GENETICS, EGYPT, AND HISTORY: INTERPRETING GEOGRAPHICAL PATTERNS OF Y CHROMOSOME VARIATION[1]

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I

Modern Egypt, the site of Africa's earliest state, lies near the crossroads of two other continents, and has had historic interactions with all its neighboring regions. This alone would make it an ideal place to study historical population biology. Egypt can also be conceptualized as a linear oasis in the eastern Sahara, one that traverses several regions of Africa. An oasis can be a way station or serve as a refugium, as well as be a place of settlement with its own special biological and cultural adaptive strategies. Both of these perspectives—crossroads and oasis/refugium—can be expected to provide insight into the processes that could have affected the Nile valley's populations/peoples. From these vantage points

[1]Discussions over a long period of time with G.A. Harrison provided useful input for the outline of this presentation, as did John Baines. P. Underhill provided useful comments that improved this manuscript. I wish to also thank F. Wendorf, F. Hassan, C. Ehret, A. Brooks, and R. Kittles, and the numerous participants at the Poznan Symposium on the Archaeology of Northeast Africa who shared data about the early Sahara, especially M. Kobusiewicz. Much more collaboration is planned with them. This piece is dedicated to John Baines, Professor of Egyptology at Oxford University, a supervisor and friend who provided much insight into ideas about, and the workings of, ancient Egypt. I would also recall the life and work of the late Larry Angel, another of my teachers, who was one pioneer in the synthesis of biological, linguistic, historical, and cultural data.

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

this presentation will examine aspects of what might be called the historical genetics of the Nile valley, with a focus on the Y chromosome. The time-frame is the late pleistocene through holocene; within this there are different levels of biocultural history. Of special interest here is patterns of north-south variation in the Egyptian Nile valley.

Bidirectional clinal variation in Egypt for various p49a,f *Taq*I Y RFLP haplotypes (Table 1) has been suggested to be likely related to specific military campaigns during and after the Middle Kingdom (Lucotte and Mercier 2003a). The events considered to have brought together northern and southern populations having different Y genetic profiles are: the Egyptian campaigns against and/or colonization of lower Nubia during the Middle and New Kingdoms (respectively primarily Dynasty XII, *ca.* 1991-1785 BCE, and Dynasty XVIII, beginning *ca.* 1490 BCE); the Nubian conquest of Egypt by the Napatan kingdom that created Dynasty XXV (*ca.* 730-655 BCE), centered near the fourth cataract (in the Republic of the Sudan); the conquest of Egypt during the Greco-Roman period by southern Europeans; and the migration of Arabic-speaking peoples from the Near East, and much later the Turks from Anatolia, both during the Islamic period. The first two of these have been suggested to explain the pattern of the three most common haplotypes: V, XI, and IV.

The object of this paper is to examine and discuss further the observed patterns in Egypt for the p49a,f *Taq*I RFLP variants, based on current available data. This will be accomplished in two ways—by examining haplotype frequencies in adjacent regions and by exploring data relevant to understanding the probable haplotype spatial variation in the Nile valley and its causes, beyond the events of the Middle Kingdom and afterwards. It is important to consider the issue of the original frequencies and origins of these variants in Egypt and other parts of Africa, as well as the adjacent regions. This is especially important given the ongoing tendency in some disciplines to label the Nile valley as Middle Eastern, in a fashion that effectively suggests that Egypt has no African context, and that also hides its biocultural Africanity in pre-Islamic times.

The approach taken here is to examine early Egypt from multiple disciplines in order to construct the most likely "narrative" that accounts for the facts as currently understood. It situates Egypt in a larger geographical and biogeographical context. The evidence to be primarily considered derives from published human biological studies, historical linguistics, and archeology. Although this presentation is not offered as a critique of previous literature, some repetition of published findings will be necessary for review, clarity, and emphasis.

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

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The term *Taq* comes from *Thermus aquaticus*, a bacterium that lives in extremely hot temperatures, and whose enzymes have proved valuable in techniques used to analyze DNA for population studies—techniques that sometimes require high temperatures. The *Taq*I endonuclease, an enzyme, cleaves DNA at particular points. Various molecular instruments called probes, that use endonucleases, can be constructed to detect variations in segments of DNA. Such variations are also called *polymorphisms*, more specifically *restriction fragment length polymorphisms* or RFLPs. The *Taq*I probes were found to detect a subset of five fragments that varied between individuals and populations and was on the non-recombining part of the Y chromosome, and therefore strictly paternally inherited (Ngo et al. 1986; Lucotte and Mercier 2003a).

The five fragments have different forms found to exist in different combinations. The different combinations for a stretch of DNA are called *haplotypes*, and can be conceptualized as a unit that is inherited. Each haplotype is given a numerical name. It should be noted that the same combination of *Taq*I fragments have occasionally arisen independently in different geographical populations. This is a case of parallel microevolution or independent mutation and can usually be distinguished from situations where migration and admixture have transferred a specific variant to another population.

The specific 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 (see Lucotte and Mercier 2003a, 2003b). Haplotype frequencies compiled and calculated from the literature are given in Tables 1, 2A, and 2B. Only the most frequently found haplotypes are reported.

