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Received 19 Oct 2016 | Accepted 20 Apr 2017 | Published 30 May 2017

DOI: 10.1038/ncomms15694 OPEN

Ancient Egyptian mummy genomes suggest an increase of Sub-Saharan African ancestry in post-Roman periods

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Egypt, located on the isthmus of Africa, is an ideal region to study historical population dynamics due to its geographic location and documented interactions with ancient civilizations in Africa, Asia and Europe. Particularly, in the first millennium BCE Egypt endured foreign domination leading to growing numbers of foreigners living within its borders possibly contributing genetically to the local population. Here we present 90 mitochondrial genomes as well as genome-wide data sets from three individuals obtained from Egyptian mummies. The samples recovered from Middle Egypt span around 1,300 years of ancient Egyptian history from the New Kingdom to the Roman Period. Our analyses reveal that ancient Egyptians shared more ancestry with Near Easterners than present-day Egyptians, who received additional sub-Saharan admixture in more recent times. This analysis establishes ancient Egyptian mummies as a genetic source to study ancient human history and offers the perspective of deciphering Egypt's past at a genome-wide level.

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NATURE COMMUNICATIONS | 8:15694 | DOI: 10.1038/ncomms15694 | www.nature.com/naturecommunications

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Front page of the article by Verena J. Schuenemann *et al.* published in open source in *Nature Communications* (8, 15694, 2017), and discussed by Jean-Philippe Gourdine, S.O.Y Keita, Jean-Luc Gourdine and Alain Anselin in the following contribution.

Première page de l'article de Verena J. Schuenemann *et al.* publié en open source dans *Nature Communications* (8, 15694, 2017), et discuté par Jean-Philippe Gourdine, S.O.Y. Keita, Jean-Luc Gourdine et Alain Anselin dans la contribution ci-après.

□ Ancient Egyptian genomes from northern Egypt: Further discussion*

Jean-Philippe GOURDINE, Shomarka O. Y. KEITA,
Jean-Luc GOURDINE and Alain ANSELIN

* *Génomes égyptiens anciens du nord de l'Égypte : poursuite de la discussion.*

Updated reprint of the article / Reproduction avec mise à jour de l'article : Gourdine, J., Keita, S., Gourdine, J., & Anselin, A. (2018, August 16). Ancient Egyptian Genomes from northern Egypt: Further discussion. <https://doi.org/10.31219/osf.io/ecwf3>.

To the memory of Alain ANSELIN – À la mémoire d'Alain ANSELIN.

1. Introduction

Schuenemann *et al.*¹ seemingly suggest, based largely on the results of an ancient DNA study of later period remains from northern Egypt, that the ‘ancient Egyptians’ (AE) as an entity came from Asia (the Near East, NE), and that modern Egyptians “received additional sub-Saharan African (SSA) admixtures in recent times” after the latest period of the pharaonic era due to the “trans-Saharan slave trade and Islamic expansion.” In spite of the implied generalization about ‘origins’ the authors do offer the caveat that their findings may have been different if samples had been used from southern Egypt, and this is a significant admission. Their conclusions deserve further discussion from multiple perspectives which cannot be fully developed due to space limitations.

There are alternative interpretations of the results but which were not presented as is traditionally done, with the exception of the admission that results from southern Egyptians may have been different. The alternative interpretations involve three major considerations: 1) sampling and methodology, 2) historiography and 3) definitions as they relate to populations, origins and evolution.

2. Sampling and methodological strategy

The samples can be questioned as to their representativeness of Egypt in terms of size, spatio-temporal and socio-cultural aspects.

- All of the samples are from the northern half of Egypt, from one nome which is 2.4% (1/42) of AE nomes. Ancient Egyptian culture originated southern Upper Egypt².

¹ Schuenemann, V. J. *et al.* Ancient Egyptian mummy genomes suggest an increase of Sub-Saharan African ancestry in post-Roman periods. *Nat. Commun.* **8**, 15694 (2017).

² Agut-Labordère, D. & García, J. C. M. *L'Égypte des pharaons: de Narmer à Dioclétien : 3150 av. J.C.- 284 apr. J.-C.* (Belin, 2016).

