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mtDNA analysis in ancient Nubians supports the existence of gene flow between sub-Sahara and North Africa in the Nile valley

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Summary. The HpaI (np3,592) mitochondrial DNA marker is a selectively neutral mutation that is very common in sub-Saharan Africa and is almost absent in North African and European populations. It has been screened in a Meroitic sample from ancient Nubia through PCR amplification and posterior enzyme digestion, to evaluate the sub-Saharan genetic influences in this population. From 29 individuals analysed, only 15 yield positive amplifications, four of them (26·7%) displaying the sub-Saharan African marker. Hpa I (np3,592) marker is present in the sub-Saharan populations at a frequency of 68·7 on average. Thus, the frequency of genes from this area in the Merotic Nubian population can be estimated at around 39% (with a confidence interval from 22% to 55%). The frequency obtained fits in a south–north decreasing gradient of Hpa I (np3,592) along the African continent. Results suggest that morphological changes observed historically in the Nubian populations are more likely to be due to the existence of south–north gene flow through the Nile Valley than to *in-situ* evolution.

1. Introduction

During past millennia the Nile valley has been the corridor that connected the Mediterranean world with the sub-Saharan Africa, allowing the movement of people from north to south and vice-versa. Following the progressive desertification of the Sahara from around 10 000 BC, the Nile has become the most important path in north–south migrations in Africa, as it represents a constant source of water. Therefore, the Nile valley was one of the most heavily inhabited areas of antiquity. Consequently, archaeologists have recovered a vast quantity of skeletal material from different sites and periods all along the valley.

Physical anthropologists have attempted to study the peopling of the valley, but conclusions have been sometimes contradictory. Traditionally, some morphological traits have been used to attribute the human samples from the Nile Valley to a 'Caucasoid' or 'Negroid' stock, depending on the predominance of traits that presumably define one or another racial group (Smith and Wood Jones 1910, Berry and Berry 1972, Batrawi 1945, 1946, Vagn Nielsen 1970, Strouhal 1969, 1981). Nasal width, facial prognathism and frontal prominence are the most widely used traits (Greene 1981). The southern populations of the valley have been regarded as being of mainly 'Negroid' type (thus displaying more ' Negroid' traits, especially wide nasal apertures and large prognathism), and the northern as mainly 'Caucasoid' type (Morant 1935). However, in Nubia (a historical region south of the first cataract, and actually included in Egypt and Sudan), the area where the admixture between 'Negroid' and 'Caucasoid' types is more apparent, even in the present-day populations, these racial attributions have sometimes become confusing and controversial.

Roughly, two different hypotheses try to explain the characteristics of the Nubian populations. Several authors (Carlson 1976, Carlson and Van Gerven 1977, Van

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Gerven 1982, Brace, Tracer, Yaroch, Robb, Brandt and Nelson 1993, among others) describe a remarkable degree of temporal biological continuity among Nubian groups. According to these authors, this suggests a long-term regional continuity, at least from the Neolithic. In contrast, other authors emphasized the cultural discontinuities and the morphological changes, supporting a multiple-migratory view of Nubian prehistory (Morant 1935, Crichton 1966, de Villiers 1968).

In this study we have tried to test these two hypotheses, using a simple mitochondrial marker that discriminates between sub-Saharan and North African populations. We have selected an ancient Nubian population from the Meroitic period (fourth to first century BC), to eliminate the major migrations in Egypt associated with the Greek, Roman and Arab expansions, which can obscure the significance of the genetic characteristics of the present-day populations. However, the ancient DNA technique has its own methodological problems that can seriously limit obtaining successful PCR amplications (Pääbo, Gifford and Wilson 1988, Hagelberg, Sykes and Hedges 1989, Horai, Hayasaka, Murayana, Wate, Koike and Nakai 1989, Hagelberg and Clegg 1991, 1993, Handt, Richards, Trommsdorff, Kilger, Simanainen, Georgiev, Bauer, Store, Hedges, Schaffner, Utterman, Sykes and Pääbo 1994a, Handt, Höss, Krings and Pääbo 1964b, Francalacci 1995, among others).

