the Kam-Sui populations.

2.2 Mitochondrial DNA

The most common Chadong haplogroups are B5a, M7b, N9a, R9b1, M7, D5, and F3a, in order of frequency, and the total percentage of these common haplogroups is 52%. In Mulam, the most common haplogroups in order of frequency are F1a, M7b, B5a, M*, N9a, F3a, B4a, C, M9b, and M7b1, comprising 58.70% of the Mulam (Fig. 3, Table S2). The characteristic mtDNA lineages of southern populations,

Table 1 Frequencies of Y chromosome haplogroups in Chadong and Mulam sample populations

Population	Sample size	Haplogroups (%)									
		C	D1	N	O1a1	O1a2	O2*	O2a1*	O3a1c	O3a2c1*	O3a2c1a
Chadong	21	23.8	9.5	4.8	0.0	0.0	19.0	19.0	4.8	9.5	9.5
Mulam	51	2.0	13.7	7.8	29.5	7.8	0.0	27.5	3.9	5.9	2.0

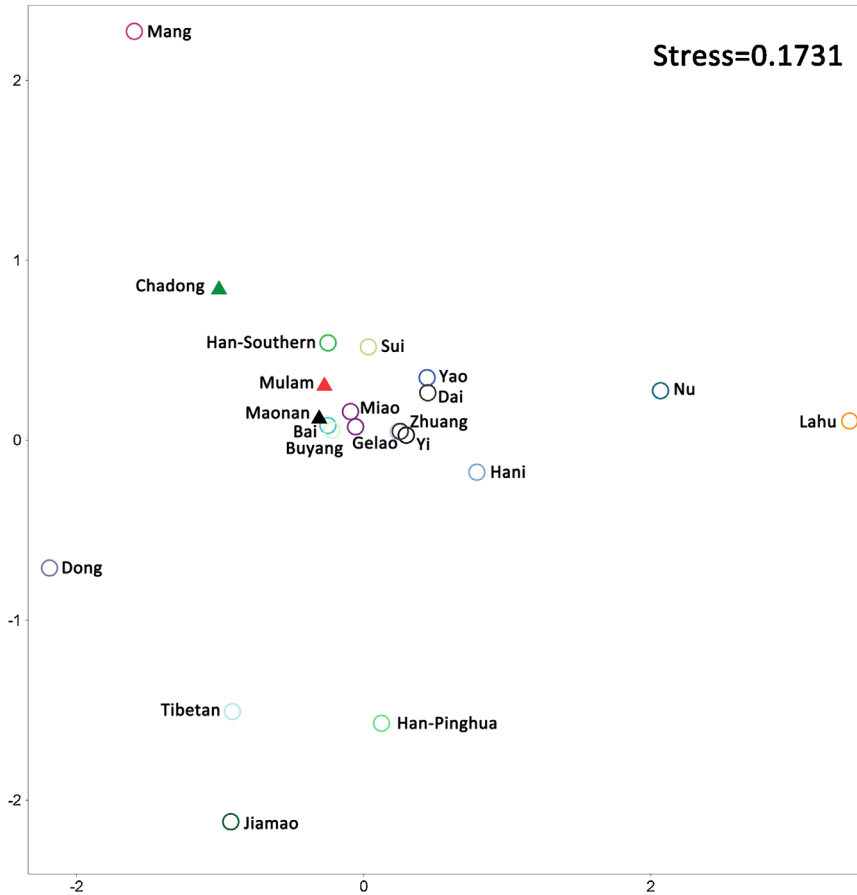


Fig. 1. Multidimensional scaling plot of 21 Chinese populations with R_{st} genetic distances based on six common Y chromosome short tandem repeats.

O2a1*-M95

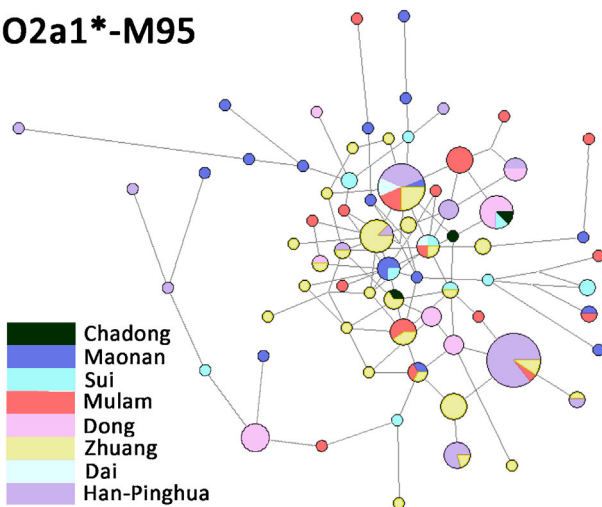


Fig. 2. Median-joining Y chromosome short tandem repeat network of O2a1*-M95 haplogroup. The length of the lines between nodes is proportional to the mutation steps.

