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The Entwined African and Asian Genetic Roots of the Medieval Peoples of the Swahili Coast

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46 **The peoples of the Swahili coast of eastern Africa established a literate urban**
47 **culture by the second millennium CE. They traded across eastern Africa and the**
48 **Indian Ocean and were among the first sub-Saharan practitioners of Islam. An open**
49 **question has been the extent to which these early interactions between Africans and**
50 **non-Africans were accompanied by genetic admixture. We report genome-wide**
51 **ancient DNA from 80 individuals in five medieval and early modern (1300-1800 CE)**
52 **coastal towns, as well as people from an inland town postdating 1650 CE. Over half**
53 **of the ancestry of most coastal individuals came from African ancestors; these**
54 **African ancestors were primarily female. A slightly smaller proportion of ancestry**
55 **was from Asia. This Asian component was approximately eighty to ninety percent**
56 **from Near Eastern males and ten to twenty percent from Indian females. Peoples of**
57 **African and Asian origins began to mix by around 1000 CE, a time when**
58 **archaeological evidence documents changes on the coast that are often interpreted**
59 **as marking the large-scale adoption of Islam. Before roughly 1500 CE, the Near**
60 **Eastern ancestry detected in the individuals was mainly Persian-related, consistent**
61 **with the narrative of the Kilwa Chronicle, the oldest history told by the Swahili**
62 **themselves. After this time, the sources of Near Eastern ancestry became**
63 **increasingly Arabian, consistent with the archaeological and historical evidence of**
64 **growing interactions between the Swahili coast and parts of southern Arabia.**
65 **Subsequent interactions of Swahili coast peoples with other Asian and African**
66 **groups further changed the ancestry of present-day peoples relative to the ancient**
67 **individuals we sequenced, highlighting how Swahili genetic legacies can be more**
68 **clearly understood with ancient DNA.**

69 **Introduction**

70 The Swahili culture of eastern Africa has been defined by a set of shared features: a
71 common language of African origin (Kiswahili), a shared predominant religion (Islam),
72 and a geographic distribution in coastal towns, many of which have long served as
73 trading centers, linking peoples across the Indian Ocean to peoples of inland Africa. In
74 the late medieval and early modern period, Swahili people lived over a vast coastal
75 region spanning present-day northern Mozambique to present-day southern Somalia and
76 including islands (Madagascar) and archipelagoes (Comoros, Kilwa, Mafia, Zanzibar,
77 Lamu) (yellow outlines in **Figure 1A**) [1, 2].

78
79 Narratives of Swahili identity have dominated research over the last 50 years, which has
80 demonstrated the autochthonous development of coastal settlement, yet questions of
81 genetic origins have remained unanswered. First millennium CE sites on the littoral,
82 beginning in the 7th century CE, were part of a shared material culture and practice
83 network across the eastern African region [3, 4] and were fully engaged in Indian Ocean
84 trading networks [5]. The annual southeast monsoons from May to October allowed
85 trading vessels to travel from India or the Arabian Peninsula to the eastern African coast,
86 and the northeast monsoons from November to March enabled their return in the same
87 year [5, 6]. Muslims were present on the coast from the 8th century CE, although
88 probably in a minority [7]. A transition can be identified in the archaeology of the coast
89 during the 11th century, with the establishment of new settlements and the elaboration of

90 older ones with coral-built mosques and tombs, all the while remaining deeply connected
91 to sites throughout eastern Africa [8]. This archaeological transition has been discussed
92 as reflecting the majority adoption of Islam [3, 9]; it can also be seen in the distinction of
93 coastal ceramics and material traditions from hinterland assemblages [10].

94
95 In the 16th century, Portuguese naval and economic dominance in the Indian Ocean
96 disrupted prior power relations [11, 12]. As Portuguese influence waned in the early 18th
97 century, the Sultanates of Oman and later Zanzibar ruled the eastern African coast [13].
98 In the 19th century, growth of overseas trade, particularly the slave trade, led to large-
99 scale movements of people from central regions of Africa to the coast and the settlement
100 of people from the Yemenite region of Hadramawt [13, 14]. In the mid-19th century,
101 other European powers, especially the British, took administrative and military control,
102 sent settlers, and precipitated significant population movements, including importing
103 workers from South Asia. In addition, there was continued interaction with other eastern
104 African groups, including pastoralist and farming groups along the coast and in the
105 interior. Because present-day people, identified as Swahili, may differ in their genetic
106 ancestry compared to populations of the 11th to 18th centuries, the origins of earlier
107 peoples of the Swahili culture cannot be reconstructed without the aid of ancient DNA.

108
109 A set of common oral traditions recorded along the coast relate the founding of coastal
110 towns to the arrival of a group known as the Shirazi, referring to a region in Persia [15-
111 17]. This Shirazi tradition was first put into writing in the Kilwa Chronicle, transcribed in
112 Portuguese in the 16th century [18]. The Swahili accounts of Shirazi roots were central to
113 the narrative constructed by mid-20th century colonialist archaeologists. They interpreted
114 second-millennium coastal eastern African sites as the remains left by Persian and Arab
115 settlers. Largely ignoring the evidence of a complex society created by peoples of African
116 origin [10], colonial archaeologists focused on cultural traits showing connections with
117 non-African peoples of the Indian Ocean world [19, 20].

118
119 Studies in the last decades have shown how Swahili elites have emphasized foreign
120 origins as part of status claims and signals of cultural and religious affinities to support
121 social stratification [21, 22]. Postcolonial research has challenged narratives of medieval
122 Swahili peoples having roots outside Africa [7, 23]. Historical linguistics has revealed
123 Kiswahili as a Bantu language, albeit with Asian loanwords [24, 25]. Archaeological
124 material culture of the people who inhabited second-millennium villages and towns
125 shows continuity with earlier settlements, including the persistence of crops,
126 domesticated animals, ceramics, and craft styles [7, 26]. Thus, postcolonial research has
127 shown that Swahili culture had autochthonous roots, coexisting with long-standing
128 engagement with Indian Ocean trade networks.

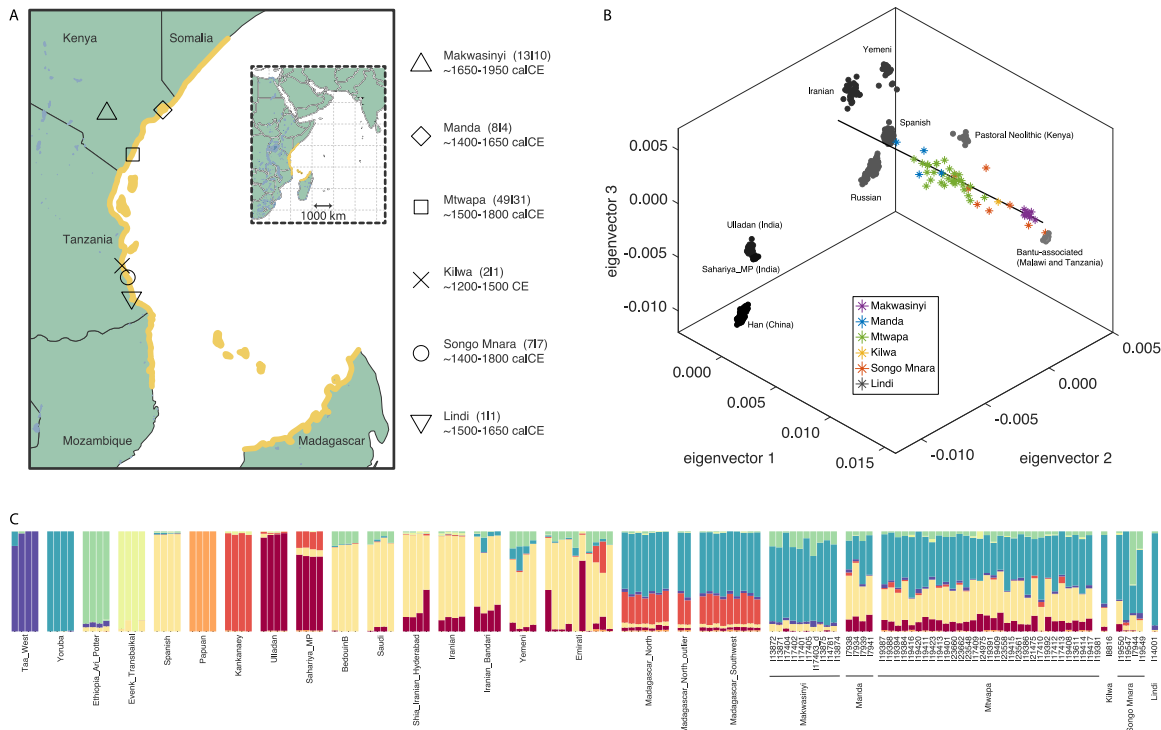
129
130 The intercontinental connections that Swahili groups maintained as part of the Indian
131 Ocean trading network probably meant that foreigners were consistently present along
132 the coast. The extent to which these foreigners immigrated, intermarried, and otherwise
133 intermingled with African residents has long been debated, thus raising questions about
134 Swahili coastal groups' ancestry [27].

136 This study presents the first genetic analysis of the medieval people of the Swahili coast
137 of eastern Africa. We generated ancient DNA data from the skeletal remains of
138 individuals found at five coastal or island towns: Manda, Mtwapa, Kilwa, Songo Mnara,
139 and Lindi. These samples date to the mid-second millennium 1300-1800 CE but provide
140 insight into genetic admixture events of the medieval period spanning from the 10th-11th
141 centuries CE onwards. We also generate DNA from the skeletal remains of individuals
142 found at the site of Makwasinyi (~1650-1950 CE), about 100 km inland from the
143 southern Kenyan coast, which has been populated by people who were in cultural contact
144 with coastal groups. We compare the newly reported data from the ancient individuals to
145 that of present-day coastal Swahili speakers [28, 29] and to published data from diverse
146 ancient and present-day eastern African [30, 31] and Eurasian groups [31-38].

147 **Data set**

148 We used in-solution enrichment for a targeted set of about 1.2 million single nucleotide
149 polymorphisms (SNPs; see Methods) to generate genome-wide ancient DNA data from
150 skeletal remains of 80 individuals buried at six second-millennium CE sites in eastern
151 Africa (black shapes in **Figure 1A**, analyzed individuals listed in **Extended Data Table**
152 **1**, see Methods and SI for an ethics statement and descriptions of archaeological and
153 genetic permissions and sampling). We also radiocarbon dated enough individuals from
154 each site to establish chronology, although from two sites (Kilwa and Lindi) the samples
155 we analyzed had insufficient collagen preservation to obtain dates. Two coastal sites were
156 from northern towns: Mtwapa (49 individuals spanning ~1500-1800 cal CE (calibrated
157 radiocarbon years)) and Manda Island (8 individuals dated to ~1400-1650 cal CE). Three
158 additional sites were from southern towns: Kilwa Island (2 individuals spanning ~1300-
159 1600 CE based on archaeological context), Songo Mnara Island (7 individuals spanning
160 ~1300-1800 cal CE), and Lindi (present-day Tanzania, 1 individual dated to ~1500-1650
161 CE). The remains of individuals buried at Mtwapa, Manda, and Songo Mnara were
162 mainly recovered from elite Muslim burials often located near mosques. We do not have
163 enough context for the Kilwa and Lindi burials to know if they followed the same pattern.
164 We also analyzed 13 individuals spanning ~1650-1950 CE from an inland site,
165 Makwasinyi (~100 km inland from the coast of present-day Kenya). While these burials
166 post-date coastal sites in our study, the Makwasinyi community traded with people in the
167 coastal towns in past centuries and has remained relatively isolated. We thus
168 hypothesized that the genetic ancestry of the Makwasinyi people might be a good proxy
169 for inland African groups that may have been in contact with people from medieval cities
170 on the northern Swahili coast in previous centuries [39, 40].

