

Original Research Article

History in the Interpretation of the Pattern of p49a,f *TaqI* RFLP Y-Chromosome Variation in Egypt: A Consideration of Multiple Lines of Evidence

S.O.Y. KEITA*

National Human Genome Center at Howard University, and Department of Anthropology,
Smithsonian Institution, Washington, DC 20060

ABSTRACT The possible factors involved in the generation of p49a,f *TaqI* Y-chromosome spatial diversity in Egypt were explored. The object was to consider explanations beyond those that emphasize gene flow mediated via military campaigns within the Nile corridor during the dynastic period. Current patterns of the most common variants (V, XI, and IV) have been suggested to be primarily related to Middle Kingdom and New Kingdom political actions in Nubia, including occasional settler colonization, and the conquest of Egypt by Kush (in upper Nubia, northern Sudan), thus initiating the Twenty-Fifth Dynasty. However, a synthesis of evidence from archaeology, historical linguistics, texts, distribution of haplotypes outside Egypt, and some demographic considerations lends greater support to the establishment, before the Middle Kingdom, of the observed distributions of the most prevalent haplotypes V, XI, and IV. It is suggested that the pattern of diversity for these variants in the Egyptian Nile Valley was largely the product of population events that occurred in the late Pleistocene to mid-Holocene through the First Dynasty, and was sustained by continuous smaller-scale bidirectional migrations/interactions. The higher frequency of V in Ethiopia than in Nubia or upper (southern) Egypt has to be taken into account in any discussion of variation in the Nile Valley. *Am. J. Hum. Biol.* 17: 559–567, 2005. © 2005 Wiley-Liss, Inc.

Biological anthropologists and geneticists have increasingly either used “history” or what might be called historicizing disciplines (e.g., archaeology, historical linguistics, and climatology) to help interpret patterns of population genetic variation, or have even undertaken to “write” a form of history using biological data as the primary evidence; migration is a major theme in many of the latter efforts. Using historical evidence, including models based on historical events, to explain a current pattern of diversity means considering various alternative scenarios, and therefore the construction of various narratives. Neglecting a strong inference approach, which in effect means not considering alternative hypotheses, is likely to weaken a research program. The construction of narratives as a primary focus is not consciously associated with *current* biological anthropology, which usually examines populations with statistical hypothesis-testing in assessing population variation and similarities. However, many of the explanations offered in population

biology for particular genetic findings very much involve writing a form of narrative.

The use of historical data to explain a genetic pattern in the linear space of the Nile Valley was undertaken by Lucotte and Mercier (2003a), who suggested that bidirectional north-south clinal variation in Egypt for the p49a,f *TaqI* Y restricted fragment length polymorphism (RFLP) haplotypes V, XI, and IV (Table 1) is likely primarily “related” to specific military campaigns during and after the Middle Kingdom, as also suggested by Krings et al. (1999) for patterns of mtDNA variants. The events suggested to have brought together northern and southern populations having different Y genetic profiles for these variants are 1) the Egyptian campaigns against and/or

*Correspondence to: S.O.Y. Keita, National Human Genome Center at Howard University, Cancer Center #615, Howard University Hospital, 2041 Georgia Ave. NW, Washington, DC 20060.

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TABLE 1. Summary of most common p49a,f Taq I Y-chromosome haplotypes in Egyptian regions¹

Region (n)	Haplotypes and percentages						
	IV	V	XI	VII	VIII	XI	XV
Lower Egypt (162)	1.2	51.9	11.7	8.6	10.5	3.7	6.8
Upper Egypt (66)	27.3	24.2	28.8	4.6	3.0	0.0	6.1
Lower Nubia (46)	39.1	17.4	30.4	2.2	2.2	0.0	0.0

¹From Lucotte and Mercier (2002).

colonization of lower Nubia during the Middle and New Kingdoms (respectively, primarily Dynasties XII, ca. 1991–1785 BC, and XVIII, beginning ca. 1490 BC), and 2) the Kushite conquest of Egypt, which created Dynasty XXV (ca. 730–655 BC). Migration events were described for other detected variants having low frequency; the presence of haplotypes XII and XV in Egypt, found at their greatest frequencies in Europe (Lucotte and Loirat, 1999), was associated with interactions during later periods.

