

1 **Title**

2 **Following the evolution of *Homo sapiens* across Africa using a**
3 **uniparental genetic guide.**

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21 **Abstract**

22 The origin and evolution of modern humans in Africa has reached a
23 multidisciplinary consensus but the age and regions where it originated
24 and evolved are current topics of discussion. In this study I put forward an
25 integrative model guided by the phylogeny and phylogeography of
26 mitochondrial DNA (and Y-chromosome) haplogroups. I propose an early
27 origin of modern humans in northwest Africa in a temporal window of
28 257-345 thousand years ago. A first population split in central Africa
29 around 175-288 thousand years ago. A subsequent northward spread with
30 additional population subdivisions during a long statistical interval that
31 culminated in a first successful out of Africa migration around 130
32 thousand years ago. A population constriction in southwest Asia
33 motivated an early return to Africa between 79 and 107 thousand years
34 ago. This ample Eurasian-ebb to Africa, detected by mitochondrial
35 haplogroup L3 and Y-chromosome haplogroup E preceded other later and
36 geographically more limited Eurasian backflows. The archaeological and
37 fossil finds that could be coetaneous to this molecular journey have been
38 integrated into this interdisciplinary model.

39 **Introduction**

40 Hypotheses about human evolution, formulated from archaeological and
41 genetics data, are mainly based on radiometric dating for the former and
42 on molecular dating for the latter [1]. These methods have the advantage
43 of locating important evolutionary events in specific places and time
44 frames where these events must have occurred. However, in many cases,
45 the frameworks established by different disciplines conflict. For example,
46 applying the molecular clock to mitochondrial DNA (mtDNA) genetic
47 variation, it has been established that modern humans had a genetic
48 African origin around 200 thousand years ago (kya) [2], and that a more
49 evolved form of that lineage left Africa colonizing Eurasia around 60 kya
50 [3]. However, Middle Stone Age (MSA) artefacts and fossils dated at the
51 site of Jebel Irhoud, Morocco placed the *Homo sapiens* emergence in
52 northwest Africa around 300 kya [4,5], and roughly at the same time MSA
53 tool assemblages replaced more primitive Acheulean tools in southern

54 Kenya [6,7]. Furthermore, fossils from Misliya Cave, Israel, dated around
55 180 kya [8], and in southern China dated around 100 kya [9], strongly
56 suggest that members of the *H. sapiens* clade left Africa earlier than
57 previously thought. It could be adduced that because mtDNA is a single
58 inherited female locus, its chronology might be discordant with those
59 obtained from whole nuclear genome analysis. However, with few
60 exceptions [10], the human demographic history deduced from genomic
61 studies highly resembles the one based on uniparental markers [11,12].
62 Therefore, the most prevalent opinion from the population genetics field
63 is that demographic human expansions from Africa to the Middle East and
64 beyond, prior to approximately 60 Kya, were ephemeral dispersals that
65 did not contributed to the modern human gene pool [13]. However, the
66 genetic chronological framework is based on an insecure evolutionary
67 rate, which in turn depends on the germline mutation rate, selective
68 constrains, and the fluctuation of the effective population size due to
69 demographic processes [14]. Certainly, new technological progresses in
70 DNA sequencing have highly refined the human germline mutation rate
71 both at the whole genome [15] and the mtDNA levels [16,17]. In addition,
72 purifying selection has been taken into account to improve evolutionary
73 rate estimations [18], but it seems that a time-dependence effect on this
74 rate [19,20], most probably due to fluctuations in population size [14], is
75 the main factor responsible of the changes detected in the evolutionary
76 rate values observed. Recently, a simple algorithm has been proposed to
77 counterbalance these effects on the mtDNA genome, which practically
78 doubles the coalescent time estimations along the human mtDNA
79 phylogenetic tree [21]. In this way, the most determinant archaeological
80 findings related to the human evolution coherently fit into the molecular
81 chronology [21].

82 In this paper, using that algorithm, with an appropriate germline mutation
83 rate, and the successive coalescent events across the human mtDNA
84 phylogeny as a molecular guide, I describe the progressive evolution of
85 modern humans into Africa using an integrative model that incorporates
86 the main archaeological and genetic evolutionary discoveries into a
87 coherent picture.

88 **Material and methods**

89 **Material:** For the phylogenetic and phylogeographic analyses I searched
90 for mtDNA complete genomes at the NCBI GenBank
91 (www.ncbi.nlm.nih.gov/genbank/), and MITOMAP
92 (www.mitomap.org/MITOMAP) databases, choosing representatives of all
93 African haplogroups and their main subgroups. Sequences were classified
94 according to the PhyloTree v.17 (<http://www.phylotree.org>) [22]. In total I
95 analysed 1,010 mitogenomes (243 for L0, 140 for L1, 73 for L5, 210 for L2,
96 8 for L6, 32 for L4, and 304 for L3). GenBank accession numbers for these
97 sequences, their haplogroup classification, and their country/ethnic
98 affiliation are detailed in supplementary (S) Table 1. A phylogenetic tree
99 showing the major mtDNA haplogroups relationships is presented as
100 supplementary(S) Fig 1. Phylogeographic trees for haplogroups L2, L6 and
101 L4 are presented in SFig 2, 3, and 4 respectively. The phylogeography of
102 haplogroups L0, L1, L5, and L3 have been studied previously [23].