such as haplogroups B, F, M7, and R9 (Li et al., 2007), accounted for the majority of matrilineal gene pools of both Chadong (62.00%) and Mulam (60.87%) populations, respectively. The frequencies of haplogroups B, M7, and R9 in the Chadong and Mulam are very similar. However, the frequency of haplogroup F is 28.26% in Mulam, more than double of the proportion in Chadong (14.00%). The high frequency of haplogroup D in Chadong (14.00%) might indicate a gene flow from Hmong-Mien or Tibeto-Burman populations to Chadong.

We used a PCA based on the distribution of mtDNA haplogroup frequencies of 26 populations to show the matrilineal genetic patterns. The distribution was a little discrete but clusters were still observed (Fig. 4). The southern populations formed one cluster in the first PC, and this pattern was mainly owed to haplogroups M7, B, and R9. The second PC resolved a close affinity between Chadong, Yao, and Sui. However, it is interesting and reasonable that Mulam and Maonan in the Kam-Sui linguistic group showed

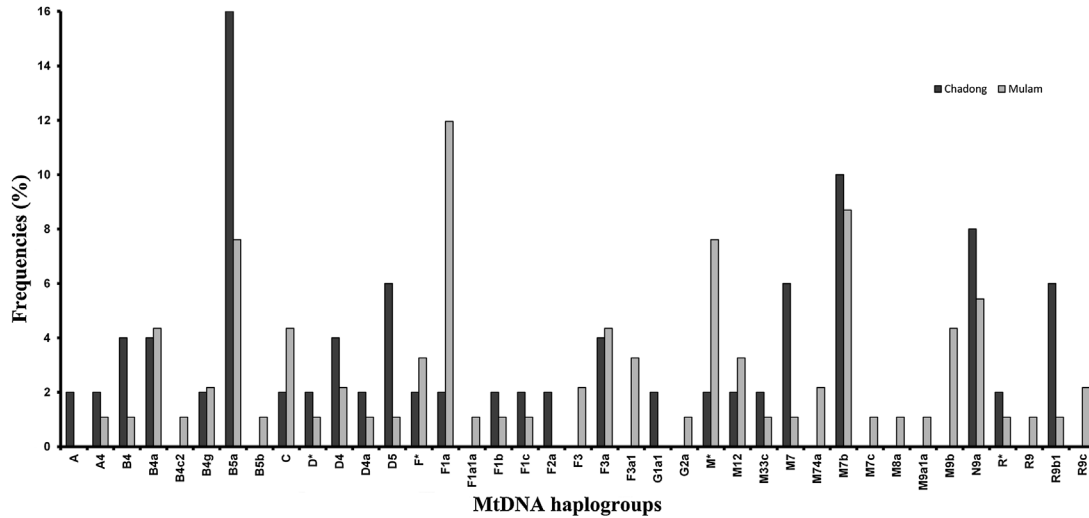


Fig. 3. Frequencies of mtDNA haplogroups of Chadong and Mulam populations.

close affinities with Kam, Sui, and Pinghua Han. It is obvious that Chadong clustered tightly with Mulam, showing more similarities to Mulam than Maonan in the maternal genetic structure.

The language of Chadong is similar to that of Mulam and Maonan; however, the Chadong people themselves believe that they are part of the Maonan minority. From the MDS and PCA results, we cannot yet tell exactly to which population the Chadong is closer. The six major mtDNA haplogroups (B4a, B5a,

F1a, M*, M7b, and N9a) encompass almost half of the Chadong, Mulam, and Maonan samples. The origins of these haplogroups may reflect the origins of the founders of the populations. A network of these six haplogroups was reconstructed for populations from the region (Fig. 5). The branch length between each of the two haplotypes in the network is proportional to the number of mutations between the individuals with the same haplogroups. If shared and/or connected haplotypes between Chadong and Maonan were observed, we would expect them to share a recent common ancestor. However, Chadong and Maonan only clustered together in the N9a haplogroup. Most Chadong haplotypes are shared or connected to Mulam haplotypes, such as in B4a, B5a, M*, and M7b. Especially in B5a, Chadong and Mulam samples formed two exclusive clades. This provides strong evidence for the affinity between the Chadong and Mulam in the maternal lineages. In the network of F1a, most Chadong and Maonan samples cluster with Tibeto-Burman in the center, indicating that most of the Chadong and Maonan people with the F1a haplogroup were derived from the Tibeto-Burman populations. It is noteworthy that some of the basal mtDNA lineages, such as M74 and M33 (Sun et al., 2006; Kong et al., 2011), were also detected in Mulam and Chadong, which might represent the ancient maternal lineages tracing back to the first settlers in South China.

