JASs Journal of Anthropological Sciences Open Access
Review Vol. 103 (2025), pp. 27 - 56 doi. 10.4436/jass10306

The mosaic of lactase persistence in Africa: from gene-culture coevolution to continental demography

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Summary - *Lactase persistence (LP), the genetically determined capacity to digest lactose beyond infancy, stands as a prime example of rapid, recent human adaptation and gene-culture coevolution. Across Africa, the distribution of genetic variants associated with LP reveals intricate patterns reflecting a complex interplay between the cultural innovation of dairying, intense positive selection, adaptation to varied environments, and diverse, continent-spanning migratory events. This review synthesizes current knowledge from genetics (including ancient DNA), anthropology, and archaeology (including lipid residue analysis of pottery and paleo proteomics of ancient dental calculus) to explore how LP variants function as powerful bioarcheological tracers of African demographic history, dietary shifts, and cultural transitions within the African continent. By integrating evidence from these multiple disciplines, I aim to illustrate how the evolution and dispersal of LP alleles mirror significant demographic events and cultural innovations throughout Africa's prehistory, highlighting one of the strongest examples of recent human adaptation.*

Keywords - *Africa, Lactase persistence, Pastoralism, Holocene, Gene-culture coevolution, Archaeology.*

Introduction

The capacity to digest lactose, the principal sugar in milk, into adulthood—a trait known as lactase persistence (LP)—represents a remarkable instance of recent human evolution driven by cultural practices (Bersaglieri et al. 2004; Feldman et al. 1996; Flatz et al. 1973; Simoons 1978; Swallow 2003; Tishkoff et al. 2007). While most mammals, including most human populations, experience a genetically programmed decline in lactase enzyme activity following weaning (lactase non-persistence, LNP), specific human groups retain high activity, allowing them to consume fresh milk and dairy products without severe lactose-related gastrointestinal effects (Arola et al. 1994; Swallow 2003; Troelsen 2005). This trait carries profound implications for understanding human adaptation, the interplay between genes and culture (gene-culture coevolution), and historical migratory patterns (Feldman and Laland 1996; Gerbault et al. 2011; Kasser et al. 2025; Tishkoff et al. 2007).

The story of LP in Africa is notably intricate and diverse. Unlike Europe, where LP is predominantly linked to a single genetic variant (-13910T, rs4988235) (Enattah et al. 2002), African populations exhibit a remarkable diversity of mutations responsible for this trait (Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2013; Ranciaro et al. 2014; Tishkoff et al. 2007). Several independently derived single nucleotide polymorphisms (SNPs) within the enhancer region of the *LCT* gene reflect distinct adaptive events arising convergently in response to similar selective pressures associated with dairy consumption (Hassan et al. 2016; Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2015; Priehodova et al. 2014; Ranciaro et al. 2014; Tishkoff et al. 2007). The geographical distribution and varying frequencies of these variants, along with the presence of the Eurasian -13910T allele in some groups due to admixture (Vicente et al. 2019), provide a unique genetic map for tracing past human movements, interactions, and environmental adaptations across the continent (Cerny et al. 2021, 2023; Coelho et al. 2005; Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2015, 2013; Macholdt et al. 2014, 2015; Priehodova et al. 2014, 2017, 2020; Ranciaro et al. 2014; Tishkoff et al. 2007; Torniainen et al. 2009).

The evolutionary pressures driving LP in Africa are closely intertwined with the adoption and intensification of pastoralism, a subsistence strategy centered on the domestication and herding of animals like cattle, sheep, and goats, first appearing in northeast Africa and the Sahara during the favorable climatic conditions of the African Humid Period (AHP), ~ 11,700–5,000 before present (BP) (Cheddadi et al. 2021; di Lernia 2021; Dunne et al. 2018, 2012; Friedrich et al. 2023; Kim et al. 2020; Kuper et al. 2006; Le Meillour et al. 2023; Liu et al. 2017; Loftus et al. 1994; Phelps et al. 2020; Salem et al. 2025). The expansion of land use for animal production coincided significantly with the termination of the AHP (~ 5,500–3,000BP) and the subsequent aridification of the Sahara, prompting a southward spread into new ecological zones (Brierley et al. 2018; Gifford-Gonzalez 2011; Gifford-Gonzalez et al. 2011; Holl 2020; Kuper 2006; Kuper and Kropelin 2006; Prendergast et al. 2019). As various groups transitioned to pastoralist or agro-pastoralist economies, particularly during the mid-to-late Holocene (~7,000 to 2,000 BP), milk became a vital nutritional resource, especially in arid and semi-arid regions where it offered calories, protein, fat, and crucial hydration (di Lernia 2021; di Lernia et al. 2013; Dunne et al. 2012). In this context, individuals capable of digesting lactose gained significant nutritional, survival, and potentially reproductive advantages (e.g., related to enhanced skeletal growth and reduced maternal mortality), leading to strong positive selection for LP-associated alleles. The selection coefficients estimated to be among the highest observed in the human genome (Bersaglieri et al. 2004; Gerbault et al. 2009; Ingram et al. 2009; Ranciaro et al. 2014; Tishkoff et al. 2007).