171
172 Of the 80 individuals for which we acquired genetic data, we removed 26 from our main
173 analyses. Of these 26, 2 had contaminated sequences, 18 had too little data for high-
174 resolution analyses, 5 were first- or possibly second-degree relatives of other individuals
175 in the dataset with better quality data, and 1 was unreliable as it was a significant outlier
176 with relatively low coverage (**Online Table 2 | newly_reported_individuals**). Of the
177 remaining 54 individuals, 24 have direct Accelerator Mass Spectrometry (AMS)
178 radiocarbon dates (**Extended Data Table 1** and **Online Table 3 | 14C_Results**).
179



180
 181 **Figure 1: Dataset overview.** A) The coastal areas associated with the Swahili culture are
 182 outlined in yellow. Sites included in this study are marked with black shapes and labeled
 183 on the zoom-in inset with the number of individuals, number of non-first-degree relatives
 184 with sufficient data to analyze extensively, and approximate date range. B) A three-
 185 dimensional principal component analysis shows present-day and ancient people studied
 186 in order to contextualize the ancestry of the Swahili individuals, labeled with asterisks.
 187 Eigenvector 1 correlates to variation maximized in sub-Saharan Africa. Together,
 188 eigenvectors 2 and 3 describe variation maximized in Eurasia. For 2D PCAs to aid
 189 visualization of the same data, see **Extended Data Figure 3**. C) Ancestry component
 190 assignment using ADMIXTURE with $K=8$ ancestral reference populations. Mtwapa,
 191 Manda, Kilwa, and some Songo Mnara individuals have evidence of shared ancestry with
 192 Near Eastern, South Asian, and African sources. Songo Mnara individuals appear to be
 193 heterogenous in their ancestry components and proportions, reflecting cosmopolitanism
 194 along the Swahili coast. The Lindi individual falls near people with western African
 195 ancestry including present-day Bantu speakers.

196 Genetic affinities of newly analyzed individuals

197 We performed principal component analysis (PCA, **Figure 1B** and **Extended Data**
 198 **Figure 3**), computing the eigenvector axes using 1286 present-day Eurasian and African
 199 individuals. Many of the newly reported ancient individuals projected onto this modern
 200 variation form a cline, with one end overlapping with ancient and present-day African
 201 groups and the other falling between present-day Persian and Indian groups. This cline
 202 suggests that the individuals might be mixed in different proportions of two source
 203 populations, where each can have multiple ancestry components. However, some coastal
 204 individuals, particularly from Songo Mnara and Lindi, do not fall along this cline.
 205 Individuals who deviate from the cline cannot be described by this same two-way

206 mixture model and must harbor alternative ancestral contributions. Similar patterns of
207 ancestry composition are evident with unsupervised clustering using ADMIXTURE
208 (**Figure 1C, Extended Data Figure 1**), which suggests sub-Saharan African-associated
209 components, Near Eastern-associated components, and East Asian or Indian-associated
210 components.

211 **Three-way mixture of Sub-Saharan African, Persian, and Indian ancestry**

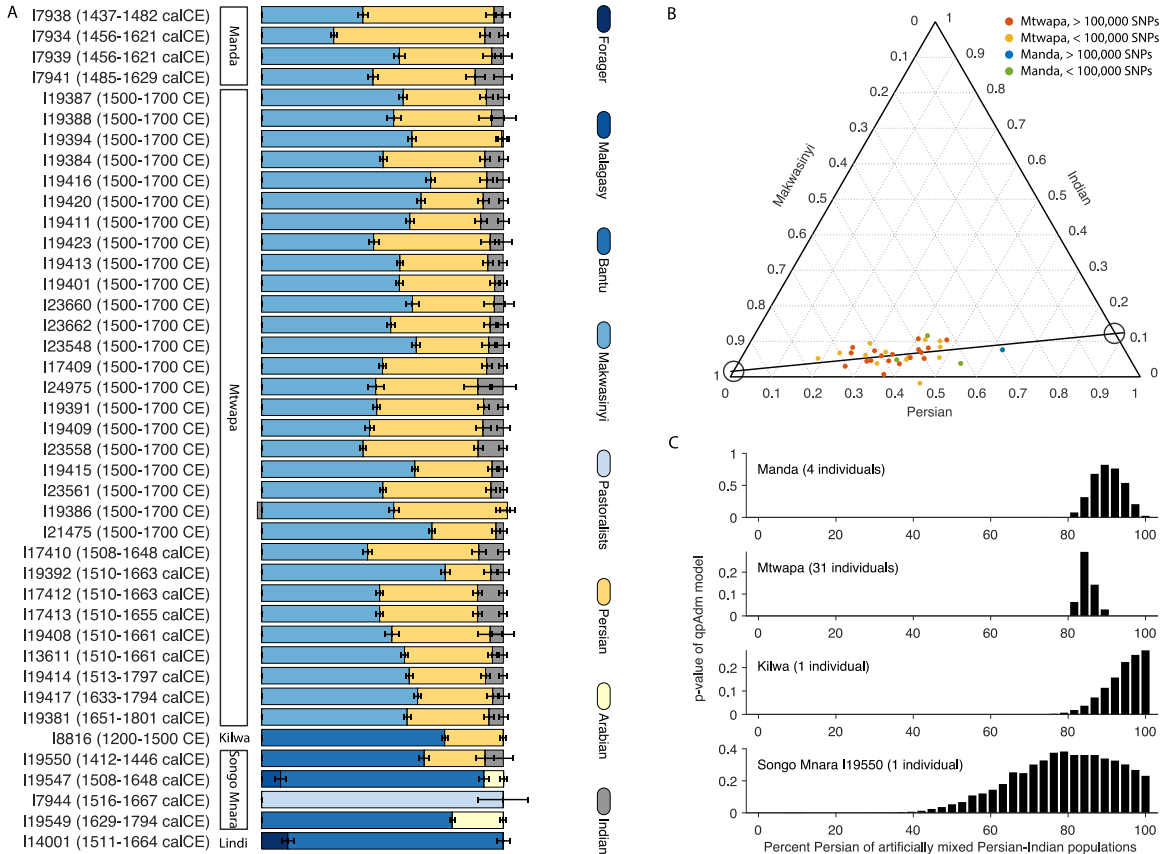
212 Using *qpAdm* [34], we identified a common three-source model that fits the data for most
213 Swahili individuals (see **Supplementary qpAdm modeling** for a description of formal
214 modeling). We used a local ancient African source and present-day Iranian and Indian
215 groups as proxies for the three ancestry components (**Figure 2A and Extended Data**
216 **Table 2**). Any model that does not include all three ancestries can be rejected with high
217 statistical confidence. This model fits the pools of Mtwapa (P value for fit 0.23) and
218 Manda (P=0.28) individuals, the Kilwa individual with good quality data (I8816)
219 (P=0.27), and at least one Songo Mnara individual (I19550) (P=0.38). In individuals with
220 relatively high proportions of African ancestry, such as the Kilwa individual, other
221 contributions are small, and the Indian proportion can fall below the threshold of
222 definitive detection.

223
224 The African source of ancestry needed to make the models fit differed between the
225 northern individuals in present-day Kenya (Mtwapa and Manda) and the southern
226 individuals in present-day Tanzania (Kilwa and Songo Mnara). Among individuals from
227 the Mtwapa and Manda sites, the best-fitting proxy source for the sub-Saharan African-
228 associated ancestry is the group from the inland Makwasinyi site (**Extended Data Table**
229 **2**). Makwasinyi individuals themselves are well-modeled as mixtures of about 80%
230 ancestry related to western African groups (an ancestry common today in speakers of
231 Bantu languages and prevalent in eastern Africa; henceforth called ‘Bantu-associated’)
232 and about a quarter ancestry from people related to ancient eastern African Pastoral
233 Neolithic individuals [30] (**Figure 3A and Extended Data Table 3**, see **Supplementary**
234 **qpAdm modeling** for a description of formal modeling). Among individuals from Kilwa
235 and Songo Mnara, the best-fitting African proxy source is Bantu-associated without a
236 Pastoral Neolithic contribution. We use the individual from this study buried at ~1600 CE
237 in Lindi as a proxy Bantu-associated source for the Kilwa individual and for the Songo
238 Mnara I19550 individual (**Extended Data Table 2**).

239
240 The ancestry proportions for individuals from Manda and Mtwapa form a cline consistent
241 with a mixture of just two source populations (**Figure 2B**). Using linear regression, we
242 extrapolated the ancestry of these two sources and inferred that one source population
243 was consistent with a 100% African origin (one standard error, **Supplementary qpAdm**
244 **modeling**). The same analysis concluded that the other source had Indian and Persian
245 ancestry. This data are consistent with sub-Saharan Africans mixing with a group that
246 already had a mix of Persian and Indian ancestry components. The finding of multiple
247 mixture events would be expected if people of mixed Persian and Indian ancestry had
248 children with people from different local African populations at different locations along
249 the coast.

250

251 When we separately analyze the Mtwapa, Manda, Kilwa, and Songo Mnara individuals,
 252 we infer possibly consistent proportions of Indian and Persian ancestry (the ranges are
 253 close and plausibly within normal variation, **Figure 2C**). Some variation in the ratio of
 254 Persian-to-Indian ancestry among the early immigrants is expected, making it difficult to
 255 distinguish between scenarios of one or many streams of Persian-Indian ancestral
 256 populations. However, there was high uncertainty for individual estimates of Indian
 257 proportions, and in some individuals (e.g., the one buried at Kilwa), it may in fact be
 258 absent (**Supplementary qpAdm modeling**). Finally, our analysis cannot determine if the
 259 Persian-Indian mixture occurred before these people arrived in eastern Africa or after.
 260



261

262 **Figure 2: Individual mixture proportions.** A) Inferences from qpAdm (bars show one
 263 standard error, see **Extended Data Table 2** and **Supplementary qpAdm modeling** for
 264 model details including source populations, proportions of admixture, and P-values for
 265 fit). Blue represents African components of ancestry: the most common are Bantu-
 266 associated (medium blue, common at southern sites), and Makwasinyi associated
 267 (medium-light blue, common at northern sites), which itself is ~80% Bantu-related and
 268 ~20% pastoralist-related. The African pastoralist-related ancestry in this diagram
 269 encompasses both Neolithic and Iron Age ancestry components from Kenya and Tanzania.
 270 Yellow represents Near Eastern ancestry: Persian (light yellow) or Arabian associated
 271 (dark yellow). Gray represents Indian ancestry. B) Ternary plot of Makwasinyi, Persian,
 272 and Indian components in Mtwapa (red points - high coverage, yellow points - low
 273 coverage) and Manda individuals (blue points - high coverage, green points - low
 274 coverage). Higher coverage individuals (>100,000 SNPs overlapping positions on the

275 *Human Origins array) are used to fit a linear regression (dashed line), which intersects at*
276 *nearly 100% Makwasinyi and nearly 0% Persian and Indian ancestries, consistent with a*
277 *Makwasinyi-related population with little or no recent Near Eastern ancestry mixing with*
278 *an already mixed Persian-Indian population to form the ancestry of northern Swahili*
279 *coast people. C) Bar graph showing P-values for a two-way qpAdm model with a local*
280 *African source (using Makwasinyi as the source for Mtwapa and Manda individuals, and*
281 *the Lindi individual as the source for the Kilwa individual and the Songo Mnara*
282 *individual) and a mixed Persian-Indian source. The x-axis specifies the proportion of*
283 *Near Eastern ancestry in this mixed source.*

284 **Male ancestors mainly from Persia; female ancestors mainly from Africa and India**

285 We tested whether male and female ancestors (based on genetically determined sex)
286 contributed equal proportions of the three ancestry components in the ancient individuals
287 sampled at Mtwapa, Manda, and Kilwa (**Table 1**). We could not carry out the same
288 analysis for Songo Mnara because there were no individuals who fit the three-way model
289 and had data of sufficient quality to permit this analysis.