In this study, most of the patrilineal and matrilineal gene pools of both Chadong and Mulam are characteristic lineages of southern China. Some ancient Southeast Asian lineages (Y chromosome haplogroups

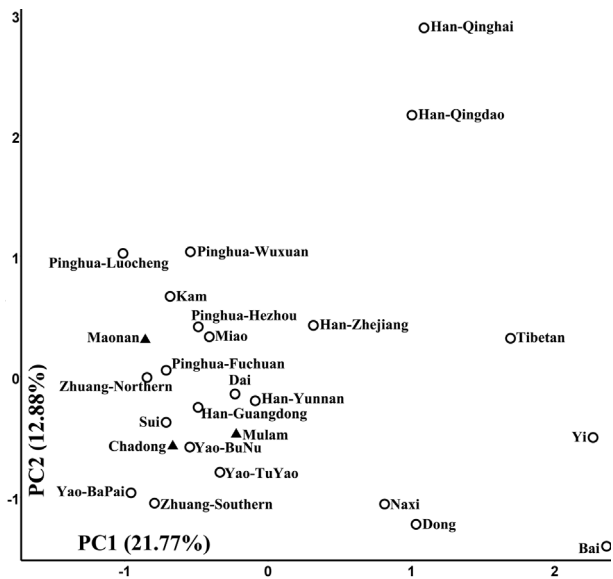


Fig. 4. Principal component analysis (PCA) plot based on mtDNA haplogroup frequencies of 26 Chinese populations.