The study of LP offers a unique opportunity to investigate gene-culture coevolution and trace ancient human migrations using genetic markers directly linked to a cultural practice (Gerbault et al. 2011; Hollox 2005; Richerson et al. 2004). Unlike neutral genetic markers, LP variants provide evidence not only of gene flow but also of the powerful selective impact of cultural transmission, revealing how technology (dairying), economy (pastoralism), and biology have intertwined to shape human history (Hollfelder et al. 2021; Macholdt et al. 2014, 2015; Ranciaro et al. 2014; Vicente et al. 2019).

Recent advancements in genomics, particularly high-throughput sequencing, and the successful retrieval of ancient DNA (aDNA) from African archaeological contexts allow researchers to directly observe genetic adaptations in time and space (Prendergast et al. 2019; Schlebusch et al. 2013; Skoglund et al. 2017; Vicente et al. 2019, 2020; Wang et al. 2020). Complementing these genetic approaches, archaeological excavations reveal the spread of dairying technologies (e.g., pottery associated with milk processing) (Dunne et al. 2012; Grillo et al. 2020; Rotunno et al. 2023; Warinner et al. 2014) and faunal remains (di Lernia 2021; di Lernia et al. 2013; Dunne et al. 2018; Gifford-Gonzalez and Hanotte 2011), while biomolecular techniques like lipid residue analysis provide direct chemical evidence of milk processing (Bleasdale et al. 2021; Dunne et al. 2012). Linguistic analyses trace the diffusion of pastoralist-related terminology across African language families, offering another layer of historical evidence (Ehret 1967).

Nevertheless, reconstructing the history of LP in Africa presents significant challenges. The continent's vast ecological diversity (Phelps et al. 2020), complex demographic histories involving deep population structures and admixture, and the often-patchy nature of archaeological and genetic data, complicate straightforward narratives (Cerny et al. 2021; Fan et al. 2019, 2023; Fortes-Lima et al. 2024, 2025; Schlebusch et al. 2018; Tallman et al. 2023; Tishkoff et al. 2009). Furthermore, cultural practices such as milk fermentation (producing yogurt, cheese, etc.), which reduces lactose content, likely predated widespread LP and may have modulated the selective advantage of the trait differently across regions and time periods, adding complexity to our understanding (Dunne et al. 2018; Grillo et al. 2020; Prendergast et al. 2019). The interpretation of archaeological proxies also requires caution; for instance, lipid residues in pottery might reflect specific processing activities (like meat/fat rendering) rather than the overall dietary importance of milk, even in highly dairy-dependent cultures (Grillo et al. 2020).

This review provides a comprehensive synthesis of current knowledge regarding LP in Africa, emphasizing its role as a marker for tracing human migrations and a prime example of gene-culture coevolution. This work explores the genetic basis of lactase persistence (LP), the distribution of associated alleles, archaeological and biomolecular evidence for dairying, and the broader implications for understanding African population history and adaptation. It also assesses methodological innovations and limitations, particularly those related to ancient DNA (aDNA) and residue analysis. By examining LP through a multidisciplinary lens, this work seeks not only to chart the migrations and adaptations of African peoples but also to illuminate the powerful processes where human biology and culture coevolve.

Molecular mechanisms and evolution of lactase persistence

Overview of lactase enzyme function and gene regulation

Lactase, an enzyme situated at the intestinal brush border, plays a pivotal role in the digestion of milk sugar by hydrolyzing lactose into its absorbable components, glucose and galactose (Troelsen 2005). This enzymatic activity is crucial, especially during infancy when milk constitutes the primary food source. The expression of the gene encoding lactase, *LCT*, located on chromosome 2q21, is primarily controlled at the transcriptional level by enhancer elements located within intron 13 of the adjacent *MCM6* gene (Jensen et al. 2011; Liebert et al. 2016; Olds et al. 2003; Tishkoff et al. 2007; Troelsen 2005; Troelsen et al. 2003). In most mammals, including most humans, lactase production significantly decreases after the weaning period, a state known as lactase non-persistence (LNP) (Swallow 2003; Troelsen 2005). However, in certain human populations, genetic variations within the *MCM6* enhancer region lead to the continued high-level expression of lactase throughout adulthood, conferring the trait of LP (Enattah et al. 2002; Jensen et al. 2011; Liebert et al. 2016; Tishkoff et al. 2007; Troelsen 2005). Understanding the regulation of the *LCT* gene is therefore fundamental to comprehend the molecular underpinnings of LP and its evolutionary history.