103 **Methods:** Phylogenetic trees were built using median-joining networks
104 [24]. To calculate coalescent absolute ages of the main haplogroups I used
105 a mutation rate of 1.6×10^{-8} per site per year (assuming a mtDNA genomic
106 length of 16,500 base pairs) that is the mean of two independent
107 empirical estimates [16,17], and applied a composite rho algorithm that
108 takes into account time-dependence effects on this mutation rate [21].
109 The procedure for obtaining coalescent ages for the main haplogroups L0,
110 L1, L5, L2, L6, L4, and L3 are detailed in STables 2, 3, 4, 5, 6, 7, and 8
111 respectively. For relative age comparisons of phylogeographically
112 representative subclades, I calculated their coalescent age using the rho
113 statistic [25] and a mutation rate for the complete mtDNA sequence of
114 one substitution in every 3,624 years, correcting for purifying selection
115 [18], but using those sequences with the largest number of mutations
116 within each clade. The reason of this is that the effects of both selection
117 (mainly purifying selection) and genetic drift tend to eliminate those
118 sequences that in a Poisson distribution, with very low mean of success,
119 have a greater number of mutations and conserve those included in the
120 largest classes that have zero or very few mutations [14].

121 Results

122 **The genus *Homo* from a genetic perspective:** *Homo* is a genus
123 represented by only a single extant species (modern humans) and several
124 extinct specimens [26], which appeared during an interval of just over two
125 million years. The first hominin species with worldwide spread, most
126 probably as result of consecutive waves of expansion [27], was *Homo*
127 *erectus s.l.* Remains of this species have been unearthed in Africa [28], the
128 Middle East [29], the Caucasus [30], China [31] and Indonesia [32]. As a
129 generalist species, *H. erectus* reached this wide geographic range with
130 migrant groups adapting to different ecological niches in isolation. In time,
131 these groups accumulated distinguishable morphological differences that
132 some anthropologists have raised to the rank of different species [33], but
133 speciation seems to be a lengthy process. Thus, molecular phylogenetic
134 studies have found a long and consistent mean time to speciation in
135 eukaryotes of around 2 million years (Myr) [34]. In fact, under climatic and
136 demographic pressures these groups came into secondary contact several
137 times. In some of these cases, recent ancient DNA (aDNA) studies have
138 confirmed that, after separations of several hundred years, archaic groups
139 as Neanderthals, Denisovans or Sima de los Huesos specimens hybridized
140 frequently confirming the existence of incomplete sexual barriers among
141 them[35–38]. The heads of these secondary encounters may be the
142 exchange of genetic variation which greatly possibilities adaptation and
143 avoids extinction. However, the tail of generalist species groups is that
144 when coming into contact they have to compete for the same resources,
145 so that the more adapted displace and outcompete the others with some
146 genetic assimilation during this process [39]. Ultimately, the rate of
147 assimilation or displacement depends on the amount of resources
148 available. Thus, there is archaeological evidence that Neanderthals
149 displaced less evolved erectus groups across Europe and archaic humans
150 in the Middle East [40]; that in turn, modern humans displaced less
151 adapted erectus groups in East and Southeast Asia [41], and Neanderthals
152 in Europe [42,43]. Furthermore, again aDNA studies have demonstrated
153 the extinction of several Neanderthal[44] and modern human populations
154 [45,46] along its recent evolutionary history. From the above

155 considerations I will consider all the groups described in this paper as sub-
 156 specific stages of a temporally evolving polytypic species.

157 **The northern African origin of the ancestor of modern humans and**
 158 **Neanderthals:** Based on the topologies obtained from non-recombinant
 159 uniparental markers (Green et al. 2008; Mendez et al. 2016; Meyer et al.
 160 2012, 2014; Petr et al. 2020)[35,36,47–49], I have proposed recently that
 161 modern humans and Neanderthals were sister clades [50], and that the
 162 topologies obtained using autosomal markers [37,48,51], which consider
 163 *Homo sapiens* as an outgroup of the sister pair Neanderthal-Denisovan
 164 were due to secondary introgression. Furthermore, I also posit that the
 165 ancestor of modern humans and Neanderthals originated in northern
 166 Africa, and that pre-Neanderthal groups crossed to Europe whereas the
 167 ancestors of modern humans remained in northern Africa, so that both
 168 groups evolved in allopatry [50].

169 **The northwest African origin of early anatomically modern humans:**
 170 Human fossil remains and Middle Stone Age (MSA) archaeological
 171 artefacts from Jebel Irhoud, Morocco, dated at 315 ± 34 thousand years
 172 ago (Kya) have situated the earliest phase of modern human evolution in
 173 northwest Africa [4,5]. Applying a variable evolutionary rate dependent of
 174 temporal fluctuations in population size to the mtDNA genome, a
 175 coalescent age for the most recent common ancestor of all extant mtDNA
 176 lineages was estimated around 300 kya [14,21] which has been replicated
 177 in this study (Table 1).

178

Branches	Mean (Kya)	95% C.I. (Kya)	Mutation rate	Study						
L0/L1'2'5'6'4'3	192	152 - 234	1.67×10^{-8}	Soares et al. 2009						
L0/L1'2'5'6'4'3	157	120 - 197	1.92×10^{-8}	Fu et al. 2013						
L0/L1'2'5'6'4'3	318	282 - 354	1.3×10^{-8} to	Cabrera						

6'4'3			0.8×10^{-8}	2020						
L0/L1'2'5' 6'4'3	312	277 - 347	4.3×10^{-8} to 1.9×10^{-8}	Cabrera 2021						
L0	320	284 - 356	1.6×10^{-8} to 0.8×10^{-8}	This study						
L0	260	228 - 293	1.6×10^{-8} to 1.9×10^{-8}	This study						
L1	333	296 - 369	1.6×10^{-8} to 0.8×10^{-8}	This study						
L1	256	223 - 289	1.6×10^{-8} to 1.9×10^{-8}	This study						
L5	386	346 - 425	1.6×10^{-8} to 0.8×10^{-8}	This study						
L5	298	263 - 335	1.6×10^{-8} to 1.9×10^{-8}	This study						
L2	332	295 - 368	1.6×10^{-8} to 0.8×10^{-8}	This study						
L2	223	192 - 253	1.6×10^{-8} to 1.9×10^{-8}	This study						
Mean branches	301	257 - 345		This study						