The object of this paper is to enlarge the discussion on the reasons for the observed patterns in Egypt for the most common p49a,f TaqI RFLP variants (V, XI, and IV) as found by Lucotte and Mercier (2003a). This issue will be explored in three ways: 1) by examining the nomenclature used to describe haplotypes, which can be taken to imply their geographical or ethnic origins; 2) by considering a range of evidence relevant to understanding the probable haplotype spatial variation in the Nile Valley before the Middle Kingdom; and 3) by integrating evidence from other kinds of Y-chromosome markers, specifically those that define lineages by biallelic markers (Hammer and Zegura, 2002). The commendable sampling strategy of Lucotte and Mercier (2003a) makes this presentation possible. It will be argued that the specific military events noted by Lucotte and Mercier (2003a) were contributory to, but not the only or even primary causes of, the basic observed patterns. Evidence from historical linguistics, archaeology, and genetics will be considered. The approach taken is to examine early Egypt from multiple perspectives in order to construct alternative narratives that account for the data as currently understood.

HAPLOTYPE AFFILIATION, APELLATIONS, AND DISTRIBUTIONS

The TaqI haplotypes of the Y-chromosome, designated by numerals, are uniparentally

inherited through males, and are not known or thought at this time to be influenced by interaction with the X-chromosome. These variants are restriction fragment length polymorphisms (RFLPs) determined by a probe described in Ngo et al. (1986), located on the nonrecombining portion of the Y-chromosome. Some TaqI haplotypes have arisen more than once, and therefore other information may be required to fully understand population relationships.

The haplotype prevalence and diversity in regions near Egypt, and/or ethnic groups historically originating in them, are suggested to be useful in assessing directions of gene flow (Lucotte and Mercier, 2003a,b). This is because it is generally assumed that the place of higher frequency in a clinal distribution is the likely source, although this may not always be true. The importance of using various lines of evidence, including comparative population data when available, cannot be overstated. Haplotype frequencies compiled and calculated from the literature are given in Tables 1 and 2A,B. They form the basis of this presentation.

The most common variants found in different studies of Egypt collectively are, in descending frequency, V, XI, IV, VII, VIII, XV, and XII (Table 2A). Haplotype V, called "Arabic" by Lucotte and Mercier (2003a), declines from lower Egypt (north) to lower Nubia (south), as do VII, VIII, XV, and XII (Table 1). Given the historical nature of the presentation of Lucotte and Mercier (2003a), the term "Arabic" suggests a southwest Asian origin for V. In contrast, haplotypes XI and IV, called "southern," with IV labeled "sub-Saharan," have their lowest frequencies in lower (northern) Egypt, but increase in upper (southern) Egypt and lower Nubia; there is no statistically significant difference in frequencies between the latter two regions for the haplotypes studied (Lucotte and Mercier 2003a).

TABLE 2A. Frequencies of *p49a,f* *TaqI* Y-chromosome haplotypes in selected African and Near Eastern countries, based on published data

Country (n)	Haplotypes and percentages						
	IV	V	XI	VII	VIII	XII	XV
Egypt (274) ¹	13.9	39.4	18.9	6.6	7.3	2.2	5.5
Lebanon (54) ²	3.7	16.7	7.4	20.4	31.5	5.6	1.9
Palestine (69) ²	1.4	15.9	5.8	13.0	46.4	0.0	4.3
Iraq (139) ³	1.4	7.2	6.4 ³	20.1	36.0	1.4	0.7
Egypt (52) ⁴	7.7	40.4	21.2	9.6	7.7	3.8	1.9
Libya (38) ⁴	7.9	44.7	10.5	0.0	5.3	13.2	0.0
Algeria (141) ⁴	8.5	56.7	5.0	1.4	7.1	4.2	5.0
Tunisia (73) ⁴	0.0	53.4	5.5	4.1	2.7	26.0	2.7
Morocco (102) ⁴	0.98	57.8	8.8	4.9	7.8	0.98	10.8
Mauretania (25) ⁴	8.0	44.0	8.0	0.0	4.0	0.0	0.0
Supra-Saharan (composite) (505) ⁴	4.4	55.0	7.7	3.2	6.3	7.1	4.2
Ethiopia (composite) (142) ⁵	0.0	45.8	26.1	0.0	16.9	0.0	0.0