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). The first three of these are of greatest interest due to their frequencies. Haplotype V, sometimes called "Arabic" (Lucotte and Mercier 2003a) declines from lower Egypt (north) at 51.9%, to upper Egypt (24.2%), and to lower Nubia (south) at 17.4%. Haplotypes VII, VIII, XV, and XII also decline (Table 1). In contrast, haplotypes XI and IV, called "southern," with IV being labeled "sub-Saharan," have their lowest frequencies in lower Egypt (XI-11.7%; IV-1.2%), but increase in upper Egypt (XI-28.8%; IV-27.3%); and lower Nubia (XI-30.4%; IV-39.1%); there is no statistically significant difference between the latter

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Table 1. Summary of the most common p49a,f *Taq*I Y-chromosome haplotypes in Egyptian regions (Lucotte and Mercier 2003a).

	Haplotypes and percentages						
Region (n)	IV	V	XI	VII	VIII	XII	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

Table 2A. Frequencies of p49a,f TaqI Y-chromosome haplotypes in selected African and Near Eastern countries (published data).

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

[1]Lucotte and Mercier (2003a)
[2]Lucotte and Mercier (2003b)
[3]Al-Zahery et al. (2003); *haplotype XI here is documented from two biallelic lineages
[4]Lucotte et al. (2000)
[5]Lucotte and Smets (1999)

two regions (Lucotte and Mercier 2003a). Haplotypes VII and VIII are most prevalent in the Near East, and XII and XV in Europe.

It is important to address the appellation of "Arabic" for haplotype V, due to names being interpreted as indicators of origins, and the inconsistencies found in the literature. This variant is found in very high frequen-

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Table 2B. *Taq*I p49a, f Y-chromosome haplotype frequencies in more restricted populations from the Horn, supra-Saharan Africa, and of Near East origin (published data).

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

[6]Lucotte et al. (1996)
References 2, 4, 5, as in Table 2A.
*Haplotype XI in groups admixed with northern Europeans is usually affiliated with haplogroup R1; in Africa it is usually associated with haplogroup E (al-Zahery 2003).

cies in supra-Saharan countries and Mauretania (collective average 55.0%), and in Ethiopia (average 45.8%) (Table 2A). In specific groups its highest prevalence is in samples from Moroccan Amazigh (Berbers) (68.9%) and Ethiopian Falasha (60.5%). Its frequency is considerably less in the Near East, and decreases from west (Lebanon, 16.7%) to east (Iraq, 7.2%) (Table 2A). The label "Arabic" for V is therefore misleading because it suggests a Near Eastern origin. In fact this variant has been called "African" (Lucotte et al. 1993:839, Lucotte et al. 1996:469), and "Berberian" (Lucotte et al. 2001:887).

Significantly, and convincingly, it has been argued that because the Falasha, more properly Beta Israel (the "black Jews" of Ethiopia, traditionally Cushitic, not Semitic speakers), have such a high frequency of V and XI and none (yet found) of VII and VIII, that this shows them to be "clearly of African origin" and to have adopted Judaism (Lucotte and Mercier 2003b: 669, Lucotte and Smets 1999). This is in contrast to their

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

being the descendants of immigrant Near Eastern Jewish communities, whose males have high frequencies of VII and VIII collectively (Tables 2A, 2B). Ironically, a noteworthy frequency of VIII has been found in a non-Jewish Ethiopian population, and this is likely due to the known interactions with Arabia in the past (see Munro-Hay 1991), with some likely amplification by genetic drift.

Given these findings, it is more accurate to call V "Horn-supra-saharan 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 primarily (but not solely) Arabic-speakers, due to language and cultural shift, and not settler colonization, as has been stated before based on biallelic lineage data (Bosch et al. 2001). High frequencies of VII and VIII characterize the indigenous core Arabic-speaking peoples of the Near East, and Jews also as noted (Tables 2A, 2B) (Lucotte and Mercier 2003b, al-Zahery et al. 2003, Lucotte et al. 1996, Lucotte et al. 1993, Santichiara-Benerecetti et al. 1993). There was no wholesale population replacement. This is not especially surprising because there is no evidence that the earliest Arabic-speakers, who came as teachers of Islam, intended to replace the indigenous populations biologically.

There is further evidence from a phylogeographic perspective for the biohistorical Africanity of haplotype V. Biallelic markers on the non-recombining portion of the Y chromosome define clades that can be associated with the *Taq*I p49a,f variants (see e.g. al-Zahery et al 2003, who present a kind of genetic Rosetta stone). Haplotype V is associated with the M35/215 subclade, as is XI (in Africa), and IV with the M2/PN1/M180 subclade, both of the YAP/M145/M213 cluster. These lineages ("subclades") subsuming haplotypes V/XI and IV, are joined by a transition mutation: "most notably the PN2 transition . . . unites two high frequency sub-clades, defined by M2/PN1/M180 mutations in sub-Saharan Africa, and M35/215 in north and east Africa." (Underhill et al. 2001:50). In one system of Y haplotype taxonomy, the subclades are in Group III (Bosch et al. 2001, Cruciani et. al. 2002). In another system of classification, these lineages are in haplogroup E (Hammer and Zegura 2002). The PN2 transition therefore defines a widespread clade. It is noteworthy that Group III is said to account for 73% of the variation in Africa (Underhill et al. 2001).

