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ORIGINAL ARTICLE

Forensic and phylogeographic characterisation of mtDNA lineages from Somalia

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Abstract The African mitochondrial (mt) phylogeny is coarsely resolved but the majority of population data generated so far is limited to the analysis of the first hypervariable segment (HVS-1) of the control region (CR). Therefore, this study aimed on the investigation of the entire CR of 190 unrelated Somali individuals to enrich the severely underrepresented African mtDNA pool. The majority (60.5 %) of the haplotypes were of sub-Saharan origin with L0a1d, L2a1h and L3f being the most frequently observed haplogroups. This is in sharp contrast to previous data reported from the Y-chromosome, where only about 5 % of the observed haplogroups were of sub-Saharan provenance. We compared the genetic distances based on population pairwise F_{st} values between 11 published East, Central and North African as well as western Asian populations and the Somali sequences and displayed them in a multidimensional scaling plot. Genetic proximity evidenced by clustering roughly reflected the relative geographic location of the populations. The sequences will be included in the EMPOP database (www.empop.org) under accession number EMP00397 upon publication (Parson and Dür Forensic Sci Int Genet 1:88–92, 2007).

Keywords Forensic genetics · mtDNA · Population data · Somalia · Control region · EMPOP

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Introduction

Somalia is located at the Horn of Africa surrounded by Djibouti to the North, Ethiopia to the west and Kenya to the south. Somalia's eastern border is formed by the Gulf of Aden and the Indian Ocean. Archaeological evidence dates the presence of modern humans on reefs off the Coast of Eritrea about 125,000 years ago [1]. According to the "Out-of-Africa" theory Somalia is accepted as the initial point of human dispersal into the rest of the world that was characterised by two major migration events. A first scenario describes a population migration southbound from the Horn of Africa across the Bab-el-Mandeb strait to the Sinai with subsequent rapid coastal settlements of Asia and Australia [2, 3]. The second migration event is suggested following a northern route through today's Egypt into the Levant [4, 5]. The existence of the northern route is under dispute being only supported by archeological data and not by genetic evidence [6–8].

Unlike the ethnically diverse nations throughout most of Africa, Somalia is largely homogenous with nearly all people identifying themselves as Somali. A remaining portion of 2 % is composed of descendents from Arabs, Persians, Indians and African people from Kenya [9]. The Somalis are typically organised in clans and speak the Somali language that is part of the Cushitic branch of the Afro-Asiatic language family. Ethnic Somalis are mainly concentrated in Somalia but are also found in Ethiopia, Yemen, Kenya, Djibouti and northern parts of Tanzania [10]. An unknown number of Somali refugees and immigrants is also found in the Middle-East, Europe and North America. It is estimated

that around 12,000 Somali individuals currently live in Denmark [10].

According to Y-chromosomal data, Somalis seem more closely related to Ethiopian and North Kenyan Cushitic speaking groups [11]. It has also been established that approximately 80 % of Somali males belong to the Y-chromosomal haplogroup E1b1b1 (previously E3b1) that was most likely introduced into the Somali population about 4,000–5,000 years ago [11, 12]. The ancestors of the Somalis have been living as nomads under isolation for many generations. There is no evidence that Somalia or other north-eastern countries were affected by the Bantu expansion that started approximately 3,500 years ago [11, 13, 14]. Instead, the genetic composition of Somalia is affected by back-migration into Africa from Eurasia and the Arabic Peninsula. Therefore, it seems that especially Somali males, are more closely related to Eurasians than to sub-Saharan African populations [11, 15–17].

Despite a few individual sequences, little is known so far about the mtDNA variation in Somalis [18, 19]. In this study for the first time whole mtDNA control region sequences of 190 unrelated Somali individuals are presented serving as basis for forensic applications.

Material and methods

Samples

A total of 192 unrelated Somali immigrants to Denmark participated in this study, which was approved by the Danish ethical committee (KF-01-037/93 and H-1-2011-081).

Extraction, amplification and sequencing

DNA was extracted from blood samples as described earlier [20] using magnetic beads and a modified protocol on Tecan Freedom EVO robotic devices. The entire mtDNA control region was amplified, sequenced and evaluated using EMPOP recommendations [21, 22] and updated nomenclature guidelines for mtDNA [23]. MtDNA haplotypes were assigned to haplogroups according to the most recent phylogeny (Phylotree, build 13: www.phylotree.org) [24] (Table 1; Table S1).