291 We first analyzed mitochondrial haplogroups transmitted entirely by females, restricting
292 to non-first-degree relatives. All but one individual carries an L* haplogroup, which
293 today is almost wholly restricted to sub-Saharan Africans [41-43]. The one individual
294 with a non-L haplogroup is from Mtwapa and carries haplogroup M30d1, which is
295 largely restricted to South Asia [42]. The mtDNA haplogroup distribution of sampled
296 coastal individuals is consistent with female ancestry deriving almost entirely from
297 African or Indian sources, with a higher proportion of African female ancestors. We also
298 expanded our mtDNA analysis to include ancient coastal and island individuals with low
299 coverage or who did not pass quality control on the autosomes but did have sufficient
300 mtDNA coverage. With this larger group of individuals, all but two have L* haplogroup
301 indicative of sub-Saharan Africa. In addition to the M30d1 haplogroup, common in South
302 Asia, we identified a male individual with haplogroup R0+16189, which is common in
303 Saudi Arabia and the Horn of Africa [44].

304

305 We also examined male-transmitted Y chromosome sequences, which tell a different
306 story than female-transmitted mitochondrial DNA. Two of three non-first-degree related
307 males from Manda belong to haplogroup J2, while the third belongs to G2; both
308 haplogroups are characteristic of Near Eastern ancestry (plausibly Persian) and are
309 largely absent in sub-Saharan Africa [45-47]. The Kilwa individual also carries a J2
310 haplogroup. Fourteen of the twenty male Mtwapa individuals belong to J-family
311 haplogroups, and two belong to R1a haplogroups, all of which are typically non-African
312 lineages. The four remaining individuals belong to E1 family haplogroups, characteristic
313 of sub-Saharan Africa. The Y chromosome haplogroup distribution is consistent with the
314 male ancestry of sampled individuals from Mtwapa deriving mostly, but not entirely,
315 from the Near East. The Y chromosome haplogroup distribution in Mtwapa differs
316 qualitatively from that in Manda and Kilwa in that it includes more J1's than J2's, but is
317 still consistent with the male ancestry of sampled individuals from Mtwapa deriving
318 mostly, but not entirely, from the Near East.

319

320 Finally, we compared ancestry estimates from chromosomes 1-22 (the autosomes), which
 321 equally reflect the contributions of females and males, to those from chromosome X,
 322 which occurs in two copies in females compared to one in males, and thus predominantly
 323 reflects the contributions of female ancestors. African ancestry estimates from the
 324 autosomes are significantly lower in the individuals from Mtwapa, Manda, and Kilwa
 325 than estimates made from chromosome X: the 95% confidence intervals are non-
 326 overlapping, and the absolute value of the Z-score for a difference between the two
 327 estimates is greater than 2. This implies that the African ancestry in medieval Swahili
 328 coast populations primarily came from females, consistent with the mitochondrial DNA
 329 and Y chromosome evidence (**Table 1**). Similarly, the Persian ancestry in all three groups
 330 primarily came from males (**Table 1**). Under the simplifying assumption that the mixture
 331 occurred in a single event over just a few generations, rather than over a period that
 332 spanned many generations, we estimate the proportion of African ancestry contributed by
 333 females: 100% in sampled individuals at Manda (95% confidence interval entirely above
 334 this value), 76-90% at Mtwapa, and 80-98% at Kilwa (Methods, **Table 1**). Using the
 335 same approach, we estimate the proportion of Persian ancestry contributed by males to be
 336 100% in sampled individuals in all three locations.

337
 338

Table 1: Inferences about mixture for three Swahili coast groups.

	Mtwapa (31 individuals)			Manda (4 individuals)			Kilwa (1 individual)	
	Africa	Persia	India	Africa	Persia	India	Africa	Persia
mtDNA haplogroups (N)	30	--	1	3	--	--	1	--
Y chrom. haplogroups (N)	4	16	--	--	3	--	--	1
Ancestry sources autosomes	56-58%	34-39%	4-9%	30-34%	55-65%	3-13%	72-76%	24-28%
Ancestry sources chrom. X	65-75%	0-24%	7-39%	49-70%	0-74%	0-75%	83-100%	0-17%
Z score autosomes vs. X for Makwasinyi	-4.7	3.4	-2.0	-5.0	1.4	-0.5	-3.3	3.3
Prop. of this ancestry female	76-90%	0%	100%	100%	0%	23-100%	80-98%	0%
Prop. of this ancestry male	10-24%	100%	0%	0%	100%	0-77%	2-20%	100%
Prop. Persian (of total Asian)	84-87%			84-97%			89-100%	
Estimated admixture dates	938-1242 CE			629-1412 CE			614-1336 CE	

339 *Notes: Ancestry estimates on chromosomes 1-22 and chromosome X are compared to infer*
 340 *proportions from female or male ancestors (Methods). Ranges for rows 3-4 are 95% confidence*
 341 *intervals based on estimated ± 1.96 standard errors, truncated if extending outside 0-100%.*

342 **All three ancestry components began mixing by about 1000 CE**

343 We used the software DATES [48] to estimate when mixture occurred. We detect strong
 344 signals of linkage disequilibrium driven by a mixture between ancestral populations of
 345 sub-Saharan African and Asian ancestry, with 95% confidence intervals for the inferred
 346 dates of 938-1242 CE for Mtwapa, 629-1412 CE for Manda, and 614-1336 CE for Kilwa
 347 (**Table 1** and **Extended Data Figure 2**). The uncertainty intervals of the three groups
 348 overlap from 938 to 1242 CE. The Songo Mnara individual that fits the three-way model
 349 does not have sufficient data to estimate a date of mixture, but since the other three date
 350 ranges overlap, it is reasonable to hypothesize that they derive from mixture in the same
 351 period. Our analysis suggests that already admixed males with both Indian and Persian
 352 ancestry were present along the coast by ~1000 CE and mixed further with primarily
 353 female sub-Saharan Africans.

354 **In recent centuries, the coast was impacted by Arabian (plausibly Omani) migration**

355 For the earliest individuals in our study with a Near Eastern ancestry component
356 (individuals from Manda, Kilwa, and the I19550 individual from Songo Mnara), there is
357 no evidence of Arabian-associated ancestry that is not well proxied by Persian sources.
358 However, later individuals can be modeled as having Arabian-related ancestry, such as
359 those buried at Mtwapa with radiocarbon dates in the 16th to 18th centuries. We were not
360 able to determine the exact source of the Arabian-associated ancestry in the Mtwapa
361 group. However, we know that it is somewhere on the genetic gradient between Arabians
362 and Persians. We are also not able to determine if there is added Persian-Arabian ancestry
363 or only added Arabian ancestry since the significant Persian admixture from ~1000 CE
364 would mask any smaller or partial subsequent additions of Persian ancestry. In one of our
365 analyses, this added Persian-Arabian ancestry source for Mtwapa is well proxied by
366 groups bordering the Strait of Hormuz, which separates the Arabian Peninsula from
367 present-day Iran. The Strait of Hormuz and the Swahili coast were under Omani control
368 simultaneously (beginning at the end of the 17th century). While Mtwapa individuals have
369 Arabian and Persian ancestries, we do not detect Arabian-associated ancestry when we
370 apply a similar analysis to the Manda individuals who lived earlier than the Mtwapa
371 individuals. Since Manda individuals lived sometime between the 15th and 17th centuries,
372 they predate Omani political dominance along the Swahili coast.

373

374 Further evidence for Arabian immigration affecting parts of the Swahili coast in the later
375 period comes from two individuals from Songo Mnara (I19547 and I19549). Both date to
376 after 1500 CE and can be modeled with Arabian-related ancestry in *qpAdm* (Figure 2A).

377 **Relationship between modern and medieval peoples of the eastern African coast**

378 We analyzed genome-wide data from 89 people previously reported by Brucato et al.
379 After removing two outliers (according to the ADMIXTURE graph in Extended Data
380 Figure 1) from analysis, we found that these present-day people who live in coastal areas
381 of Kilifi, Lamu, and Mombasa in Kenya and who identify as Swahili [28] typically have
382 a small genetic inheritance from ancient people who lived in nearby coastal areas
383 (proxied by the individual buried at Kilwa) (**Figure 3A** and **Extended Data Table 3**,
384 **Supplementary qpAdm modeling**). We infer point estimates in the three coastal
385 populations of 79-86% Bantu-associated ancestry proxied by the Lindi individual (all
386 standard errors about 3%); 2-15% Pastoral Iron Age-associated ancestry [30] (all
387 standard errors about 3%); and 6-14% ancestry from medieval Swahili-associated
388 ancestry (all standard errors about 4%) (**Figure 3A**).

389

390 We also examined mitochondrial and Y chromosome haplotype determinations published
391 in the same study [28]. A total of 231 of 237 individuals with mitochondrial DNA
392 haplogroup determinations (97%) were from the L and M1 lineages, which are
393 widespread in Africa, consistent with almost all female-lineage ancestry being from
394 Africa [49-52]. Of 107 Y chromosome haplogroups, 102 (95%) are typically African,
395 which is very different from medieval coastal individuals from whom almost all Y
396 chromosome haplogroups are Near Eastern associated (Table 1).

397

398 The Brucato et al. Y chromosome haplogroup frequencies are not characteristic, however,
 399 of all modern coastal populations that identify as Swahili. Raaum et al. carried out an
 400 independent study of these frequencies, investigating mitochondrial and Y chromosomes
 401 of 179 present-day Swahili men from thirteen locations along the Kenyan coast (8 in the
 402 Lamu archipelago, 3 near Mtwapa and 2 near the Tanzanian border) [29]. The Raaum et
 403 al. study found that the African-associated Y haplogroup frequency was 45%, which was
 404 much less than the 95% in Brucato et al. albeit also substantially larger than the 17% in
 405 the medieval individuals (see Table 2). Thus, although Brucato and Raaum are sampling
 406 Swahili groups from roughly the same areas in Kenya, their findings are qualitatively
 407 different, implying population structure in modern day Swahili. The Raaum et al. study
 408 may have been biased toward upper-class Swahili society because they recruited
 409 participants through snowball sampling relying on initial contacts known to field
 410 assistants, while the Brucato et al. sampling strategy relied on public meetings. The
 411 medieval Swahili sample may more closely resemble the sample in the Raaum et al.
 412 study because our excavations focused on graves located near mosques, likely biasing
 413 toward more elite residents. Still, both studies were in agreement in showing a large
 414 increase in the proportion of African haplogroups relative to the medieval sample.
 415