2. Material and methods

2.1. The sample

The sample comes from the Amir-Abdallah site, situated near Abri, between the Second and the Third Cataract, in a narrow curve to the east of the river Nile. The site was excavated during the 1978–81 period, by the Spanish mission in Sudan (financed by the Duran-Vall Llosera foundation). Burials were oriented north–south; each body was fully extended and sometimes placed in a simple wooden coffin. Occasionally the arid climatic conditions of the region have produced a natural mummification of the soft tissues. Five radiocarbon dates, which have yielded ages around 2130–2320 BP, are available (Trancho 1986). This dating places the Amir-Abdallah site in the Meroitic period. Thus, the necropolis was probably inhabited from the third to the first centrury BC.

Twenty-nine samples (12 of cortical tissue from long bones, 16 teeth and one of hair from a mummified individual), mainly from adult individuals, have been selected for ancient DNA analysis (table 1).

2.2. The sub-Saharan African marker

The HpaI African marker corresponds to a point mutation at np3,594 (C > T) of the mitochondrial genome, which creates a recognition site for the Hpal enzyme at np3,592 (Denaro, Blanc, Johnson, Chen, Wilmsen, Cavalli-Sforza and Wallace 1981). Although the polymorphism is located in a coding region, the polypeptide sequence is not altered and therefore, the mutation can be considered to be selectively neutral (Denaro *et al.* 1981).

The Hpa I (np3,592) marker has an extremely high incidence in African populations, especially in those from sub-Saharan areas (table 2), while it is virtually absent in Asia and Europe (Denaro *et al.* 1981, Scozzari, Torroni and Semino 1988, Scozzari, Torroni, Semino, Cruciani, Spedini and Santachiara-Benerecetti 1994, Brega, Mura, Caccio, Semino, Brdicka and Santachiara-Benerecetti 1994, Chen, Torroni, Excoffier, Santachiara-Benerecetti and Wallace 1995). The widespread presence of this marker in the African continent would suggest its ancestral character (Denaro *et al.* 1981),

Table 1. Ancient Nubian samples analyzed in the study.

Specimen	Sample	Age and Sex	Amplification +
1-AM 110·2	Bone	Adult female	+
2-AM 110·1	Bone	Adult female	+
3-AM 110·3	Bone	Infantile	+†
4-AM 170·1	Bone	Adult female	+
5-AM 170·2	Bone	Infantile	
6-AM 170·3	Bone	Infantile	
7-AM 328·0	Bone	Adult male	
8-AM 188·0	Bone	Adult female	
9-AM 110·1	Hair	Adult female	
10-AM 181·0	Bone	Adult female	+
11-AM 176·0	Bone	Adult male	+
12-AM 197·0	Bone	Adult female	+
13-AM 328·0	Bone	Adult male	+
14-AM 339	Tooth	Juvenile male	+†
15-AM 343	Tooth	Adult female	+
16-AM 333	Tooth	Adult female	+
17-AM 100	Tooth	Adult undetermined	+†
18-AM 402	Tooth	Adult undetermined	
19-AM 418	Tooth	Adult undetermined	
20-AM 303	Tooth	Adult female	
21-AM 269	Tooth	Adult male	
22-AM 362	Tooth	Adult female	+
23-AM 370	Tooth	Adult female	+†
24-AM 313	Tooth	Infantile	
25-AM 397	Tooth	Adult male	
26-AM 291	Tooth	Adult female	+
27-AM 253	Tooth	Juvenile	
28-AM 189	Tooth	Adult male	
29-AM 343	Tooth	Adult female	

† Specimens with the Hpa I (np3,592) sub-Saharan African marker.