Investigation for close maternal relatedness using STRs

Individuals with identical mitochondrial haplotypes were further investigated using STR analysis in order to detect unknown, unreported, close maternal relatedness or unintentional repeated analyses of the same individual according to [25]. The STR genotypes were determined using the AmpFISTR Identifiler system (Applied Biosystems, Foster

Table 1 Diversity indices for 3,109 published HVS-1 mtDNA sequences including 190 Somali samples from this study

Population	SOM[a]	SOM	YEM	SOQ	SAU	KEN	LBY	ETH	CAF	CMR	COD	GAB	EGY
No. of samples	190	190	185	65	553	100	129	171	56	363	39	946	312
Reference	This study	This study	Cerny [29]	Cerny [30]	Abu-Amero [28]	Brandstätter [35]	Ottoni [31]	Poloni 2009 [34]	Quintana-Murci [33]	Quintana-Murci [33]	Quintana-Murci [33]	Quintana-Murci [33]	Saunier [32]
No. of haplotypes	114	88	108	17	269	83	20	95	11	81	10	267	204
No. of unique haplotypes	83	53	75	6	192	71	6	56	3	44	4	147	150
Haplotype diversity	0.98	0.98	0.98	0.88	0.99	0.99	0.67	0.99	0.81	0.89	0.8	0.98	0.99
Mean pairwise differences	15.9±7.1	8.2±3.8	7.7±3.6	5.1±2.5	7.1±3.3	9.6±4.4	4.1±2.1	10.3±4.7	6.0±2.9	8.0±3.7	6.9±3.3	9.7±4.5	6.9±3.2

HVS-1 motives span from 16030 to 16370. Length variation around position 16193 was disregarded. The comparison was performed among 12 populations (abbreviated according to the international three-letter code).

[a] Values based on complete CR data

City, CA, USA). Relevant pedigrees were created and evaluated with the software DNA-VIEW (Charles H. Brenner, Oakland, CA, USA) to calculate likelihood ratios (LR) using an in-house database containing Somali allele frequencies. Cut-off values for exclusion scenarios were applied according to [26].

Random match probability

The random match probability was calculated as the sum of squared haplotype frequencies based on mtDNA CR sequences excluding C insertions in length heteroplasmic regions around positions 16193, 309 and 573.

Population-genetic analyses

Molecular diversity indices, pairwise differences between and within populations as well as analysis of molecular variance were calculated using ARLEQUIN version 3.5 [27]. We compared our data to previously published work describing populations in Saudi Arabia [28], Yemen [29], Soqotra (an island belonging to Yemen in the Gulf of Aden) [30], Libya [31], Egypt [32], Central African Republic [33], Cameroon [33], Congo [33], Gabon [33], Ethiopia [34] and Kenya [35]. All sequences were aligned and trimmed to the greatest common range 16030–16193 and 16194–16370. Multidimensional scaling (MDS) analysis was performed to illustrate the inter-population structure. The two-dimensional MDS plot (Fig. 1) was based on the average values of the pairwise population differences (Table S2).

Results

Identification of closely maternally related individuals

Individuals with identical mtDNA haplotypes were investigated for close maternal relatedness using autosomal STRs. As a result, one sequence was excluded from the study as the identical STR genotype suggested unintended double analysis of the same sample. Likelihood ratios were calculated for full and half sibling constellations vs. unrelated for 106 sample pairs with identical CR haplotypes. In 102 cases, the LR calculation did not indicate maternal relatedness (LR<10). In one case, the LR calculation indicated the presence of full siblings (8.39×10^7), and one of the two sequences was excluded from the sample set. In three remaining cases, LR calculation did not indicate the presence of full or half sibling but potentially a more distant relationship ($LR_{Full\ sibling}$—570, 0.36 and 107 and $LR_{Half\ sibling}$—503, 12.6 and 219, respectively); those sample pairs remained in the sample set, which finally resulted in a total set of 190 CR sequences.

Haplotypes and diversity indices

In the dataset of 190 Somali sequences we observed 114 distinct haplotypes of which 83 were unique (Table 1; Table S1). The two most frequent haplotypes belonged to haplogroups L0a1d (eight individuals, 16129A, 16148T, 16168T, 16172C, 16187T, 16188G, 16189C, 16223T, 16230G, 16293G, 16311C, 93G, 152C, 185A, 189G, 236C, 247A, 263G, 315.1C, 523DEL, 524DEL and 553T)