- The socio-cultural dynamics are not fully considered: the information on the origin and social status is incomplete, or unknowable in fact. The mummies are clearly *assumed* to be representative of the local population based on an incomplete archaeological report, in spite of the historical information provided about northern Egypt's interaction with the Near East since the Predynastic, and the known settlements of Greeks, and others, in northern Egypt in later periods.
- The timeline is not representative of AE history ~ 3,000 years is missing (e.g. Predynastic, Early Dynastic, Old Kingdom, Middle Kingdom²).
- The samples cannot be convincingly said to represent true breeding populations or those that truly integrate historical information.
- The authors use Bayesian reconstruction of population size changes through time with BEAST, for which there is generally a discrepancy between the marginal prior and the original prior distribution. The available information on the comparison between original and marginal priors, and on prior and posterior distributions, does not take into account possible population substructure.
- Sex-biased sampling (mtDNA) cannot recover population demography of the whole country unless the sample size is large enough and representative in terms of chronology, regional variation, "ethnicities" (including the foreign presence), class and geography. It suffers from many biases that can affect the assessment of the effective population size: population size changes, mutation bias, and natural selection.
- The whole genome sample size is too small (n=3) to accurately permit a discussion of all Egyptian population history from north to south.

3. Historiography and misinterpretation

- The authors do not consider explanations based on historical narrative, although they present historical information. NE input in AE could also be explained by old mercantile relationships with Lower Egypt (e.g. Maadi-Buto complex ~4,000 BC³), Egyptianized Asiatic rulers and migrants (e.g. Hyksos ~1,650 BC), NE prisoners of war (e.g. from Thutmose III's military campaign in NE ~ 1,490 BC), from diplomatic marriages² (e.g. Amenhotep III and Mitanni princess, Gilukhipa ~ 1,380 BC), etc.
- The authors completely dismiss the results of PCR methods used on AE remains. As a Habicht *et al.*⁴ states, PCR based methods were used successfully on mummified Egyptian cats and crocodiles without creating extensive debate. Results that are likely reliable are from studies that analyzed short tandem repeats (STRs) from Amarna royal mummies⁵ (1,300 BC), and of Ramesses III (1,200 BC)⁶; Ramesses III had the Y

³ Teeter, E. *Before the Pyramids: The Origins of Egyptian Civilization*. (Oriental Institute of the University of Chicago, 2011). <https://oi-idb-static.uchicago.edu/multimedia/88/oimp33.pdf>

⁴ Habicht, M. E., Bouwman, A. S. & Rühli, F. J. Identifications of ancient Egyptian royal mummies from the 18th Dynasty reconsidered. *Am. J. Phys. Anthropol.* **159**, S216–31 (2016).

⁵ Hawass, Z. *et al.* Ancestry and pathology in King Tutankhamun's family. *JAMA* **303**, 638–647 (2010).

⁶ Hawass, Z. *et al.* Revisiting the harem conspiracy and death of Ramesses III: anthropological, forensic, radiological, and genetic study. *BMJ* **345**, e8268 (2012).

chromosome haplogroup E1b1a, an old African lineage⁷. Our analysis of STRs from Amarna and Ramesside royal mummies with popAffiliator⁸ based on the same published data^{5,6} indicates a 41.7% to 93.9% probability of SSA affinities (see Table 1); most of the individuals had a greater probability of affiliation with “SSA” which is not the only way to be “African” a point worth repeating.