perhaps attributable to a proto-khoisan stock (Scozzari *et al.* 1988), prior to the divergence of Khoisan and Negroids (Scozzari *et al.* 1994). Using the intragroup mtDNA sequence divergence (mtDNA evolution rate of 2·2–2·9%/Myr), Chen *et al.* (1995) estimated an age of 98 000–130 000 years BP for the haplogroup L, characterized by the HpaI site gain at np3,592. Hpa I (np3,592) is present in around 90–100% of Khoisan and Pygmies (Denaro *et al.* 1981, Soodyall and Jenkins 1992, Johnson, Wallace, Ferris, Rattazzi and Cavalli-Sforza 1983, Chen *et al.* 1995), while in northern populations, such as Senegal and Cameroon, it diminishes to around 60–80% (Scozzari *et al.* 1988, 1994, Graven, Passarino, Semino, Boursot, Santachiara-Benerecetti, Langaney and Excoffier 1995) (figure 1). The present-day Arabian population from Israel displays Hpa I (np3,592) at a frequency of 12·8% (Bonné-Tamir, Johnson, Natali, Wallace and Cavalli-Sforza 1986). The residual presence of Hpa I (np3,592) in some European populations (such as 4·4% in Sicilian individuals) is tentatively attributed to the introduction of African slaves during the Roman period, or to the presence of a sub-Saharan African genetic component in the Moslem settlers (Semino, Torroni, Scozzari, Brega, DeBenedictis and Santachiara-Benerecetti 1989).

In populations from other continents, for example Asia or America (Denaro *et al.* 1981, Brega, Gardella, Semino, Morpurgo, Astaldi-Ricotti, Wallace and Santachiara-Benerecetti 1986a), far from possible African contacts, the HpaI (np3,592) marker is always absent.

Table 2. Absolute values of the HpaI morph 3 (np3,592) haplotype in populations from Africa, Europe and Asia.

	n	HpaI (np3,592)	Percentage
Africa			
Bushmen (San) (Botswana) (1)	41	38	92·68
Sekele (San) (Namibia) (2)	49	46	98·88
Nama (Khoikhoi) (Namibia) (2)	46	35	76·09
!Kung (Botswana) (3)	34	33	97·06
Aka Pigmies (Central African Republic) (1)	44	42	95·45
Pigmies (Central African Republic) (18)	17	17	100·00
Pigmies (Zaire) (18)	22	22	100·00
Bantús (Zulú and others) (South Africa) (1)	48	34	70·83
Kwengo (Namibia) (2)	10	8	80·00
Bantu (South Africa) (3)	40	28	70·00
Wolof (Senegal) (4)	110	71	64·55
Peuls (Senegal) (4)	47	32	68·09
Tukolor (Senegal) (4)	12	9	75·00
Others (Senegal) (4)	17	9	52·94
Mandenka (Senegal) (13)	119	93	78·15
Bamileke (Cameroon) (5)	77	48	62·34
Bakaka (Cameroon) (5)	18	8	44·44
Herero (Namibia) (6)	54	6	11·11
Dama (Namibia) (6)	43	15	34·88
Ambo (Namibia (6)	22	16	72·73
Total sub-Saharan Africa	831	571	68·71
Jews (Ethiopia) (7)	57	24	42·11
Jews (Morocco) (7)	22	1	4·55
Total Africa	910	596	65·49
Near east			
Jewish Ashkenazi (Israel) (7)	75	2	2·66
Arabs (Israel) (7)	62	8	12·90
Total	137	10	7·30
Asia			
Jews (Turkey) (7)	8	0	0·00
Jews (Iraq) (7)	26	0	0·00
Jews (Yemen) (7)	65	0	0·00
Jews (Habban, Arabia) (7)	17	0	0·00
Asiatic (China, Taiwan, Japan) (1)	48	0	0·00
Thauru (Nepal) (8)	91	0	0·00
Total	255	0	0·00
Europe			
Caucasoids (Europe and USA) (1)	54	0	0·00
Caucasoids (Europe) (3)	50	0	0·00
Sicilians (Italy) (9)	90	4	4·44
Sardinians (Italy) (10, 11)	134	0	0·00
Romans (Italy) (10, 11)	87	1	1·15
Calabrians (Italy) (12)	60	0	0·00
Czechoslovakia (14)	64	0	0·00
Italia (north) (14)	99	0	0·00
Italia (center) (14)	28	0	0·00
Italia (north) (15)	103	0	0·00
Lithuanian (16)	155	0	0·00
Finnish (17)	110	0	0·00
Total	1034	5	0·48