Discovery and characterization of functional variants

The breakthrough in elucidating the genetic basis of LP was the identification of the C/T polymorphism at position -13910 upstream of the *LCT* gene, where the derived T allele is strongly associated with LP in Europeans (Enattah et al. 2002). Subsequent investigations revealed that this variant alone could not explain LP prevalence in many African and Middle Eastern populations (Bersaglieri et al. 2004; Mulcare et al. 2004). This led to the discovery of several other SNPs within the same *MCM6* enhancer region, each independently capable of enhancing *LCT* expression and sustaining lactase activity into adulthood (Enattah et al. 2008; Ingram et al. 2007; Liebert et al. 2016; Tishkoff et al. 2007). Key variants identified in African populations include G/C at position -14010 (rs145946881), found in pastoralists in the Horn of Africa and parts of East Africa *(*Breton et al. 2014*;* Coelho et al. 2009*;* Macholdt et al. 2015*;* Ranciaro et al. 2014*;* Tishkoff et al. 2007*);* T/G at -13915 (rs41380347), frequent in Middle Eastern populations and present in Northeast Africa as well (Cerny et al. 2007; Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2015; Priehodova et al. 2014, 2017,2020; Ranciaro et al. 2014; Tishkoff et al. 2007); C/G at -13907 (rs41525747), primarily found in East Africa pastoralists (Hollfelder et al. 2021; Jones et al. 2015; Ranciaro et al. 2014; Tishkoff et al. 2007); and T/G at -14009 (rs869051967), also occurring in East African groups, often those with Arabian admixture (Hollfelder et al. 2021;

Ingram et al. 2009; Jones et al. 2013; Ranciaro et al. 2014; Tishkoff et al. 2007) (Tab. 1). The Eurasian -13910T allele is found at lower frequencies in some North and West African groups, most notably among Fulani populations, reflecting historical admixture and long-distance contact (Vicente et al. 2019). Functional studies, such as luciferase reporter assays, have confirmed that these derived alleles enhance the transcriptional activity of the *LCT* promoter, thereby maintaining lactase production into adulthood (Ingram et al. 2007; Jensen et al. 2011; Liebert et al. 2016; Olds and Sibley 2003; Tishkoff et al. 2007). While rare or population-specific alleles continue to be reported (Hollfelder et al. 2021), these SNPs represent the primary known drivers of LP in African populations.

Convergent evolution, independent origins and strong selection pressure

The ability to digest lactose into adulthood arose through multiple independent mutations within the *MCM6* regulatory region of the lactase gene (Enattah et al. 2002; Ingram et al. 2007; Mulcare et al. 2004; Tishkoff et al. 2007). Genetic studies show that the major LP alleles found in different world regions—such as −13910T in Europe and −14010C, −13907G, and −13915G across African and Afro-Arabian populations—occur on different haplotype backgrounds, confirming that they originated independently and represent a clear case of convergent evolution (Babiker et al. 2011; Enattah et al. 2002; Ingram et al. 2007; Jones et al. 2015, 2013; Priehodova et al. 2014; Ranciaro et al. 2014; Tishkoff et al. 2007). This demonstrates that the cultural innovation of dairying repeatedly and independently triggered similar adaptive responses (Feldman and Laland 1996; Gerbault et al. 2011, 2009; Laland et al. 2001; Odling-Smee et al. 2003). Phylogenetic analyses further confirm these separate origins, indicating that the cultural innovation of pastoralism independently triggered similar adaptive genetic responses in different parts of the world (Anagnostou et al. 2009; Gallego Romero et al. 2012; Holden et al. 2009; Itan et al. 2009; Zadro et al. 2017). Moreover, in Africa, the spatial and temporal distribution of these alleles is inextricably linked to the dispersal of domesticated cattle, sheep, and goats, first appearing in Northeast Africa and the Sahara during the favourable climatic conditions of the AHP (~12,000–5,000 BP) (deMenocal et al. 2000; di Lernia 2021; Dunne et al. 2018; Gifford-Gonzalez 2011; Gifford-Gonzalez and Hanotte 2011; Hanotte et al. 2002, 2000; Kuper 2006; Kuper and Kropelin 2006; Marshall et al. 2002; Pereira et al. 2009). In fact, the molecular dating of these mutations consistently aligns their emergence with the archaeological evidence for the spread of herding economies. While the European T-13910 allele is estimated to have arisen between ~7,500 and 9,000 BP (Bersaglieri et al. 2004; Itan et al. 2009), the East African −14010C variant is estimated to have emerged more recently, likely between ~2,700 and 6,800 BP (Tishkoff et al. 2007). This East African timeline critically overlaps with the Pastoral Neolithic (PN) period and, crucially, coincides with the climatic shift from the favourable Holocene Climatic Optimum to subsequent periods of aridification that began around 5,000 BP (Brierley et al. 2018; Kuper 2006; Marshall and Hildebrand 2002; Phelps et al. 2020; Prendergast et al. 2019) (Tab.2).

In fact, these increasingly dry conditions would have exerted immense selective pressure on herding groups (deMenocal et al. 2000). Aridity rendered mobile pastoralism an essential subsistence strategy, making the ability to safely consume fresh milk—a stable source of calories and hydration—a strong evolutionary advantage (Dunne et al. 2012; Marshall and Hildebrand 2002). Thus, the ascendancy of specialized pastoralism in East Africa is intricately linked to both the initial spread of domestic animals and the intensification of genetic selection driven by this environmental drying (Marshall et al. 2011; Prendergast 2023; Prendergast et al. 2019; Tishkoff et al. 2007). The estimated timing of the emergence of these variants generally aligns with the archaeological evidence for the development and spread of herding economies in the respective regions, occurring primarily within the last 10,000 years (Ranciaro et al. 2014; Tishkoff et al. 2007).

