RESEARCH ARTICLE SUMMARY

AFRICAN GENETICS

Ancient DNA reveals a multistep spread of the first herders into sub-Saharan Africa

Mary E. Prendergast*†, Mark Lipson*†, Elizabeth A. Sawchuk*†, Iñigo Olalde, Christine A. Ogola, Nadin Rohland, Kendra A. Sirak, Nicole Adamski, Rebecca Bernardos, Nasreen Broomandkhoshbacht, Kimberly Callan, Brendan J. Culleton, Laurie Eccles, Thomas K. Harper, Ann Marie Lawson, Matthew Mah, Jonas Oppenheimer, Kristin Stewardson, Fatma Zalzala, Stanley H. Ambrose, George Ayodo, Henry Louis Gates Jr., Agness O. Gidna, Maggie Katongo, Amandus Kwekason, Audax Z. P. Mabulla, George S. Mudenda, Emmanuel K. Ndiema, Charles Nelson, Peter Robertshaw, Douglas J. Kennett, Fredrick K. Manthi, David Reich*

INTRODUCTION: Cattle, sheep, and goats appeared in eastern Africa 5000 years ago, catalyzing the spread of herding throughout sub-Saharan Africa. Archaeologists have long debated the geographic origins of eastern Africa's first herders, the extent to which people moved with livestock, and relationships among food-producing and foraging communities. In this work, we integrate ancient DNA with archaeological, linguistic, and genetic evidence to explore how pastoralism developed within this region, establishing the roots of one of Africa's dominant economic strategies.

RATIONALE: Research into the spread of herding has been limited by patchy archaeological data and poorly preserved human remains. Ancient DNA has the potential to untangle patterns of movement and interaction underlying this economic and cultural transition.

We generated genome-wide ancient DNA data from the remains of 41 individuals (35 directly radiocarbon dated) associated with Later Stone Age (n = 3), early pastoral and Pastoral Neolithic (n = 31), Iron Age (n = 1), and Pastoral Iron Age (n = 6) traditions in what are now Kenya and Tanzania to study how ancient individuals were related to each other and to people living today.

RESULTS: We document a multistep spread of herding and farming into eastern Africa. Ancient individuals genetically correlate with their archaeological associations: Later Stone Age individuals form part of a forager genetic cline, early pastoral and Pastoral Neolithic individuals are most closely related to present-day Afro-Asiatic speakers, and Pastoral Iron Age individuals show affinities to present-day Nilotic speakers. A child buried at an Iron Age agricultural site has shared ancestry with western Africans and Bantu speakers.

We propose a four-stage model that fits the data. First, admixture in northeastern Africa created groups with approximately equal proportions of ancestry related to present-day Sudanese Nilotic speakers and groups from northern Africa and the Levant. Second, descendants of these northeastern Africans mixed with foragers in eastern Africa. Third, an additional component of Sudan-related ancestry contributed to Iron Age pastoralist groups. Fourth, western African–related ancestry, similar to that found in present-day Bantu speakers, appeared with the spread of farming.

We also observe a high frequency of a Y chromosome lineage associated with the spread of pastoralism, as well as a single individual with a genetic variant conferring adult lactase persistence. We do not detect any differentiation among individuals associated with two distinctive Pastoral Neolithic artifact traditions, suggesting that these represent cultural rather than ancestral differences.

CONCLUSION: Archaeological and now genetic evidence suggest complex spreads of herding and farming in eastern Africa involving multiple movements of ancestrally distinct peoples as well as gene flow among these groups. Models formulated on the basis of ancient DNA are a starting point for further exploration through additional archaeological, linguistic, and genetic research. ■

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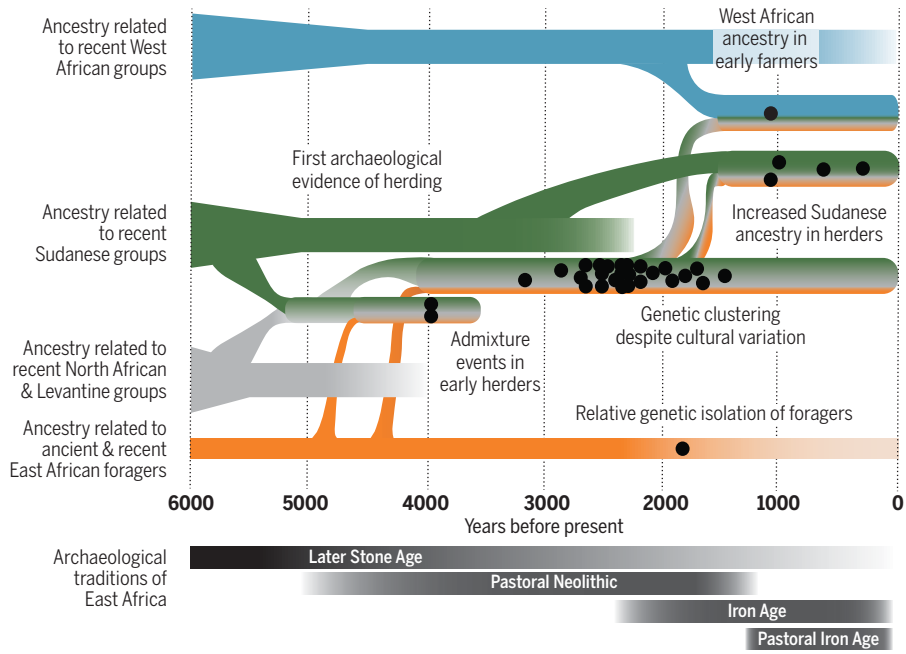

Admixture events contributing to ancestry of ancient eastern Africans. Results were inferred from genome-wide ancient DNA data from 41 individuals from archaeological sites in Kenya and Tanzania, analyzed together with published ancient and present-day genetic data. Black circles represent reported individuals, placed at their median calibrated radiocarbon dates (six individuals, five of whom have forager-related ancestry, had insufficient collagen for dating and thus are not represented here). Ancestry components depicted in green and gray continue to the present day (outside of eastern Africa) but are truncated for readability.

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RESEARCH ARTICLE

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Ancient DNA reveals a multistep spread of the first herders into sub-Saharan Africa

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How food production first entered eastern Africa ~5000 years ago and the extent to which people moved with livestock is unclear. We present genome-wide data from 41 individuals associated with Later Stone Age, Pastoral Neolithic (PN), and Iron Age contexts in what are now Kenya and Tanzania to examine the genetic impacts of the spreads of herding and farming. Our results support a multiphase model in which admixture between northeastern African–related peoples and eastern African foragers formed multiple pastoralist groups, including a genetically homogeneous PN cluster. Additional admixture with northeastern and western African–related groups occurred by the Iron Age. These findings support several movements of food producers while rejecting models of minimal admixture with foragers and of genetic differentiation between makers of distinct PN artifacts.

Domestic sheep, goats, and cattle of southwest Asian origin were first introduced to northeastern Africa ~8000 calibrated years before the present (B.P.) and spread into eastern Africa beginning ~5000 B.P., ultimately reaching southernmost Africa by ~2000 B.P. (*1*, *2*). How pastoralism—a way of life centered on herding animals—spread into eastern Africa is unclear. Livestock appear in northern Ethiopia and Djibouti relatively late [~4500 to 4000 B.P. (*3*)] and are poorly documented elsewhere in the Horn of Africa and in South Sudan. Instead, the earliest known domesticated animals in sub-Saharan Africa are found in Kenya at the beginning of the Pastoral Neolithic (PN) (~5000 to 1200 B.P.) era near Lake Turkana, where archaeological evidence documents groups that pursued fishing and herding and constructed elaborate monumental cemeteries (*4*–*6*). Although livestock spread quickly through the Turkana Basin, herding practices were not transmitted farther south for many hundreds of years. Sheep, goats, and pottery typical of Turkana began to trickle into Kenya's south-central Rift Valley ~4200 B.P. (*7*, *8*), but it was not until ~3300 B.P. that specialized pastoralism spread across Kenya and northern Tanzania, transforming the economic, social, and physical landscapes of the region (*9*–*11*).