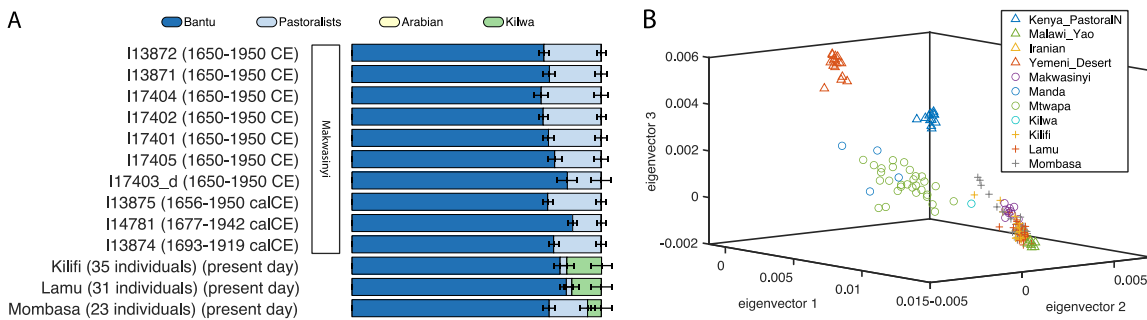
416 **Table 2: Comparison of medieval Swahili haplogroup distribution with those from two**
 417 **studies of present-day Swahili individuals.**

Likely Y chromosome haplogroup origin	Present-day Raaum et al [29]	Present-day Brucato et al [28]	Medieval Present study
Africa	45%	95%	17%
Near East	35.5%	3%	83%
Other	19.5%	2%	0%
Likely mtDNA HG origin	Raaum et al [29]	Brucato et al [28]	Present study
Africa	94%	97%	97%
South or East Asia	4%	2%	3%
Other	2%	1%	0%

418 **Ancient non-coastal groups are genetically similar to present-day coastal groups**

419 The predominant genetic profile of Bantu-associated and pastoralist-associated ancestry
 420 found in present-day Kenyan coastal populations is similar to that in the Makwasinyi
 421 individuals located 100 km inland from the Kenyan coast (**Figure 3A**). The Makwasinyi
 422 individuals date to the last three centuries. They are from a relatively isolated population
 423 located deep into the Tsavo region and nearly 50 kilometers from their nearest neighbors.
 424 The Makwasinyi group fits as an African ancestry proxy source for *qpAdm* modeling of
 425 the Mtwapa and Manda individuals. Unlike the Mtwapa and Manda individuals,
 426 Makwasinyi individuals have no evidence of any recent Asian ancestry according to
 427 *qpAdm*. Instead, they are well modeled as 21.3±1.2% Pastoral Neolithic-associated
 428 ancestry and 78.7±1.2% Bantu-associated ancestry (**Figure 3A**). Herders were present in
 429 eastern Africa from at least 3000 BCE but are not documented beyond northernmost
 430 inland Kenya until two millennia later [30]. They persisted after people who practiced
 431 farming spread from west to east Africa in the first millennium CE, often associated with
 432 the Bantu expansion [26]. The sex-bias determination in the Bantu-Pastoral Neolithic

433 mixture in Makwasinyi varies depending on the individual used as the Bantu-associated
 434 proxy source. When we use the 600BP individual buried at Makangale Cave on Pemba
 435 Island, we infer that Bantu-related ancestors were 37-50% female and 50-63% male,
 436 whereas KPN-related ancestors were 48-100% female and 0-52% male (Methods,
 437 **Supplementary qpAdm modeling**). However, when we calculate male and female
 438 ancestry proportions using the individual buried at Lindi, we infer that Bantu-related
 439 ancestors were 48-74% female and 26-52% male, whereas KPN-related ancestors were 0-
 440 60% female and 40-100% male. The variation could reflect the inherently poor statistical
 441 resolution of the X chromosome estimates and different degrees of sex-biased mixture in
 442 the source populations themselves. The average date for the Bantu-Pastoral Neolithic
 443 mixture is ~300-1200 CE (**Extended Data Figure 2**), with most of this date range
 444 consistent with the archaeological evidence for the impact of the Bantu expansion on this
 445 region.
 446



447 **Figure 3: Relation of medieval Swahili people to modern and ancient eastern Africans.**
 448 *A) Graphical representation of individual and population level qpAdm models for*
 449 *Makwasinyi individuals (this study) and present-day people from Kilifi (n=35), Lamu*
 450 *(n=31), and Mombasa (n=23) who identify as Swahili [28]. The green ancestry*
 451 *component represents the modeled contribution from medieval Swahili coast people, as*
 452 *represented by the individuals buried in Kilwa. B) PCA with the same present-day people*
 453 *from Kilifi, Lamu, and Mombasa, as well as present-day people from Malawi, Iran, and*
 454 *Yemen (triangles) [31, 32, 37, 53], and ancient individuals from eastern Africa published*
 455 *in this study (open circles) and previously (triangles) [30, 31] projected onto the first*
 456 *three eigenvectors.*

458 **Outliers past and present highlight the cosmopolitanism of the Swahili coast**

459 While the main patterns of variation in the dataset are driven by admixture involving
 460 people with African, Persian, and Indian ancestries; there are some individuals at Songo
 461 Mnara and Lindi that do not have any evidence of recent Asian ancestry (I14001 dating
 462 to 1511-1664 calCE and I7944 dating to 1516-1667 calCE) (**Figure 3A** and **Extended**
 463 **Data Table 3, Supplementary qpAdm modeling**). We detect possible Arabian or
 464 Omani-associated ancestry in the Mtwapa group (**Supplementary qpAdm modeling**)
 465 and perhaps in two third-degree relatives from Songo Mnara (I19547 dating to 1508-1648
 466 calCE and I19549 dating to 1629-1794 calCE) (**Figure 3A** and **Extended Data Table 3,**
 467 **Supplementary qpAdm modeling**). In addition, we find the possibility of Malagasy-
 468 associated ancestry in Songo Mnara (I19547 dating to 1508-1648 calCE) (**Figure 3A** and
 469 **Extended Data Table 3, Supplementary qpAdm modeling**). These coastal individuals

470 who differ genetically compared to the others from similar times or geographic locations
471 testify to the cosmopolitan nature of this region and its involvement within the inter-
472 continental Indian ocean trading network.

473

474 **Discussion**

475 A key finding of this study (**Figure 4** and **Table 1**) is genetic evidence of admixture at
476 roughly 1000 CE between people of African and people of Persian ancestry. This
477 admixture is consistent with one strand of the history recorded by the Swahili themselves,
478 the Kilwa Chronicle, which describes the arrival of seven Shirazi (Persian) princes on the
479 Swahili coast. At Kilwa, coin evidence has dated a ruler linked to that Shirazi dynasty,
480 Ali bin al-Hasan, to the mid-11th century [54]. Whether or not this history has a basis in
481 an actual voyage, ancient DNA provides direct evidence for Persian-associated ancestry
482 deriving overwhelmingly from males and arriving on the eastern African coast by about
483 1000 CE. This timing corresponds with archaeological evidence for a substantial cultural
484 transformation along the coast, including the widespread adoption of Islam [3, 8, 9]. It is
485 difficult to distinguish between a scenario in which a mixture event occurred within a few
486 generations and one drawn out over dozens of generations. While we can be confident
487 that mixture had begun by 1000 CE, in theory, it could have started earlier and continued
488 later. We emphasize that the people of African ancestry made the largest genetic
489 contribution to the mixed population.

490

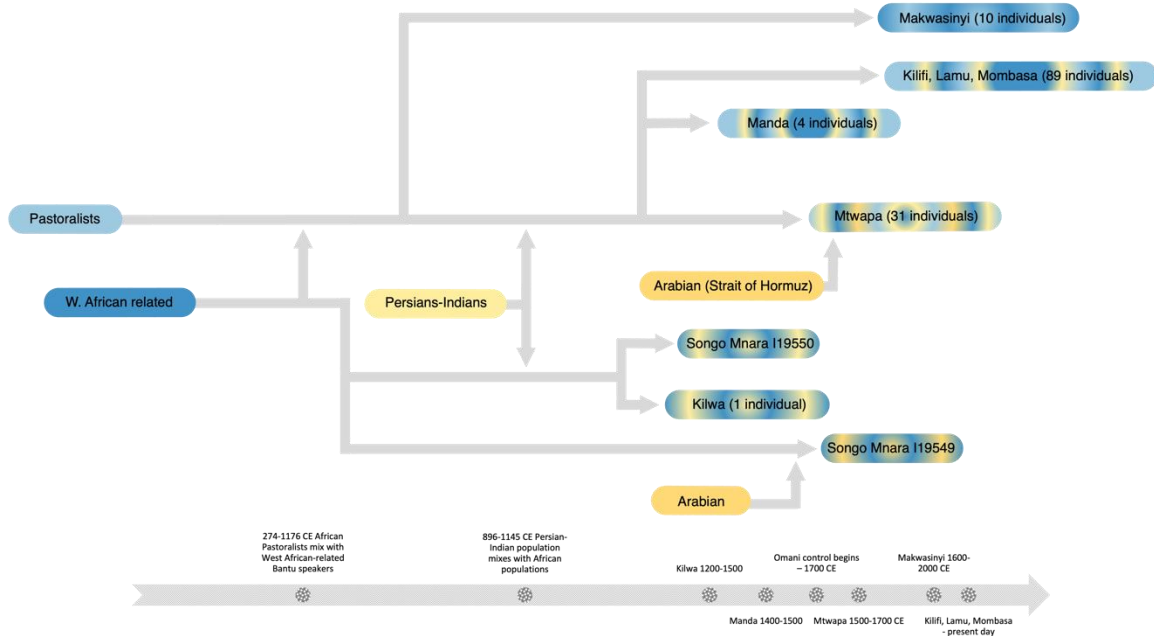
491 The genetic findings are important to interpret in light of the archaeological evidence.
492 The samples analyzed here are from the 14th – 18th centuries, and mostly from elite
493 contexts. While it is notable that elite burials of this period had significant Persian
494 ancestry, we do not fully understand the contexts in which this admixture first occurred.
495 Coastal sites of around 1000 CE had less evidence for elite distinction, and it is notable
496 that these later elites developed from admixed populations. Two of the sites (Mtwapa
497 and Songo Mnara) did not exist as towns during the period of admixture, and so these
498 admixed populations moved to those towns during the succeeding centuries.

499

500 The genetic findings are also important to interpret in light of the linguistic evidence.
501 Kiswahili is a Bantu language, and given our finding that most of the female ancestry of
502 individuals in this study derived from Africans, our results point to a scenario in which
503 the children of immigrant men of Asian origin adopted the languages of their mothers, as
504 is common in matrilocal cultures [55]. But Kiswahili also has non-African influences
505 consistent with the genetic and archaeological findings and reflecting 1500 years of
506 interaction with societies around the Indian Ocean rim. Persian loanwords contribute up
507 to 3% of Kiswahili, but it is unclear if they derive directly from Persian or through
508 adoption into other Indian Ocean languages [56]. Arabic loanwords are the single largest
509 non-Bantu element in Kiswahili (16-20%) [56]. However, these words, which
510 predominantly relate to religion, jurisprudence, trade, and maritime vocabulary, may be
511 primarily due to incorporations after around 1500 CE [25].

512

513



514
 515 **Figure 4: Proposed admixture events of groups along the eastern African coast.**
 516 African populations are depicted in variations of blue. Near eastern and south Asian
 517 populations are depicted in variations of yellow. Mixtures of different colors represent
 518 populations that are admixed between the respective proxy source populations with those
 519 colors.

520 A repeated theme in this study is the different participation of males and females in
 521 population mixture events both on the coast and inland throughout the medieval period.
 522 For example, we find evidence of predominantly male Near Eastern ancestors mixing
 523 with predominantly female African and, to a much lesser extent, female Indian ancestors
 524 in the lineages of medieval Swahili coast people. This finding testifies to asymmetric
 525 social interactions between groups as cultural contact occurred, although genetic data
 526 cannot determine the processes that contributed to these patterns. We can learn more
 527 about the nature of these interactions through archaeological, ethnographic, linguistic,
 528 and historical evidence.