TABLE 2B. *TaqI* *p49a,f* Y-chromosome haplotype frequencies in more restricted populations from Horn, supra-Saharan Africa, and Near Eastern origin, from published data

Population (n)	Haplotypes and percentages						
	IV	V	XI	VII	VIII	XII	XV
Falasha (38) ⁵	0.0	60.5	26.3	0.0	0.0	0.0	0.0
Ethiopians, non-Falasha (104) ⁵	0.0	40.4	25.9	0.0	23.1	0.0	0.0
Berbers (Morocco) (74) ⁴	1.4	68.9	2.8	1.4	6.8	4.1	0.0
"Sephardic" Jews (381) ²	8.4	18.6	6.8	19.9	34.1	4.2	2.1
"Oriental" Jews (56) ²	1.8	8.9	0.0	7.1	78.6	0.0	1.8
"Near Eastern" Jews (27) ⁶	0.0	7.4	0.0	7.4	85.1	0.0	0.0
Ashkenazi Jews (256) ²	0.0	3.1	15.2 ⁷	22.7	24.6	9.0	10.9

¹Lucotte and Mercier (2003a).²Lucotte and Mercier (2003b).³al-Zahery et al. (2003); haplotype XI here is documented from two biallelic lineages.⁴Lucotte et al. (2000).⁵Lucotte and Smets (1999).⁶Lucotte et al. (1996).⁷Haplotype XI in groups admixed with Northern Europeans is usually affiliated with haplogroup R1; in Africa, it is usually associated with haplogroup E (al-Zahery et al., 2003).

Haplotype V is found in very high frequencies in supra-Saharan countries and Mauretania (collective average, 55.0%) and in Ethiopia (average, 45.8% for reported groups). Its highest prevalence to date is in samples from specific populations: Ethiopian Falasha (60.5%) and Moroccan Berbers (68.9%). Haplotype V's frequency is considerably lower in the Near East, and decreases from west (Lebanon, 16.7%) to east (Iraq, 7.2%) (Table 2A). The appellation "Arabic" for V is therefore misleading, because it suggests an origin external to Africa that is not supported by the evidence. In fact, this variant was called African by Lucotte et al. (1993, p. 839; 1996, p. 469), as well as "Berberian" (Lucotte et al., 2001, p. 887). Significantly, it was convincingly argued by

these same researchers and their associates that because the Falasha (the "black Jews" of Ethiopia) have such a high frequency of V and XI and none (yet found) of VII and VIII, this shows them to be "clearly of African origin" and to have adopted Judaism (Lucotte and Mercier, 2003b, p. 669; Lucotte and Smets, 1999). This is in contrast to their being the descendants of males from immigrant Near Eastern Jewish communities.

Given these findings, it is more accurate to call V "Horn-supra-Saharan African" (or simply African), not "Arabic;" it is indigenous to Africa. The first speakers of Arabic, a Semitic language, came into Africa from the Near East. Using the same logic as applied to the Falasha, supra-Saharan Africans are pri-

marily Arabic-speakers due to language shift, and not settler colonization, since high frequencies of VII and VIII collectively characterize the indigenous core Arabic-speaking peoples of the Near East, and Jews also (Table 2A, B) (Lucotte and Mercier, 2003b; al-Zahery et al., 2003; Lucotte et al., 1993, 1996; Santichiara-Benerecetti et al., 1993). It is important to establish the biogeographical origin of V for the populations in this discussion.