The core PN era (~3300 to 1200 B.P.) in Kenya and Tanzania witnessed the development of diverse herder societies, some heavily reliant on livestock (*2*). However, pastoralism did not fully replace Later Stone Age (LSA) economies present in the region since ~50,000 B.P., creating a mosaic of herding and foraging communities on the landscape. Two contemporaneous pastoralist traditions have been identified: Elmenteitan and Savanna Pastoral Neolithic (SPN) (*12*, *13*). Elmenteitan sites are found between the central Rift Valley and the western Lake Victoria Basin of Kenya. Occupants used a particular obsidian source, left behind distinctive lithic and ceramic traditions, and practiced primarily cremation burial. By contrast, SPN sites are found across a wider part of Kenya and Tanzania. Occupants used different obsidian sources, had greater diversity in material culture, and mainly buried their dead in cairns. The heterogeneous SPN category likely encompasses multiple groups. Some distinctions between SPN and Elmenteitan traditions, such as mortuary practices, are variable (*6*), and relationships between PN groups—both cultural and genetic—remain uncertain. In addition, little is known about herder interactions with LSA foragers or about relationships among later PN herders and the first iron-using herders after ~1200 B.P. By this time, farming is also documented in the region (*14*, *15*).

Archaeologists have debated the cultural and genetic affinities of the first pastoralists in eastern Africa and the role that movement of people played in the spread of herding to the region. Because the oldest instances of livestock remains and associated pottery and stone tool traditions have been found near Lake Turkana, it has been hypothesized that pastoralism was introduced by migrants from Sudan and/or Ethiopia, potentially in a series of small movements, and that their descendants gave rise to PN traditions farther south (*12*, *13*, *15*, *16*). However, there are no unambiguous cultural connections between Kenya's earliest herders and northern groups, and archaeological evidence supports the local adoption of herding to some degree (*8*, *16*, *17*). Other archaeological and linguistic evidence has been jointly used to hypothesize two expansions into eastern Africa: an initial expansion of herders speaking Afro-Asiatic (specifically proto–Southern Cushitic) languages from the Horn of Africa linked with the SPN, and a second expansion of herders speaking Nilo-Saharan (specifically Nilotic) languages linked with the Elmenteitan.

People of the second expansion have also been hypothesized to be ancestral to some Iron Age groups (*18*, *19*). One subset of Rift Valley sites is designated Pastoral Iron Age (PIA) (~1200 B.P. to recent years) on the basis of material culture and evidence for herding, whereas other sites appear connected to farming and are classified into early, middle, and later Iron Age (IA) (~2500 B.P. to recent) variants (*2*, *14*). Iron-working first entered eastern Africa via the Lake Victoria Basin ~2500 B.P. and spread toward the coast by 2000 B.P. (*14*). This expansion may have brought

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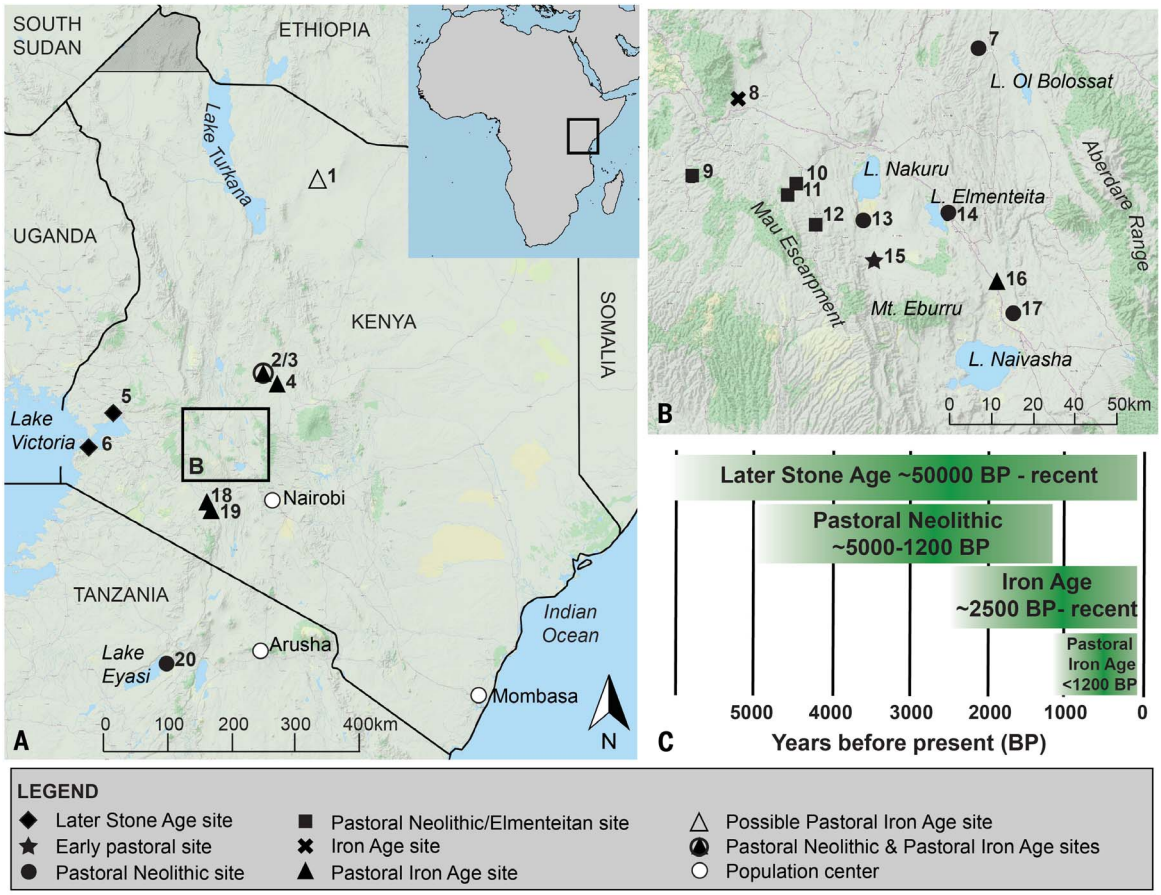

Fig. 1. Map of the study area and regional chronology. (**A**) Locations of sampled archaeological sites in Kenya and Tanzania, with (**B**) detail of the south-central Rift Valley. (**C**) A timeline for eastern African archaeological traditions highlights their degree of overlap and diffuse endpoints. Numbers in (A) and (B) correspond to sites listed in Table 1. Location of 7 is approximate. [Terrain basemaps: © www.thunderforest.com; data: © www.osm.org/copyright; adapted under CC-BY-SA 2.0]

early IA farmers, thought to have spoken Bantu languages originating in equatorial western Africa, into contact with PN herders, although iron-working is not widely attested among herders until ~1200 B.P. at PIA sites (*2*, *15*). Alternatively, PIA sites may reflect other iron-working traditions entering from the north, potentially associated with additional movements of Nilotic-speaking pastoralists into and within the Rift (*2*). This complex mosaic of foragers, herders, and farmers gave rise to much of the present day ethnolinguistic landscape of eastern Africa (*20*).

Rigorous testing of models for the spread of herding has been inhibited by several factors. A spatial and chronological gap exists between the earliest evidence of pastoralism in the Turkana Basin and the later PN expansion, with few material culture similarities. Additionally, relationships among PN and diverse Iron Age groups remain poorly understood. Human skeletal material from relevant contexts tends to be fragmentary, limiting bioarchaeological analysis, and reliable radiocarbon dates are rare. Finally, the persistence of foraging groups raises questions about interaction networks during this period (*12*, *15*), as well as whether food production spread primarily via demic expansion or via local adoption of novel practices and livestock.

To address these debates, we generated genome-wide ancient DNA data from individuals buried at sites associated with LSA (n = 3), early pastoral and PN (n = 31), IA (n = 1), and PIA (n = 6) archaeological traditions in what are now Kenya and Tanzania (Fig. 1, Table 1, and table S1). We extracted DNA from a combination of tooth and bone samples and enriched for a targeted set of ~1.2 million single nucleotide polymorphisms (SNPs) (*21*). Surprisingly, given the tropical climate and variable curatorial conditions, we obtained excellent data quality, with a median of approximately 0.51× coverage, or 440,000 SNPs covered by at least one sequence, for the 41 newly reported individuals (from a total of 67 sequencing libraries; table S2). The data scored well in standard ancient DNA authenticity metrics for all but two individuals [I12391 and I13970, whom we excluded from genome-wide analyses but for whom we obtained Y chromosome and mitochondrial DNA (mtDNA) haplogroups (*21*)]. We also generated direct radiocarbon dates for 35 individuals (tables S3 and S4 and fig. S1). We analyzed these data jointly with sequences from published ancient African individuals (*22*–*27*) as well as from people living in eastern Africa today (*28*–*31*).