529
 530 A limitation of this work is its sparse sampling of present-day and ancient populations
 531 both in space and time. The shortage of present-day and ancient samples means that the
 532 data that we have access to may not represent the precise sources or precise regions of
 533 Persia or Arabia, but rather be proxies for the true sources. The sampling of ancient
 534 Africans is similarly limited. The geographical coverage is skewed toward Kenya—with
 535 the individuals from Tanzanian sites such as Songo Mnara, Kilwa, and Lindi sufficient to
 536 identify similarities and differences in ancestry profiles from Kenya but not sufficient to
 537 define a general pattern—and does not incorporate groups from present-day Somalia,
 538 Mozambique, the Comoros Islands, and Madagascar. In addition, the individuals we
 539 analyzed were not fully representative of all social and economic groups in Swahili
 540 society. Nearly all the coastal graves and tombs occupied prominent positions within
 541 medieval and early modern townscapes (see **Supplementary Archaeological site**

542 **summaries**). With the exceptions of Makwasinyi and possibly Kilwa and Lindi, the
543 individuals we analyzed were from elite contexts within high-profile coastal sites.
544 However, the Swahili cultural world included many non-stone and non-elite settlements
545 whose residents are not represented here and whose ancestry would potentially be
546 systematically different [57], and indeed modern Swahili populations retain differences
547 today. Finally, none of the burials we analyzed pre-dated the 13th century; sampling of
548 individuals who lived before and after the mixture events around 1000 CE would provide
549 insights about the population changes that occurred that cannot be discerned based on the
550 datasets we analyze here.

551

552 Narratives of ancestry have a complex history on the eastern African coast. The data
553 presented here add to that complexity. Ancient DNA data shows that there was also a
554 complicated and ongoing cultural mix on the coast, where African people and society
555 interacted and had families with visitors from other parts of Africa and many parts of the
556 Indian Ocean world.

557

558

559

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745
746
747

748 **Methods**

749

750 **Ethics Statement**

751 The present-day communities of the Swahili coast have strong traditions of connection to
752 the people of the medieval coastal towns—including a tradition of descent from the
753 people who lived in these communities, as well as shared language and religion—and
754 hence community consultation is an important part of this work. Many medieval and
755 present-day coastal people are also Muslim, and hence it is important to carry out any
756 analysis in ways that are sensitive to Muslim proscriptions against disturbing the dead.
757 The sampling for this study emerged from decades⁷-long community-based archaeology
758 projects—including by co-authors Sibel and Chapurukha Kusimba in the Kenya region,
759 and by co-authors Wynne-Jones, Fleisher, Tanzanian Antiquities, and the Songo Mnara
760 ruins committee in the Tanzania region—that involved participation in and return of
761 results to local communities, following rules for handling and reburial of remains
762 agreed by the communities. Prior to submission of this study for publication, the
763 corresponding authors of this study held return-of-results consultation meetings with
764 local groups in Lamu, Songo Mnara, and Kilwa Kisiwani, and feedback from these
765 engagements helped us to ensure that the final research was reflective of community
766 perspectives.

767

768 **Ancient DNA sample preparation, DNA extraction, library preparation,
769 enrichment, sequencing, and bioinformatic analysis**

770 To generate the genetic data for the samples in **Extended Data Table 1** and **Online
771 Table 2 | newly_reported_individuals** (and by-library metrics in **Online Table 1 |
772 newly_reported_libraries**), we used established protocols in dedicated clean rooms,
773 involving first sampling about 40 milligrams of powder from skeletal remains, then
774 extracting DNA using methods designed to retain short, damaged fragments [58], then
775 building individually barcoded libraries [59-61] after incubation with uracil DNA
776 glycosylase (UDG) with the goal of removing characteristic errors typical of ancient
777 DNA in the interiors of sequences [62, 63]. We amplified these libraries and carried out
778 in-solution enrichment of DNA libraries for about 1.2 million single nucleotide
779 polymorphisms (SNPs) [64-66] as well as baits targeting the mitochondrial genome [67],
780 and sequenced the enriched products along with a small amount of unenriched library on
781 Illumina NextSeq 500 or HiSeq X Ten instruments. The resulting sequenced paired-end
782 reads were separated into respective libraries and stripped of identification tags and
783 adapter related sequences. Read pairs were merged prior to alignment, requiring a
784 minimum of 15 base pair overlap, allowing one mismatch if base quality was at least 20
785 or, up to three mismatches at lower base quality. We restricted to sequences that were at
786 least 30 base pairs long. The resulting sequences were aligned using *samse* from *bwa-
787 v0.6.1* [68] separately to (a) the human genome reference sequence (*hg19*), and (b) the
788 mitochondrial RSRG genome [69] to allow the targeted nuclear and mitochondrial
789 specific sequences to be assessed.

790

791 We performed a series of quality control measures. Specifically, we inferred the rate of
792 mismatch of the sequences mapping to the mitochondrial consensus sequence (of
793 libraries with at least 2-fold coverage) and tested if the upper bound of the inferred match

794 rate was at least 95% [64]; we tested if the ratio of Y chromosome to the sum of X and Y
795 chromosome sequences was in the range expected for DNA entirely from a female (<3%)
796 or male (>35%); we tested if the rate of cytosine to thymine substitution in the final
797 nucleotide was at least 10% for single stranded libraries or 3% for double stranded
798 libraries as expected for authentic ancient DNA; and we examined the rate of
799 polymorphism on the X chromosome to estimate a rate of contamination flagging an
800 individual as appreciable contaminated if the lower bound of the inferred contamination
801 rate was at least 1% [70].

802

803 We represented each position in the genome based on a single randomly selected
804 sequence, and 80 individuals passed quality control screening. The analyses in this study
805 focus on the 54 non-outlier individuals that are not first- or second-degree relatives of
806 another individual in the study for which we have better quality data and for which we
807 have data on a minimum of 15,000 SNPs. **Online Table 1 | newly_reported_libraries**
808 provides a full report of sequencing results on both libraries that yielded data passing
809 standard measures of ancient DNA authenticity and libraries that failed screening; we
810 report negative results as a guide to help in future sampling efforts.

811

812 **Human Origin sample collection and data generation**

813 We generated genotype data for 29 present-day individuals from the United Arab
814 Emirates and Madagascar on the Affymetrix Human Origins array [34]. We applied
815 quality control analyses from [32].

816

817 The Madagascar samples analyzed in this study were collected during 2007–2014 with
818 ethical approval by the Human Subjects' Ethics Committees of the Health Ministry of
819 Madagascar and by French committees (Ministry of Research, National Commission for
820 Data Protection and Liberties and Persons Protection Committee). Individuals all gave
821 written consent before the study. DNA was purified from saliva using the Oragen Kit
822 (DNA Genotek Inc.). The north and south Madagascar sampling was based on a grid
823 sampling approach, in which “spots” 50 km in diameter were placed all over Madagascar
824 (taking into account population density data), and three to four villages were sampled in
825 each spot. Sampled villages were founded before 1900, and sampled individuals were 61
826 ± 15 y old, with the maternal grandmother and paternal grandfather born within a 50-km
827 radius of the sampling location. Subjects were surveyed for current residence, familial
828 birthplaces, and a genealogy of three generations to establish lineage ancestry and to
829 select unrelated individuals. Global Positioning System locations were obtained during
830 sampling.

831

832 The Emirati samples were collected from Emirati nationals from the city of Al Ain,
833 United Arab Emirates. Ethical approval was obtained from the Al Ain District Human
834 Research Ethical Committee. The samples were collected from healthy adults and
835 initially used as controls for a study of rare disease using a different SNP array [71].

836

837 A list of the newly reported HO individuals and some relevant information can be found
838 in Online Table 4 | newly_reported_HO_data.

839

840 **Principal component analysis (PCA)**

841 We used smartpca version 18180 from EIGENSOFT version 8.0.0 [72, 73] with optional
842 parameters (numoutlieriter: 2, numoutevec: 3, lsqproject: YES, newshrink: YES, and
843 hiprecision: YES). We computed eigenvectors of the covariance matrix of SNPs from
844 present-day individuals from Africa and Eurasia genotyped on the Affymetrix Human
845 Origins (HO) SNP array which targets approximately 600,000 SNPs that are a subset of
846 those targeted by in-solution enrichment (see SI for a list of populations used). Ancient
847 individuals and present-day individuals (most genotyped on the HO SNP array, and some
848 also genotyped on the Illumina Human Omni5 Bead Chip [28]) were projected into the
849 three-dimensional (3D) eigenspace determined by the first three principal components.

850
851 **ADMIXTURE analysis**

852 For the ADMIXTURE [74] plots in **Figure 1C** and **Extended Data Figure 1**, we use a
853 dataset of 728 populations containing 7279 non-American Human Origins present-day
854 populations and Swahili coast samples that were converted with convertf from the
855 PACKEDANCESTRYMAP format to the PACKEDPED format for pruning in PLINK2
856 [75]. We applied the maf 0.01 option, which only includes SNPs that have a minor allele
857 frequency of at least 0.01. We then pruned SNPs based on LD, using the indep-pairwise
858 option with a window size of 200 variants, a step size of 25 variants, and a pairwise r^2
859 threshold of 0.4. After pruning the SNP dataset, we ran 4 replicates of ADMIXTURE
860 with random seeds with $K = 4$ to $K = 12$ ancestral reference populations.

861
862 **Quantitative estimation of mixture proportions**

863 We used *qpAdm* (ADMIXTOOLS version 7.0.2) [34] to test if the Makwasinyi, Manda,
864 Mtwapa, Kilwa, and Songo Mnara target populations can be formally modeled as having
865 derived from a set of source populations (termed “left” groups) relative to a set of
866 reference populations (termed “right” groups). See **Supplementary qpAdm modeling**
867 for further details of this process that are population- or sample-specific.

868
869 The *qpAdm* workflow builds on the *qpWave* framework. The null hypothesis of *qpWave*
870 is that a set of left populations (L_1, L_2, \dots, L_{N_L}) and a set of right populations
871 (R_1, R_2, \dots, R_{N_R}) form clades with respect to one another. *qpWave* builds a matrix of
872 $f_4(L_i, L_j; R_m, R_n)$ that encompass all non-redundant f_4 -statistics for the left and right
873 population sets. If the left groups form clades with respect to the right groups, then these
874 f_4 -statistics will be statistically consistent with zero. The rank of the matrix will be 1 since
875 any additional rows or columns will not provide any linearly independent information.
876 But if there is gene flow between the left and right groups, then the null hypothesis is
877 rejected (we use a $p < 0.1$ threshold) and the rank of the matrix will increase for every
878 independent gene flow between right and left groups.

879
880 *qpAdm* builds on *qpWave* by adding a target population to the left groups. The
881 assumption is that the left groups and right groups still form a clade with respect to one
882 another after the addition of this target; in other words, there is no independent gene flow
883 between the target and the right populations that does not also pass through a common
884 ancestral population with other left groups. The *qpAdm* P value for fit tests if this
885 assumption is met, that is, if there is no *qpWave* rank increase after adding the target

886 population. It then models the target as a linear combination of f_4 -statistic vectors
887 associated with the other left groups, normalizing the weights to sum to one in which case
888 they can be interpreted as unbiased estimates of mixture proportions.

889
890 In our use of *qpAdm*, we use a cycling approach, treating the target as a linear
891 combination of all possible subsets of the candidate source populations, and moving the
892 other candidate source population to the right. Cycling populations to the right allows us
893 to test if a proposed set of left source populations is consistent with being more closely
894 related to the target than other populations. Thus, we can build the closest admixture
895 model within the constraints of our dataset and test its fit to the data. *qpAdm* uses a Block
896 Jackknife, removing a different block of SNPs in each iteration, to determine the mean
897 coefficient and its standard error for each source population in the model.