There is further Y-chromosome evidence from a phylogeographic perspective for the biohistorical Africanity of haplotype V. Although unfortunately not assessed by Lucotte and Mercier (2003a), biallelic markers define clades (Hammer and Zegura, 2002) that can be associated with the *TaqI* p49a, f variants (e.g., al-Zahery et al., 2003; Semino, personal communication). These markers are found on the nonrecombining portion of the Y-chromosome, and transmitted through male lineages. Haplotype V is associated with the M35/215 (or 215/ M35) subclade, as is XI (in Africa), and IV with the M2/PN1/M180 lineage, both of the YAP/M145/M213 cluster. These lineages that in Africa subsume haplotypes V, XI, and IV are joined by a transition mutation: "Most notably the PN2 transition... unites two high frequency subclades, defined by M2/PN1/M180 mutations in sub-Saharan Africa, and M35/215 in north and east Africa" (Underhill et al., 2001, p. 50; see also Cruciani et al., 2002). It is of great interest that the PN2 clade or family indicates that numerous African populations with diverse morphologies (skin colors, physiognomies, body builds, and hair forms) share ancient common male ancestry with each other, before they share ancestry with groups from other regions who are grossly more similar anatomically.

The geography of these haplotypes and their associated lineages notably overlap the spatial distributions of specific language phyla, and this is postulated here to have implications for patterns of Y diversity in the Egyptian Nile Valley. The haplotype V and XI data can be related to the spatial range of the Afroasiatic linguistic phylum, which a cautious interpretation of the evidence suggests most likely originated in, and had its primary history in, Africa; only one member (Semitic) is found in southwest Asia (the Near East) (Bender, 1975; Greenberg, 1966, 1973; Fleming, 1974;

Diakonoff, 1981, 1998; Ruhlen, 1987; Blench, 1993; Nichols, 1997; Ehret, 1984, 1995, 2000). The spatio-temporal interpretation by Underhill et al. (2001, p. 51) of the PN2/M35 lineage corresponds to the core range of Afroasiatic (East Africa north to Egypt and west to Mauretania): "We suggest that a population with this subclade of the African YAP/M145/M213/PN2 cluster expanded into the southern and eastern Mediterranean at the end of the Pleistocene." ('Southern' here refers to northern Africa.) Also, "a Mesolithic population carrying Group III lineages with M35/M215 mutation expanded northwards from sub-Saharan to north Africa and the Levant" (Underhill et al., 2001, p. 55; see also Bosch et al., 2001; Bar-Yosef, 1987).

Haplotype IV, on the M2/PN1 subclade, is notably found in west, central, and subequatorial Africa in speakers of the Niger-Congo (Niger-Kordofanian) languages, and also at noteworthy frequency in at least one group of Nilosaharan speakers: Nubians, some Afroasiatic speakers, and upper Egyptians, who have linguistically shifted branches within Afroasiatic (ancient Egyptian/Coptic to Semitic). The three major language phyla of Africa are thought to have originated in supraequatorial Africa (Blench, 1993; Ehret, personal communication); hence there is no geographical problem in terms of proximity to the Sahara.

Haplotype XI has its highest frequencies in the Horn and the Nile Valley, and also has an African origin in this region. This haplotype has arisen independently several times in different regions, as indicated by its affiliation with lineages defined by different biallelic markers (e.g., al-Zahery et al., 2003; Passarino et al., 2001; Semino, personal communication).

A careful, critical reading of the *data* presented in the published literature reinforce these Y-chromosome findings, although samples are frequently small and not spatially comprehensive, for understandable reasons. The following discussion is based on data in Lucotte and Smets, 1999; Lucotte and Mercier, 2003a,b; Lucotte et al., 2000, 2001; Underhill et al., 2001; Nebel et al., 2002; Manni et al., 2002; Luis et al., 2004; Cruciani et al., 2004; and Semino et al., 2002, 2004. The major interest here is in assessing the data in order to understand the likely *original* frequencies, or those at different time depths, in order to understand