Overview of genetic affinities of ancient eastern Africans

We used principal components analysis (PCA) of the genome-wide data to visualize the genetic structure of the ancient individuals (Fig. 2 and table S5). We defined PCs using a small set of present-day groups [southern Africans, northeastern Africans, and non-Africans (*21*)] and projected a large number of diverse individuals onto these axes. An alternative analysis with western Africans additionally used to compute the axes yielded almost identical results (fig. S2). Present-day groups from Sudan mostly lie along a cline extending from Copts (upper right, near individuals from northern Africa and the Levant) to Nilotic speakers such as Dinka and Nuer (lower left). Afro-Asiatic speakers (mostly from Ethiopia) form a second cline, with the right end near Sudanese Beja and Nubians and the left end extending toward eastern African foragers [who themselves form a south-to-north gradient (*22*)]. Present-day Kenyans largely fall in the space

Table 1. Ancient individuals reported in this study, ordered by start of calibrated radiocarbon date range. Site codes, where available, follow a standardized system for Africa (*49*). Calibrated years before the present were calibrated in OxCal v.4.3.2 (*50*), modeling for an unspecified mixture of IntCal13 (*51*) and SHCal13 (*52*) curves and rounding to the nearest decade. PN, Pastoral Neolithic; ELM, Elmenteitan; IA, Iron Age; PIA, Pastoral Iron Age; LSA, Later Stone Age. N/A, not applicable; ND, not determined. Prob., probably; cov., coverage.

Lab ID	Site	Map no.	Latitude (°)	Longitude (°)	Archaeological association	Genetic cluster	Sex	mtDNA haplogroup	Y chromosome haplogroup	Average cov. (reads per site)	Uncalibrated years before present (lab no.)	Calibrated years before present (B.P.), 2σ
I12533	Prettejohn's Gully (GsJi11)	15	−0.545	36.106	Early pastoral?	PN outlier	M	K1a	E2(xE2b); E-M75	0.83	3670 ± 20 (PSUAMS-4982)	4080–3890
I12534	Prettejohn's Gully (GsJi11)	15	−0.545	36.106	Early pastoral?	PN outlier	F	L3f1b	N/A	0.69	3640 ± 20 (PSUAMS-4983)	4060–3860
I8874	Cole's Burial (GrJj5a)	14	−0.442	36.267	PN	PN cluster	M	L3i2	E1b1b1a1a1b1; E-CTS3282	3.90	3070 ± 20 (PSUAMS-4723)	3350–3180
I8809	Kisima Farm, A5/Porcupine Cave	2	0.458	36.709	PN	PN cluster	M	M1a1	E1b1b1b2b2a1; E-M293	3.48	2855 ± 20 (PSUAMS-4510)	3030–2860
I8820	Kisima Farm, A5/Porcupine Cave	2	0.458	36.709	PN	PN cluster	F	M1a1f	N/A	0.07	2675 ± 20 (PSUAMS-4717)	2840–2740
I12398/9*	Rigo Cave (GrJh3)	12	−0.464	35.971	PN/ELM	PN cluster	M	L3f	E1b1b1b2b2a1; E-M293	0.89	2480 ± 20 (PSUAMS-4945); 2570 ± 15 (PSUAMS-4946)	2710–2380; 2750–2510
I8759	Naishi Rockshelter	13	−0.458	36.081	PN	PN outlier	M	L3x1a	E1b1b1b2b; E-V1515 (prob. E-M293)	0.07	2550 ± 15 (PSUAMS-4715)	2750–2500
I13980	Gishimangeda Cave	20	−3.476	35.348	PN	PN cluster	M	HV1b1	E1b1b1a1b2; E-V22	2.72	2530 ± 20 (PSUAMS-5655)	2740–2490
I13981	Gishimangeda Cave	20	−3.476	35.348	PN	PN cluster	F	L0a	N/A	0.36	2510 ± 20 (PSUAMS-5656)	2730–2460
I8758	Naishi Rockshelter	13	−0.458	36.081	PN	PN cluster	M	L0a2d	A1b(xA1b1b2a); A-P108	0.29	2470 ± 15 (PSUAMS-4624)	2700–2370
I8804	Keringet Cave?†	9	−0.358	35.699	PN	PN cluster	M	L4b2a1	A1b1b2; A-L427	0.50	2465 ± 20 (PSUAMS-4716)	2700–2360
I8923	Rigo Cave (GrJh3)	12	−0.464	35.971	PN/ELM	PN cluster	M	M1a1b (likely)	E1b1b1b2b2; E-V1486 (prob. E-M293)	0.15	2440 ± 20 (PSUAMS-4512)	2690–2350
I13979	Gishimangeda Cave	20	−3.476	35.348	PN	PN cluster	F	L3x1	N/A	2.56	2410 ± 20 (PSUAMS-5654)	2490–2350
I8922	Rigo Cave (GrJh3)	12	−0.464	35.971	PN/ELM	PN cluster	M	L4b2a2c	E1b1b1b2b2a1; E-M293	2.79	2400 ± 15 (PSUAMS-4725)‡	~2460–2350
I8814	Naivasha Burial Site	17	−0.663	36.410	PN	PN cluster	F	L4b2a2b	N/A	2.53	2400 ± 20 (PSUAMS-4784)	2480–2340
I13978	Gishimangeda Cave	20	−3.476	35.348	PN	PN outlier	F	L4b2a1	N/A	0.56	2355 ± 20 (PSUAMS-5653)	2400–2310
I8830	Naivasha Burial Site	17	−0.663	36.410	PN	PN cluster	M	M1a1b	xBT (prob. A)	0.10	2320 ± 20 (PSUAMS-4720)	2360–2210
I8920	Naivasha Burial Site	17	−0.663	36.410	PN	PN cluster	M	L3h1a1	E1b1b1b2b2a1; E-M293	1.68	2310 ± 15 (PSUAMS-4724)	2350–2210
I8919	Naivasha Burial Site	17	−0.663	36.410	PN	PN cluster	M	L4a1	A1b1b2b; A-M13	1.84	2255 ± 20 (PSUAMS-4789)	2340–2160
I8918	Naivasha Burial Site	17	−0.663	36.410	PN	PN cluster	M	L3x1a	E1b1b1b2b2a1; E-M293	2.45	2235 ± 20 (PSUAMS-4744)	2320–2150