A limited review of Y chromosome studies for supra-Saharan Africa demonstrates a consistency with each other once equivalences are determined. There is a modal frequency of particular lineages from Egypt to Morocco that is distinct from those in the Near East, Europe, and tropi-

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cal Africa, although Egypt is perhaps the most diverse—a not unexpected finding (cf. Bosch 2001, Rosser et al. 2000, and Manni et al. 2002, Lucotte and Mercier 2003a). The southwest Asian (Near Eastern) lineages decline from east to west. However, in some of the studies, only individuals from northern Egypt are sampled, and this could theoretically give a false impression of Egyptian variability (contrast Lucotte and Mercier 2003a with Manni et al. 2002), because this region has received more foreign settlers (and is nearer the Near East). Possible sample bias should be integrated into the discussion of results.

The geography of the p49a,f haplotypes and their associated subclades notably overlap the spatial distributions of specific language phyla, and this may have implications for understanding aspects of early African population history, including the patterns of Y diversity in the Egyptian Nile valley. The genetic data, specifically the M35 subclade affiliated with haplotype V in Africa, can be related to the spatial range of much of the Afroasiatic linguistic phylum, which evidence suggests most likely originated in Africa; only one member (Semitic) is found in the Near East (see Bender 1975, Greenberg 1966, 1973, Fleming 1974, Nichols 1997, Ehret 1984, 1995, 2000).

The peoples of the Egyptian and northern Sudanese Nile valley, and supra-Saharan Africa now speak Arabic in the main but, as noted, this largely represents language shift. Ancient Egyptian is Afroasiatic, and current inhabitants of the Nile valley should be understood as being in the main, although not wholly, descendants of the pre-neolithic regional inhabitants, although this apparently varies by geography as indicated by the frequency of Near Eastern haplotypes/lineages (Table 1, Lucotte and Mercier 2003a, Manni et al. 2002, Cruciani 2002). An accurate spatiotemporal interpretation of the PN2/M35 lineage corresponds to the northern core range of Afroasiatic: "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" (Underhill et al. 2001:51). ("Southern" here refers to supra-Saharan Africa.) . . . 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. 2001:55).

The Mushabi culture in the Levant might have been created by a "mesolithic" (epipaleolithic) population from the Nile valley (Bar Yosef 1987), and the Iberomarusian in the Maghreb as well, as suggested by Bosch et al. (2001). Interestingly, late pleistocene/early Holocene migration, broadly corresponding with this geographical, linguistic, and genetic pattern, was also hypothesized from skeletal data. Angel (1972, 1973)

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interpreted some of his findings as indicating evidence of migration from Africa to the Levant and to Anatolia; he also saw a connection between some indigenous Africans in eastern Africa, the Nile valley, and the Maghreb (Angel and Kelley 1986). However, it is important to be wary of assuming an obligatory association of linguistic affiliation, molecular genetic variants, and morphometric patterns of skeletal variation, although sometimes there is congruence for some of these (see e.g., Poloni et al. 1997). Furthermore, the archeological industries in these regions are not the same, and would not be necessarily so, even if the peoples who created them were biologically related.

The caveat to the above scenario is that if the M35 mutation is a lot older—50,000 years in one unlikely scenario considered by Bosch et al (2001), then it may have originally reached northwest Africa at an earlier time; this would not, of course, negate later migrations. Origin and dispersal times need not be the same. The Dabban, in Cyrenaica, is Late Stone Age/Upper Paleolithic, and dates to at least 40,000 bp, but seems to have no clear local antecedents (McBurney 1960, Smith 1982, Phillipson 1985). The Aterian, its predecessor in the general region, including the Sahara, is older, and associated remains at Dar as Soltan (possibly dating to 60,000 bp) are anatomically modern. The various archeological industries that have been described are not uniformly spread over the region west of Egypt. The relationships of the later epipaleolithic and neolithic cultures in the area from Libya to Morocco (e.g., Iberomarusian, Oranian, Capsian, Capsian of Neolithic Tradition, Libyco-Capsian) to each other have not been fully resolved (see e.g., Smith 1982). Nor have possible relationships with Nile valley industries been firmly established when they have been considered (see Close 1980-81, Connor and Marks 1986, Midant-Reynes 2000). Some lithic stylistic similarities have been noted between some late pleistocene/early holocene Nile Valley industries and those of the northwest Africa: Iberomarusian, Libyco-Capsian, and Eastern Oranian (Close 1980-81). This may have some relevance to how biocultural diversification and migration are conceptualized in Saharan and supra-Saharan Africa. It is important to state that most archeologists do not interpret the Capsian as being of Near Eastern origin.

Haplotype IV, designating the M2/PN1 subclade, as noted, is found in high frequency in west, central, and sub-equatorial Africa in speakers of Niger-Congo—which may have a special relationship with Nilosaharan—spoken by Nubians; together they might form a superphylum called Kongo-Saharan or Niger-Saharan (see Gregersen 1972, Blench 1995), but this is not fully supported. The spatial distribution of p49a,f *Taq*I haplotypes in the geographically-widespread speakers of Nilosaharan languages

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

has not been fully characterized, but the notable presence of haplotype IV in Nubians speaking the Eastern Sudanic branch is interesting in that this subgroup is in the Sahelian branch of speakers, whose ancestors may have participated in the domestication of cattle in the eastern Sahara (Ehret 2000, Wendorf and Schild 2001). Sometimes haplotype IV (and the M2 lineage) is seen as being associated with the "Bantu expansion" (~2000-3000 bp), but this does not mean that it is not much older, since expansion and origin times cannot be conflated. Haplotype IV has substantial frequencies in upper Egypt and Nubia , greater than VII and VIII, and even V. Bantu languages were never spoken in these regions or Senegal, where M2 is greater than 90 percent in some studies.