179

180 This mtDNA coalescence matches the archaeological and fossil estimates
181 in Morocco but there is a lack of specific mtDNA lineages in this area to
182 directly support a northwest African origin. However we have indirect
183 evidence of the existence of an old genetic component in the Maghreb.
184 Thus, Late Pleistocene northern African remains derived one-third of their
185 genomic ancestry from a complex sub-Saharan African gene pool [52].
186 Curiously, this component was not detected in subsequent Neolithic
187 periods [53]. On the other hand, it is interesting to point out that,
188 although most of the Y-chromosome lineages in Morocco (J-M267; E-M81)
189 are of recent implantation [54], one of the most ancient lineages of the Y-
190 Chromosome, A0a1 (xP114) has been detected in Moroccan Berbers [55].
191 Accepting the northwest African origin hypothesis implies that other
192 contemporaneous hominin lineages as the Broken Hill (Zambia) skull
193 dated to 299 ± 25 kya [56], or the Kenyan Guomde calvarium dated to

194 around 270 kya [57] possibly did not directly contribute to the origin of
 195 our species.

196 **The west central African southern African mtDNA bifurcation:** The next
 197 phylogenetic step in the human mtDNA evolution was the split of the
 198 earliest L0 lineages from the L1'2'5'6'4'3 ancestor that seems to have
 199 occurred somewhere in central Africa around 230 kya (Table 2).

Haplogroup	Lineages	Mutations	mean Age (years)	95% C.I. (years)
L0	291	952	231,263	174,578 - 287,948
L1	130	483	230,892	142,562 - 319,222
L5	73	240	235,072	157,948 - 312,196
L2	201	593	143,505	110,785 - 176,225
L3'4'6	329	1,172	185,017	105,878 - 264,157
L6	4	26	35,992	17,235 - 54,750
L3'4	333	1,151	130,838	87,634 - 184,042
L4	26	194	122,872	94,828 - 150,196
L3	291	952	93,348	79,476 - 107,220

200

201 Subsequent subdivisions of L0 probably happened around the Zambezi
 202 river approximately 200 kya (Table 3)[58], whereas the L1 and L5
 203 bifurcations occurred nearly at the same time in central Africa (Table 2).

Haplogroups	Sequences	mean mutations	95% C.I.	Coalescent (years)	Geographic origin
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L0a	5	45.00	43.73 - 47.07	164,757	East Africa	
L0f	4	55.00	52.75 - 57.25	199,595	East Africa	
L0k	4	53.50	52.58 - 54.42	194,152	South Africa	
L0d	5	53.00	51.48 - 54.52	192,337	South Africa	
L1b	5	35.00	34.12 - 35.88	127,015	Northern Africa	
L1c	5	55.00	52.37 - 57.63	199,595	Central Africa	
L5	5	51.40	47.42 - 55.38	186,531	East Africa	
L2a	5	29.40	27.98 - 30.82	106,693	Central Africa	
L2b	5	41.00	38.85 - 43.15	148,789	African	
L6	5	16.60	15.49 - 17.71	60,241	East Africa	
L4a	5	32.60	30.72 - 34.48	118,305	East Africa	
L4b	5	36.00	32.71 - 39.29	130,644	African	
L3a	3	19.67	18.23 - 21.10	71,382	East Africa	
L3b'f	10	21.60	20.12 - 23.30	78,386	East Africa	
L3b	5	20.60	19.92 - 21.28	74,757	Central Africa	
L3f	5	22.60	21.92 - 23.28	82,015	East Africa	
L3c'd	6	21.50	20.50 - 23.10	78,023	East Africa	
L3c	1	21.00	-	76,209	East Africa	
L3d	5	21.60	20.49 - 22.71	78,386	Central Africa	
L3e'i'k'x	14	19.36	17.02 - 21.7	70,257	East Africa	
L3e	5	21.20	19.58 -	76,935	Central -	

			22.82		West Africa	
L3h	4	33.50	28.18 - 39.32	121,572	East Africa	

204

205 Although L0, mainly the L0d'k clade, is considered a signature of the
206 Khoe-San people [59], not all L0 branches remained in Southern Africa.
207 Some of them as L0a and L0f had an early implantation in central and
208 eastern Africa. Likewise, although L1c is representative of the western
209 pygmy populations of central Africa, and L0a and L5 of the eastern ones
210 [60], subsequent ramifications extended further to eastern Africa and
211 beyond. Similarly, the two deepest Y-chromosome lineages, haplogroups
212 A and B, branched out in these areas with some A lineages that seem
213 autochthonous of central African pygmies as A1-P305, other of southern
214 African Khoisan as A1b1a-M14, and other present in both areas as A1b1b-
215 M32 [61–63]. The case of haplogroup B is similar, in fact Y-Hg B is a
216 primary branch of the complex Y-Hg A [64], its deepest lineages in the B2-
217 M182 clade are prevalent in western and central African pygmies,
218 whereas other more derived branches as B2b1-P6 and B2b4-P8 are
219 restricted to southern African Khoisan or to eastern Africans as B2b2
220 M169 [61–63]. Although subsequent expansions extended the geographic
221 range of Y haplogroups A and B it seems that was in central Africa where
222 both lineages originated [65].