Lab ID	Site	Map no.	Latitude (°)	Longitude (°)	Archaeological association	Genetic cluster	Sex	mtDNA haplogroup	Y chromosome haplogroup	Average cov. (reads per site)	Uncalibrated years before present (lab no.)	Calibrated years before present (B.P.), 2σ
I13762	Gishimangeda Cave	20	−3.476	35.348	PN	PN cluster	M	L3i2	E1b1b1b2b2a1; E-M293	1.81	2140 ± 15 (PSUAMS-5458)	2150–2020
I10719	Njoro River Cave II	11	−0.389	35.917	PN/ELM	PN cluster	F	L3h1a2a1	N/A	1.11	2070 ± 15 (PSUAMS-4758)	2110–1930
I13970	Gishimangeda Cave	20	−3.476	35.348	PN	N/A	F	L3h1a2a1	N/A	0.03	2030 ± 20 (PSUAMS-5650)	2000–1900
I13977	Gishimangeda Cave	20	−3.476	35.348	PN	PN cluster	M	L0f2a1	E1b1b1b2b2; E-V1486 (prob. E-M293)	0.30	2005 ± 20 (PSUAMS-5652)	2000–1890
I8808	Jawuoyo Rockshelter	5	−0.067	34.667	LSA	Forager cline	M	L4b2a2c	E1b1b1a1b2; E-V22	1.37	1895 ± 15 (PSUAMS-4783)	1880–1750
I8805	Egerton Cave (GrJh10)	10	−0.375	35.933	PN/ELM	PN cluster	F	L0a1d	N/A	3.79	1880 ± 15 (PSUAMS-4741)	1870–1740
I12384	Ol Kalou	7	−0.300§	36.400§	PN	PN cluster	M	L3d1d	E1b1b1b2b2a1; E-M293	0.51	1800 ± 20 (PSUAMS-4940)	1810–1620
I13972	Gishimangeda Cave	20	−3.476	35.348	PN	PN outlier	M	T2+150	E1b1b1b2b2; E-V1486 (prob. E-M293)	0.09	1780 ± 25 (PSUAMS-5651)	1740–1580
I12394	Keringet Cave (GrJg4)	9	−0.358	35.699	PN/ELM	PN cluster	F	K1a	N/A	0.42	1585 ± 15 (PSUAMS-4943)	1530–1400
I8892	Ilkek Mounds	16	−0.603	36.374	PIA	PIA cluster	M	L0f2a	E2(xE2b); E-M75	0.10	1170 ± 15 (PSUAMS-4788)	1170–980
I8802	Deloraine Farm (GqJh6)	8	−0.183	35.809	IA	IA other	M	L5b1	E1b1a1a1a1a; E-M58	2.65	1160 ± 15 (PSUAMS-4625)	1170–970
I8901	Kisima Farm, C4	3	0.458	36.709	PIA	PIA cluster	M	L3h1a1	E2(xE2b); E-M75	0.02	1110 ± 15 (PSUAMS-4743)	1060–940
I12391	Kasiole 2 (GvJh54)	18	−1.326	35.939	PIA	N/A	M	L3h1a2a1	E1b1b1b2b; E-V1515 (prob. E-M293)	0.02	1110 ± 15 (PSUAMS-4942)	1060–940
I12381	Laikipia District Burial (GoJl45)	4	0.380	36.893	PIA	PIA cluster	F	L0a1c1	N/A	0.92	635 ± 15 (PSUAMS-4939)	650–560
I12379	Emurua Ole Polos (GvJh122)	19	−1.396	35.983	PIA/recent	PIA cluster	M	L3h1a2a1	E1b1b1b2b2a1; E-M293	3.38	270 ± 15 (PSUAMS-4938)	420–160
I13763	Gishimangeda Cave	20	−3.476	35.348	PN	Forager cline	F	ND	N/A	0.01	Insufficient collagen	N/A
I13982	Gishimangeda Cave	20	−3.476	35.348	PN	Forager cline	F	ND	N/A	0.02	Insufficient collagen	N/A
I13983	Gishimangeda Cave	20	−3.476	35.348	PN	Forager cline	M	ND	BT (low cov.; prob. B)	0.02	Insufficient collagen	N/A
I8904	Kokurmatakore	1	3.132	37.433	PIA?¶	PN outlier?	M	L3a2a	E1b1b1; E-M35 (not E-M293)	0.09	Insufficient collagen	N/A
I8930	White Rock Point (GrJb2)	6	−0.450	34.321	LSA	Forager cline	M	L2a4	BT(xCT) (low cov.; prob. B)	0.03	Insufficient collagen	N/A
I8931	White Rock Point (GrJb2)	6	−0.450	34.321	LSA	Forager cline	F	L0a2 (likely)	N/A	0.03	Insufficient collagen	N/A

*Samples are from the same individual but provided slightly different radiocarbon dates. †The context of this individual is uncertain; see (21) for details. ‡Indirect date on a bone that may be from a different individual (table S1). All other dates are direct on the individual for whom DNA data are reported. §Approximate location. ¶New attempts to date this individual failed, but a published date on bone apatite from this individual suggests a PIA association, despite genetic clustering with PN individuals; see (21) for details.

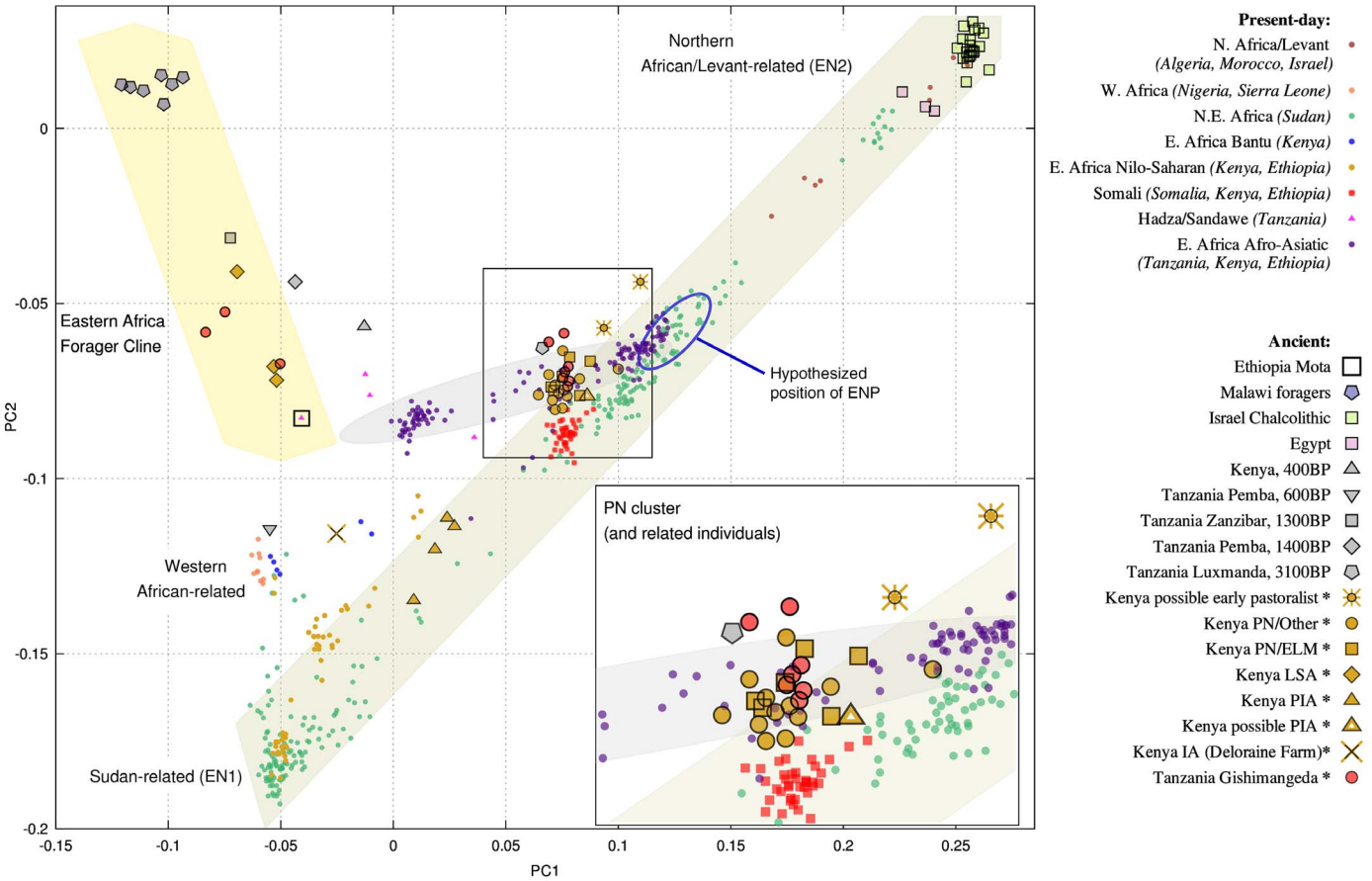

Fig. 2. Principal components analysis. Shaded regions are drawn to highlight notable clines of ancestry. Ancient individuals from this study are indicated in the key with asterisks. Dates for published ancient individuals outside of Kenya and Tanzania are ~4500 B.P. for Mota, ~8100 to 2500 B.P. for Malawi foragers, ~6500 to 5800 B.P. for Israel Chalcolithic, and ~3600 to 2000 B.P. for Egypt. ELM, Elmenteitan; LSA, Later Stone Age; PN, Pastoral Neolithic; IA, Iron Age (I8802); PIA, Pastoral Iron Age; ENP, early northeastern pastoralist. See (*21*) for more details and table S5 for the full list of individuals shown.

between Sudanese, Ethiopians, and western Africans, with their language family affiliations tending to predict their broad-scale genetic affinities.