Tab. 1 - ***Major African lactase persistence (LP) variants. Summary of the main LP-associated variants in African populations (−13910T, −13907G, −13915G, −14009G, and −14010C), located upstream of the LCT gene within intron 13 of MCM6. These variants arose independently and represent convergent adaptive responses to dairying across different African regions.***

LP VARIANT	RS ID	AFRICAN DISTRIBUTION	FUNCTIONAL/ SELECTIVE FEATURES	KEY REFERENCES
−13910T	rs4988235	Dominates West of Lake Chad among pastoralists and North African groups (e.g., Fulani, Tuareg, Moors). Highest at Sahara–Sahel interface.	Classic enhancer variant; strong selection in Europe; introduced to Africa via gene flow; long haplotypes in Fulani; selection signals in Sahel pastoralists.	Tishkoff et al. 2007; Ranciaro et al. 2014; Vicente et al. 2019; Priehodova et al. 2020; Cerny et al. 2023. See text for more related references.
−13907G	rs41525747	Primarly found in East African pastroalists; detected in S. Ethiopian, Sudanese and Kenyan afro-asiatic cushitic-speaking groups.	One of the multiple independent region-specific LP variants; detectable selection; often co-occurs with -13915G regionally.	Tishkoff et al. 2007; Ranciaro et al. 2014; Jones et al. 2013. See text for more related references.
−13915G	rs41380347	Present into the Horn, Northeast Africa and it the Eastern Sahel. Also frequent in Middle Eastern populations.	Associated with Arabian-derived pastoral ancestry diffusion into the Eastern Sahel. Its expansion in the Eastern Sahel is estimated around 1,300–1,800 BP.	Tishkoff et al 2007; Ingram et al. 2007; Ranciaro et al. 2014; Hollfelder et al. 2017; Priehodova et al. 2014; Cerny et al. 2021. See text for more related references.
−14009G	rs869051967	Occurs in East African groups, often pastoralists and with Arabian admixture; low frequency.	Another variant reflecting the diversity of convergent evolution in East Africa; rare; functional activity observed in vitro.	Tishkoff et al. 2007; Ingram et al. 2009; Ranciaro et al. 2014; Hollfeleder et al. 2021. See text for more related references.
−14010C	rs145946881	Highest in Horn and East African pastoralists (e.g. Maasai, Beja, Datog). Also found in southern African populations (e.g. Nama) due to recent migrations (~35% in Nama via East African admixture; ~6% Kuvale). Rare in farmers.	Most frequent African LP allele; very strong selection (s ≈ 0.04–0.10); extended haplotype homozygosity (EHH). Estimated to have emerged between 2,700 and 6,800 years ago and spread South via herder migration ~2 ka BP.	Tishkoff et al. 2007; Coelho et al. 2009; Ranciaro et al. 2014; Macholdt et al. 2014; Vicente et al. 2021. See text for more related references.

These alleles have shown that LP alleles in Africa exhibit very strong signatures of recent positive selection. The −14010C allele in East African pastoralists is associated with extended haplotype homozygosity over more than 2 Mb, while −13907G and −13915G show similarly long haplotypes (~1.4 Mb and ~1.1 Mb, respectively) in Sudanese and Kenyan populations (Ranciaro et al. 2014; Tishkoff et al. 2007). These patterns are classic indicators of a recent and intense selective sweep, with estimated strength of selection coefficients (s) of 0.04–0.097, among the strongest selection coefficients estimated for any human trait underscoring the intense selective advantage conferred by milk access in arid environments (Segurel et al. 2017; Tishkoff et al. 2007). Such strong selection was required to explain the rapid increase in allele frequency from an initial rare state to the high levels seen today, confirming the profound survival advantage conferred by reliable access to milk. For example, selection appears to be stronger and more recent in

Tab. 2 - Archaeological timeline of the Holocene in Africa. Timeline illustrating the emergence and spread of key elements, including pottery, cattle domestication, and lactase persistence (LP) genetic variants, across different times and regions. The table highlights the interplay among climate change (e.g. Saharan desiccation), human migration, technological innovation, and biological adaptation across Africa.

	EARLY HOLOCENE (~11,700 TO 8000 BP)	**MID-HOLOCENE (~8000 TO 4,500 BP)**	**LATE HOLOCENE (~4,500 BP -PRESENT)**
REGIONS	Eastern Sahara, Middle Nile Valley.	North & Northeast Africa, gradually expanding South.	Continental spread (East, West, South Africa).
CLIMATE CONTEXT	End of Ice Age. Start of African Humid Period "Green Sahara" wet phase.	Peak and end of African Humid Period. Gradual aridification/desiccation of the Sahara, pushing populations South and North.	Aridification of the Sahara and modern climate patterns.
ARCHAEOLOGY & FOSSILS	Early Sahara pottery appears early (~9,000-8,000 BP), independent of agriculture. Debate over early local cattle management (faunal remains).	Earliest African milk residues (~7,000 BP) in Saharan ceramics. Widespread of domestic cattle (from Near East origin likely) and caprines. Emergence of sophisticated pastoral societies.	Diversification of pastoral/agricultural systems. Appearance of "Iron Age" package in some regions much later (e.g., Southern Africa ~2,000 BP).
LINK TO LP VARIANTS	No direct link. Populations were hunter-gatherers or very early proto-pastoralists.	Pastoralism establishes the *cultural practice* necessary for the genetic trait to be advantageous.	Lactase Persistence (LP) Genetic Variants become prevalent in specific cattle-rearing populations (e.g., in East Africa and the Sahel), as a gene-culture co-evolutionary adaptation to milk consumption.