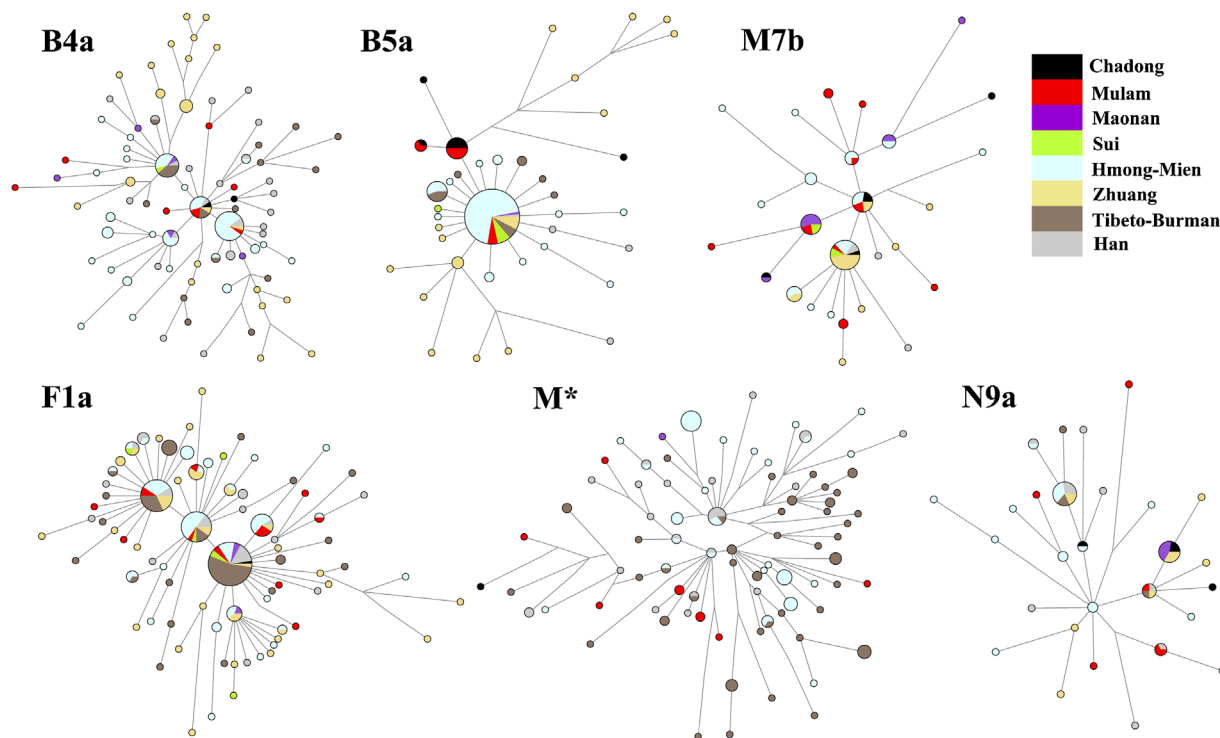


Fig. 5. Mitochondrial DNA hypervariable segment I networks of the six major haplotypes in Chadong, Mulam, and Maonan samples (B4a, B5a, F1a, M*, M7b, and N9a). The length of the lines between nodes is proportional to the mutation steps.

C and D, mtDNA haplogroups M*, M33, M74, and R*) were also identified in Chadong and Mulam. The two populations also showed patterns of the Y chromosome and mtDNA diversities similar to other southern populations, especially Kam-Sui populations, which was actually in accordance with linguistic classification. However, the origins of Chadong and Mulam seem to be much more complex. Recent gene flow from Sino-Tibetan populations is detected in the patrilineal side of Chadong and Mulam, such as haplogroups O3a1c, O3a2c1*, and O3a2c1a, probably through the expansion and dispersal of Han Chinese. From the matrilineal aspect, most mtDNA haplogroups of Chadong and Mulam also clustered together with Hmong-Mien, and obvious gene flow from Tibeto-Burman populations to Chadong was also observed in haplogroup F1a. Taken together, the origins of Chadong and Mulam are mainly results of an admixture between surrounding populations with the indigenous Kam-Sui populations. Within the Kam-Sui populations, Chadong is more closely related to Mulam than to Maonan, especially from the matrilineal side.

Acknowledgements This work was supported by the Natural Science Foundation of Guangxi (Grant No. 2011GXNSFA018240), the National Natural

Science Foundation of China (Grant Nos. 31071098, 91131002), the National Excellent Youth Science Foundation of China (Grant No. 31222030), the Shanghai Rising-Star Program (Grant No. 12QA1400300), the Shanghai Commission of Education Research Innovation Key Project (Grant No. 11zz04), and Shanghai Professional Development Funding (Grant No. 2010001).

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. *Nature Genetics* 23: 147.
- Anthony D, Edmondson JA, Luo YX eds. 2008. *The Tai-Kadai languages*. London: Routledge.
- Bandelt HJ, Forster P, Rohl A. 1999. Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16: 37–48.
- Excoffier L, Laval G, Schneider S. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1: 47–50.
- Jobling MA, Tyler-Smith C. 1995. Father and sons: The Y chromosome and human evolution. *Trends in Genetics* 11: 449–456.
- Karafet TM, Mendez FL, Meilerman MB, Underhill PA, Zegura SL, Hammer MF. 2008. New binary polymorphisms