- There are some philosophical issues as well for which space does not permit a full discussion. Conceptually what genetic markers are considered to be “African” or “Asian” needs discussion--and of what “defines” Africa as well. For example, the E1b1b1 (M35/78) lineage found in one Abusir el-Meleq sample is found not only in northern Africa, but is also well represented in eastern Africa⁷ and perhaps was taken to Europe across the Mediterranean before the Holocene (Trombetta, personal communication). E lineages are found in high frequency (>70%) among living Egyptians in Adaima⁹. The authors define all mitochondrial M1 haplogroups as “Asian” which is problematic. Gene history is not population history: ultimate “origins” and later sources to a specific region/population are conceptually different. Gene history is not also ethnic or linguistic history. M1 has been postulated to have emerged in Africa¹⁰, and there is no convincing evidence supporting an M1 ancestor in Asia: many M1 daughter haplogroups (M1a) are clearly African in origin and history¹⁰. The M1a1, M1a2a, M1a1i, M1a1e variants found in the Abusir el-Meleq samples¹ predate Islam and are abundant in SSA groups¹⁰, particularly in East Africa. Furthermore, SSA groups indicated to have contributed to modern Egypt do not match the Muslim trade routes that have been well documented¹¹ as SSA groups from the great lakes and southern African regions were largely absent in the internal trading routes that went north to Egypt. It is important to note that “SSA” influence may not be due to a slave trade, an overdone explanation; the green Sahara is to be considered as Egypt is actually in the eastern Sahara. SSA affinities of modern Egyptians from Abusir El-Meleq might be attributed to ancient early settlers as there is a notable frequency of the “*Bushmen canine*”- deemed a SSA trait in Predynastic samples dating to 4,000 BC⁹ from Adaima, Upper Egypt. Haplogroup L0f, usually associated with southern Africans, is present in living Egyptians in Adaima⁹ and could represent the product of an ancient “ghost population” from the Green Sahara that contributed widely. Distributions and admixtures in the African past may not match current “SSA” groups¹².

4. On the Definition of African

Schuenemann *et al.*¹ seem to implicitly suggest that only SSA equals Africa and that there are no interconnections between the various regions of Africa not rooted in the slave trade, a favorite trope. It has to be noted too that that in the Islamic armies that entered Egypt that there were a notable number of eastern Africans. It is not clear why there is an emphasis on ‘sub-Saharan’ when no Saharan or supra-Saharan population samples--empirical or modelled are considered; furthermore, there is no one way to be “sub-Saharan.” In this

⁷ Rowold, D. *et al.* At the southeast fringe of the Bantu expansion: genetic diversity and phylogenetic relationships to other sub-Saharan tribes. *Meta Gene* **2**, 670–685 (2014).

⁸ Pereira, L. *et al.* PopAffiliator: online calculator for individual affiliation to a major population group based on 17 autosomal short tandem repeat genotype profile. *Int. J. Legal Med.* **125**, 629–636 (2011).

⁹ Crubézy, E. Le peuplement de la vallée du Nil. *Archéo-Nil* **20**, 25–42 (2010).

¹⁰ Pennarun, E. *et al.* Divorcing the Late Upper Palaeolithic demographic histories of mtDNA haplogroups M1 and U6 in Africa. *BMC Evol. Biol.* **12**, 234 (2012).

¹¹ Lovejoy, P. E. *Transformations in Slavery: A History of Slavery in Africa*. (Cambridge University Press, 2011).

¹² Busby, G. B. *et al.* Admixture into and within sub-Saharan Africa. *Elife* **5**, (2016).

study northern tropical Africans, such as lower and upper Nubians and adjacent southern Egyptians and Saharans were not included as comparison groups, as noted by the authors themselves.

5. Conclusion

The paleolithic past has to be distinguished from the biocultural emergence in the Holocene of any society, including Europe. Egypt long before the pyramids was culturally and linguistically African as evidenced by numerous studies^{3,13,14} based on standard research which accept Egypt's place in the Nile corridor as having local origins. The symbolism found in the Badarian or Naqadan graves, etc. nor the pyramids were brought from Asia (Near East). The Egyptian Neolithic cannot be shown as an entity to have come from Asia, although some domesticates were borrowed on local terms into a system of indigenous foraging in the Fayum². Historical linguistics shows ancient Egyptian to be Afroasiatic with borrowings from other African language phyla¹⁵. Archaeological data would seem to indicate an early integration of the eastern delta, in northern Egypt, by early Upper Egyptian rulers since Iry Hor from Abydos (~3,250 BC), who already wrote royal inscriptions in Egyptian² in a script and symbolic system that used African flora and fauna^{3,13}. This region of Egypt, and northern Egypt had long had social intercourse with the Near East. The ancient Egyptians in “origin” were not settler colonists akin to the European colonists in Africa. Schuenemann *et al.*¹ study is best seen as a contribution to understanding a local population history in northern Egypt as opposed to a population history of all Egypt from its inception.