223 The deep segregation of the ancestors of southern African populations
224 from the rest was confirmed in a study of southern African ancient
225 genomes in which the modern human divergence was estimated to 260 to
226 350 kya [66]. Furthermore, it was observed that differences between
227 Khoisan genomes were greater than those between geographically very
228 distant Eurasian genomes [67]. However, there is genomic evidence of
229 secondary contacts among extant populations of Khoisan, rainforest
230 pygmies, and click speakers Hadza and Sandawe from Tanzania which
231 diverged by 100 – 120 kya [58,68]. In a similar vein, an ancient genomic
232 divergence between the ancestors of the rainforest pygmies and West
233 African Yoruba farmers was estimated to 90 – 150 Kya [69]. On the other
234 hand, ancient DNA studies of a 2,330 years old South African skeleton

235 observed the extinction of some L0d mtDNA lineages even in recent times
236 confirming an evolution-extinction process in these populations [70].

237 In apparent contradiction with the mtDNA phylogeny, some genome
238 based studies proposed that the deepest splitting branch in modern
239 Africans leads to central African pygmies instead of southern African
240 Khoisan [71], In my opinion, under a neutral view, this discrepancy can be
241 explained as due to the non-recombining nature of the maternal lineages.
242 Autosomal phylogenies are based on differences in genetic diversity, but
243 in mtDNA, in addition, it is also based on the relative age of the mutations
244 accumulated in the no recombining mtDNA genome. Due to this, although
245 the central African pygmy L1c lineages show a mean number of mutations
246 similar to, or greater than, the Khoisan L0 lineages (Table 3). The mtDNA
247 phylogeny clearly shows that L0 is the deepest branch of the human tree
248 (Sfig 1), and that the relative accumulation of mutations in the different
249 lineages is, most probably, a result of their different demographic
250 processes [14]. The surprising find that central African pygmies have
251 reduced chromosome X to autosome diversity ratios relative to all other
252 sub-Saharan Africans has also been explained by demography [12]. Thus,
253 genetic age estimations situated the ancestor of modern humans in
254 Central-Southern Africa in a temporal window contemporary with the
255 Sangoan/Lupemban lithic technologies [72,73] and hominin specimens as
256 Kabwe [56], Florisbad [74] or *Homo naledi* [75]. However, this
257 phylogenetic jump from northwestern to central Africa leaves a
258 geographic gap that is covered by western Africa. Regrettably, although its
259 archaeological record is still scarce, western Africa seems to be a region of
260 delayed and stagnant hominin evolution. Putative Oldowan, Acheulean,
261 Sangoan and other Middle Stone Age incipient industries are sensibly
262 more recent in West Africa[76–78] than their counterparts in eastern and
263 central-southern Africa[7,79]. Likewise, the scarce hominin fossils remains
264 unearthed show primitive features even at recent Pleistocene to
265 Holocene boundaries as is the case of the Nigerian Iwo Eleru remains,
266 reflecting either admixture with archaic humans or long-term survival of
267 primitive anatomical features at recent (11.7 -16.3 Ka) times[80,81]. On its
268 hand, mtDNA does not present any deep split that could be specifically
269 related to West Africa (Table 3). Nevertheless, the deepest Y-chromosome

270 branch (Hg A00) with a coalescent age around 300 kya has been detected
271 only in present day Cameroon populations, with particular prevalence
272 among Mbo (6.3%) and Bangwa (40.3%) groups [82]. Furthermore, this
273 basal lineage has been found in Late Pleistocene / Holocene forager
274 remains from Shum Laka also in Cameroon [71]. It has been suggested
275 that the presence of Hg A00 in modern humans could be the result of
276 admixture with archaic hominins [71] but even if we excluded this
277 haplogroup, there are other Y-chromosome basal lineages, as A0a1a
278 observed in Cameroonian Bakola directly related to the A0a1 (xP114)
279 present in Berbers from Algeria, or the primitive A1a clade observed in
280 Fulbe and Tuareg from Niger and also found in Moroccan Berbers, that
281 consistently points to an early migratory input from northwest to western
282 Africa[64]. In addition, the genome-wide study of the above mentioned
283 Shum Laka fossil specimens clearly showed that these individuals are most
284 similar to the present-day Central African pygmies than to the actual
285 Cameroonian populations. This fact is reinforced by the presence of the
286 central African Y-chromosome B2b-M112 and mtDNA L1c haplotypes in
287 those specimens [71]. These results could be explained as the result of a
288 post-Pleistocene turnover of a primitive autochthonous West African
289 population or, most probably, as the retraction and subsequent
290 substitution of a previously much more large central African population as
291 also could be the case for the southern Chad [83].

292 **The geographic northeast progression of the mtDNA phylogeny:**

293 Haplogroup L5 was the next branch splitting off from macro-haplogroup
294 L5'2'6'4'3 at approximately 235 Kya (STable 4). However, its basal sub-
295 branches (L5a, L5b, and L5c) suffered long periods of stagnation not
296 having subsequent ramifications until favorable climatic conditions during
297 the last interglacial period (130-74 Kya), around 30 Kya, and after the
298 LGM, in Holocene times. The core geographic area for this haplogroup
299 comprises Tanzania, Kenya, Ethiopia and southern Sudan [84,85].
300 However, secondary branches are predominant today in more specific
301 regions or ethnic groups. For example, L5a1c1 is prevalent in Mbuti
302 pygmies from central Africa, L5a1c2 concentrate in Kenya, and L5a2 and
303 its subsequent radiations occur in southeastern African regions. Possible
304 Y-chromosome counterparts of these early expansions through east and

305 northward Africa could be the A3b2-M13 and B2a1-M218 lineages [86,87].
306 Even today, the geographic preeminence of L0, L1 and L5 basal lineages in
307 southern, central and eastern Africa respectively, seems to be the
308 remnants of a very ancient maternal structure in the African continent. It
309 is interesting to compare this vision with the very similar results obtained
310 from the analysis of ancient genome-wide genotype data from terminal
311 Late Pleistocene and early Holocene African hunter gatherers that
312 showed, in the same geographic area, a clinal pattern with individual
313 genomes well represented by varying proportions of Central African
314 pygmy, Southern African, and Ethiopian related ancestries [88]. However,
315 in general, ancient DNA genome based studies focus on more recent
316 population movements and turnovers and on the evidence of archaic
317 introgression in the majority of the populations analyzed [71,89,90].