- reshape and increase resolution of the human Y chromosomal haplogroup tree. *Genome Research* 18: 830–838.
- Kivisild T, Tolk HV, Parik J, Wang Y, Papiha SS, Bandelt HJ, Villems R. 2002. The emerging limbs and twigs of the East Asian mtDNA tree. *Molecular Biology and Evolution* 19: 1737–1751.
- Kong QP, Sun C, Wang HW, Zhao M, Wang WZ, Zhong L, Hao XD, Pan H, Wang SY, Cheng YT, Zhu CL, Wu SF, Liu LN, Jin JQ, Yao YG, Zhang YP. 2011. Large-scale mtDNA screening reveals a surprising matrilineal complexity in east Asia and its implications to the peopling of the region. *Molecular Biology and Evolution* 28: 513–522.
- Kong QP, Yao YG, Sun C, Bandelt HJ, Zhu CL, Zhang YP. 2003. Phylogeny of East Asian mitochondrial DNA lineages inferred from complete sequences. *American Journal of Human Genetics* 73: 671–676.
- Li H, Cai X, Winograd-Cort ER, Wen B, Cheng X, Qin Z, Liu W, Liu Y, Pan S, Qian J, Tan CC, Jin L. 2007. Mitochondrial DNA diversity and population differentiation in southern East Asia. *American Journal of Physical Anthropology* 134: 481–488.
- Li H, Wen B, Chen SJ, Su B, Pramoongjago P, Liu Y, Pan S, Qin Z, Liu W, Cheng X, Yang N, Li X, Tran D, Lu D, Hsu MT, Deka R, Marzuki S, Tan CC, Jin L. 2008. Paternal genetic affinity between Western Austronesians and Daic populations. *BMC Evolutionary Biology* 8: 146.
- Li JF. 2001. Brief introduction of Chadong dialect. *Minority Languages of China* 1: 67–80. (in Chinese)
- Liu X, Shan KR, Qi XL, He Y, Zhao Y, Wu CX, Li CY, Chu X, Ren XL. 2006. Y-SNP analysis of Bouyei, Gelao, Mulao, Maonan, and Zhuang populations in Guizhou. *Hereditas* 28: 1350–1354. (in Chinese)
- Loo JH, Trejaut JA, Yen JC, Chen ZS, Lee CL, Lin M. 2011. Genetic affinities between the Yami tribe people of Orchid Island and the Philippine Islanders of the Batanes archipelago. *BMC Genetics* 12: 21.
- Pakendorf B, Stoneking S. 2005. Mitochondrial DNA and human evolution. *Annual Review of Genomics and Human Genetics* 6: 165–183.
- 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. 2010. A mitochondrial revelation of early human migrations to the Tibetan Plateau before and after the last glacial maximum. *American Journal of Physical Anthropology* 143: 555–569.
- Shi H, Zhong H, Peng Y, Dong YL, Qi XB, Zhang F, Liu LF, Tan SJ, Ma RZ, Xiao CJ, Wells RS, Jin L, Su B. 2008. Y chromosome evidence of earliest modern human settlement in East Asia and multiple origins of Tibetan and Japanese populations. *BMC Biology* 6: 45.
- Su B, Xiao C, Deka R, Seielstad MT, Kangwanpong D, Xiao J, Lu D, Underhill P, Cavalli-Sforza L, Chakraborty R, Jin L. 2000. Y chromosome haplotypes reveal prehistorical migrations to the Himalayas. *Human Genetics* 107: 582–590.
- Sun C, Kong QP, Palanichamy MG, Agrawal S, Bandelt HJ, Yao YG, Khan F, Zhu CL, Chaudhuri TK, Zhang YP. 2006. The dazzling array of basal branches in the mtDNA macro-haplogroup M from India as inferred from complete genomes. *Molecular Biology and Evolution* 23: 683–690.
- Underhill PA, Shen P, Lin AA, Jin L, Passarino G, Yang WH, Kauffman E, Bonn -Tamir B, Bertranpetit J, Francalacci P, Ibrahim M, Jenkins T, Kidd JR, Mehdi SQ, Seielstad MT, Wells RS, Piazza A, Davis RW, Feldman MW, Cavalli-Sforza LL, Oefner PJ. 2000. Y chromosome sequence variation and the history of human populations. *Nature Genetics* 26: 358–361.
- van Oven M, Kayser M. 2009. Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Human Mutation* 30: 386–394.
- van Oven M, H mmerle JM, van Schoor M, Kushnick G, Pennekamp P, Zega I, Lao O, Brown L, Kennerknecht I, Kayser M. 2011. Unexpected island effects at an extreme: Reduced Y chromosome and mitochondrial DNA diversity in Nias. *Molecular Biology and Evolution* 28: 1349–1361.
- Wang CC, Yan S, Qin ZD, Lu Y, Ding QL, Wei LH, Li SL, Yang YJ, Jin L, Li H. the Genographic Consortium. 2013. Late Neolithic expansion of ancient Chinese revealed by Y chromosome haplogroup O3a1c-002611. *Journal of Systematics and Evolution* 51: 280–286.
- Wang J, Zheng GQ. 1980. A sketch of Mulam. Beijing: The Ethnic Publishing House. (in Chinese)
- 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, Xie X, Gao S, Li H, Shi H, Song X, Qian T, Xiao C, Jin J, Su B, Lu D, Chakraborty R, Jin L. 2004b. Analyses of genetic structure of Tibeto-Burman populations reveals sex-biased admixture in southern Tibeto-Burmans. *American Journal of Human Genetics* 74: 856–865.
- Wen YT. 2010. Exploration on the origin of Mulam. *Guangxi Ethnic Studies* 2: 131–135. (in Chinese)
- Yan S, Wang C-C, Li H, Li S-L, Jin L. Genographic Consortium. 2011. An updated tree of Y-chromosome Haplogroup O and revised phylogenetic positions of mutations P164 and PK4. *European Journal of Human Genetics* 19: 1013–1015.
- Yao YG, Kong QP, Bandelt HJ, Kivisild T, Zhang YP. 2002. Phylogeographic differentiation of mitochondrial DNA in Han Chinese. *American Journal of Human Genetics* 70: 635–651.
- Yao YG, Zhang YP. 2002. Phylogeographic analysis of mtDNA variation in four ethnic populations from Yunnan Province: New data and a reappraisal. *Journal of Human Genetics* 47: 311–318.