898 899 **mtDNA and Y-chromosome haplogroup determination**

900 Mitochondrial haplogroups were determined using HaploGrep 2 [76]. Y chromosome
901 haplogroups were determined according to the Yfull tree.

902 903 **Sex-bias determination based on the different autosome and X chromosome** 904 **representation in the genome of males and females**

905 We measured Sex-bias per source population by comparison of the inferences of
906 proportions of ancestry on chromosomes 1-22 (the autosomes) which reflect 50% female
907 and 50% male inheritance ($C_A = (m + f)/2$), and on the X chromosome which reflect
908 67% female and 33% male ancestry ($C_X = (2f + m)/3$). We determined Z-scores as in
909 [77]. For each of Mtwapa, Manda, Kilwa, and Makwasinyi, we determine sex-bias in the
910 following manner. (1) We sample 10^6 sets of coefficients by generating random numbers
911 from a multivariate normal distribution based on the *qpAdm*-determined jackknife mean
912 coefficients and the error covariance matrix for both the autosomes the X-chromosome,
913 separately. Since the values in the covariance matrix from *qpAdm* were rounded, we
914 ensure that the eigenvalues of the matrices are all greater or equal to zero by adding a
915 small offset to the matrices determined as the absolute value of its respective minimum
916 eigenvalue. (2) We remove from consideration all infeasible sets of coefficients, namely
917 those that include a coefficient below 0. (3) We take 95% confidence intervals of all the
918 sampled sets of ancestry proportions. To do so, we determine how extreme each set of
919 proportions are by finding their distance to the jackknife mean coefficients. We remove
920 the 2.5% of samples with the greatest distance and the 2.5% of samples with the least
921 distance. (4) We next calculate the female and male proportions of ancestry for each
922 source population. Given the coefficient C_A on the autosomes and the coefficient C_X on
923 the X chromosome, we can determine the likely proportion of female and male ancestry
924 from any given source by solving the system of two above equations, giving $f = 3C_X -$
925 $2C_A$ and $m = 4C_A - 3C_X$. We calculate these f and m proportions for each source
926 population for the sampled set of autosomal and X chromosome coefficients. (5) We
927 normalize the proportions of female and male ancestry as $\hat{f} = f/(f + m)$ and $\hat{m} =$
928 $m/(f + m)$ for each source for the sampled sets. (6) We find the mean and standard
929 deviation of all the \hat{f} and \hat{m} values from the sampled set for each of the source
930 populations. The values are recorded as ranges in **Table 1**. Under the simple model of all
931 the mixture occurring at once, these formulae can be interpreted as estimating the fraction

932 of ancestors at the time of mixing that are on the male or female side. However, if the
933 mixture was more gradual, the interpretation is more complicated albeit still informative
934 about sex bias.

935

936 **Determining the composition of the two latest source populations in the African-** 937 **Persian-Indian admixture**

938 We plot all the Mtwapa and Manda individuals on a ternary plot with their respective
939 proportions of Makwasinyi, Iranian, and Indian ancestry. We apply a linear regression to
940 the high coverage individuals from Mtwapa (I19381, I19394, I19384, I19414, I19420,
941 I19413, I19417, I19401, I23662, I17409, I19391, I13611, I17412, I17413, I23558,
942 I19415, I23561, and I21475) and Manda (I7934) as seen in the ternary plot (see **Figure**
943 **2B** and **Figure S3**) with an equivalent Cartesian equation of $f(x) = 0.09856 \cdot x +$
944 0.01301 . The line intersects the Makwasinyi axis at $98 \pm 6\%$ (left circle in **Figure 2B** and
945 **Figure S3**), which would allow for $2 \pm 6\%$ Indian ancestry. This is statistically consistent
946 with 100% Makwasinyi and 0% Iranian and 0% Indian. A parsimonious scenario would
947 thus be that the Iranian and Indian ancestry came from the same source population. The
948 other end of the regression line intersects the Indian axis (right circle in **Figure 2B** and
949 **Figure S3**) at $12 \pm 5\%$ Indian ancestry and $88 \pm 5\%$ Iranian ancestry. We further
950 consolidated this uncertainty by jackknifing the qpAdm analyses and applying a separate
951 linear regression to each bin. Through this we determine that one admixing source
952 population is composed of $98.4 \pm 2.5\%$ Makwasinyi ancestry, which is also consistent with
953 a parsimonious model of 100% Makwasinyi ancestry at that end of the cline. The other
954 source population is composed of $12.2 \pm 2.8\%$ Indian ancestry with $87.8 \pm 2.8\%$ Iranian
955 ancestry (see **Supplementary qpAdm modeling**).

956

957 **Determining the date of mixture using admixture linkage disequilibrium**

958 DATES measures the covariance coefficient between each two genome positions in an
959 ancient individual for an admixture model with two source populations, as described in
960 Narasimhan et al. [48]. With multiple individuals, this analysis is applied separately to all
961 individuals and the curves are combined to increase resolution. The statistical power of
962 DATES increases when we use groups with large sample sizes as sources. The surrogate
963 source populations and estimated elapsed generations can be seen in **Extended Data**
964 **Figure 2**. We use a 28 ± 2 year-to-generation conversion estimate [78] to calculate the
965 average date of the admixture, which is listed in the text and in **Table 1** and in **Extended**
966 **Data Figure 2**.

967

968 **Data availability**

969 The aligned sequences are available through the European Nucleotide Archive, accession
970 PRJEBxxxxx [to be made available upon publication].

971

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994

995 **Author contributions**

996 ESB, JF, SWJ, SW, JM, MEP, DR, and CMK conceptualized the study; ESB, KS, and
997 SM formally analyzed the genetic data; ESB, NB, KC, EC, LI, AL, JO, LQ, KS, NW, FZ,
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1002

1003 **Competing interests** The authors declare no competing interests.

1004

1005 **Supplementary Information** The online version contains supplementary material
1006 available at [to be made available upon publication].

1007

1008 **Correspondence and requests** for materials should be addressed to Esther S. Brielle,
1009 Jeffrey Fleisher, Stephanie Wynne-Jones, David Reich, and Chapurukha M. Kusimba.

1010

1011 **Peer review information** to be added after review.

1012

1013 **Reprints and permissions information** is available at [to be made available upon
1014 publication].

1015

1016 **Extended Data Table 1 | Ancient individuals with high coverage genome-wide data**
1017 **newly reported in this study.** Makwasinyi Family A has 4 members. I13873 has a son
1018 I13872 and a brother I13875 (who is genetically a second or third degree relative of
1019 I13872), and all three males are second- or third-degree relatives of I17402. Manda
1020 Family A has 4 members. I7934, I7942, I7943, and I19407 are all first-degree relatives of
1021 one another. Mtwapa Family A has 2 members who are second- or third-degree relatives,
1022 I19401 and I13611. Mtwapa Family B has 8 members. Of them, I23550 and I17409 are
1023 first degree relatives. Second or third-degree relatives are I17409 to I19391, I19394 to

1024 I23558, I19394 to I19391, I19391 to I19393, I19394 to I19423, and I19394 to I19388.
 1025 Mtwapa Family C has 3 members. I21475 and I19419 are first degree relatives. I21475
 1026 and I19384 are second- or third-degree relatives. Mtwapa Family D has 2 members who
 1027 are second- or third-degree relatives, I19416 and I19417. Mtwapa Family E has 2
 1028 members who are second- or third-degree relatives, I19414 and I19415. Mtwapa Family
 1029 F has 2 Members who are second- or third-degree relatives, I23662 and I19398. Songo
 1030 Mnara Family A has 2 members who second or third-degree relatives, I19547 and
 1031 I19549.

ID	Date	Locality	SNPs	Sex	Y haplogroup	mtDNA haplogroup	Comments
I14781	1698-1950 calCE	Taita Taveta, Makwasinyi	532619	F	----	L0a1a+200	
I13872		Taita Taveta, Makwasinyi	598510	M	E1b1a1a1a2a1a	L4b2a	
I13875	1667-1843 calCE	Taita Taveta, Makwasinyi	537980	M	E1b1a1a1a2a1a3b1d1c	L2a1+143	
I13874	1709-1927 calCE	Taita Taveta, Makwasinyi	446807	M	E1b1a1a1a2a1a3a1d~	L3a2	
I13871		Taita Taveta, Makwasinyi	181981	F	----	L3d1a1a	
I13873		Taita Taveta, Makwasinyi	240344	M	E1b1a1a1a2a1a	L2a1+143	Removed family A
I17404		Taita Taveta, Makwasinyi	93611	F	----	L3d1a1a	
I17402		Taita Taveta, Makwasinyi	593614	M	E1b1a1a1a2a1a3b1d1c	L1c3b1a	
I17401		Taita Taveta, Makwasinyi	228632	F	----	L3f2a1	
I17405		Taita Taveta, Makwasinyi	110661	F		L0f2a	
I17403		Taita Taveta, Makwasinyi	36275	F		L5a1a	
I7934	1456-1621 calCE	Lamu, Manda Kenya	403873	F	----	L2d1a	
I7939	1456-1621 calCE	Lamu, Manda Kenya	44918	M	J2	n/a (<2x)	
I7941	1485-1629 calCE	Lamu, Manda Kenya	44105	M	G2a	L3e3a	
I7942	1457-1626 calCE	Lamu, Manda Kenya	391682	M	J2b2a2~	L2d1a	Removed family A
I19407	1510-1668 calCE	Lamu, Manda Kenya	25216	M	J2	L2d1a	Removed family A
I7938	1437-1482 calCE	Lamu, Manda Kenya	71503	F	----	L2a1b1	
I17410	1508-1648 calCE	Kilifi, Mtwapa Kenya	144148	M	J1a2a1a2d2b~	L3d1a1a	
I17409		Kilifi, Mtwapa Kenya	636684	M	J1a2a1a2d2b~	M30d1	
I19381	1651-1801 calCE	Kilifi, Mtwapa Kenya	367125	M	J1a2a1a2d2b~	L2a1a	
I19387		Kilifi, Mtwapa Kenya	183657	F	----	L2a1b1a	
I19388		Kilifi, Mtwapa Kenya	26134	M	E1b1b	L0a2a2a	
I19394		Kilifi, Mtwapa Kenya	202755	M	E1b1b1b2a1a1a1a1f~	L0a2a2a	
I19390		Kilifi, Mtwapa Kenya	19762	F	----	L3b1a+@16124	outlier
I19392	1510-1663 calCE	Kilifi, Mtwapa Kenya	134037	F		L3b1a1	
I19384		Kilifi, Mtwapa Kenya	463984	F		L3b1a1a	
I19414	1513-1797 calCE	Kilifi, Mtwapa Kenya	902017	F		L1c3a1b	
I19419		Kilifi, Mtwapa Kenya	126541	M	J1a2a1a2	L3f1b1a1	Removed family C
I19416		Kilifi, Mtwapa Kenya	121558	M	R1a1a1	L3b1a1a	
I19420		Kilifi, Mtwapa Kenya	193510	M	R1a1a1	L3e1d1	
I19411		Kilifi, Mtwapa Kenya	163986	F	----	L1c3a1b	
I19423		Kilifi, Mtwapa Kenya	56327	M	E1b1b	L0d3	
I19408	1510-1661 calCE	Kilifi, Mtwapa Kenya	33031	M	J1a2a1a2d2b~	L3e3a	
I19413		Kilifi, Mtwapa Kenya	725990	M	J1a2a1a2d2b~	L1b1a	
I19417	1633-1794 calCE	Kilifi, Mtwapa Kenya	193918	M	J1a2a1a2	L3e3a	
I19401		Kilifi, Mtwapa Kenya	765624	M	J1a2a1a2d2b~	L0a2a2a	
I23660		Kilifi, Mtwapa Kenya	38908	M	J	L3d1a	
I23662		Kilifi, Mtwapa Kenya	214343	M	J2a1a1a2a2b	L0a2a1a2	
I23550		Kilifi, Mtwapa Kenya	20760	F	----	M30d1	Removed family B
I24975		Kilifi, Mtwapa Kenya	19369	F		n/a (<2x)	
I19391		Kilifi, Mtwapa Kenya	222944	M	J1a2a1a2d2b~	L0a2a2a	
I19409		Kilifi, Mtwapa Kenya	92063	M	J1	L0a1b1a	
I13611	1510-1661 calCE	Kilifi, Mtwapa Kenya	525800	F	----	L3b1a11	
I17412	1510-1663 calCE	Kilifi, Mtwapa Kenya	973533	M	J1a2a1a2d2b~	L0a2a1a2	
I17413	1510-1655 calCE	Kilifi, Mtwapa Kenya	636350	F	----	L0a1b2a	
I19386		Kilifi, Mtwapa Kenya	80546	M	J1	L3e3a	
I19415		Kilifi, Mtwapa Kenya	518120	F	----	L0a2a1a2	
I23548		Lamu, Pate Island, Faza	132420	M	E1b1a1a1a2a1a	L3e3a	
I23558		Mtwapa Kenya	699608	F	----	L0a1b1a	
I21475		Mtwapa Kenya	928732	F		L3f1b1a1	
I23561		Mtwapa Kenya	753944	F		L3a2	
I7944	1516-1667 calCE	Songo Mnara Tanzania	633887	M	E1b1b1b2b2a1a~	L3a1b	
I19551	1294-1392 calCE	Songo Mnara Tanzania	19083	M	R1a	L3e3a	
I19548	1418-1450 calCE	Songo Mnara Tanzania	79001	M	E1b1a1~	L3e2b	
I19552	1402-1437 calCE	Songo Mnara Tanzania	31712	F	----	L3e2b1a2	
I19547	1508-1648 calCE	Songo Mnara Tanzania	472669	F		L3d1a1a1	
I19550	1412-1446 calCE	Songo Mnara Tanzania	66333	F		L3d1a1a	
I19549	1629-1794 calCE	Songo Mnara Tanzania	248300	M	E1b1b1a1a1b2~	L3d1a1a1	
I8816	1300-1600 CE	Kilwa, Coast Tanzania	880458	M	J2a2a1a1a2a~	L2a1h	