318 The wide chronological window open in eastern Africa by the L5
319 coalescent interval (95% CI: 312 – 158 kya) allows to include in it the most
320 notable fossil and stone assemblages excavated in this area as are the
321 modern human remains recovered at Omo-Kibish (Ethiopia) and dated to
322 more than 200 kya[91,92], or the Herto (Ethiopia) remains dated around
323 160 kya[93]. The Sangoan-Lupemban lithic industries of equatorial Africa,
324 mentioned above, have also been found at Lake Eyasi in Tanzania[94], and
325 in Kenya at the Muguruk site[95], even most interesting is the presence of
326 stratified Sangoan-Lupemban assemblages as far as northern Sudan, at Sai
327 Island, dated around 230 kya that has been interpreted as the result of a
328 possible human norward dispersal from equatorial Africa during the MIS 7
329 interglacial period[96,97].

330 **An earlier out of Africa:** The next bifurcation in the mtDNA genomic tree
331 separated two sister branches, L2 and the composite L3'4'6 with
332 coalescent ages of 143 (111 – 176) kya and 185 (106 – 264) kya,
333 respectively (Table 2). Based on its subsequent ramifications and present-
334 day phylogeography, it has been suggested a western African origin for
335 haplogroup L2 [98,99]. This seems to be in contradiction with the eastern
336 geographic spread of its ancestral branch L5, and with the clear
337 northeastern spread of its sister branch L3'4'6 [23,85,100]. However, as
338 the earliest radiations of L2 occurred rather late, at around 60 kya,

339 involving eastern and western expansions, it seems more equidistant to
340 assume a central African origin for L2, an alternative hypothesis also
341 contemplated by other authors[98,99]. In any case, haplogroup L2 is a
342 typical sub-Saharan African lineage that likewise their predecessors L0, L1
343 and L5 did not participate in the out of Africa spread. It is the northeastern
344 L3'4'6 cluster the progenitor of the entire Eurasian maternal diversity [23].
345 Haplogroup L6 was the first lineage to split off from that composite clade.
346 This rare lineage presents mean frequencies below 1% in northeastern
347 Africa but, in spite of this, it is found at similar frequencies in Saudi
348 Arabia[23] and in higher frequencies in Yemen[101,102]. Based on the L6
349 tree[23] it appears that not all of the Arabian lineages are a subset of the
350 African lineages, so that an early expansion of modern humans from Africa
351 across Arabia has been suggested based on the haplogroup L6
352 phylogeography[101]. In a similar vein, haplogroup L4, another minor
353 eastern African mitochondrial lineage, has Arabian representatives in all
354 their main sub-branches, excepting L4b2b [23], which also points to an
355 early phylogeographic extension of this clade into the Arabian Peninsula.
356 The sister clade of L4 is haplogroup L3 that houses the Eurasian branches
357 M and N which contain all of the mtDNA diversity outside Africa [103]. It
358 has been proposed that after the radiation of L3 in eastern Africa, the
359 ancestors of M and N crossed the Bab al Mandab strait about 60 – 70 Kya
360 (the previously calculated coalescent age for L3) and, following a southern
361 coastal route, they spread all over the world [100,104–106]. As an
362 alternative hypothesis, we have proposed that the clade L3'4'6 already
363 extended its geographic range to southwestern Asia and that the splits of
364 the L6 and L3'4 branches (Table 2) occurred at the outside margins of
365 Africa, being the Y-chromosome counterpart of this early spread the
366 haplogroup CT-M168 that includes the Eurasian haplogroups C, D and F
367 and the African haplogroup E[23]. The ample statistical range of these
368 mtDNA coalescent ages (Table 2) includes important archaeological finds
369 in the region as the presence of early modern human populations in the
370 Levant at Misliya Cave from 177 to 194 kya[8], and at Qafzeh[107,108] and
371 Skhul[109,110] caves from 90 to 130 kya. These findings are in support of
372 an early expansion of modern humans from northeast Africa through the
373 northern Levantine route[111] which has also been proposed by mtDNA

374 [103,112] and genomic[113] data. However, fossil and previous genetic
375 models propose different chronologies as the mtDNA and Y-chromosome
376 dispersions are limited by the younger coalescent age of haplogroup L3
377 and CT-M168 respectively, and those based on genomic data by the levels
378 of haplotype diversity of the population outside Africa and the genome
379 mutation rate. In addition, it seems that the comparison of the lithic
380 industries, prevalent in the areas implied in the two routes out of Africa,
381 show stronger technological and typological similarities between
382 assemblages from the Horn of Africa and the Nile Valley and Arabia than
383 any of these regions and the Levant[114,115], however, alternatives to
384 this vision exist [116]. On the other hand, mainly two MSA archaeological
385 eastern African connections with Arabia have been identified, suggesting
386 early expansions of modern humans from the former to the later. The first
387 involves the Jebel Faya 1 site (United Arab Emirates) assemblage C, dated
388 to about 125 kya[117], which lithic technologies show similarities with
389 MSA assemblages in northeast Africa, particularly with the late Sangoan
390 [118]. The second evidence is founded on the similarities of the Dhofar
391 (Oman) lithic material and the Late Nubian Complex a specific African
392 industry that in Dhofar is dated at 106 kya[119]. These potential arrivals
393 coincide with wet stages of MIS5, with the split of the mtDNA L3'4 clade
394 (Table 2), and also with genomic results that place indigenous Arabs as
395 direct descendants of the first Eurasian populations [120], showing a
396 comparative excess of Basal Eurasian ancestry [121]. However, recent
397 archaeological sequences excavated in different regions of Arabia have
398 evidenced hominin presence since 400 kya in the Nefud Desert [122], and
399 since 210 kya at Jebel Faya[123] enabling much older hominin expansions
400 into the Peninsula or even to an autochthonous hominin evolution in
401 southwest Asia that got extinct by adverse climatic cycles and/or the
402 arrival of modern humans. Finally, it should be mentioned that an exit
403 through the Bab al Mandab Strait does not guarantee the existence of a
404 southern coastal route since an inland northward expansion is also
405 possible [124]. Furthermore, from the gathered evidence, both, the
406 northern and southern migratory routes could have been followed alike
407 [125]. At this respect, the detection of Nubian assemblages at the Negev