different levels of history, to borrow a concept from Braudel (1982). It was found that the ancestral state of the M35 (or 215/M35) subclade is found only in East Africa, including the Horn. The major downstream mutations within this subclade are M78 (found in the Horn, Egypt, and Maghreb) and M81 (found in the Maghreb, predominantly among Amazigh (Berber) speakers). M78 was also found in the Levant and the Aegean/Balkan region, and over time, variation in this lineage has emerged as indicated by other markers; it is not clear how much of this latter variation may have emerged before the lineage went with migrants from Africa. There are also other 215/M35 lineages, e.g., M123. In Egypt, haplotypes VII and VIII are associated with the J haplogroup, which is predominant in the Near East proper (al-Zahery et al., 2003; Semino et al., 2004), and has a high frequency in some samples from northern Egypt (e.g., Luis et al., 2004). Other studies are interpreted as showing a spatial continuity with populations in the Near East for the living Egyptian population, which is not unexpected, but this is apparently due to gene flow into a preexisting population in the Nile Valley, and not settler colonization of the proto-Egyptian population from Asia Minor (see Y chromosome data in Manni, 2003, and previously cited work). Gene flow connects biopopulations, regions, and ethno-social units, thereby conferring "new" ancestries. Documentable populations and individuals from the Near East and Europe at various times have settled in Egypt throughout post-Middle Kingdom history. On the whole, the diversity of non-African lineages would be expected to be greatest in northern Egypt generally, but there may also have been selective places of settlement in upper Egypt.

DISCUSSION

The high prevalence of V in Ethiopia, south of Egypt, alone would seem to indicate that movements associated with Dynasty XII and XVIII Egyptian military colonizations are not necessarily sufficient explanations for frequencies in lower Nubia (which is statistically the same as upper Egypt). Ethiopian (and Falasha) frequencies are higher than in upper Egypt. Leaving aside the notably lower frequencies of the other haplotypes, and the likely migrations asso-

ciated with them (Lucotte and Mercier, 2003a), what other interactions may help explain the patterns of the distributions of V, XI, IV, VII, and VIII in Africa and southwest Asia (the Near East)? What were their pre-Middle Kingdom frequencies in the Egyptian Nile Valley, and what events may have helped shape them? It is hypothesized that processes involving migration and interactions are the major mechanisms that account for the haplotype patterns, and that prevalence locates their most parsimonious geographical sources, assuming a minimal number of unusual founder, expansion, or extinction events.

The distribution and high prevalence of haplotype V (and less so, XI; in the Nile Valley primarily) and Afroasiatic speakers in Africa correspond with the geography of the Horn-supra-Saharan arc. The spread of the language phylum and genes may illustrate the concept of kin-structured migration (Fix, 1999), with founder effect in some instances (e.g., high frequency in Moroccan Berbers).

In the Nile Valley, V (and XI) may have been established with early Afroasiatic speakers, whose reconstructed vocabulary on available evidence suggests that they were hunters and intensive plant users, not food producers (for a discussion of cultural reconstruction from language, see Ehret, 1984, 1988, 2000; Blench, 1993; Ehret et al., 2004). Interestingly this subsistence pattern characterizes a late Paleolithic site from Wadi Kubanniya in southern Egypt (Wetterstrom, 1993) and subsequent Epipaleolithic sites. Early Afroasiatic speakers, along with those of Nilosaharan, were likely drawn into the early less arid Sahara (see below).

A moister, more inhabitable eastern Sahara was colonized in the late Pleistocene-early Holocene, after a long near-absence of people associated with a long period of aridity (Wendorf and Schild, 1980; Hassan, 1988; Ehret, 1993; Midant-Reynes, 2000; Wendorf et al., 2001). The people drawn into the Sahara were not likely to have been biologically or linguistically homogeneous, if the ethnographic present can be used to form an analogy, as well as the research results of historical linguistics. A dynamic diachronic interaction consisting of the fusion and fission of populations can easily be envisioned in the fluctuating environment of the Holocene Sahara, where oases

can be conceptualized as a kind of refugia supporting populations that interacted intermittently, perhaps at ceremonial centers like Nabta Playa (Wendorf et al., 2001), and making decisions about group relationships and mate exchanges. This situation describes that of a metapopulation under environmental pressure, perhaps causing selection and drift: the Sahara could be modeled as an evolutionary processor and pump of people who over time lost most of its population, and whose subsegments contributed significantly to circum-Saharan regions (Keita, 1990). This metapopulation-evolution dispersal model would explain aspects of culture and biology, but simulation studies would help improve its parameters.