Haplotype XI has its highest frequencies in the Horn and the Nile valley, but has been called "Oriental" (see Lucotte for this appellation 1996:469), which is also misleading. The high frequency in both Nilosaharan and Afroasiatic speakers in northeast Africa is striking. This haplotype has arisen independently several times as indicated by its affiliation with lineages defined by different biallelic markers (see e.g., al-Zahery 2003, O. Semino, personal communication). The notable frequency in Askenazic Jews is likely primarily of European, not African, origin (the EU19 lineage, see Passarino et al. 2000), or in haplogroup R (see al-Zahery 2003). In northwestern Africa (Tunisia) it is likely to be of both African and European origin due to the region's populations' various historical interactions with Europe.

The widespread distribution of the PN2 clade in the major language phyla of Africa, its existence in the Levantine-Iraq region and even in the Aegean, and its likely post-glacial maximum date are significant and show how numerous bioculturally diverse peoples can be connected, even at relatively shallow time depths. This should give pause to those who have trouble escaping racial thinking. The diversification and early expansion of PN2 bearing populations likely started in the northeast quadrant of Africa (defined by bisecting the continent along its north-south axis and at the equator). This region is postulated to be the ancestral home of two of the three major language phyla of supra-equatorial Africa: Nilosaharan and Afroasiatic (Blench 1993, Ehret 1984, personal communication).

It is significant that bearers of the PN2 mutation are geographically widespread and diverse in external morphology and language family affiliation. There is also biological diversity even within the speakers of language families (in their "homelands") that could be seen by some as problematic. The range of external morphologies in the continental African speakers of Afroasiatic cannot be viewed as problematic from an evolu-

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

tionary (versus racio-typological) perspective, and indicates the richness and complexity of indigenous African biocultural microevolution and its diversity (Hiernaux 1974, Keita and Kittles 1997, Kittles and Keita 1999). Conceptual racio-typological approaches that only interpret variation in terms of the interaction of primordial pre-existing distinct biocultural units will not easily explain phenomena like the PN2 distribution.

Accepting even the lower putative age of the mutation (Hammer and Zegura 2002 vs. Bosch et al. 2001), and language phyla (Ehret 1984), it can be suggested that PN2 and descendants perhaps arose in a population that antedates these language groupings, and which later heavily contributed to, or became the biopopulation base of, the nascent speech communities. Alternatively, it could mean that there was extensive interaction between the speakers of the ancestral linguistic families, postulating that the descendant mutations arose in these, with a subsequent different distribution in populations of various speech families. Haplotypes V and XI are somewhat ubiquitous in African language families (see Poloni 1997). In either case it is likely that a very successful subsistence strategy in the northeast quadrant of Africa made this possible (see e.g., Connor and Marks 1986, Wetterstrom 1993).

As noted, VII and VIII are the major indigenous Near Eastern haplotypes, and found to predominate in extant core descendant communities: Near Eastern Arabic speakers and Jews. In comparison to those of V their frequencies are small in supra-Saharan Africa (Tables 2A, 2B). Again employing the Falasha and northern Africa cases as a models, and the genetic evidence, it can be postulated that selected M35 carriers, speakers (from Africa) of a stage of ancestral Semitic (pre-proto-Semitic) entered the Near East, where indigenous peoples adopted it, and via ongoing language shift and population growth eventually became numerically greater than the original speakers of the ancestor.

As noted with reservation, the archeological "signal" for such movement might be the presence of the Mushabi industry in the Levant that has Nile Valley affinities (Bar-Yosef 1987, Midant-Reynes 2000). The large number of Mushabi sites suggests a major migration (see comments in Bar-Yosef 1987). However, this can only be tentatively suggested because there may be little concordance between language family and the distribution of archeological artifacts. Also the Mushabi may be indigenous to the Levant. The point is that an African proto-language grouping was adopted by indigenous Near Eastern peoples, based on linguistics and genetics. Eventually attestable Semitic emerged; reconstruction of this Common Semitic indicates that its speakers were food producers and not hunters and gatherers, as were the speakers of undifferentiated Afroasiat-

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ic (see Diakonoff 1981, and revision 1998, Ehret 1984, 1995, personal communication).

Later there is some movement into Africa after the domestication of plants and ovacaprines, which happened in the Near East nearly 2000 years before it occurred in Egypt (Hassan 1988, Wetterstrom 1993). Early neolithic levels in northern Egypt contain the Levantine domesticates, and show some influence in material culture as well (Kobusiewicz 1992). Ovacaprines appear in the western desert before the Nile valley proper (Wendorf and Schild 2001). However, it is significant that the ancient Egyptian words for the major Near Eastern domesticates—sheep, goat, barley, and wheat—are not loans from either Semitic, Sumerian, or Indo-European. This argues against a mass settler colonization (at replacement levels) of the Nile valley from the Near East at this time. This is in contrast with some words for domesticates in some early Semitic languages, which are likely Sumerian loan words (Diakonoff 1981).