(1): Denaro *et al.* 1981; (2); Soodyall and Jenkins 1992; (3): Johnson *et al.* 1983; (4): Scozzari *et al.* 1988; (5): Scozzari *et al.* 1994; (6): Soodyall and Jenkins 1993; (7): Ritte *et al.* 1993; (8): Brega *et al.* 1986a; (9): Semino, Torroni, Scozzari, Brega, De Benedictis and Santachiara-Benerecetti 1989; (10): Brega, Scozzari, Maccioni, Iodice, Wallace, Bianco, Cao and Santachiara-Benerecetti 1986b; (11): Santachiara-Benerecetti, Scozzari, Semino, Torroni, Brega and Wallace 1988; (12): De Benedictis, Rose, Caccio, Picardi and Quagliariello 1989; (13): Graven *et al.* 1995; (14): Brega *et al.* 1994; (15): Sartoris, Varelto, Migone, Cappelo, Piazza, Ferrara and Ceppellini 1988; (17): Kucinskas 1994; (17): Vilkki, Savontaus and Nikoskelainen 1988; (18): Chen *et al.* 1995.

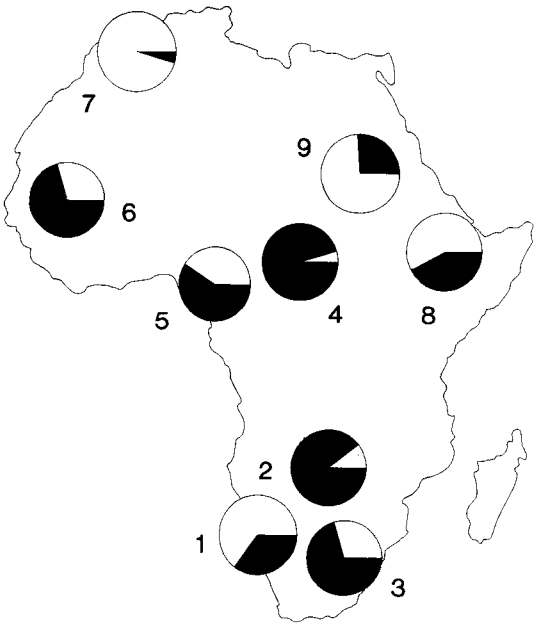

Figure 1. Frequencies of HpaI (np3,592) marker (in black) in African populations, grouping them by geography and ethnic affinities. **1:** Populations of Namibia; Kwengo, Herero, Dama and Ambo (Soodyall and Jenkins 1992, 1993); **2:** Khoisan populations; San, Nama. !Kung (Denaro *et al.* 1981, Soodyall and Jenkins 1992, Johnson *et al.* 1983); **3:** Bantu-speaking populations from South Africa (Denaro *et al.* 1981, Johnson *et al.* 1983); **4:** Pigmies (Denaro *et al.* 1981, Chen *et al.* 1995); **5:** populations of Cameroon (Scozzari *et al.* 1994); **6:** Senegalese populations (Scozzari *et al.* 1988, Graven *et al.* 1995), **7:** Jews from Morocco (Ritte, Neufeld, Prager, Gross, Hakim, Khatib and Bonné-Tamir 1993); **8:** Jews from Ethiopia (Ritte *et al.* 1993), **9:** Meroitic Nubian population from Amir (present study).

2.3. DNA extraction

DNA has been extracted from 29 ancient samples, following the procedure of Hagelberg and Clegg (1991) and Hagelberg (1994), slightly modified. The treatment of the teeth is a modification of that of Ginther, Issel-Tarver and King (1992). The detailed methodology of DNA extraction and amplification can be found elsewhere (Lalueza 1995, 1996).

Teeth were immersed in 15% hydrochloric acid and ethanol, and posteriorly irradiated 10–15 min under UV light (254 nm). The surfaces of the bone specimens (approximately 1–2 g of cortical bone) were removed using a Sandblaster (CIE Dentalfarm). Both teeth and bone samples were ground in a cryogenic impact grinder (Spex Industries Inc.) and the powder obtained was washed with 0·5 M EDTA pH 8·0; 10 ml of lysis buffer, containing 8·5 ml 0·5 M EDTA pH 8·0–8·5, 1 ml 5% SDS, 0·5 ml 1 M Tris and 100 µl proteinase K (1 mg/ml), was added to the tubes containing the samples and incubated overnight at 37°C with agitation. After this the tubes were centrifuged for 5 min at 2000 rpm, and the supernatant extracted twice with phenol/chloroform (1 : 1) and finally only with chloroform. The 10 ml of the resultant sample were concentrated and purified using Centricon-30 microconcentrators (Amicon Inc.), for 30 min at 4000 rpm. The final volume obtained was 100–500 µl.