Stimulated by mid-Holocene droughts, migration from the Sahara contributed populations and/or cultures to the Nile Valley (Hassan, 1988; Kobusiewicz, 1992; Wendorf and Schild, 1980; Wendorf et al., 2001; Kobusiewicz et al., 2004); the predynastic of upper Egypt and later Neolithic in lower Egypt show clear Saharan affinities. It is noteworthy that archaeological evidence indicates an occupation hiatus in the Egyptian Nile Valley between 10,000–6000 BC (Midant-Reynes, 2000), which might mean that some peoples went into the Sahara (with some of their descendants later returning). A striking increase in pastoralists' hearths are found in the Nile Valley dating to between 5000–4000 BC (Hassan, 1988). There is evidence for shared culture between Sudan and Egypt in the Neolithic (Kroeper, 1996). Post-Neolithic/predynastic population growth, as based on extrapolations from settlement patterns (Butzer, 1976), would have led to relative genetic stability. The population of Egypt at the end of the predynastic is estimated to have been greater than 800,000 (Butzer, 1976), but was not evenly distributed along the valley corridor, being most concentrated in locales of important settlements. The Egyptian population continued to grow, and it is not likely that incursions by a few thousand soldiers would have had a recoverable impact, unless there had been some systematic policy-driven effort to foster gene flow, for which there is no evidence.

Interactions between Nubia and Egypt (and the Sahara as well) occurred in the period between ~4000–~3000 BC. Some items of material culture were shared in the phase (called Naqada I) between the

Nubian A-group and upper Egypt (~3900–3650 BC). There is good evidence for a zone of cultural overlap and therefore a basis for social interaction (Wilkinson, 1999, after Hoffman, 1982; and citing evidence from Needler, 1984; Williams, 1986; Adams, 1996).

There is a caveat for lower Egypt. If the initial Neolithic/predynastic northern Egyptian populations were characterized by relatively higher frequencies of VII and VIII (from Near Eastern sources), then immigration could have actually brought more V and XI from Saharan sources in the later northern Neolithic, or even via immigration from upper Egypt. The ancient Egyptians interpreted their unifying king, Narmer (either the last of Dynasty 0, or the first of Dynasty I), as having been upper Egyptian and moving from south to north with victorious armies (Gardiner, 1961; Hassan, 1988; Wilkinson, 1999), although this "unification" may not have involved a military campaign. However, it remains true, based on archaeological evidence, that southern predynastic culture, the basis of the dynastic Egypt, had moved north by the end of the predynastic period (Bard, 1994), regardless of the amount of population emigration.

It is possible that the current VII and VIII frequencies reflect, in the main, movements during the Islamic period (vs. the Neolithic) and the effects of polygamy (Salem et al., 1996; Nebel et al., 2002), as well as some of the impact of Near Easterners who settled in the delta at various times in ancient Egypt (Gardiner, 1961), and even more recently in the colonial era due to political events. Cosmopolitan northern Egypt is less likely to have a population representative of the core indigenous population of the most ancient times.

Dynasty I brought the political conquest (and cultural extirpation or absorption?) of the A-group Nubian kingdom Ta Seti by Egyptian kings (Wilkinson, 1999). It is important to note that Ta Seti (or Ta Sti, or Ta Sety) was the name of the southernmost nome (district) of upper Egypt recorded in later times (Gardiner, 1961). Egypt continued activities in Nubia in later Dynasty I (Wilkinson, 1999; Emery, 1961). A different reading of the documents interpreted as indicating the defeat of Nubia by Dynasty I Egyptian kings is that these rulers were defending Nubian allies who had assisted them in consolidating Egypt from attacks

by other Nubians (Trigger, 1976; for the hypothesis of a more direct Nubian intervention in predynastic upper Egypt, see also Williams, 1986). Over the dynastic period, Nubians were continuously brought into Egyptian armies as mercenaries, sometimes even to fight other Nubians (Trigger, 1976). There was steady Nubian contact, especially in upper Egypt. In later times, kings or leaders from the south, with southern armies and sometimes Nubian mercenaries, restored unity to Egypt; this was the case for the Dynasty XI rulers who made possible the Middle Kingdom, and whose pharaohs subsequently also raided Nubia (as noted by Lucotte and Mercier, 2003a), establishing forts there. However, Middle Kingdom forts did not hold large populations (Trigger, 1976), and therefore likely had little population impact.