The positions of ancient eastern Africans on the PCA strongly correlate with archaeological associations. The three individuals from LSA cultural contexts all cluster with previously reported ancient foragers, falling intermediately between those from southern Ethiopia (Mota) and coastal Tanzania (Zanzibar and Pemba islands), consistent with their geographic position (*22*, *24*). Individuals from pastoralist contexts [including one from Luxmanda in Tanzania (*22*)] are highly differentiated from foragers, with the exception of three individuals uncertainly assigned a pastoral context at Gishimangeda Cave in Tanzania, who cluster with foragers. PN individuals, including Elmenteitan and those within the heterogenous SPN category (whom we refer to as "other PN"), mostly form a tight cluster near present-day Afro-Asiatic speakers, with a small number of modest outliers, including the two individuals buried at Prettejohn's Gully, whose earlier date (~4000 B.P.) coincides with the initial limited spread of herding into the area. Finally, five Iron Age individuals are shifted to the left in the PCA: four PIA individuals toward Nilotic speakers and an IA child from Deloraine Farm (I8802)—the earliest agricultural site in Kenya's Rift Valley (*32*)—toward western Africans and Bantu speakers.

We also examined the uniparentally inherited loci (mtDNA and Y chromosomes) of the sampled individuals. The most pronounced pattern is the high frequency among the PN individuals (7 to 12 out of 17 males; table S6) of the E-M293 haplogroup (E1b1b1b2b2a1), a Y chromosome lineage that has been hypothesized to be associated with the spread of pastoralism in the Horn of Africa, Kenya, and Tanzania and from there to southern Africa, on the basis of its present-day distribution and diversity (*33*, *34*). Other males also carried haplogroups most frequently found in present-day eastern Africa, with the exception of E-M58 (E1b1a1a1a1a; predominantly western African) in the IA individual I8802, consistent with his position in the PCA. The observed mtDNA lineages form more of a mosaic pattern, including types most closely associated with eastern and northeastern Africans, eastern African foragers, and northern Africans and western Eurasians (table S7).

Formal modeling of admixture

To obtain quantitative inferences about the genetic relationships among the ancient and present-day individuals, we used the *qpAdm* software (*35*, *36*), which provides a flexible framework for testing admixture models and estimating mixture proportions. Guided by the PCA, we began by using three groups of individuals—present-day Dinka (*28*), ancient Chalcolithic-period individuals from Israel (*25*), and the ~4500 B.P. forager from Mota, southern Ethiopia (*24*)—to represent distinct components of ancestry plausibly found in ancient and present-day eastern Africans, with present-day western Africans among the outgroups (*21*). Note that the use of these proxy groups in *qpAdm* modeling does not imply an assumption that they are directly ancestral to the true sources contributing to the individuals we analyzed. Instead, for a model to be properly formulated, the reference groups only need to be more closely related to the true sources

than are the outgroups, without substantially different admixture (35). Thus, for example, ancestry related to the Chalcolithic Israel reference individuals could plausibly have originated anywhere in northeastern Africa or the Levant and could have been present in northeastern Africa for many thousands of years. We use the Chalcolithic individuals in this study because we lack genetic data from a phylogenetically adjacent reference group from Egypt, Sudan and/or South Sudan, or the Horn. Additionally, *qpAdm* does not require any assumptions regarding the internal phylogeny relating the references and outgroups, and it provides both standard errors for mixture proportion estimates and a *P* value for overall model fit quality (35).

Our *qpAdm* modeling reveals that the PN individuals had substantial proportions of all three ancestry components (~40% each for those represented by Dinka and by the Chalcolithic Israel individuals and ~20% related to Mota) (Fig. 3 and tables S8 and S9), with no evidence of western African–related ancestry. The individuals from Prettejohn's Gully can also be well modeled using the same three components, but in a modestly different ratio. The Iron Age group as a whole (including the more recent ~300 B.P. individual from Emurua Ole Polos but excluding the possible PIA individual from Kokurmatakore) does not fit well under a three-way model, but the fit improves markedly when we exclude the Deloraine Farm individual I8802 (P = 0.009 versus 0.0003). The remaining four individuals (who are confidently assigned to PIA contexts) are inferred to have substantially more Sudan (Dinka)–related ancestry (~60%) than is seen in the PN. We also observe similar patterns for present-day groups falling near the ancient individuals in PCA [using data from (31)], whereby the three-way model fits better for Afro-Asiatic– and Nilo-Saharan–speaking groups than for Bantu-speaking groups (table S8). Consistent with the PCA results, Afro-Asiatic speakers are inferred (as in PN) to have relatively even proportions of the components represented by Dinka and by Chalcolithic Israel (but with varying proportions of Mota-related ancestry), whereas Nilo-Saharan speakers are inferred to have more Sudan-related ancestry. Alternative model formulations in which we use either ancient individuals from Taforalt in Morocco (27) in place of the Chalcolithic Israel group or present-day Lemande from Cameroon (28) in place of Dinka (with Dinka moved to the outgroup set) fit significantly worse for most test groups (table S8).

From these results, we formulated a four-part hypothesis to explain the origins of the ancestries in the sampled eastern African groups. First, admixture in northeastern Africa, likely associated with the spread of pastoralism, created groups (as yet unsampled with ancient DNA) with approximately equal proportions of ancestry related to (i) present-day Nilotic speakers such as Dinka and Nuer and (ii) sampled ancient and present-day groups from northern Africa and the Levant. We refer to this combination as early northeastern African pastoralist-associated ancestry (henceforth "early northeastern pastoralist," or ENP) and the two subcomponents as EN1 and EN2. Second, descendants of these groups mixed with local foragers in eastern Africa, leading to the ~20% Mota-related ancestry in the PN individuals. Third, an additional period of Sudan-related gene flow occurred before the Iron Age and contributed to PIA groups. Fourth, close to the same time, western African–related ancestry related to present-day Bantu speakers [also seen in an individual buried on Pemba Island ~600 B.P. (22)] appeared in the Rift Valley (notably at Deloraine Farm), in association with the spread of farming.

To test these hypotheses and gain further insight into changes in ancestry over time, we carried out a second round of analysis in *qpAdm* using pairs of reference groups linked more closely with each historical phase. For the initial spread of pastoralism, we used Hadendowa [Sudanese Beja (29)] plus Mota. It is likely that