1032 **Extended Data Table 2 | Ancient individuals with high coverage genome-wide data**
 1033 **newly reported in this study that have Persian and often Indian ancestry.** The
 1034 African proxy source is the Makwasinyi group from this study for individuals buried at
 1035 Mtwapa and Manda, and is the Lindi individual from this study for the Kilwa individual
 1036 and the Songo Mnara individual I19550. The Persian proxy source in all cases is the HO
 1037 Iranian group [32, 37]. The Indian proxy source in all cases is the HO Sahariya_MP
 1038 group [33].

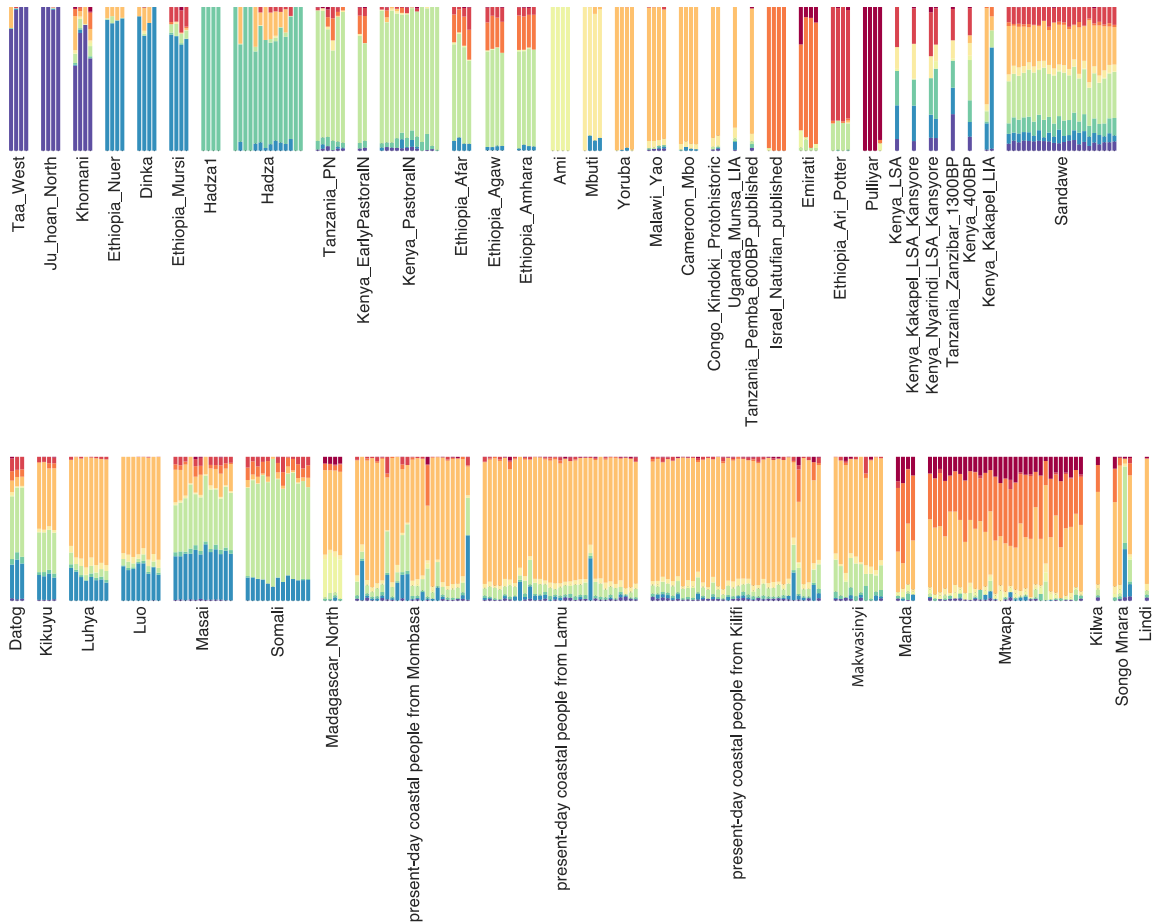
Date	ID	Swahili group	local African source	P value	African ancestry	Persian ancestry	Indian ancestry
1300-1600 CE	I8816	Kilwa	Lindi (Bantu proxy)	0.2742	0.76±0.01	0.24±0.01	--
1412-1446 calCE	I19550	Songo Mnara	Lindi (Bantu proxy)	0.3758	0.67±0.02	0.25±0.04	0.08±0.04
1437-1482 calCE	I7938	Manda	Makwasinyi	0.4391	0.42±0.02	0.54±0.03	0.04±0.03
1456-1621 calCE	I7934		Makwasinyi	0.7001	0.3±0.01	0.63±0.02	0.08±0.02
1456-1621 calCE	I7939		Makwasinyi	0.3931	0.57±0.02	0.38±0.04	0.05±0.04
1485-1629 calCE	I7941		Makwasinyi	0.6402	0.46±0.02	0.42±0.04	0.12±0.04
1500-1700 CE	I19387	Mtwapa	Makwasinyi	0.2390	0.59±0.02	0.34±0.03	0.07±0.02
1500-1700 CE	I19388		Makwasinyi	0.7668	0.55±0.03	0.41±0.05	0.05±0.05
1500-1700 CE	I19394		Makwasinyi	0.0020	0.62±0.02	0.37±0.02	0.01±0.02
1500-1700 CE	I19384		Makwasinyi	0.0547	0.5±0.02	0.42±0.02	0.08±0.02
1500-1700 CE	I19416		Makwasinyi	0.8258	0.7±0.02	0.23±0.03	0.07±0.02
1500-1700 CE	I19420		Makwasinyi	0.3127	0.66±0.02	0.26±0.02	0.08±0.02
1500-1700 CE	I19411		Makwasinyi	0.2720	0.61±0.02	0.29±0.03	0.1±0.02
1500-1700 CE	I19423		Makwasinyi	0.7124	0.46±0.02	0.48±0.04	0.05±0.04
1500-1700 CE	I19413		Makwasinyi	0.4221	0.57±0.01	0.36±0.02	0.06±0.02
1500-1700 CE	I19401		Makwasinyi	0.0468	0.57±0.01	0.39±0.02	0.04±0.02
1500-1700 CE	I23660		Makwasinyi	0.1056	0.62±0.03	0.34±0.04	0.04±0.04
1500-1700 CE	I23662		Makwasinyi	0.0024	0.53±0.02	0.41±0.02	0.05±0.02
1500-1700 CE	I23548		Makwasinyi	0.7622	0.64±0.02	0.3±0.03	0.06±0.03
1500-1700 CE	I17409		Makwasinyi	0.4021	0.5±0.01	0.43±0.02	0.07±0.02
1500-1700 CE	I24975		Makwasinyi	0.4748	0.47±0.03	0.42±0.06	0.1±0.06
1500-1700 CE	I19391		Makwasinyi	0.2653	0.48±0.02	0.44±0.02	0.08±0.02
1500-1700 CE	I19409		Makwasinyi	0.2347	0.45±0.02	0.47±0.03	0.08±0.03
1500-1700 CE	I23558		Makwasinyi	0.0003	0.42±0.01	0.48±0.02	0.1±0.02
1500-1700 CE	I19415		Makwasinyi	0.7634	0.63±0.01	0.32±0.02	0.05±0.02
1500-1700 CE	I23561		Makwasinyi	0.2154	0.5±0.01	0.45±0.02	0.05±0.02
1500-1700 CE	I19386		Makwasinyi	0.4199	0.55±0.02	0.47±0.03	-0.02±0.03
1500-1700 CE	I21475		Makwasinyi	0.2545	0.71±0.01	0.27±0.02	0.03±0.01
1508-1648 calCE	I17410		Makwasinyi	0.7735	0.44±0.02	0.46±0.03	0.1±0.02
1510-1663 calCE	I19392		Makwasinyi	0.2057	0.76±0.02	0.19±0.03	0.05±0.02
1510-1663 calCE	I17412	Makwasinyi	0.0616	0.49±0.01	0.41±0.02	0.11±0.02	
1510-1655 calCE	I17413	Makwasinyi	0.0616	0.49±0.01	0.41±0.02	0.11±0.02	
1510-1661 calCE	I19408	Makwasinyi	0.7674	0.54±0.03	0.41±0.05	0.05±0.05	
1510-1661 calCE	I13611	Makwasinyi	0.5060	0.59±0.02	0.36±0.02	0.05±0.02	
1513-1797 calCE	I19414	Makwasinyi	0.2761	0.61±0.01	0.32±0.02	0.07±0.02	
1633-1794 calCE	I19417	Makwasinyi	0.4274	0.65±0.02	0.31±0.02	0.04±0.02	
1651-1801 calCE	I19381	Makwasinyi	0.0255	0.6±0.02	0.34±0.02	0.06±0.02	

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 1041 **Extended Data Table 3 | Ancient individuals with high coverage genome-wide data**
 1042 **newly reported in this study that do not have evidence of Persian ancestry.** The
 1043 forager proxy source for the Lindi individual I14001 is the Hadza group genotyped on the
 1044 Human Origins array [32] and the Bantu proxy source is the Malawi_Yao group [31].
 1045 The Pastoral Neolithic and Pastoral Iron Age proxy sources for the Songo Mnara
 1046 individual I7944 are the 1240K capture Kenya_PastoralN group [30] and the 1240K
 1047 capture Kenya_IA_Pastoral_published group [30], respectively. The Malagasy proxy
 1048 source for the Songo Mnara individual I19547 is the Madagascar_North group, the Bantu
 1049 proxy source is the Malawi_Ngoni group, and the Arabian proxy source is the

1050 Yemeni_Highlands_Raymah individual. The Bantu proxy source for the Songo Mnara
 1051 individual I19549 is the 1240K capture Tanzania_Pemba_600BP_published individual
 1052 [31] and the Arabian proxy source is the Emirati group. The Bantu proxy source for the
 1053 Makwasinyi group is the 1240K capture Tanzania_Pemba_600BP_published individual
 1054 [31] and the Pastoral Neolithic proxy source is the 1240K capture Kenya_PastoralN
 1055 group [30]. The Bantu proxy source for all the present-day groups from Kilifi, Lamu, and
 1056 Mombasa is the 1240K Lindi individual from the present study. The medieval Swahili-
 1057 speaking proxy source is the Kilwa individual from the present study for the present-day
 1058 groups. The Pastoral Iron Age proxy source for the present-day groups is two published
 1059 individuals from [30], I8892_published and I12381.