Maasai pastoralists than in Europeans (Gerbault et al. 2009; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007), consistent with the younger estimated age of the East African −14010C allele (~2,700–6,800 years) (Tishkoff et al. 2007) compared to the European −13910T allele (~7,500–9,000 years) (Bersaglieri et al. 2004; Itan et al. 2009). The estimated age of the East African allele aligns closely with archaeological and biomolecular evidence for intensified dairy use during the PN (Dunne et al. 2018, 2012; Gifford-Gonzalez 2011; Grillo et al. 2020, 2018; Hildebrand et al. 2018; Prendergast et al. 2019). Together, these genomic and archaeological signatures underscore how convergent selection for lactase persistence accompanied independent pastoral transitions in Europe and Africa, driven by ecological stress, mobility, and reliance on milk as a crucial resource.

Distribution of LP variants and tracing migrations

The distribution of LP alleles across Africa reflects deep entanglement between demography, ecology, language history, and pastoral subsistence systems, with patterns shaped not by simple geographic gradients but by historically layered, admixture, mobility, sex-biased gene flow and cultural transmission (Blench 1997; Breton et al. 2014; Buckova et al. 2013; Cerny et al. 2009, 2007; Cizkova et al. 2017; di Lernia 2021; Dunne et al. 2012; Ehret 1967; Fortes-Lima et al. 2025; Gifford-Gonzalez 2000; Hildebrand et al. 2018; Hollfelder et al. 2017; Kuper and Kropelin 2006; Macholdt et al. 2014; Mous 2020; Prendergast et al. 2019; Priehodova et al. 2017; Sereno et al. 2008; Tishkoff et al. 2009; Trombetta et al. 2015; Vicente et al. 2021; Waring et al. 2021).

Across the continent, pronounced heterogeneity in LP allele frequencies reflects subsistence mode, climate, and demographic history rather than geographic distance alone, with the highest values consistently found among mobile pastoralists in arid and semi-arid environments (Schlebusch and Jakobsson 2018). East Africa constitutes the most diverse and ancient core of LP evolution (Hassan et al. 2016; Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2015, 2013; Ranciaro et al. 2014; Tishkoff et al. 2007). Here, the −14010C allele reaches its highest frequencies among Cushitic- and Nilotic-speaking pastoral groups such as the Maasai, Datog, Beja, Afar, and Somali, in some communities approaching ~40–60%, while additional enhancer variants including −13907G, −13915G, and −14009G occur at lower but meaningful frequencies across the Horn, Ethiopia, and the Turkana Basin (Hollfelder et al. 2021; Ingram et al. 2007, 2009; Jones et al. 2015, 2013; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007; Wagh et al. 2012). These genetic distributions mirror recurrent expansions of Afroasiatic-speaking agro-pastoralists from the Horn and interactions with Nilo-Saharan pastoral groups and later Bantu-speaking farmers, aligning with linguistic phylogenies suggesting early Cushitic and Nilotic pastoral dispersals from Northeast Africa. This allele mosaic reflects convergent evolution in populations independently adopting dairying across ecologically similar dryland zones, supported by successive waves of pastoral gene flow (Ranciaro et al. 2014; Tishkoff et al. 2007).

Population-genetic studies, including haplotype-based analyses, show that these East African LP alleles are embedded in distinct haplotype backgrounds with extended linkage disequilibrium, reflecting strong, recent selection (Jones et al. 2013; Mulindwa et al. 2020; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007; Walsh et al. 2020). Pastoral groups in Ethiopia and South Sudan show enriched pastoralist-associated ancestry tracts relative to neighboring agriculturalists, demonstrating sustained herder mobility and network continuity across millennia (Babiker et al. 2011; Bird et al. 2023; Hollfelder et al. 2021; Hollfelder et al. 2017). Fine-scale Ethiopian genetic structure further aligns with linguistic boundaries among Cushitic, Semitic, and Omotic speakers, reinforcing that language history and subsistence ecology jointly shaped regional population structure (Bird et al. 2023; Ingram et al. 2007; Jones et al. 2015, 2013; Mulindwa et al. 2020; Pagani et al. 2012, 2015). In Sudan, genomic structure differentiates Nubians, Nilotic pastoralists, and Arab-associated groups, with the −13915G allele enriched among Arabic-speaking communities and lower among Nubians and Nilotes, consistent with asymmetric diffusion of Arabian-derived pastoral ancestry and LP alleles (Bird et al. 2023; Hassan et al. 2016; Hollfelder et al. 2021; Ingram et al. 2009; Jones et al. 2015; Priehodova et al. 2014, 2017; Ranciaro et al. 2014; Tishkoff et al. 2007).