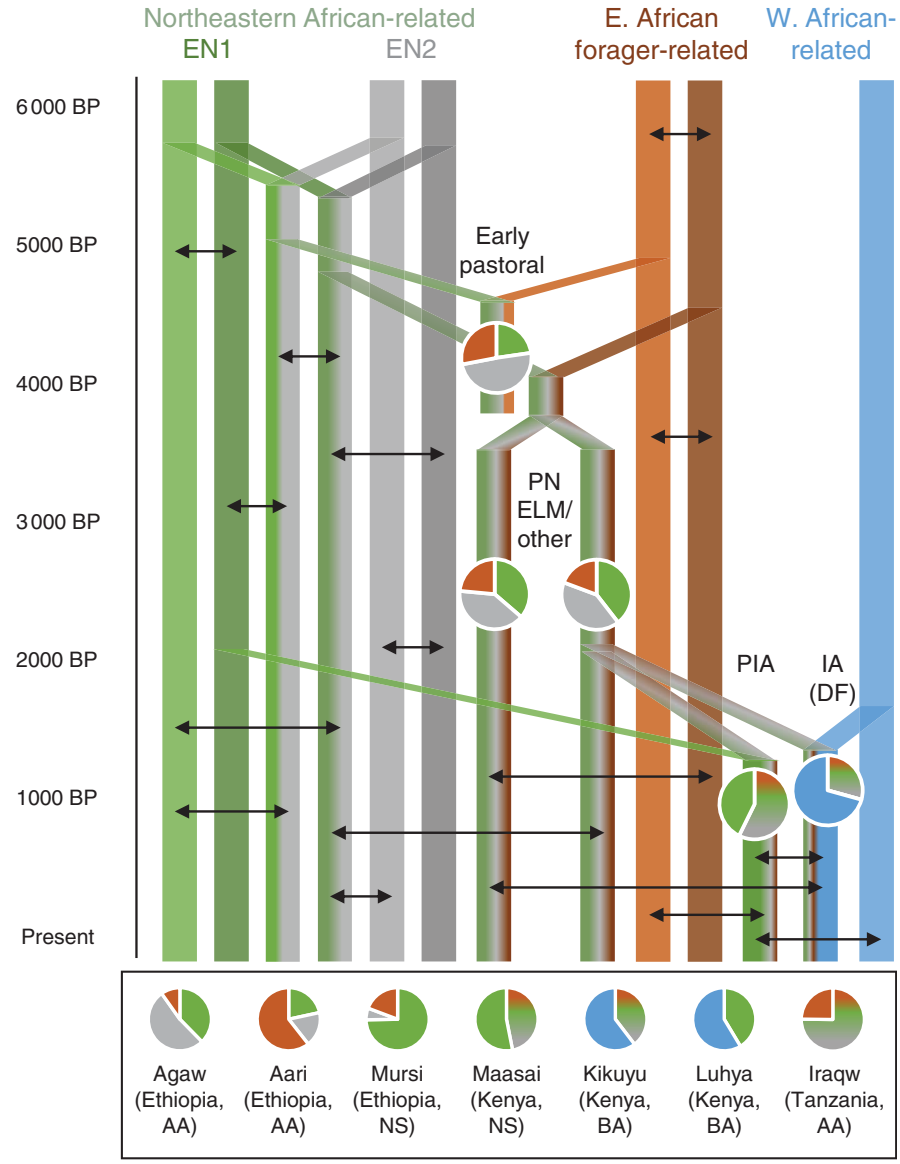

Fig. 3. Proposed model of admixture for ancestry in eastern Africans. Solid-color bars represent lineages of northeastern African (EN1/Sudan-related in green, EN2 in gray), eastern African forager-related (orange), and western African-related (blue) ancestry, and mixed-color bars represent admixed groups (hypothesized early northeastern pastoralists, green plus gray). Pie charts show ancestry proportions for sampled ancient (embedded in figure at approximate date points) and present-day (bottom) groups inferred from *qpAdm* (PN-related ancestry as mixed-color sections). Black arrows represent likely ongoing interactions and not specific admixture events inferred from the data. EN1 and EN2, early northeastern pastoralist source groups; PN, Pastoral Neolithic; ELM, Elmenteitan; PIA, Pastoral Iron Age; IA (DF), Iron Age (Deloraine Farm); AA, Afro-Asiatic; NS, Nilo-Saharan; BA, Bantu.

the genetic landscape of northeastern Africa has changed substantially since the time of the events we are modeling, so we do not propose that Hadendowa are descended directly from ENP; rather, we chose them to serve as a proxy for the (approximate) mixture of ancestries hypothesized to be present in the true ENP-related source (on the basis of the PCA and *qpAdm* results above). This two-way model yields a good fit for the PN individuals ($P = 0.45$) but not for Iron Age individuals (either the PIA cluster or the IA individual from Deloraine Farm) or present-day Nilotic- and Bantu-speaking groups (all $P < 1 \times 10^{-6}$; table S8). We also attempted to fit PN as a mixture of possible early Kenyan pastoralist (represented by Prettejohn's Gully) and forager-related ancestry, but this combination was rejected ($P < 1 \times 10^{-6}$ using either Mota or the three Kenyan LSA individuals to represent the forager component), suggesting that the two ancient pastoralist groups are not simply differentiated by their proportions of forager-related ancestry.

Finally, to study later transformations, we built models using PN as one proxy source and Dinka (Sudan-related), Mota (forager-related), or Lemande (western African-related) as the other. We obtain improved fits for the Iron Age individuals and for present-day Kenyan Nilotic- and Bantu-speaking groups in this framework: The PIA cluster can be fitted as a mixture of ~57% PN-related and ~43% Sudan-related ancestry, whereas the Deloraine Farm individual can be modeled as a mixture of ~29% PN-related and ~71% western African–related ancestry (Fig. 3). Similar models also yield good fits for present-day Maasai (~47% PN-related and ~53% Sudan-related) and Kikuyu (~40% PN-related and ~60% western African–related), whereas Luhya can be fit as a mixture of Sudan-related (~41%) and western African–related (~59%) ancestry (Fig. 3).

We also used direct tests of asymmetry in allele frequencies to investigate the fine-scale genetic structure of the PN cluster and related individuals (table S10). First, in agreement with their colocalization in PCA, we do not detect any significant differences in allele-sharing between Elmenteitan and other PN individuals relative to a set of 27 comparison groups, including the Iron Age and possible early pastoralist groups from this study (maximum nominal Z score = 2.1; see also Fig. 4). There are hints of differentiation (maximum $Z = 2.6$) between the main PN cluster and individual I8904 from Kokurmatakore [previously dated to the PIA (*37*)], but this individual's ancestry is much more similar to other PN individuals than to PIA (Fig. 2 and table S10). We also find only minor asymmetry between the primary Kenyan and Tanzanian PN clusters (maximum $Z = 2.5$). However, four PN-period individuals who appear as outliers on PCA do have statistically significant ancestry differences as compared with the PN cluster. In particular, two individuals from Gishimangeda Cave (I13972 and I13978) and the previously reported ~3100 B.P. pastoralist individual from Luxmanda in Tanzania (*22*) have evidence of more or different forager-related ancestry relative to Sudan-related ancestry [e.g., f_4(Ancient South African foragers, Dinka; X, PN) > 0, $Z = 3.2$, 5.1, and 6.8, respectively; Fig. 4 and tables S8 and S10], whereas individual I8759 (an early PN individual buried at Naishi Rockshelter in Kenya) has evidence of less forager-related ancestry [e.g., f_4(Ancient South African foragers, Europeans; I8759, PN) < 0, $Z = -4.4$]. We also confirm the differences in ancestry between the PN cluster and the two possible early pastoralist individuals from Prettejohn's Gully (both $Z > 5$). Although the individuals from Prettejohn's Gully fall relatively far apart on PCA (Fig. 2), their ancestry is only weakly differentiated via f statistics (maximum $Z = 2.2$; table S10).

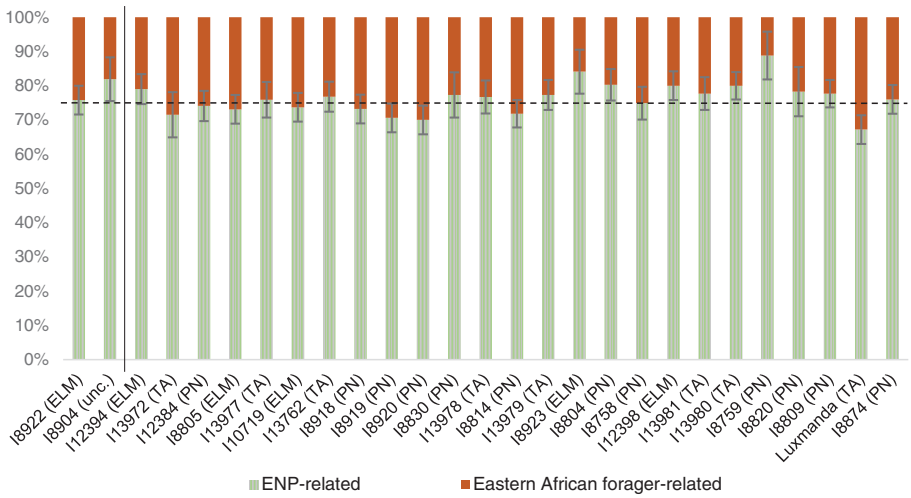

Fig. 4. Mixture proportions for PN individuals. Results are from a two-component *qpAdm* model using Hadendowa (green-and-gray striped bars) and the ancient individual from Mota, Ethiopia (orange bars) as proxy sources [for early northeastern pastoralist (ENP) and eastern African forager–related ancestry, respectively]. Radiocarbon-dated individuals (to the right of the solid line) are ordered from most ancient on the right (I8874, 3350 to 3180 B.P.) to most recent on the left (I12394, 1530 to 1400 B.P.). Bars show two standard errors in each direction. The dashed line represents the Kenya PN group-level estimate (74.7 ± 1.0% ENP-related ancestry). Note that the linear regression coefficient for forager-related ancestry is not significantly nonzero as a function of date ($R^2 = 0.03$, $P = 0.39$) or latitude ($R^2 = 0.03$, $P = 0.37$). ELM, Elmenteitan; PN, other Kenyan Pastoral Neolithic; TA, Tanzanian PN [including the Luxmanda individual from (*22*)]; unc., uncertain.