The New Kingdom (which was made possible by Dynasty XVII southern upper Egyptians who expelled the Hyksos) later conquered and effectively colonized lower and upper Nubia to the fourth cataract for 500 years. There was an Egyptianization of Nubian elites that later extended to the masses, and Egyptians were even settled deep in upper Nubia (central Sudan) (Trigger, 1976); some Nubians came or were brought to upper Egypt. In contrast to this New Kingdom colonization, the Nubian control of Egypt was less than 100 years, and there was no program of settler colonization. *Given the Egyptian vs. Nubian actions, it is striking how small the percentage of haplotype V in Nubia is, vs. IV and XI in upper Egypt (Table 1), if these military events alone are viewed as being responsible for extant regional genetic profiles.*

Taking a long and synthetic view, one compelling scenario is as follows: Afro-asiatic-speaking populations, who can be inferred to have had predominantly, but not only, haplotype V (and XI), and Nilosaharan speakers (mainly haplotypes IV and XI) became established in the eastern Sahara and Nile Valley after the postglacial maximum. The Egyptian valley was apparently abandoned for some reason between 10,000–6000 BC; some peoples may have gone into the Sahara, and others into the Levant. Perhaps at the beginning of this period, or near it (Bar-Yosef, 1987), marks when pre-Neolithic migrants with haplotype V would have established pre-*proto-Semitic* in the Levant, whose descendant *Semitic* became prominent via language shift in

populations with VII and VIII; the later Common *Semitic* (CS) was spoken by an agricultural population (Diakonoff, 1998). Early Amazigh speakers in the northern Sahara in this model would have gone west.

Later, mid-Holocene climatic-driven migrations led to a major settlement of the valley in upper Egypt and Nubia, but less so in lower Egypt, by diverse Saharans with haplotypes IV, XI, and V. These people fused with the indigenous valley peoples, as did Near Easterners with VII and VIII, but perhaps also some V. With population growth, the genetic profiles would have become stabilized. Nubian and upper Egyptian proximity (and on some level, shared culture), Nubia's possible participation in Egyptian state-building and later political absorption in Dynasty I, and ongoing interactions before the Middle Kingdom provided the circumstances for ongoing social intercourse and gene flow. This would have created or reinforced a basic similarity that likely existed at the beginning of the predynastic between groups that were ethno-linguistically and initially politically distinct. The evidence suggests that some Nubians became Egyptians, and vice versa. Considering all of this, the later military migrations suggested by Lucotte and Mercier (2003a) would have mildly reinforced a basically established genetic profile, but would not have been its primary cause.

This interpretation has explanatory power for the mtDNA variant patterns of Krings et al. (1999), who also considered these military invasions as primary explanations of the north-south distribution of variants that they geographically labeled to indicate origin (of emergence). Their calculated coalescence dates would fit with the Saharan metapopulation-evolution dispersal model, which does not attempt to account for the ultimate geographical origin of all genetic variation. Notably, no artistic or textual evidence indicates that Egyptian or Nubian women formed a significant part of the armies of their societies (Baines, personal communication), and furthermore, even if they did, it is not likely that they would have allowed themselves to be impregnated by enemies to the degree that would account for the observed patterns. Nor can it be assumed that they would have left their children in foreign countries. There is also no evidence that any women accompanying male armies would have remained in the foreign territories to make genetic contributions.

In conclusion, late Pleistocene, early and mid-Holocene, and Dynasty I population movements that can be related to language family dispersals, droughts, and Nile Valley settlement, respectively, as well as mating patterns, social interactions other than warfare, and the effects of state-level conflicts, should all be integrated into discussions of Nile Valley biopopulation history. It is hypothesized that the events of the early settling of the Nile Valley and interactions through Dynasty I, and ongoing population growth, likely had as much of a role in generating the Nile Valley profile for the p49a,f *TaqI* Y haplotypes as did events in the Middle Kingdom and later. In this view, these later events, while contributory, were not the primary determinants of the patterns now observed.

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