2.4. DNA amplification

Two blank controls (a control extract amplification and a no-template PCR control) were performed, to check for contamination in the reagents. The first control was obtained by adding distilled water to the extraction buffer and following the procedure of extraction. The second control was made with no DNA template in the amplification, to monitor any possible contamination of the PCR reagents.

Samples were run as a 25 µl reaction mix containing 0·5–1·5 units of Taq DNA Polymerase (Perkin-Elmer Cetus), 10 × reaction buffer, 25 mM $MgCl_2$ (2·5 mM, final concentration), 200 µM of each dNTP, 200 pM of each primer and 1 µl of the DNA extract. Samples were denatured, annealed and extended at 94°C, 55°C and 72°C, respectively. The process was repeated for 35 cycles, each step lasting 1 min, except for the first denaturation, which lasted 5 min. To screen for the Hpa I (np3,592) mitochondrial marker, one pair of primers delineating the region has been designed (L3556 (Anderson, Bankier, Barrell, deBruijn, Coulson, Dronis, Eperon, Nierlich, Ree, Sanger, Schrier, Smith, Standen and Young 1981); 5′-CTCACCATCGCTCTTC-3′, H3630; 5′-AACGGCTAGGCTAGAG-3′). The region amplified was only 109 bp in length; owing to the high level of fragmentation of the ancient DNA, described by several researchers (Handt *et al.* 1994b, Pääbo *et al.* 1988), this small length is likely to give good positive results.

2.5. Restriction enzyme digestion and gel electrophoresis

Unpurified PCR product (17–20 µl) were incubated overnight at 37°C with the addition of 5 units of the Hpa I enzyme. The product was electrophoresed through a 3% NuSieve low-melting agarose gel for 2–3 h, stained with ethidium bromide and visualized with UV light. The digestion of the PCR product (presence of the Hpa I sub-Saharan marker) yields two bands in the gel (of 50 and 59 bp), while in the absence of digestion only one band of 109 bp is observed.

3. Results

Only 15 individuals, which corresponds to 51·7% of the total sample, have been successfully amplified (table 1). The low efficiency of amplification of the Nubian remains can be attributed to the antiquity of the site and/or to the arid environmental conditions, probably not favourable to the preservation of ancient DNA in bones. Seven samples (46·6% of the amplified specimens) have been analysed twice in the same laboratory, all yielding the same results and thus confirming the reproducibility of the analysis. In addition, we have attempted to amplify a 228 bp D-loop region for sequencing, with negative results in all samples.

Four of the amplified samples displayed the mutation at np3,594 and, consequently, were digested by the Hpa I enzyme at position 3,592. Thus, the proportion of individuals with the sub-Saharan African marker is approximately 26·7% (allelic frequency of 0·267 ± 0·114) in the Amir Abdallah population. A confidence interval can be computed; the resulting values of allelic frequency range from 0·153 to 0·381. Although the sample size is recognized to be small, the frequency obtained is concordant with a broad geographic gradient in the African continent (sub-Saharan Africa, 68·7%; Ethiopian (Jews), 42%; Israeli Arabs, 12·9% (see figure 1).

3.1. Contamination

The appearance of false-positive reactions is one of the main problems in ancient DNA studies, favoured by the damage of the DNA template in the ancient samples

and the sensitivity of the PCR technique (Hagelberg, Sykes and Hedges 1989, Francalacci 1995). However, the adoption of different precautions can minimize the risk of contamination (Brown and Brown 1992, Handt *et al.* 1994b, Hagelberg 1994). In our laboratory we maintain a clear physical separation of working areas and material between pre-PCR and post-PCR phases, in order to prevent carry-over contamination. During the study of the Nubian samples all PCR controls were negative. Thus, the existence of reagent contamination can be discarded. Also the existence of Nubian individuals with the sub-Saharan African marker supports the reliability of our results, since the remains were exclusively handled by Europeans during the excavation, and the laboratory work was undertaken by a European researcher who lacks the np3,592 Hpa I marker.