This evidence indicates that the northern Nile valley peoples apparently incorporated the Near Eastern domesticates into a Nilotic foraging subsistence tradition on their own terms (Wetterstrom 1993). There was apparently no "neolithic revolution" brought by settler colonization, but a gradual process of neolithicization (Midant-Reynes 2000). While some Neolithic movement took place, there is the problem of sifting the results of this from later migration. (Also some of those emigrating may have been carrying haplotype V, descendents of earlier migrants from the Nile valley, given the postulated "Mesolithic" time of the M35 lineage emigration). It is more probable that the current VII and VIII frequencies, greatest in northern Egypt, reflect in the main (but not solely) movements during the Islamic period (Nebel et al. 2002), when some deliberate settlement of Arab tribes was done in Africa, and the effects of polygamy. There must also have been some impact of Near Easterners who settled in the delta at various times in ancient Egypt (Gardiner 1961). More recent movements, in the last two centuries, must not be forgotten in this assessment.

The mode and patterns of migration discussed above would account for the opposing east-west clines of V versus VII+VIII in southwest Asia, and the higher frequency of V nearer Africa (Egypt). The Greco-Roman incursions (Gardiner 1961) are the earliest text-supported migrations that may account for XII and XV in Egypt. There is little evidence for earlier movements, but these likely did occur to Egypt's Mediterranean coast. Both of these haplotypes have high frequencies in Europe (Perischetti et al. 1992, Lucotte and Loriat 1999), and are found on different biallelic lineages than the most frequent haplotypes found in Egypt (cf. Hammer and Zegura 2002, Underhill et al 2001, al-Zahery et al 2003).

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The very noteworthy frequency of XII in Tunisia might reasonably in part be attributed to the settlement of numbers of Roman soldiers and administrators and their families after the defeat of Carthage, perhaps increased by some form of sexual or social selection. There was also likely "Copper-Age" migration from Sardinia (Camps 1982), and ongoing contact with nearby islands in the Mediterranean. Somewhat surprising for Tunisia is the relative paucity of VII+VIII given the Phoenician settler colonies, and its later role in the Islamic period. This is likely due to sampling since other studies suggest a larger Near Eastern impact (Hammer, personal communication).

This is a reminder that genes, languages, and nationalities are not intrinsically linked, and that numerous samples would be helpful in getting an accurate assessment. The well-known Greek colonies in urban Cyrenaica (in modern Libya) also must not be forgotten in this regard, as well as the reflux of European converts to Islam back into Africa, after the expulsion of Jews and Muslims from Europe in the fifteenth century. This last event might account for the frequency of haplotype XV in Morocco.

III

The data for Egypt, north to south, are rendered more interesting in light of the distributions in adjacent regions. The high prevalence of V in Ethiopia, south of Egypt, would alone seem to indicate that movements associated with Dynasty XII and XVIII Egyptian military colonizations are not sufficient explanations for frequencies in lower Nubia and upper Egypt, statistically the same. The decreasing cline does not continue. Ethiopian (and Falasha) frequencies are higher than in upper Egypt. This observation is not the case for haplotypes VII, VIII, XII, and XV, although, ironically, haplotype VIII has a notable presence in a sample of non-Falasha Ethiopians from north of Addis Ababa (Lucotte and Smets 1999).

Leaving aside the smaller frequencies of the "European" haplotypes, and the likely migrations associated with them (see 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? We hypothesize that early holocene settlement and population interactions, not later military incursions, are the major mechanisms that accounts for the haplotype patterns, and that prevalence locates their most parsimo-

https://doi.org/10.1353/hia.2005.0013 Published online by Cambridge University Press

nious geographical sources, assuming a minimal number of unusual founder, expansion, and extinction events.

It is possible that the spread of the haplotypes bears some relationship to the spread of language families. Recall that the languages spoken in the Nile valley, Horn, and supra-Saharan Africa west of Egypt, as well as the central and southern Sahara, belong primarily to the Afroasiatic and Nilo-Saharan phyla (or families) (Greenberg 1966, Ehret 1984, Ruhlen 1987). Nubian in the Nile valley is Nilo-Saharan. Ancestral (proto-)Afroasiatic may date from 15,000 to 13,000 BCE (Ehret 1984), or more. Its differentiation through space and time and movement occurred primarily in Africa, producing at least six families: Omotic, Cushitic, Chadic, ancient Egyptian, Berber, and Semitic. In a phylogenetic model these last four are concluded to be the "younger" members of the family, but the nature of the process of linguistic differentiation might make certain dating difficult.

Hypotheses that bring Afroasiatic from Asia or Europe with agriculture are not parsimonious (Ehret, personal communication). The Nostratic hypothesis that proffers this view has largely been modified and abandoned; most Nostraticists now see Afroasiatic as a sister of Nostratic and not a daughter (Ruhlen 1991). The common parent to these would reach back into a time not generally believed to be validly accessible to standard linguistic methods (Nichols 1997), although there is dissent on this point.

The distribution and high prevalence of haplotype V (and less so of XI, Nile valley primarily), and Afroasiatic speakers in Africa correspond with the geography of the Horn-supra-Saharan arc. This is suggestive. The spread of the language phylum and genes may illustrate a case of kin-structured migration (Fix 1999), with founder-effect in some instances (e.g., high frequency of V in Moroccan Berbers). In the southern Nile valley V (and XI) might 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 (see Ehret 1988, 2000, for a discussion of cultural reconstruction from language, and Ehret 1984).

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 Sahara, which was less arid in the late pleistocene in the early holocene after the last glacial maximum. Over time, as Afroasiatic differentiated and populations migrated, founder effect with kin-structured migration may have led to the basic distribution of V seen in the Horn and northern Africa today. Haplotype V has a

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much lower frequency among core Semitic-speaking descendant communities in the Near East (i.e., Arabs and Jews).