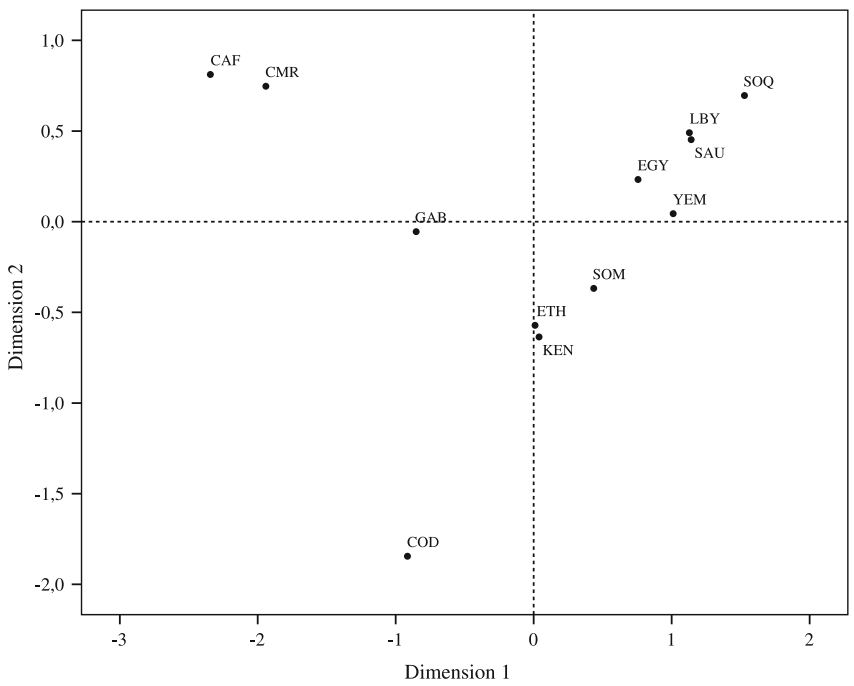

Fig. 1 MDS plot reflecting genetic proximity between the observed populations from Somalia (*SOM*), Saudi Arabia (*SAU*) [28], Yemen (*YEM*) [29], Soqotra (*SOQ*) [30], Libya (*LYB*) [31], Egypt (*EGY*) [32], Central African Republic (*CAF*) [33], Cameroon (*CMR*) [33], Congo (*COD*) [33], Gabon (*GAB*) [33], Ethiopia (*ETH*) [34] and Kenya (*KEN*) [35] based on HVS-1 sequences with a common reading from 16030 to 16370. Length variants around position 16193 were disregarded

Table 2 Haplogroup frequencies of 190 samples from Somalia based on full mtDNA control region sequences (16024-576); haplogroup nomenclature according to Phylotree build 13 [24]

HG	Number	Per cent
HV1b1	3	1.6
K1a	9	4.7
L0a1′4	5	2.6
L0a1a	3	1.6
L0a1d	12	6.3
L0a2a2	1	0.5
L1b1a2a	1	0.5
L2a1*	6	3.2
L2a1a3	8	4.2
L2a1b1	1	0.5
L2a1h	21	11.1
L2b	1	0.5
L3*	7	3.7
L3a	3	1.6
L3b1b	4	2.1
L3d	4	2.1
L3f*	10	5.3
L3f1b	1	0.5
L3f2*	1	0.5
L3f2a	2	1.1
L3h2	9	4.7
L3i1a	1	0.5
L3i2	2	1.1
L3x*	1	0.5
L3x1	4	2.1
L3x1b	1	0.5
L4a1	4	2.1
L4b2	1	0.5
L6	1	0.5
M1*	9	4.7
M1a1*	7	3.7
M1a1d	10	5.3
M1a5	3	1.6
N1a	10	5.3
N1b	8	4.2
N1e′I	1	0.5
R0*	2	1.1
R0a*	6	3.2
R0a1a*	1	0.5
R0a1a2	2	1.1
U3a	3	1.6
U9a	1	0.5

and M1a1d (eight individuals, 16093C, 16129A, 16189C, 16223T, 16249C, 16311C, 16359C, 16519C, 73G, 150T, 189G, 195C, 198T, 263G, 315.1C, 489C, 523DEL and 524DEL). Other frequent haplotypes belonged to haplogroups L2a1h (seven individuals, 16092C, 16183C, 16189C, 16192T, 16223T, 16278T, 16291T, 16294T, 16390A, 73G, 143A, 146C, 152C, 195C, 263G and 315.1C), N1b (six individuals, 16176G, 16223T, 16258C, 16390A, 16519C, 73G, 152C, 263G, 315.1C, 523DEL and 524DEL) and L3h2 (six individuals, 16111T, 16184T, 16223T, 16304C, 16519C, 73G, 150T, 195C, 263G, 315.1C, 318C, 523DEL and 524DEL). Ignoring length variation at positions 16193, 309 and 573, the mean number of pairwise differences between two random Somali individuals was 15.9±7.1 and the probability of two mtDNA sequences being identical was 1.5 %, which corresponds to a power of discrimination of 98.5 %.

Heteroplasmic positions

Heteroplasmic positions were observed in nine samples at eight different positions of which two were well known transversions (16182M and 16183M) and six transitions (16170R, 16187Y, 16301Y, 16311Y, 195Y and 513R). The affected positions were described previously [36] with the exception of 16170 and 513.