Moreover, aDNA provides key chronological context: early herders in Kenya and Tanzania ~5,000 BP consumed dairy yet carried very low LP allele frequencies, confirming that dairying preceded genetic adaptation enabling adult lactose digestion (Hildebrand et al. 2018; Prendergast 2023; Prendergast et al. 2019). Pastoral Neolitic individuals from East Africa lacked LP alleles despite consuming milk, supporting a cultural-first, genetic-later process wherein fermentation and mixed subsistence strategies buffered lactose intolerance for millennia (Prendergast et al. 2019; Vicente and Schlebusch 2020; Wang et al. 2020). Climatic pulses, including megadroughts, triggered multiple pastoral expansions around the Horn that intensified dairy reliance and selection on −14010C (Dunne et al. 2018; Fan et al. 2023; Gifford-Gonzalez and Hanotte 2011; Ranciaro et al. 2014; Schlebusch and Jakobsson 2018; Schlebusch et al. 2013; Tishkoff et al. 2007). Afroasiatic linguistic reconstructions show proto terms for cattle and milk shared across Cushitic and Semitic branches, suggesting pastoral knowledge transmission predating widespread genetic adaptation (Blench 1997; Ehret 1967) (Fig. 1).

North Africa presents parallel yet distinct dynamics. Moderate-to-high LP frequencies in North Africa are driven mainly by the Eurasian

Fig. 1 - Photographs illustrating individuals from pastoralist populations across eastern, west-central, and southern Africa, highlighting the cultural and phenotypic diversity of groups that share livestock-based subsistence systems while inhabiting distinct ecological and social environments. Image–label correspondences follow a left-to-right, top-to-bottom order: Fulani (Cameroon); Herero (Botswana); Maasai (Kenya); Pokot (Kenya); Surma (Ethiopia). Image credit: Dr. Sarah Tishkoff's laboratory.

–13910*T and Arabian –13915*G alleles (di Lernia 2021; Fregel et al. 2018; Hassan et al. 2016; Henn et al. 2012; Ingram et al. 2009; Lucas-Sanchez et al. 2021; Pereira et al. 2009; Secher et al. 2014).

Ancient DNA from Holocene Saharan pastoralists demonstrates continuity with local foragers and only limited external gene flow, indicating that early North African pastoralism emerged through cultural transmission and modest admixture rather than wholesale replacement (di Lernia 2021; di Lernia et al. 2013; Fregel et al. 2018; Salem et al. 2025). These findings reinforce that dairying in North Africa emerged through cultural adoption layered on deep regional ancestry, consistent with Sahara-based pastoral networks operating before major Eurasian migrations (Salem et al. 2025). Linguistic reconstructions of the Proto-Berber likewise indicate early pastoral terminology, matching genomic evidence for long-term pastoral continuity punctuated by episodic inputs from the Levant and Arabian Peninsula (Blench 2006; Ehret 2019). Together, these data show that deep North African ancestry predates back-to-Africa events, while subsequent recurrent Near Eastern gene flow contributed to Amazigh genetic diversity (Anagnostou et al. 2020; Henn et al. 2012; Vila-Valls et al. 2024). Finally, divergent haplotypes patterns around −13910T and −13915G in Maghreb versus Egypt further illustrate region-specific selection histories associated with distinct cultural and demographic processes (Hassan et al. 2016).

As the Sahara dried after ~5,500 BP, pastoral populations moved southward into the Sahelian savanna corridor, establishing a transcontinental pastoral highway (Kuper 2006; Kuper and Kropelin 2006), where mobile herding societies mediated new routes of demographic exchange and selection for lactase persistence in transitional environments bridging North and sub-Saharan Africa (Henn et al. 2008; Marshall and Hildebrand 2002; Prendergast et al. 2019; Ranciaro et al. 2014; Schlebusch and Jakobsson 2018; Skoglund et al. 2017; Smith 2009). The Sahel forms the ecological and demographic connection between North and East African pastoral spheres and West Africa. A striking geographic partition marks the Sahel: the −13910T allele dominates West of Lake Chad among Fulani, Tuareg, and Moors (Cizkova et al. 2017; Fortes-Lima et al. 2025; Ranciaro et al. 2014; Vicente et al. 2019), while −13915G is concentrated East of Lake Chad among Arabic-speaking pastoralists (Cerny et al. 2009, 2023, 2007; Haber et al. 2016; Hollfelder et al. 2021; Jones et al. 2015; Ranciaro et al. 2014). The −13910T variant expanded in Fulani ~7,500–9,700 ya, matching Middle-Holocene Saharan pastoral origins, while −13915G expanded ~1,300–1,800 ya, corresponding to historically documented Arabian movements into the eastern Sahel (Cerny et al. 2021; Haber et al. 2016; Priehodova et al. 2014, 2017, 2020; Ranciaro et al. 2014; Vicente et al. 2019) (Tabs. 1,2). Comprehensive analysis of >1,200 Sahelian individuals confirmed this spatial duality, with −13910T exclusively in western pastoralists and −13915G dominant in eastern groups (Priehodova et al. 2020). Fulani carry a more diverse −13910T haplotype set than Tuareg, and coalescent modeling indicates earlier, slower expansion in Fulani (~8,500 ya) versus rapid expansion in Tuareg (~1,500–2,000 ya), reflecting distinct demographic histories (Priehodova et al. 2020). The −13910T haplotype in Fulani is shared with Near-Eastern-related populations, consistent with a Northeast African-to-Saharan origin (Fregel et al. 2018; Henn et al. 2012; Lucas-Sanchez et al. 2021; Priehodova et al. 2020; Triska et al. 2015). Sedentary Sahelian farmers show negligible LP allele frequencies, highlighting subsistence-driven genetic structure and limited gene flow between farmers and nomadic herders (Novackova et al. 2020). Pastoral mobility and transhumance underpin genetic cohesion and endogamy among herders, consistent with ethnographic data. The Sahelian pastoralist lifestyle, characterized by seasonal movements, fostered milk as both food and hydration source, contributing to improved childhood nutrition relative to farming groups (Buckova et al. 2013; Pedersen et al. 2007). Seasonal transhumance in the Sahel enhanced the adaptive value of milk as both food and hydration, amplifying fitness advantage in arid ecologies.