Dates of admixture

The fact that we observe tight clustering of PN individuals via PCA and *qpAdm*, with little if any spatial or temporal structure as revealed by direct dating (Fig. 4 and table S9), suggests that the admixture responsible for forager-related ancestry in the PN had largely ceased before the lifetimes of our sampled individuals. To test this hypothesis, we used the MALDER software (*38*, *39*) to estimate dates of admixture for pairs of high-coverage individuals with similar direct radiocarbon dates and locations (*21*). All pairs have inferred dates that point to distant average times of admixture (mean ~4600 B.P. for PN and ~5300 B.P. for Prettejohn's Gully; Fig. 5 and table S10), with the concordance among the PN estimates providing an independent line of evidence for a lack of substantial ongoing mixture. We infer a more recent average date (~2200 B.P.) for two late PIA individuals, likely associated with additional Sudan-related ancestry (table S11). Our power to detect multiple waves of admixture is limited with ancient data, but for one pair of PN individuals from Naivasha Burial Site, we are confidently able to identify two separate events, the first at ~5100 B.P. and the second at ~4000 B.P. We also infer two waves for a pair of individuals from Gishimangeda Cave, dating to ~6000 B.P. and ~4000 B.P. In light of our *qpAdm* results, and given the associated MALDER amplitudes (table S11), these multiple dates plausibly represent estimates of the times of (i) the formation of admixed ENP ancestry and (ii) admixture in eastern Africa between local foragers and descendants of the first mixture, leading to the three-component ancestry of PN individuals. In this context, the single (and intermediate) estimated dates for other PN pairs can be interpreted as averages of these two processes (Fig. 5).

Incorporating genetic evidence into models for the spread of food production

The four-phase model emerging from our genetic and radiocarbon dating results builds on archaeological reconstructions for the spread of herding into eastern Africa, supporting some theories while rejecting others that until now have been considered plausible. Under a proposed "moving frontier" model, herders entering new environments would interact in diverse ways with Indigenous foragers, resulting in varying cultural responses and blurred archaeological boundaries

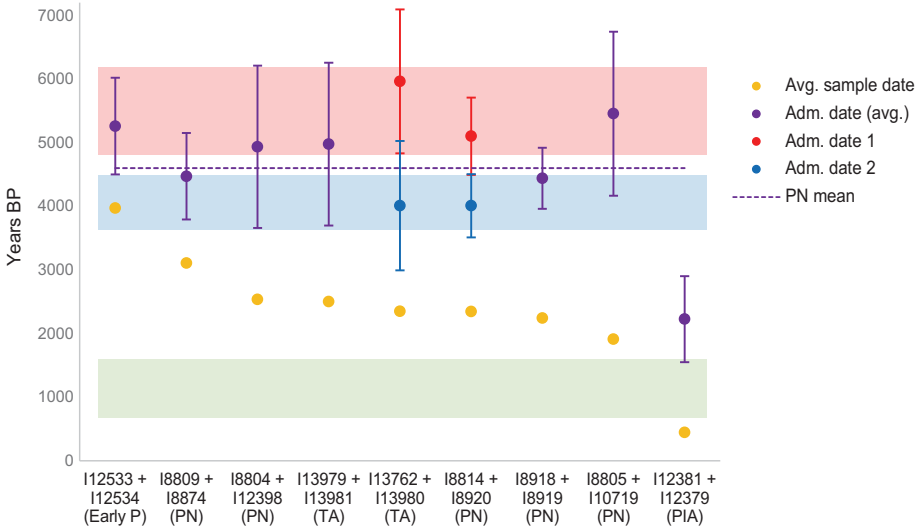

Fig. 5. Dates of admixture inferred for pairs of ancient individuals. Bars show two standard errors in each direction. The shaded areas represent implied periods of admixture (Adm.): ENP (early northeastern pastoralist; red), forager-related (blue), and additional Sudan-related (green). Early P, early pastoralists; PN, Pastoral Neolithic; PIA, Pastoral Iron Age; TA, Tanzanian PN. See also table S11.

as groups adopted some of each other's cultural practices. In the ensuing "static frontier," more intensive herding and/or competition would transform initial relationships into more stable, long-term patterns (*40*). Archaeologists interpret the construction of cemeteries by the first herders in the Turkana Basin and the apparent trickle of people with similar material culture into the south-central Rift Valley as part of a moving frontier, whereas the explosion of pastoralist cultures in the PN reflects more established, static herder-forager relationships (*6*, *15*).

On the basis of genetic data from a wide sampling of PN individuals, we infer two phases of admixture associated with the spread of pastoralism: the first likely ~6000 to 5000 B.P. in northeastern Africa and the second ~4000 B.P. between this admixed ENP group and eastern African foragers. Archaeological data show that the Nile Valley was important for herders seeking reliable water sources toward the end of the African Humid Period (~7000 to 6000 B.P.) (*1*, *41*). Herders plausibly traced the White Nile southward, following unknown trajectories through South Sudan and/or southern Ethiopia to arrive in the Turkana Basin ~5000 B.P. (*5*, *6*). Alternatively, they may have moved via the Horn of Africa, but current evidence for herding in that region postdates that of Turkana (*3*). Our results support archaeological hypotheses that no matter the routes they took, early herders interacted with local foragers as they spread (*16*, *42*). In eastern Africa, extensive forager-herder interactions have been proposed, both in the Turkana Basin and during the initial trickle of herding into the south-central Rift Valley (*6*–*10*, *16*, *17*). Either area, or another unsampled region, could have witnessed the admixture we document between descendants of the (already admixed) ENP group and local foragers, giving rise to the groups who then developed the PN cultural traditions of southern Kenya and northern Tanzania.

Our attempts to extract DNA from early herders in Turkana were unsuccessful (*21*), so the genetic ancestry (or ancestries) of the first eastern African pastoralist groups remains uncertain. However, some lineages may be reflected in a man and a woman buried at Prettejohn's Gully ~4000 B.P. There are few associated artifacts, but the individuals' genetic profiles suggest that they may represent an initial limited dispersal of herders into the south-central Rift Valley that did not leave large numbers of descendants. Previously, evidence of herding before ~3300 B.P. was limited to Turkana-related Nderit pottery found sporadically, and usually undated, in the area (*8*), and to sheep or goat remains associated with a date of ~4200 B.P. at a site 33 km south of Prettejohn's Gully (*7*). Genetically, the two individuals are most similar to those from PN sites, but they fall outside the range of sampled PN (and present-day) variation and cannot be modeled as directly related to PN. They also have a suggestively older date of admixture, and the male individual (I12533) carries a Y chromosome haplogroup (E2; E-M75) not found in any of our sampled PN individuals. Our results thus imply at least two chronologically distinct movements of herders through eastern Africa, consistent with archaeological evidence of complex spreads (*2*), while adding new information by showing that one group (the one that gave rise to the PN cluster) was eventually much more demographically successful than the others.

Although Prettejohn's Gully may represent a limited trickle of herders into the south-central Rift Valley, numerous PN sites after ~3300 B.P. attest to successful specialized pastoralism. Archaeologists attribute this florescence to herder innovations that allowed them to overcome environmental and disease barriers, likely facilitated by strong social networks reflected in widespread material cultural traditions (*8*–*11*). The dense cluster of PN individuals in our PCA—including burials >450 km apart—suggests that these networks formed among people with shared ancestry, with the close relatedness perhaps reinforced by ongoing mobility and gene flow. Moreover, it is notable that individuals in our sample buried with distinctive Elmenteitan material culture display minimal genetic differentiation from those of other PN burials. Strong Elmenteitan material cultural traditions may reflect maintenance of social boundaries, but our results do not support the view that these people were genetically distinct (*12*, *18*). In comparison to present-day groups, all PN individuals (associated with both the SPN and Elmenteitan material cultures) show the greatest genetic affinity to Afro-Asiatic speakers, supporting the hypothesis that the initial large-scale expansion of pastoralism in eastern Africa was linked to the spread of Afro-Asiatic languages (*18*, *19*).