It should be reiterated that using the same logic as applied to assess the Falasha, and the Arabic speakers of supra-Saharan Africa, it can be postulated that the ancestor of undifferentiated Semitic was adopted in the Near East by peoples having a prevalence of haplotypes VII and VIII. The levels and cline of V in the region are consistent with this hypothesis. Haplotype V in northern Egypt may also have had recurrent sources: in addition to a neolithic return of some having haplotype V, the Libyan kings of dynasties XXII-XXIV (~950-750 BC), based in the delta, might also have settled their countrymen. These would have been Amazigh (Berber)-speaking populations probably with a predominant frequency of haplotype V. It is difficult to judge the impact of these.

Archeological data, or the absence of it, have been interpreted as suggesting a population hiatus in the settlement of the Nile Valley between the epipaleolithic and the neolithic/predynastic, but this apparent lack could be due to material now being covered over by the Nile (see Connor and Marks 1986, Midant-Reynes 2000, for a discussion). Analagous to events in the Atacama Desert in Chile (Nuñez et al 2002), a moister more inhabitable eastern Sahara gained more human population in the late pleistocene-early holocene (Wendorf and Schild 1980, Hassan 1988, Wendorf and Schild 2001). If the hiatus was real then perhaps many Nile populations became Saharan.

Later, stimulated by mid-holocene droughts, migration from the Sahara contributed population to the Nile valley (Hassan 1988, Kobusiewicz 1992, Wendorf and Schild 1980, 2001); the predynastic of upper Egypt and later neolithic in lower Egypt show clear Saharan affinities. A striking increase of pastoralists' hearths are found in the Nile valley dating to between 5000-4000 BCE (Hassan 1988). Saharan Nilosaharan-speakers may have been the initial domesticators of African cattle found in the Sahara (see Ehret 2000, Wendorf et. al. 1987). Hence there was a Saharan "neolithic" with evidence for domesticated cattle before they appear in the Nile valley (Wendorf et al. 2001). If modern data can be used, there is no reason to think that the peoples drawn into the Sahara in the earlier periods were likely to have been biologically or linguistically uniform.

Conceptually, modeling the early to mid-holocene eastern Sahara, including the Nile valley, as being the locale of a metapopulation in a deteriorating habitat, and undergoing reduction from dispersal might help explain the current Nile valley diversity (see Gyllenberg and Hanski 1997, Gandon and Michalakis 1999, Hanski and Ovaskainen 2000, Duncan et

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al. 2001, Poethke and Hovestadt 2002, Nuñez et al. 2002). A dynamic diachronic interaction consisting of the fusion, fissioning, and perhaps "extinction" of populations, with a decrease in overall numbers as the environment eroded, can easily be envisioned in the heterogeneous landscape of the eastern Saharan expanse, with its oases and wadis, that formed a reticulated pattern of habitats. This fragile and changing region with the Nile valley in the early to mid-holocene can be further envisioned as holding a population whose subdivisions maintained some distinctiveness, but did exchange genes. Groups would have been distributed in settlements based on resources, but likely had contacts based on artefact variation (Wendorf and Schild 2001). Similar pottery can be found over extensive areas. Transhumance between the Nile valley and the Sahara would have provided east-west contact, even before the later migration that largely emptied parts of the eastern Sahara.

Early speakers of Nilosaharan and Afroasiatic apparently interacted based on the evidence of loan words (Ehret, personal communication). Nilosaharan's current range is roughly congruent with the so-called Saharo-Sudanese or Aqualithic culture associated with the less arid period (Wendorf and Schild 1980), and therefore cannot be seen as intrusive. Its speakers are found from the Nile to the Niger rivers in the Sahara and Sahel, and south into Kenya. The eastern Sahara was likely a micro-evolutionary processor and pump of populations, who may have developed various specific sociocultural (and linguistic) identities, but were genealogically "mixed" in terms of origins.

These identities may have further crystallized on the Nile, or fused with those of resident populations that were already differentiated. The genetic profile of the Nile Valley via the fusion of the Saharans and the indigenous peoples were likely established in the main long before the Middle Kingdom. 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, but was not evenly distributed along the valley corridor, being most concentrated in locales of important settlements (Butzer 1976). Nubia, as noted, was less densely populated.

Interactions between Nubia and Egypt (and the Sahara as well) occurred in the period between 4000 and 3000 BCE (the predynastic). There is evidence for sharing of some cultural traits between Sudan and Egypt in the neolithic (Kroeper 1996). Some items of "material" culture were also shared in the phase called Naqada I between the Nubian A-Group and upper Egypt (~3900-3650 BCE). There is good evidence for a

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zone of cultural overlap versus an absolute boundary (Wilkinson 1999 after Hoffman 1982, and citing evidence from Needler 1984 and Adams 1996). Hoffman (1982) noted cattle burials in Hierakonpolis, the most important of predynastic upper Egyptian cities in the later predynastic. This custom might reflect Nubian cultural impact, a common cultural background, or the presence of Nubians.

Whatever the case, there was some cultural and economic bases for all levels of social intercourse, as well as geographical proximity. There was some shared iconography in the kingdoms that emerged in Nubia and upper Egypt around 3300 BCE (Williams 1986). Although disputed, there is evidence that Nubia may have even militarily engaged upper Egypt before Dynasty I, and contributed leadership in the unification of Egypt (Williams 1986). The point of reviewing these data is to illustrate that the evidence suggests a basis for social interaction, and gene exchange.