4. Discussion

The degree of genetic admixture in ancient Nubia can be estimated using the model of Bernstein (1931), from two parental populations (A and B, with a gene frequency of P_A and P_B, respectively). The proportion of these genes in the population resulting from the admixture of A and B is P_M. From this,

$$P_M = MP_A + (1 - M)P_B$$

$$P_M = P_B + M(P_A - P_B)$$

$$M = P_M - P_B/P_A - P_B$$

where M is the proportion of migrant genes. When the allele used in this model is absent in one parental population and is present at high frequencies in the other, the model is a good approximation to the M value (Cavalli-Sforza and Bodmer 1971). In the case of Nubia, $P_B = 0{\cdot}00$ (initial frequency of HpaI in Nubia, considering it initially as a Caucasoid population), $P_A = 0{\cdot}69$ (average frequency of HpaI (n 3,592), in present-day populations from sub-Saharan Africa) and $P_M = 0{\cdot}27$ (the frequency of HpaI observed in the sample from Amir Abdallah site in Nubia), then $M = 0{\cdot}27/0{\cdot}69 = 0{\cdot}39$. Thus, the proportion of migrant genes in Nubia during the Meroitic period could be as high as 39% (with a confidence interval from 55% to 22%). To estimate P_A the present-day data have been used. The frequency of Hpa I (np3,592) in sub-Saharan populations at the Meroitic period is obviously unknown. However, due to the ancestral character of this marker, it can be hypothesized that it might have been very high in ancient times, possibly similar to that observed in present-day populations. Also, the original populations from which the gene flow or the migration took place are unknown; thus the best approximation is to consider the average frequency of all available sub-Saharan samples. On the other hand, the value obtained for M seems concordant with the intermediate 'Negroid–Caucasoid' characteristics described in skeletal and present-day Nubian populations at morphological level (Trancho 1986).

Although the sample size successfully amplified is small, the presence of the Hpa I (np3,592) marker in the Amir-Abdallah site is an interesting result that suggests the existence of a south–north gene flow along the Nile Valley, at least during or before the Meroitic period. In absence of selection the presence of these individuals in this site must be attributed to the entrance of genes from sub-Saharan Africa, which has produced a geographic genetic gradient. Arranging the available African populations roughly distributed along the direction of the Nile rive (figure 2), a progressive decreasing of the HpaI (np3,592) marker from South Africa to Europe

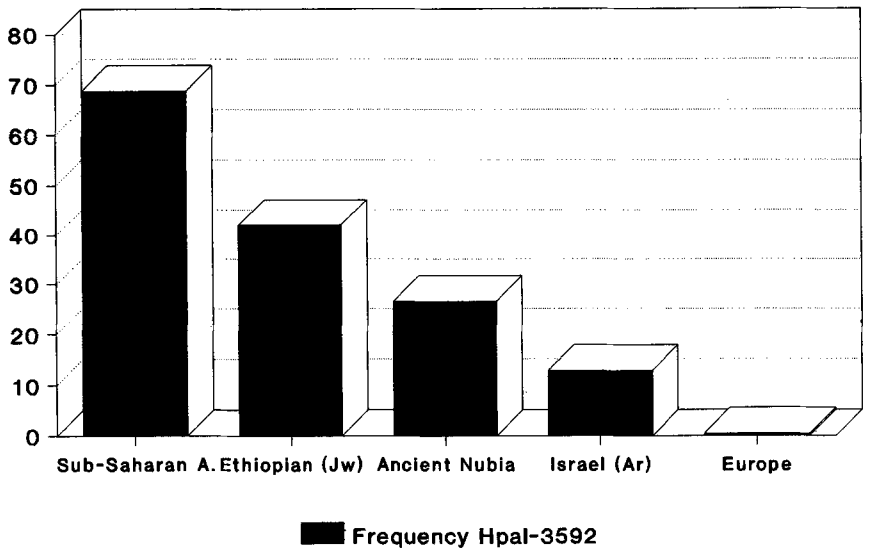

Figure 2. Frequency of Hpa I (np3,592) in African populations roughly arranged along a hypothetical south–north line. References are listed in Table 2; the Nubian data correspond to the present study.

can be observed. Although data for Ethiopian Jews are only available from East Africa, this Jewish community shows a clear genetic affinity to other Ethiopians, as estimated by nuclear genome analyses (Zoossmann-Diskin, Ticher, Hakim, Goldwitch, Rubinstein and Bonné-Tamir 1991). Ethiopian Jews are probably a local group that converted to Judaism and, thus, represent a good estimate of HpaI (np3,592) in Ethiopia.