408 highlands in the southern Levant dated to the MIS5 humid period is
409 relevant [126].

410 **An earlier return to Africa:** After a period of maturation and stasis in
411 southwestern Asia, mtDNA haplogroup L3 split in the region and while the
412 ancestors of the L3 African subclades returned to Africa, the ancestors of
413 the Eurasian branches M and N began their exodus eastwards[23].
414 According to the new coalescent ages for the L3 subclades (Table 3), the
415 first radiations in eastern Africa took place around 75 kya, at the beginning
416 of the arid MIS 4 period. It was at this stage when an early modern human
417 displacement by the Neanderthals in the Levant was attested [40]. The Y-
418 chromosome counterpart of this mtDNA back flow to Africa was
419 haplogroup E [127]. The detection, in the extant population of Saudi
420 Arabia, of the basal African Y-chromosome lineage E-M96*[128] is in
421 support of this back flow. Furthermore, whole genome sequence analyses
422 also favor models involving possible African returns 70-60 kya[129,130].
423 Interestingly, a similar model, involving back flow to Africa, has been
424 proposed to explain the complex mtDNA phylogeography of hamadryas
425 baboons lineages present in Africa and Arabia [131].

426 The evidence gathered from the fossil and archaeological records for the
427 proposed return to Africa has been only occasionally mentioned but,
428 without generalized acceptance. Thus, it has been suggested that the Early
429 Nubian Complex, developed at the end of MIS 6 beginning of MIS5 (145 –
430 125 Kya) in northeast Africa, extended to Arabia where the Late Nubian
431 Complex occurred and from there was reintroduced into Africa during
432 MIS5a (85-75 kya)[132]. It is known that an early Nubian technology
433 appeared at Gademotta (Ethiopia) after 180 kya[133], and that it succeeds
434 the Lupemban at Sai Island (Sudan) after 150 kya[96]. In addition, at
435 Sodemein Cave (Egypt), stratigraphic layers dated to 121 ± 15 kya and $87 \pm$
436 9 kya are associated respectively with Early and Later Nubian complexes
437 [134]. Potential modern human fossils coetaneous of these assemblages
438 could be the Herto (Ethiopia) skull, dated to between 160 and 154 kya
439 [135], and the Singa (Sudan) skull dated to 133 ± 2 kya[136]. Other Late
440 Nubian assemblages could be mentioned, for instance, at Aduma
441 (Ethiopia) where it is associated with skeletal remains dated to 79-105 kya

442 [137] and in Taramsa Hill (Egypt) where it is at the same level of a child
443 burial dated to 68.6 ± 8.0 kya[138]. After the dry MIS4, a transformed
444 Nubian technology is present at Nazlet Khater (Egypt) associated with
445 modern human skeletal remains dated to around 40 kya[139], already
446 within a generalized MIS 3 population fragmentation that propitiated the
447 cultural differentiation evidenced by the Later Stone Age African diversity.
448 It should be emphasized that the proposed return to Africa, inferred from
449 the non-recombinant maternal haplogroup L3 and paternal haplogroup E
450 lineages, was earlier, had a broader geographic distribution, and greater
451 genetic impact than later Eurasian penetrations into Africa. At this respect,
452 it is suffice to note that, on average, maternal L3 lineages represent 27%
453 and paternal E lineages 72% of the female and male African genetic pools
454 respectively [23]. Subsequent pre-Holocene and Holocene Eurasian waves
455 into Africa, signaled mainly by mtDNA haplogroups M1 and U6 [140–144],
456 and Y-chromosome haplogroups J1-M267, R-V88 and T-M70 [87,145–147]
457 had more limited impact affecting mainly northern and northeastern
458 Africa. Due to the fact that these secondary Eurasian flows did not reach
459 southern Africa, the delayed presence in South Africa of Nubian
460 technology dated to 60-50 kya[148], and the analysis of the Hofmeyr skull,
461 dated at 36.2 ± 3.3 kya, and showing strongest morphometric affinities
462 with Upper Paleolithic Eurasians rather than present-day Khoisan [149],
463 might be explained as the late arrival to the south of the proposed
464 southwestern Asian reflux into Africa. The morphological affinities found
465 between Hofmeyr and Nazlet Khater crania [150] are also in accordance
466 with this hypothesis.

467

468 **Discussion**

469 **Journey and evolution of modern humans throughout Africa:** The
470 proposition that the population from which modern humans evolved was
471 located in northwest Africa is based on two main premises: first, it was the
472 most probable place in which an ancestral hominin population bifurcated
473 giving rise to the ancestors of the European Neanderthals and the African

474 humans [50]; second, it has been there where the oldest remains of our
475 species have been found [5].