¹³ Anselin, A. Some Notes about an Early African Pool of Cultures from which Emerged the Egyptian Civilisation. in *Egypt in its African Context. Proceedings of the Conference held at The Manchester Museum, University of Manchester* (ed. Exell, K.) 43–53 (Oxford, BAR International, 2009).

¹⁴ Wengrow, D., Dee, M., Foster, S., Stevenson, A. & Ramsey, C. B. Cultural convergence in the Neolithic of the Nile Valley: a prehistoric perspective on Egypt's place in Africa. *Antiquity* **88**, 95–111 (2014).

¹⁵ Takács, G. Sibilant and velar consonants of South Cushitic and their regular correspondences in Egyptian and other Afro-Asiatic branches. in *Afroasiatica Tergestina. Papers from the 9th Italian Meeting of Afro-Asiatic (Hamito-Semitic) Linguistics, Trieste* 393–426 (1998).

Table 1: Geographical region affinities of Amarna and Ramesside mummies based on popAffiliator 1⁸ analysis of 8 pairs of STR

Sample Name	CSF1PO	D2S1338	D7S820	D13S317	D16S539	D18S51	D21S11	FGA		Pop Affiliator Ethnic group probability SSA (Sub-Saharan Africa), EA (Eurasia), A (Asia)							
								24	26								
Thuya*	7	12	19	26	10	13	9	12	11	13	8	19	26	35	24	26	SSA 93.4%, EA 6.3%, A 0.3%
Yuya*	9	12	22	27	6	15	11	13	6	10	12	22	29	34	20	25	SSA 93.7%, EA 6%, A 0.3%
KV35ELa,c*	9	12	22	26	10	15	11	12	6	11	19	22	26	29	20	26	SSA 71.9%, EA 21.8%, A 6.3%
Amenhotep III (KV35)*	6	9	16	27	6	15	10	16	8	13	16	22	25	34	23	31	SSA 93.7%, EA 6%, A 0.3%
KV55b,c*	9	12	16	26	15	15	10	12	11	13	16	19	29	34	20	23	SSA 41.7%, EA 41.5%, A 16.7%
KV35YLc*	6	12	16	26	6	10	10	12	8	11	16	19	25	29	20	23	SSA 88.3%, EA 31.2%, A 0.5
Tutankhamun (KV62)c*	6	12	16	26	10	15	10	12	8	13	19	19	29	34	23	23	SSA 93.9%, EA 4.6%, A 1.5%
Rameses III**	7	10	15	28	6	15	9	12	8	11	8	12	28	35	24	34.2	SSA 93.6%, EA 6.1%, A 0.3%
Unknown Man E**	7	10	19	28	6	13	9	13	8	12	12	26	29.2	35	24	26	SSA 91.2%, EA 7%, A 1.1%

Table 1: Geographical region affinities of Amarna and Ramesside mummies based on popAffiliator 1⁸ analysis of 8 pairs of STR

8/13 pairs of STR from Combined DNA Index System were used by Hawass *et al.*^{5,6}, nevertheless, data suggest main sub-Saharan affinities of pharaonic mummies from the 18th and 20th dynasty (circa 1,300 BC), far in the past before Islamic slave trade.

Disclaimer: The geographical regions affinities were defined according to popAffiliator⁸, we acknowledge there might be problems with any type of classification. (data from Hawass *et al.*^{5,6} available here <http://bit.ly/Pop-Affi-STR-Mummies>)*

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Contributions

Jean-Philippe Gourdine and Shomarka O. Y. Keita performed the PopAffiliator analysis, drew tables, wrote and reviewed the main genetic, statistical, anthropological and Egyptology portions of the article. Jean-Luc Gourdine wrote and review the statistical portion. Alain Anselin wrote and reviewed Egyptological/linguistics portion.