Supplementary Material

The following supplementary material is available for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12009/supinfo>:

Table S1. Y chromosome single nucleotide polymorphism (SNP) and short tandem repeat (STR) data of Chadong and Mulam samples.

Table S2. Mitochondrial DNA haplogroups and hypervariable segment I (HVS-I) motif of Mulam and Chadong samples.

Appendix I Members of the Genographic Consortium

Janet S. ZIEGLE (Applied Biosystems, Foster City, CA, USA)

Li JIN (Fudan University, Shanghai, China)

Hui LI (Fudan University, Shanghai, China)

Shilin LI (Fudan University, Shanghai, China)

Pandikumar SWAMIKRISHNAN (IBM, Somers, NY, USA)

Laxmi PARIDA (IBM, Yorktown Heights, NY, USA)

Daniel E. PLATT (IBM, Yorktown Heights, NY, USA)

Ajay K. ROYYURU (IBM, Yorktown Heights, NY, USA)

Lluis QUINTANA-MURCI (Institut Pasteur, Paris, France)

R. John MITCHELL (La Trobe University, Melbourne, Australia)

Marc HABER (Lebanese American University, Beirut, Lebanon)

Pierre A. ZALLOUA (Lebanese American University, Beirut, Lebanon)

Syama ADHIKARLA (Madurai Kamaraj University, Madurai, India)

ArunKumar GANESHPRASAD (Madurai Kamaraj University, Madurai, India)

Ramasamy PITCHAPPAN (Madurai Kamaraj University, Madurai, India)

Varatharajan Santhakumari ARUN (Madurai Kamaraj University, Madurai, India)

R. Spencer WELLS (National Geographic Society, Washington DC, USA)

Himla SOODYALL (National Health Laboratory Service, Johannesburg, South Africa)

Elena BALANOVSKA (Research Centre for Medical Genetics, Russian Academy of Medical Sciences, Moscow, Russia)

Oleg BALANOVSKY (Research Centre for Medical Genetics, Russian Academy of Medical Sciences, Moscow, Russia)

Chris TYLER-SMITH (The Wellcome Trust Sanger Institute, Hinxton, UK)

Daniela R. LACERDA (Universidade Federal de Minas Gerais, Belo Horizonte, Brazil)

Fabício R. SANTOS (Universidade Federal de Minas Gerais, Belo Horizonte, Brazil)

Pedro Paulo VIEIRA (Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil)

Jaume BERTRANPETIT (Universitat Pompeu Fabra, Barcelona, Spain)

David COMAS (Universitat Pompeu Fabra, Barcelona, Spain)

Begoña MARTÍNEZ-CRUZ (Universitat Pompeu Fabra, Barcelona, Spain)

David F. SORIA-HERNANZ (Universitat Pompeu Fabra, Barcelona, Spain)

Christina J. ADLER (University of Adelaide, Adelaide, Australia)

Alan COOPER (University of Adelaide, Adelaide, Australia)

Clio S. I. Der SARKISSIAN (University of Adelaide, Adelaide, Australia)

Wolfgang HAAK (University of Adelaide, Adelaide, Australia)

Matthew E. KAPLAN (University of Arizona, Tucson, AZ, USA)

Nirav C. MERCHANT (University of Arizona, Tucson, AZ, USA)

Colin RENFREW (University of Cambridge, Cambridge, UK)

Andrew C. CLARKE (University of Otago, Dunedin, New Zealand)

Elizabeth A. MATISOO-SMITH (University of Otago, Dunedin, New Zealand)

Matthew C. DULIK (University of Pennsylvania, Philadelphia, PA, USA)

Jill B. GAIESKI (University of Pennsylvania, Philadelphia, PA, USA)

Amanda C. OWINGS (University of Pennsylvania, Philadelphia, PA, USA)

Theodore G. SCHURR (University of Pennsylvania, Philadelphia, PA, USA)

Miguel G. VILAR (University of Pennsylvania, Philadelphia, PA, USA)