The Fulani exemplify layered admixture, trans-Sahelian mobility, and LP evolution. Their genomes reflect West African ancestry blended with Saharan and Levant-related sources (Cerny et al. 2023; Fortes-Lima et al. 2025; Schlebusch and Jakobsson 2018; Tishkoff et al. 2009; Vicente et al. 2019). Eurasian-related ancestry in Fulani arrived via North Africa rather than directly from Europe (Fan et al. 2019; Fregel et al. 2018; Henn et al. 2012; Lucas-Sanchez et al. 2021; Triska et al. 2015; Vicente et al. 2019), and multiple admixture pulses involved Berber-related and eastern Sahel populations (Fortes-Lima et al. 2022; Priehodova et al. 2020; Triska et al. 2015; Vicente et al. 2019). Y-chromosomes frequently carry E-M81 and E-M78, while maternal lineages are predominantly West African L, consistent with male-mediated herder migration and female incorporation into Fulani communities (Cerny et al. 2009; Fortes-Lima et al. 2025; Priehodova et al. 2017; Trombetta et al. 2015). Linguistic evidence further supports this scenario with Fulfulde pastoral vocabulary showing Afroasiatic influence consistent with Saharan pastoral networks (Blench 1997, 2006; Ehret 1967).

South of the Sahel, LP remains extremely low (or absent) among Central African rainforest foragers and Bantu-speaking farmers, reflecting ecological limits on cattle herding (Ranciaro et al. 2014). The Bantu expansions ~3,000 ya primarily disseminated agriculture and small livestock rather than intensive dairying, explaining persistently low LP frequencies across central and much of southern Africa (Fortes-Lima et al. 2024; Grollemund et al. 2015; Koile et al. 2022; Li et al. 2014). Structural ecological barriers—including disease environments, humidity, and tsetse fly distribution—further constrained cattle herding in tropical regions, maintaining weak selective pressure for LP (Akinsola et al. 2024; Bradley et al. 1994; Hanotte et al. 2002; Kim et al. 2020; Koch 2020). By contrast, in southern Africa, LP variation reflects the arrival and spread of East African pastoralists during the late Holocene (Schlebusch and Jakobsson 2018; Smith 2009). Nama pastoralists exhibit ~35% −14010C allele introduced through admixture with East African herders ~2,000 BP, as shown by autosomal, haplotype, and aDNA evidence (Macholdt et al. 2014, 2015; Ranciaro et al. 2014; Schlebusch and Jakobsson 2018; Skoglund et al. 2017). Multiple waves of East African ancestry shaped southern pastoral communities and patterns of admixture highlight this demographic process (Bajic et al. 2018; Breton et al. 2014; Coelho et al. 2009; Henn et al. 2008; Macholdt et al. 2014, 2015; Vicente et al. 2021). Admixture dating (~1,000–2,000 BP) aligns with archaeological evidence for the arrival of livestock and ceramic traditions linked to East African pastoralists (Coelho et al. 2009; Henn et al. 2008; Pleurdeau et al. 2012). In southwestern Angola, Kuvale herders show ~6% −14010C and high Khoe-San maternal input (~22% mtDNA), reflecting sex-biased gene flow and the incorporation of local women into immigrant herding populations (Coelho et al. 2009). LP alleles appear in the Xhosa but not in Akan, reinforcing that pastoralism spread from East Africa through Khoe intermediaries rather than from West Africa (Bajic et al. 2018; Coelho et al. 2009; Marks et al. 2015; Ranciaro et al. 2014; Torniainen et al. 2009; Vicente et al. 2021). Genome-wide analyses indicate that Khoe-Kwadi-speaking Nama and Khwe carry the highest East African-related ancestry (~7–8%), with decreasing proportions in other southern Khoe-San populations (Vicente et al. 2021). These ancestry segments date to ~1,000–2,000 BP and show clear male bias in East African contributions, consistent with patrilineal herder transmission (Coelho et al. 2009; Henn et al. 2008; Vicente et al. 2021). Uniparental markers independently corroborate this scenario: the East African pastoral Y-chromosome lineage E-M293 is found from Tanzania to Namibia and Botswana, with reduced Short Tandem Repeats (STR) diversity in southern Africa indicating a founder event ~2,000 BP and a demic migration distinct from the later Bantu expansion (Chan et al. 2019; Henn et al. 2008; Vicente et al. 2021). Linguistic diffusion parallels these genetic patterns: borrowing of livestock vocabulary into Khoe languages reflects contact with East African pastoralists and shared pastoral knowledge network (Blench 2006; Ehret 1967). Therefore, South of the Sahel, where ecological constraints limited cattle herding and fresh milk consumption, LP frequencies remained extremely low and selective pressure weaker than in the Horn or Sahel (Breton et al. 2014; Jones et al. 2015; Ranciaro et al. 2014).