476 Uniparental marker phylogenies point to Central/Southern Africa as the
477 place where the first split of that population occurred. The association of
478 these groups with Sangoan and Lupemban lithic technologies agree in
479 time and space, however, it seems a cultural throwback that descendant
480 of the makers of Mousterian MSA industries [4] opted for more primitive
481 lithic strategies, although this could be justified as a special adaptation to
482 new environments. At this respect, it should be mentioned the presence
483 of a Sangoan of northeastern Africa technology included over a
484 northwestern Africa Levallois Mousterian substratum at Wadi Lazalim in
485 southern Tunisia [97]. Afterward, molecular markers signal a clear
486 northward geographic progression signaled by L5 and L3'4'6 mtDNA
487 clades at the eastern African region and, less evidently, by the L2 clade at
488 the central region. In northeastern Africa it seems that the sub-Saharan
489 Sangoan/Lupemban was replaced by the Early Nubian technology [132]. It
490 is also probable that in northern Africa it was the Aterian which evolved
491 from previous sub-Saharan lithic industries [151]. Nevertheless, the out of
492 African migrants carrying maternal clade L3'4'6 and paternal clade CT-
493 M168 only could brought an Early Levantine Mousterian industry to the
494 Levant and a possible related Lupemban technology to southern Arabia
495 [117] and, afterwards, an Early Nubian technology that spread and
496 differentiated across the whole peninsula [152]. These early demic
497 spreads out of Africa into Eurasia, coinciding with humid periods as the
498 end of MIS7 (around 190 ka) and MIS5e (around 130 kya), could
499 satisfactorily explain the detection of anatomically modern human teeth
500 in southern China dated to 120-80 Kya[9], the presence of an early
501 modern human tooth in Sumatra at 73-63 kya[153], the archaeological
502 evidence of a possible human arrival to northern Australia around 65 kya
503 [154], or the genomic evidence of an ancient split between Africans and
504 Papuans around 120 kya[10].

505 Although the non-recombining uniparental markers have drawn a clear
506 trajectory of modern humans across Africa, this certainly has not been the
507 case. The presence of other primitive human groups along the way had

508 undoubtedly promoted genetic admixture events that, unnoticed by
509 uniparental markers, have been reflected in the genome of modern
510 Africans [155,156] and their Eurasian descendants several times [157,158].
511 Furthermore, extinction events generated by simple genetic drift could
512 affect more frequently to uniparental markers than whole genomes. Thus,
513 some early demographic expansions detected by the analysis of complete
514 genomes in current populations might not be perceived by the same
515 analysis in uniparental markers. However, in spite these caveats, the
516 phylogeny and phylogeography of mtDNA and Y-chromosome lineages
517 seem to find a coherent reflection in the archaeological and
518 anthropological records and might open the way for more detailed
519 interdisciplinary studies.

520 A graphical map of the proposed modern human route and its cultural,
521 physical, and genetic evolution across Africa is depicted in Fig 1.

522 **Fig 1. Modern human evolution across Africa and beyond**

523 **The first back to Africa of modern humans:** The first out of Africa and
524 back again for modern humans was proposed based on a nested cladistic
525 analysis of the Y-chromosome variation (Hammer [159], and was
526 supported by applying a most parsimonious criterion at an unbiased Y-
527 chromosome tree [127]. Searching for a female counterpart, it was
528 suggested that mtDNA haplogroup L3 also signals an early return to Africa
529 [23] and, recently, this backflow to Africa has also been detected by whole
530 genomic data [129]. The relatively closer morphological affinities of some
531 African fossils with coetaneous Eurasian remains rather than with current
532 African groups that have never abandoned the African continent [150],
533 could also be taken in favor of this return to Africa. However, the
534 archaeological support is much weaker because, although the temporal
535 margins of the appearance and development of the Early and Late Nubian
536 technological complexes are into the range proposed by the genetic
537 markers, a clear geographical and temporal separation between these two
538 lithic variants have not been yet determined. Therefore, it remains to
539 deepen into this possibility suggested only by a few [132].

540 A graphical map of the proposed early return to Africa of modern humans
541 and its genetic and archaeological support is depicted in Fig 2.

542 **Fig.2 Modern human early return to Africa from southwest Asia.**

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1223

1224 **Supporting information captions**

1225 S1 Fig. Phylogenetic relationships between the main mtDNA African
1226 clades.

- 1227 S2 Fig. Phylogeography of mtDNA haplogroup L2
- 1228 S3 Fig. Phylogeography of mtDNA haplogroup L6
- 1229 S4 Fig. Phylogeography of mtDNA haplogroup L4
- 1230 S1 Table. Mitochondrial sequences utilized for the phylogenetic and
- 1231 phylogeographic analyses.
- 1232 S2 Table. Age of the African mtDNA haplogroup L0.
- 1233 S3 Table. Age of the African mtDNA haplogroup L1.
- 1234 S4 Table. Age of the African mtDNA haplogroup L5.
- 1235 S5 Table. Age of the African mtDNA haplogroup L2.
- 1236 S6 Table. Age of the African mtDNA haplogroup L6.
- 1237 S7 Table. Age of the African mtDNA haplogroup L4.
- 1238 S8 Table. Age of the African mtDNA haplogroup L3.
- 1239