There is a caveat for lower Egypt. If neolithic/predynastic northern Egyptian populations were characterized at one time by higher frequencies of VII and VIII (from Near Eastern migration), then immigration from Saharan sources could have brought more V and XI in the later northern neolithic. It should further be noted that 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, Wilkinson 1999). However, this may only be the heraldic "fixation" of an achieved political and cultural *status quo* (Hassan 1988), with little or no actual troup/population movements. Nevertheless, it is upper Egyptian (predynastic) culture that comes to dominate the country and emerges as the basis of dynastic civilization. Northern graves over the latter part of the predynastic do become like those in the south (see Bard 1994); some emigration to the north may have occurred—of people as well as ideas.

Interestingly, there is evidence from skeletal biology that upper Egypt in large towns at least, was possibly becoming more diverse over time due to immigration from northerners, as the sociocultural unity proceeded during the predynastic, at least in some major centers (Keita 1992, 1996). This could indicate that the south had been impacted by northerners with haplotypes V, VII, and VIII, thus altering southern populations with higher than now observed levels of IV and XI, if the craniometric data indicate a general phenomenon, which is not likely. The recoverable graves associated with major towns are not likely reflective of the entire population. It is important to remember that population growth in Egypt was ongoing, and any hypothesis must be tempered with this consideration.

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Dynasty I brought the political conquest (and cultural extirpation?) of the A-Group Nubian kingdom Ta Seti by (*ca.* 3000 BC) Egyptian kings (Wilkinson 1999). Lower Nubia seems to have become largely "depopulated," based on archeological evidence, but this more likely means that Nubians were partially bioculturally assimilated into southern Egypt. Lower Nubia had a much smaller population than Egypt, which is important to consider in writing of the historical biology of the population. It is important to note that Ta Seti (or Ta Sti, Ta Sety) was the name of the southernmost nome (district) of upper Egypt recorded in later times (Gardiner 1961), which perhaps indicates that the older Nubia was not forgotten/obliterated to historical memory.

Depending on how "Nubia" is conceptualized, the early kingdom seems to have more or less became absorbed politically into Egypt. 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 kings is that these rulers were defending Nubian allies who had assisted them in consolidating Egypt from attacks by other Nubians (see Trigger 1976). 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. Nubians were allegedly carried off into Egypt in great numbers during the Old Kingdom (Dynasties III to VI). (Emery 1961, Wilkinson 1999). In the First Intermediate Period Nubian mercenaries assimilated into the Upper Egyptian population (Fischer 1961).

In later times it was also kings or leaders from the south, with southern armies and sometimes Nubian mercenaries, who restored unity to Egypt; this was the case for the Dynasty XI, whose rulers made possible the Middle Kingdom, and whose pharaohs subsequently also raided Nubia, establishing forts there and an apparently small presence. Middle Kingdom forts did not hold large populations (Trigger 1976). It also seems likely that C-Group Nubian population and culture "disappears" because of biocultural assimilation into Upper Egyptian society in the Second Intermediate Period (Hafsaas, 2004). This is another possible source of variation assuming that they were different in the first place.

In the tradition of southern Egyptian leaders, the later Nubian kings (Dynasty XXV) who conquered Egypt saw themselves as restorers and revivalists in some sense, and not apparently as foreigners; this would have likely influenced their behavior toward ordinary Egyptians. Evidence for this is found in the Victory Stela of Pi(ankhy), founder of Dynasty XXV; the text does not suggest an attitude seeking settler colonization or

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territory (see translations by Lichtheim 1980, Goedicke 1998). It is worth noting that during the Islamic period that Christian Nubians sometimes controlled, or had great influence in, upper Egypt (Shinnie and Shinnie 1965).

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. Lower Nubia was not the threat, but rather the kingdom of Kush, whose rulers had allied themselves with the Asiatic Hyksos between the Middle and New Kingdoms. This colonization lasted 500 years, to the end of the New Kingdom. There was an Egyptianization of Nubian elites that later extended to the masses, and Egyptians were even settled deep in upper Nubia. Prisoners and enslaved locals were sometimes sent to Egypt and settled there (Trigger 1976), but it is difficult to quantify the number of translocated persons. No doubt some assimilated individuals also went to Egypt.

After the New Kingdom, Egyptians either returned home or simply fused with the local population. In contrast to Egyptian New Kingdom colonization, the Nubian control of Egypt was less than 100 years in duration, and there is no record of a program of settler colonization. Given the Egyptian versus Nubian actions it is striking how small the percentage of V in Nubia is, versus IV and XI in upper Egypt (Table I), if these military events alone are viewed as being responsible for extant regional genetic profiles, and if these variants are treated as being ethnically specific.

Taking a long and synthetic view, one compelling scenario is as follows: after the early late pleistocene/holocene establishment of Afroasiatic-speaking populations in the Nile valley and Sahara, who can be inferred to have been predominantly, but not only V (and XI), and of Nilosaharan folk in Nubia, Sudan, and Sahara (mainly XI and IV?), 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 having haplotypes IV, XI, and V in proportions that would significantly influence the Nile valley-dwelling populations.

These mid-Holocene Saharans are postulated to have been part of a process that led to a diverse but connected metapopulation. These peoples 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 became stabilized. Nubian and upper Egyptian proximity and on some level, shared culture, Nubia's possible participation in Egyptian state-building, and later partial political absorption in Dynasty

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I, would have reinforced biological overlap (and been further "stabilized" by ongoing population growth).