With regard to the moving frontier model, we find that although sampled PN individuals carry ~20% admixture from local forager groups, almost all of this gene flow occurred well before the core PN era, as herders entered new environments. By contrast, the rapid spread of pastoralists into Kenya and Tanzania after ~3300 B.P. involved minimal gene flow between herders and foragers, plausibly due to the formation of a static frontier along which social barriers prevented large-scale gene flow, despite possible social and economic interaction (*8*, *15*). Alternatively, population densities of foragers may have been so low that gene flow between the groups had little demographic impact on the more numerous pastoralists (*12*). Static frontiers were not absolute, however, in agreement with ethnographic and ethnohistoric records that testify to some intermarriage between foragers and food producers (*43*, *44*). Today, for example, the Eyasi Basin is an important interaction zone for diverse foraging and food-producing groups (*44*) and is home to speakers of each of the four main African language phyla. In our data, the ancestries of the individual buried at Luxmanda (*22*), the southernmost known PN site (*11*), and two newly reported individuals from Gishimangeda Cave in the Eyasi Basin attest to additional admixture with foragers beyond the events contributing to the possible early pastoralists from Prettejohn's Gully and to the main PN cluster. Furthermore, at Gishimangeda Cave, we observe three individuals clustering genetically with foragers, which may reflect social ties between people with different ancestry and/or ways of life. However, given that the three forager-related individuals produced insufficient collagen for radiocarbon dating and genetic data with substantially lower coverage than that of the pastoralist-related individuals, we speculate that the observation of distinct ancestry types is more likely to be a consequence of multiple burial phases at the site (i.e., greater antiquity for the forager-related individuals).

Low frequency of genetic adaptation to milk consumption

To test whether the success of PN groups in eastern Africa was aided by genetic adaptations linked to diet, we also evaluated the sequenced individuals for presence or absence of genetic variants associated with adult lactase persistence (LP) (table S12). Although our coverage is limited for some individuals and some SNPs, we observe only one instance of an LP-conferring mutation, in individual I13762, from Gishimangeda Cave in Tanzania. This individual, who falls within the main PN genetic cluster and lived during the later PN (2150 to 2020 B.P.), carried the derived allele at the rs145946881 (G/C-14010) SNP, which is the most common LP mutation found among eastern African groups today. The other ancient individuals could possibly have carried different variants conferring the same phenotype, but the assayed SNPs are found at high frequencies in some present-day eastern African groups and thus are likely to have been important historically (*45*). This finding suggests that eastern African pastoralists were mostly lactose intolerant as recently as 3000 to 1000 years ago and that the LP alleles only recently rose in frequency, although our results also demonstrate that the G/C-14010 mutation was present and could have been a target for natural selection by the PN period. Direct evidence for dairying is currently lacking in the region, despite the specialized pastoralist lifestyle inferred from faunal remains at PN sites (*8*). However, culinary innovations such as fermentation could have enabled dairy consumption even in the absence of LP.

Increasing complexity in the Iron Age

The eastern African Iron Age can be summarized archaeologically as a mosaic in which foragers, herders, and early farmers with distinct traditions and ways of life overlapped in space and time (*2*, *14*, *15*, *19*). This complexity is reflected in the ancient individuals we analyzed. The young boy buried at Deloraine Farm—the site with the earliest direct evidence of farming in the Rift Valley (*32*)—shows affinity to western Africans and speakers of Bantu languages (both genome-wide and on the Y chromosome). This is the earliest documentation of western African–related ancestry in eastern Africa, in a region where today such ancestry is widespread and the majority of people speak Bantu languages (*46*).

The Deloraine Farm child's genetic distinctiveness as compared with the PN cluster is notable in light of similarities in artifacts between Elmenteitan sites and Deloraine Farm, viewed as evidence of continuity from the Elmenteitan to the Iron Age (*32*, *47*). By contrast, four PIA individuals spanning an ~800-year period show greater affinity to present-day Nilotic speakers and are associated with an influx of Sudan (Dinka)–related ancestry. Similarities between archaeologically and ethnographically documented material culture suggest that PIA sites may be associated with ancestors of present-day Kenyan Nilotic speakers such as the Kalenjin or Maasai (*32*, *47*). Both the PIA individuals and present-day Maasai retain substantial components of PN-related ancestry, showing that the ancestry composition of PIA and more recent pastoralists reflects mixture with previously established herder groups in eastern Africa. For other groups, such as Luhya (who speak a Bantu language), there is little evidence of PN-related ancestry, suggesting that their ancestors spread into Kenya without mixing substantially with local herders. Boundaries between foragers and food producers may have been maintained during the Iron Age, as we do not observe a significant increase in forager ancestry in the PIA or IA individuals, but we cannot rule out a small proportion of additional forager-associated admixture. Overall, we caution that these interpretations are limited by small sample sizes and may not reflect the more nuanced regional dynamics within this mosaic.

Genetic diversity of eastern African foragers

Archaeological evidence of foragers across Holocene eastern Africa encompasses an array of material culture and subsistence traditions (*48*). This study adds to our understanding of LSA genetic variation by reporting ancient DNA from additional foragers without pastoralist-related admixture, including from fisher-foragers near Lake Victoria who may have been living contemporaneously with PN herders in the broader region. These individuals fall in an intermediate position between Ethiopian and Tanzanian foragers on a genetic cline that is well correlated (among sampled ancient individuals) with geographical location (*22*). Broadly, however, the similarity of foragers buried in the Victoria and Eyasi basins to individuals living on the Kenya coast and in Ethiopia and coastal Tanzania (*22*, *24*) suggests that shared forager ancestry extended widely across the region, as also attested by present-day genetic data (*20*).

Outlook

Genome-wide data from 41 ancient eastern Africans show that archaeological complexity during the spreads of herding and farming is also reflected in genetic patterns, which indicate multiple movements of and gene flow among ancestrally distinct groups of people. We identify three components of ancestry harbored by ancient pastoralists and propose a sequence of admixture events to explain our observations; future archaeological and ancient DNA research in the Turkana Basin, the Horn of Africa, and other parts of northeastern Africa will be necessary to confirm the earliest stages of the spread of herding into the region. At the other end of our timeframe, we document multiple admixture events affecting Iron Age groups associated with heterogeneous economic, cultural, and linguistic patterns. This complexity can be further explored through additional comparisons of genetic and archaeological diversity. Ancient DNA offers a new source of information about eastern African Holocene prehistory, and an important next direction is to integrate this information rigorously with insights provided by the longer-established disciplines of archaeology and linguistics.

Materials and methods summary

Human skeletal remains from eastern African archaeological sites, including the petrous portion of the skull, teeth, and other bones, were sampled from the National Museums of Kenya and Tanzania and the Livingstone Museum in Zambia, following protocols to minimize both destruction and contamination. Bioarchaeological data on the analyzed individuals, along with detailed information about archaeological context, are provided in the full materials and methods (*21*). DNA was extracted from bone powder in dedicated clean rooms at Harvard Medical School using protocols optimized for ancient DNA. Illumina sequencing libraries were prepared with uracil-DNA-glycosylase (UDG) to reduce deamination-induced errors. Before sequencing, libraries were enriched for molecules overlapping ~1.2 million genome-wide SNPs. Of the 77 samples processed for this study, 43 (from 41 distinct individuals) provided genome-wide ancient DNA data. Direct radiocarbon dates were generated at the Pennsylvania State University (PSU) Radiocarbon Laboratory via accelerator mass spectrometry (AMS).

Raw sequencing data were filtered and aligned to the human reference genome. One sequence per individual was chosen randomly from those overlapping each targeted SNP to represent that individual at that position. On the basis of authenticity metrics, two individuals were excluded from genome-wide analyses. The other 39 individuals were analyzed in conjunction with published genetic data from ancient individuals and present-day groups, using a variety of statistical approaches. Multiple population genetics methods were applied to investigate proportions, sources, and dates of admixture, with a particular emphasis on testing of proposed admixture models through the *qpAdm* software.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 and S2
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Data S1

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