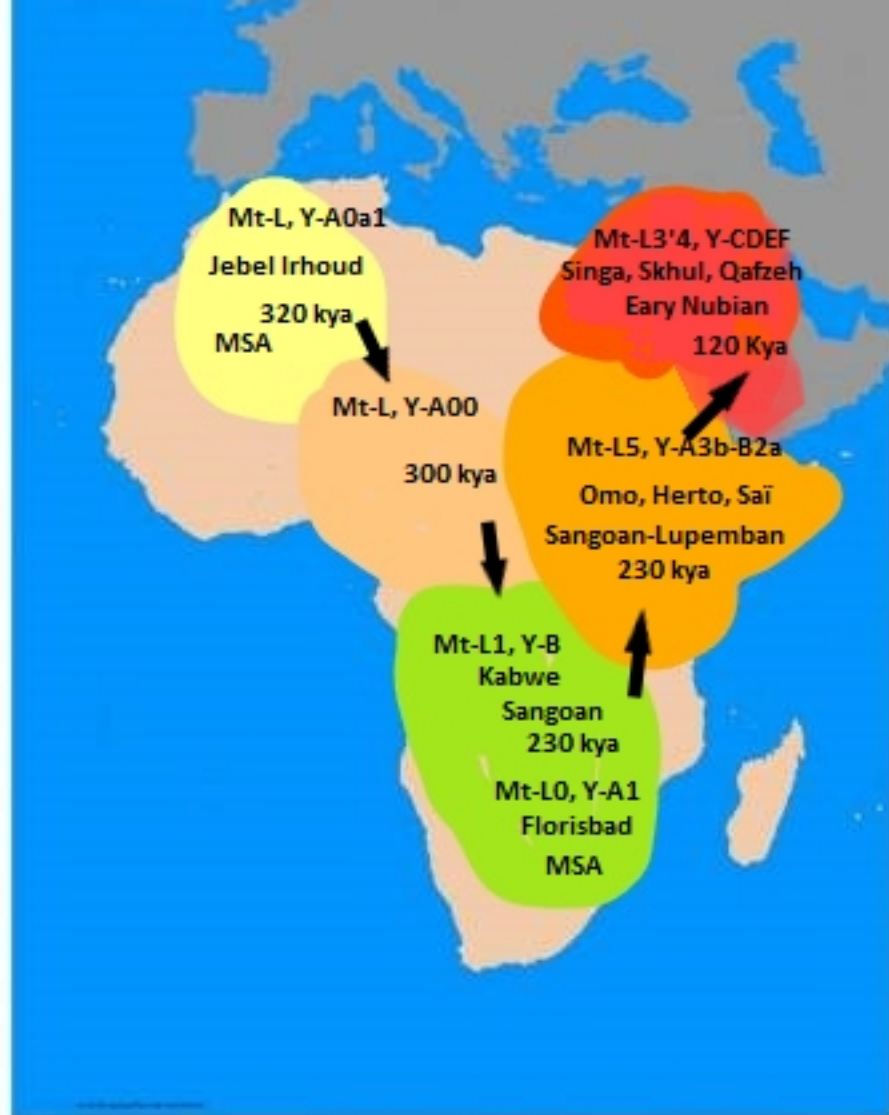


Figure 1

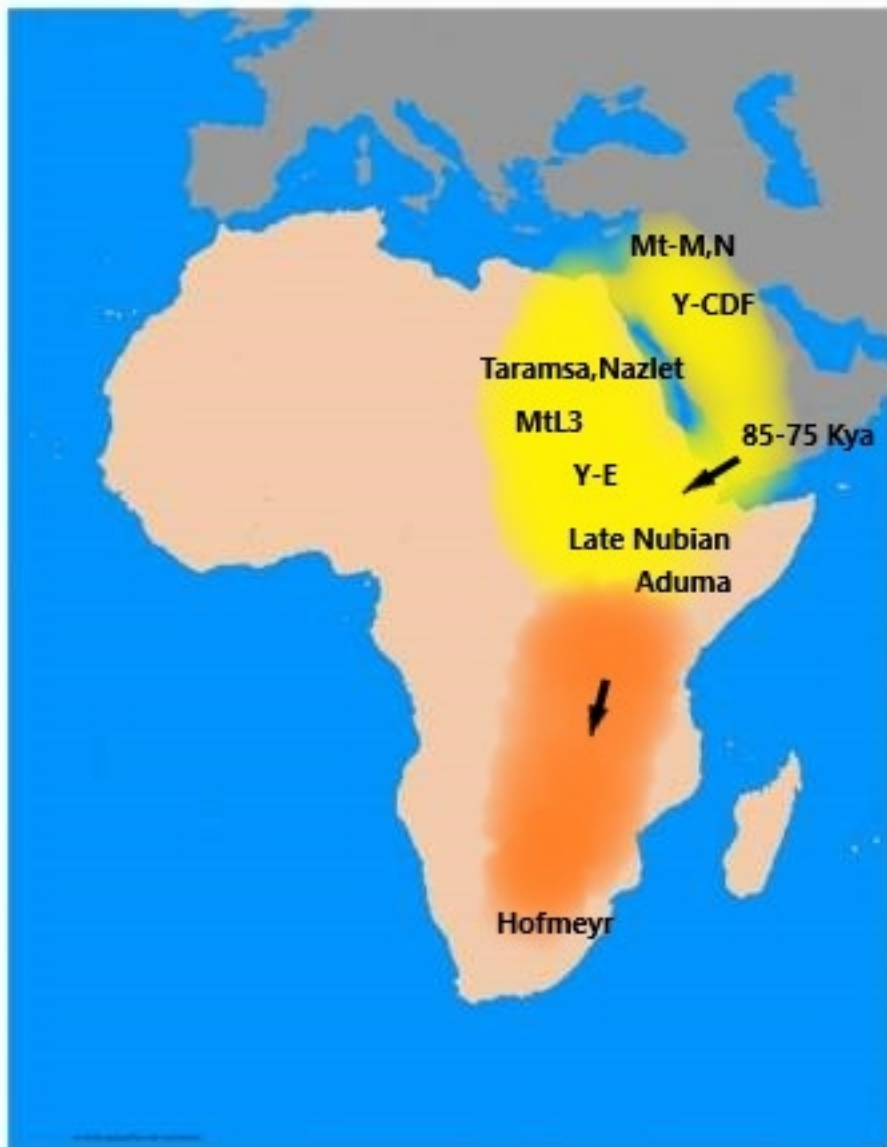


Figure 2