In this model much later migrations would have not created the genetic profile, only helped to maintain it. Although Nubia was occupied for some 500 years during the New Kingdom, there apparently was no genocidal settler colonization. However, there is evidence for the Egyptianization of Nubians and other enslaved southerners (Nubians proper and others) being taken to Egypt, but it is hard to imagine that the assimilation of these individuals would have greatly affected gene frequencies, all other things being equal. The relatively brief non-colonizing control of Egypt by Nubians would not have had the effect of a half millennium of occupation unless there was some specific policy of assimilation. These interactions, in the view advocated here, would have reinforced a basic genetic pattern long present in southern Egypt.

Considering the possible explanations for the Y variation, the clinal patterns observed for mtDNA variants (Krings et al. 1999) become subjects of interest. This DNA is usually only inherited maternally. The mtDNA variants' distributions have been been used to interpret the Nile valley as a zone of intergradation, created by the admixture populations of distinct northern and southern origin having different haplotypes. Movement up and down the Nile corridor is the mechanism postulated to have produced the pattern (from the Mediterranean to the southern Sudan). The three military invasions have also been invoked to explain the mtDNA patterns (Krings et al 1999:1173). This is a less tenable explanation for these variants, since women were not soldiers in ancient Egypt and Nubia, and wives of soldiers would not likely have contributed to the gene pools of the conquered. The translocation of a lot of the population of the victorious parties is not attested.

However, the coalescence times for the slowly evolving northern and southernmost haplotypes by region should be considered (see Krings et. al. 1999). These would seem to place the ancestor in the epoch of the less arid Sahara, in the early to pre-mid-holocene, when it was more populated or shortly after, when droughts were influential in causing emigration. Hence it can be argued that the scenario presented for the Y chromosome variation—of Saharan interactions and migrations into the valley—and later events would also have some power in explaining the distributions of the mtDNA variants, at least in part. Differential bidirectional north-south migration by itself would not likely be the only explanation for the findings. One needs also to consider under what social circumstances would delta Egyptian women come to be in the southern Sudan, unless only the village-to-village transfer of DNA is postulated.

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The more recent upheavals in the Sudan may also have altered patterns. The social context/circumstances of gene flow must always be considered, and ideally understood. The historical linguistic data reported earlier would apply in the case of maternal lineages as well. It can also be argued that it is not likely that the "northern" genetic profile is simply due to "Eurasians" having colonized supra-Saharan regions from external African sources. It might be likely that the greater percentage of haplotypes called "Eurasian" are predominantly, although not solely, of indigenous African origin. As a term "Eurasian" is likely misleading, since it suggests a single locale of geographical origins. This is because it can be postulated that differentiation of the L3* haplogroup began before the emigration out of Africa, and that there would be indigenous supra-Saharan/Saharan or Horn-supra-Saharan haplotypes. More work and careful analysis of mtDNA and the archeological data and likely probabilities is needed. Early hunting and gathering paleolithic populations can be modeled as having roamed between northern Africa and Eurasia, leaving an asymmetrical distribution of various derivative variants over a wide region, giving the appearance of Eurasian incursion.

It is of some interest that the patterns observed in the Nile valley across ethno-national boundaries for both types of lineage DNA do not apparently conform to those found in idealized strictly patrilineal/patriarchal societies that admit diverse women to their ranks as mates, but exclude foreign males (Salem et al. 1996, al-Zahery 2003, Richards et al. 2003). The diversity in male and female lineages by regions is striking. This also justifies a more complex model of interpretation for the observed genetic variation beyond one that only considers linear migration in the Nile corridor, and exchange between formerly "pure" ethnopopulations.

It is important to consider more complex models of population genesis, which allow for historically visible "groups" to be heterogeneous at origin, due to evolutionary (or social) processes, instead of interpreting heterogeneity as a necessary sign of admixture between distinct historically-known groups with different haplotypes or gene frequencies. Also models can be explored that postulate populations to be a blend of different historically known (or reported) ethno-ancestral groups, yet be genetically relatively "homogeneous," as well as those that have a known (or reported) single ethnic origin, but yet are genetically "heterogeneous."

Obviously, the time depth of "origins" and what this means must be carefully defined. Flexibility in model-building may help interpret situations that may be foreign to our current conceptions and paradigms. It is possible for a biologically-defined group to change cultural-linguistic

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iidentities due to adoption/language shift, and for a cultural-linguistically defined/maintained community to change biologically because it diachronically and bioculturally assimilates numerous individuals who were genetically and/or morphologically different.

In summary, late pleistocene, early and mid-holocene, and Dynasty I population movements that can be related to language family dispersals, Saharan aridity, droughts and Nile Valley settlement, mating patterns, social interactions other than warfare, as well as the effects of state-level conflicts should be integrated into discussions of Nile valley population histories.

This is generally applicable. Movements from the west and east to the Nile Valley, and north and south within the Nile corridor played a role in its population history. It is hypothesized that the events of the early settling of the Nile valley and interactions through Dynasty I and the Old Kingdom, and ongoing population growth, likely had as much of a role in generating the current Nile Valley pattern for the p49a,f *Taq*I Y haplotypes, as did events occurring in the Middle Kingdom and later. In this view these latter events, while contributory, were not the primary determinants of the distributions now observed. Future research, using computer simulation, might enable choosing the best model to explain the observed patterns of variation.

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