At the morphological level (e.g. in the skin colour or the nasal index), a similar geographic gradient is also observable in present-day populations. According to the data of the HpaI (np3,592) mitochondrial marker, it seems that this morphological cline in the Nile Valley is more likely to be due to migration and gene flow from sub-Saharan Africa, than to the result of selection operating through the action of solar radiation on people who were already there. Our results are also compatible with a counter-current movement southwards by Caucasian mitochondrial types. However, the present-day distribution of the HpaI (np3,592) marker suggests that the migration up from sub-Saharan Africa associated to the desertification of the Sahara is the most feasible explanation. Obviously, it should be interesting to study the HpaI (np3,592) marker in a set of populations (both ancient and modern) along the Valley, to better characterize this genetic cline. The screening of this simple genetic marker is potentially of great interest in ancient DNA studies, and can shed new light on the patterns of human movements between sub-Saharan Africa and the Mediterranean world.

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Zusammenfassung. Der mitochondriale DNA-Marker HpaI (np3, 592) ist eine selektionsneutrale Mutation, die bei afrikanischen Bevölkerungen aus sub-saharischen Regionen häufig vorkommt, während sie bei nordafrikanischen und europäischen Populationen fast völlig fehlt. Um den genetischen Einfluss sub-saharischer Bevölkerungen auf eine meroitische Stichprobe aus dem ehemaligen Nubien zu analysieren, wurde die Stichprobe mittels PCR-Amplifikation und späterer enzymatischer Aufspaltung auf diesen DNA-Marker untersucht. Lediglich bei 15 von 29 analysierten Individuen war die Amplifikation erfolgreich, vier von ihnen (26·7%) wiesen den für sub-saharischen Regionen spezifischen Marker auf. Damit läßt sich die Genfrequenz dieses Markers in meroitischen nubischen Populationen aus dieser Region auf ca. 39% schätzen (mit einem Konfidenzintervall von 22% bis 55%). Die beobachtete Frequenz passt zu einem in Süd-Nord-Richtung abnehmenden Gradienten von HpaI (np3, 592) entlang des afrikanischen Kontinents. Die Ergebnisse legen nahe, dass die historisch beobachteten morphologischen Veränderungen in nubischen Populationen vermutlich eher durch die Existenz eines Genflusses von Süd nach Nord durch das Niltal erklärt werden können, als durch lokale Evolutionsprozesse.

Résumé. Le marqueur HpaI (np3, 592) d'ADN mitochondrial est une mutation sélectivement neutre, très commune en Afrique sub-saharienne alors qu'elle est presque absente en Afrique du Nord et en Europe. Elle a été identifiée dans un échantillon méroïtique de l'ancienne Nubie par amplification PCR puis digestion enzymatique, et étudiée afin d'évaluer les influences génétiques sub-sahariennes dans cette population. Des 29 individus analysés, seulement 15 ont fourni des amplifications positives, quatre d'entre-eux (26·7%) présentant le marquer africain sub-saharien. Le marquer HpaI (np3, 592) est présent dans les populations sub-sahariennes avec une fréquence moyenne de 68·7%. Les gènes de cette origine dans la population méroïtique de Nubie peuvent donc être estimés voisins de 39% (avec un intervalle de confiance de 22% à 55%). La fréquence obtenue s'insére harmonieusesment dans un gradient sud-nord de HpaI (np3, 952) traversant le continent africain. Ces résultats suggèreraient que les changements morphologiques observés historiquement dans les populations nubiennes, seraient plus vraisemblablement le fait d'un flux génique orienté sud-nord dans la vallée du Nil, que d'une évolution *in-situ*.