Haplogroup distribution

All 190 haplotypes were assigned to haplogroups according to the mitochondrial phylogeny (Phylotree, build 13 [24]). A total number of 42 discernible haplogroups were found in the dataset (Table 2). In total, 60.5 % of the mtDNA haplotypes belonged to the African haplogroups L1–L4 and L6. The remaining 39.5 % were attributed to haplogroups M1 (15.3 %), N1 (10.0 %) and R (14.2 %).

Population comparison

The Somali dataset was compared to a total of 2,919 mtDNA sequences of 11 African and western Asian populations with a common HVS-1 range from 16030 to 16193 and 16194 to 16370. Within this reading frame, the Somali dataset contained 88 different haplotypes 53 of which were unique; 31 of the Somali haplotypes were also found in the other investigated populations. The majority of the observed variance (80.3 %) was attributable to differences within populations, and 19.7 % represented differences among the populations. Intra-population diversity values (expressed as average number of pairwise differences) ranged from 4.1± 2.1 in Libyans to 10.3±4.7 in Ethiopians. The intra-population diversity in the Somalis was 8.2±3.8. Within the MDS plot (Fig. 1), the Somali population clustered with the geographically closest populations from Ethiopia and Kenya. The genetic distances in the MDS plot roughly corresponded to the geographical location of the Somali and the other populations.

Discussion

In the present study, about 60 % of the detected mitochondrial lineages were of ancient African origin (L haplogroups), 25 %

were of Asian provenience (M1 and N1 haplogroups) and roughly 15 % showed West Eurasian background (R, U and K haplogroups). This distribution is in sharp contrast to earlier investigations of the paternal lineages in the same samples. There, according to Y-STR typing only 5 % of Y-chromosomal haplogroups were attributable to sub-Saharan origin [11], whereas the vast majority (85 %) belonged to haplogroup E1b1b1, which is considered to be of North East African origin and to have spread out of Africa by more recent events and a later back migration [37]. This was confirmed by a study that gave a comparable Y-chromosomal haplogroup distribution in Somali immigrants to Norway [38].

The relative contribution of older African mtDNA lineages in surrounding populations is 77 % in Kenya [35], 52 % in southern Ethiopia [34], 46 % in Yemen [28], 36 % in southern Ethiopia [39] and 29 % in Egypt [40] confirming the established trend of decreasing haplogroup L frequencies with a south to north direction in Africa [41]. The relatively high contribution of haplogroup M1(15–18 %) in our Somali dataset, in Egyptians [40] and in the northern populations of Ethiopia [39] with decreasing frequencies further south is consistent with the model of a back-migration of M1 lineages passing the Levant corridor and moving eastbound [42, 43]. Similar distributions were observed within haplogroup N and some of its subhaplogroups that show decreasing frequencies from North to South (Saudi Arabia, 81 % [28]; Egypt, 50–60 % [28, 40]; Yemen, 45–50 % [28, 40]; Northern Ethiopia, 31 % [39]; Somalia, 25 %; Kenya, ~3–6 % [28, 35]; and southern Ethiopia, ~2 % [34]). A total of 19 sequences (10 %) belonged to haplogroups N1a, N1b and N1e′I. Haplogroup N1 was observed with similar frequencies in Egypt (5–9 %) [34, 40], northern Ethiopia (4 %) [39], Yemen (5–8 %) [27, 39] and Saudi Arabia (7 %) [28] but diminished in more southern regions such as southern Ethiopia, Kenya and Tanzania [28, 34, 35].

Also, the haplogroup frequencies of R and U lineages in Saudi Arabia (42 %) [28], Yemen (27–40 %) [28, 39], Egypt (24–29 %) [34, 40], southern Ethiopia (30 %) [34], northern Ethiopia (17 %) [39], Somalia (15 %; this study) and Kenya (3 %) [35] are consistent with the back migration model from the Arabian Peninsula to East Africa. Similarly, the gene flow between both regions is also indicated by the occurrence of HV1b1 in Somalia (albeit represented by a single haplotype), which is reported to be dispersed on the Arabian peninsula [44, 45].

Interestingly, we did not observe any U6 lineages which is reported to be common in North African populations and on the Iberian Peninsula reaching frequencies up to 29 % in Algerian Berbers [46]. Subhaplogroup U6a is dispersed throughout northern Africa, West Africa [47] to the Near East [41, 45, 48]. Excluding sampling bias, the absence of haplogroup U6 in our dataset could reflect a gradient of U6 diminishing to the south, which is supported by its low frequencies in Ethiopia and Kenya (3 and 1 %, respectively [35, 39]).

Forensic genetic implications

The Somali population has a high number of unique mtDNA haplotypes and a high power of discrimination (98.5 %) based on sequencing of the entire mtDNA control region providing a valuable tool for forensic genetic investigations.

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