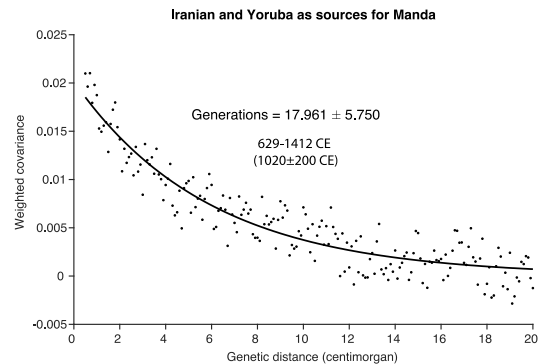
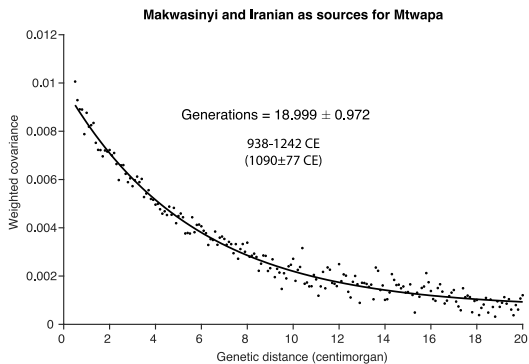
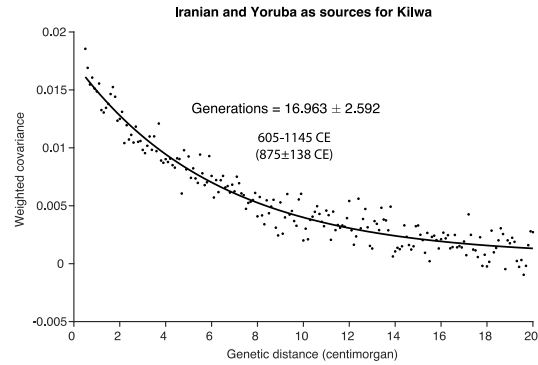
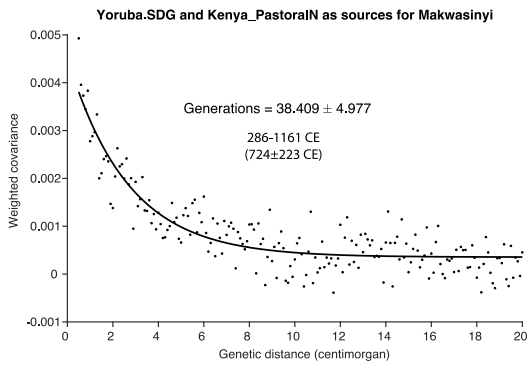
Date	ID	Individual	P value	Forager	Malagasy	Bantu	Pastoral Neolithic	Pastoral Iron Age	Arabian	Manda
1511-1664 calCE	I14001	Lindi	0.5996	0.11±0.03		0.89±0.03				
1508-1648 calCE	I19547	Songo Mnara	0.1261		0.08±0.02	0.84±0.02			0.08±0.01	
1516-1667 calCE	I7944		0.9535				0.03±0.07	0.98±0.07		
1629-1794 calCE	I19549	Makwasinyi	0.1421			0.79±0.01			0.21±0.01	
1650-1950 CE	I13872		0.5336			0.77±0.02	0.23±0.02			
1650-1950 CE	I13871		0.6913			0.79±0.02	0.21±0.02			
1650-1950 CE	I17404		0.0138			0.76±0.03	0.24±0.03			
1650-1950 CE	I17402		0.3717			0.77±0.02	0.23±0.02			
1650-1950 CE	I17401		0.3161			0.79±0.02	0.21±0.02			
1650-1950 CE	I17405		0.1396			0.81±0.03	0.19±0.03			
1650-1950 CE	I17403_d		0.3585			0.86±0.04	0.14±0.04			
1667-1843 calCE	I13875		0.3751			0.79±0.02	0.22±0.02			
1698-1950 calCE	I14781		0.4857			0.89±0.02	0.12±0.02			
1709-1927 calCE	I13874	0.3811			0.81±0.02	0.19±0.02				
present day	Kilifi (35 individuals)	Kilifi	0.5919			0.84±0.03		0.03±0.03		0.14±0.04
present day	Lamu (31 individuals)	Lamu	0.3589			0.86±0.03		0.02±0.03		0.12±0.04
present day	Mombasa (23 individuals)	Mombasa	0.3465			0.79±0.03		0.15±0.03		0.06±0.04

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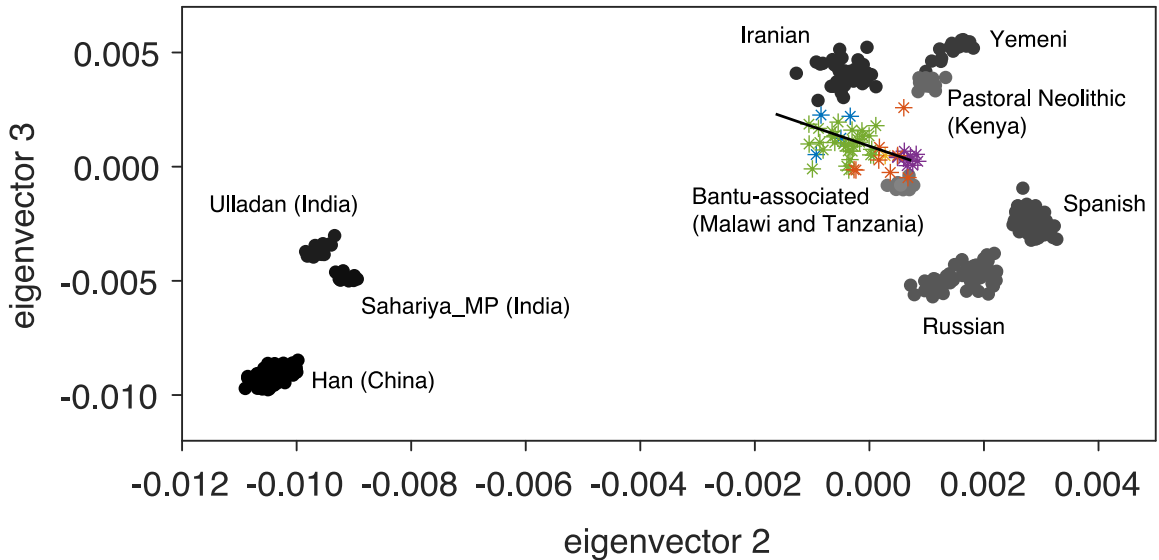
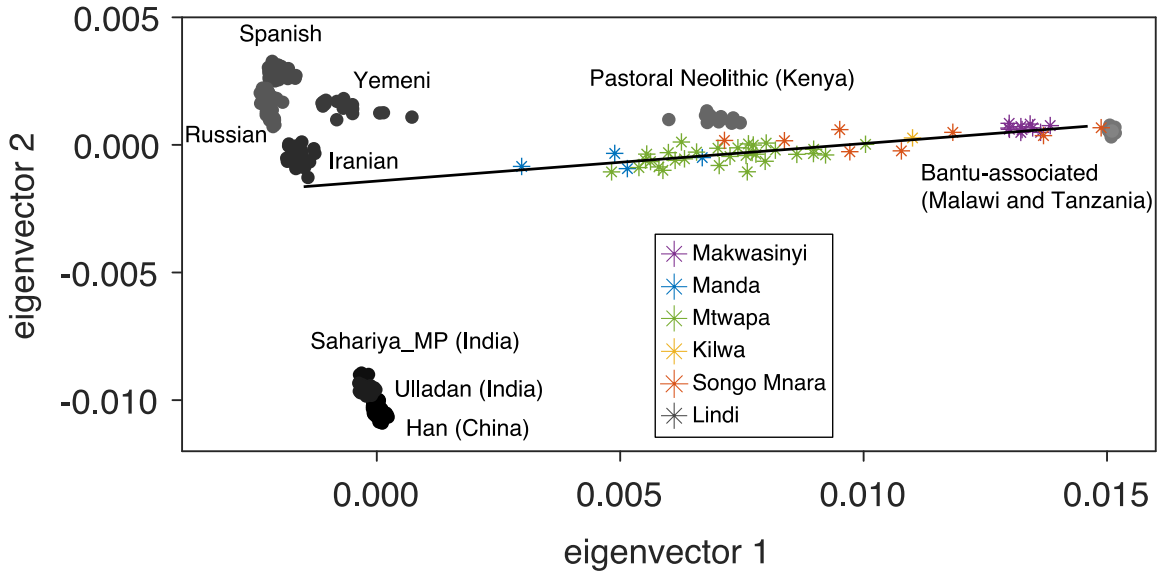
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Extended Data Figure 1 | ADMIXTURE analysis, with K=10 ancestral reference populations. We used 262 populations (2248 individuals) including African populations genotyped with the Human Origins array along with some 1240K capture ancient samples from present-day Kenya, present-day Tanzania, and surrounding areas, Swahili coast present-day samples [28], ancient Israel_Natufian_published, and Pulliyar samples from present-day India. We were able to view a variety of African pastoral, farming, and forager ancestries within coastal and inland Swahili-speaking populations of the Human Origins dataset. Makwasinyi components of ancestry resemble those of the present-day coastal populations sampled by Brucato and colleagues [28], albeit with different proportions.



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Extended Data Figure 2 | DATES curves. Curves that show the exponential decay of linkage disequilibrium generated by mixture between two populations related differentially to the two sources as a function of the number of elapsed generations since the mixture event. Multiplying by a 28 ± 2 year-to-generation conversion estimate and subtracting from the average calibrated radiocarbon dates of the ancient individuals (or the archaeologically estimated date) gives calendar years [78].



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 1082 **Extended Data Figure 3 | Two dimensional PCAs.** (Top) A PCA of the first and second
 1083 eigenvectors for the same data as in Figure 1B. (Bottom) A PCA of the second and third
 1084 eigenvectors for the same data as in Figure 1B.