Together, genomic, linguistic, and archaeological evidence demonstrates that while Bantu dispersals reshaped the demographic landscape of sub-Saharan Africa, they did not carry a dairying economy. Instead, LP in southern Africa was introduced via an earlier East African pastoral expansion, followed by local assimilation and cultural exchange (Henn et al. 2008; Macholdt et al. 2014, 2015; Ranciaro et al. 2014; Schlebusch and Jakobsson 2018; Vicente et al. 2021). Because humid environments and mixed subsistence regimes limited fresh milk consumption outside pastoral groups, selective pressure for LP remained weak, explaining extremely low LP frequencies south of the Sahel compared to the Horn and Sahel belt.

Therefore, African pastoral history reflects deep coevolution of herders, livestock, languages, and landscapes, shaped by mobility, resilience, and cultural innovation over millennia.

Archaeological and biomolecular evidence of dairying

Archaeological research across Africa provides essential, independent lines of evidence for early emergence, dispersal, and cultural complexity of dairying traditions, which form the behavioral substrate for selection on LP alleles. It integrates faunal remains, ceramic technologies, monumental mortuary architecture, rock art depicting cattle and milking, and increasingly, biomolecular signatures including lipids, proteins, and isotopic data preserved in ceramics, dental calculus, and sediments (Bleasdale et al. 2021; di Lernia 2021; di Lernia et al. 2013; Dunne et al. 2012; Grillo et al. 2018; Hildebrand et al. 2018; Prendergast et al. 2019; Rotunno et al. 2023; Warinner et al. 2014). Together, these converging lines of evidence demonstrate that milk use in Africa has deep antiquity and that cultural innovations in dairy production and processing long preceded widespread genetic adaptation for lactase persistence.

The earliest unequivocal African evidence for milk exploitation derives from the central Sahara during the African Humid Period (AHP) (Fig. 2), when vast savannas supported cattle and caprine herding. Lipid residue analyses from Tadrart Acacus and Takarkori in southwest Libya indicate ruminant dairy processing by ~7,000 BP (di Lernia 2021; Dunne et al. 2018, 2013, 2012) (Tab. 3).

These findings align with high-resolution paleoenvironmental records identifying the abrupt collapse of the African monsoon system around 5,500 BP and the subsequent desiccation of the Sahara (Kuper 2006; Kuper and Kropelin 2006). Ceramic lipid residues also suggest that early Saharan herders employed fermentation and other processing strategies to reduce lactose content (di Lernia 2021; Dunne et al. 2013, 2012; Rotunno et al. 2023), consistent with genetic evidence showing minimal LP allele frequencies among Holocene pastoralists in northern Africa (Lucas-Sanchez et al. 2021; Schlebusch and Jakobsson 2018; Vicente and Schlebusch 2020; Xue 2018) (Tab. 2).

Recent reassessments of Saharan pastoral origins emphasize that herding developed through complex, punctuated cultural transmission processes rather than uniform demographic replacement (di Lernia 2021; Prendergast 2023; Prendergast et al. 2019). Early domesticated caprines appear in the Tadrart Acacus region (a mountain range located in southwestern Libya, Sahara Desert, near the border with Algeria) by ~8,300 BP, arriving from the eastern Sahara and Nile corridor rather than being locally domesticated (di Lernia 2021) (Tab. 3). These small pioneer herding groups entered landscapes occupied by robust forager–fisher–hunter communities (Sereno et al. 2008), who engaged in selective adoption and reconfiguration of pastoral practices rather than wholesale acculturation. Rock art from Messak Settafet and Wadi Teshuinat depicts cattle with enlarged udders and milking scenes, underscoring the ritual and symbolic prominence of dairying from the earliest pastoral phases (di Lernia 2021; di Lernia et al. 2010; Mori 1965) (Tab. 3). Moreover, bioarcheological evidence for ceremonial cattle deposition at sites like Uan Muhuggiag and the Gobero complex highlights the integration of livestock into cosmologies, burial practices, and emergent social hierarchies (Holl 2020; Sereno et al. 2008; Stojanowski et al. 2014) (Tab. 3; Fig. 2).

The end of the AHP initiated major demographic reorganization. Radiocarbon syntheses document widespread abandonment of Saharan interior sites after ~5,300 cal BC as mobile pastoral families retreated toward ecological refugia such as the Nile Valley and major desert oases (deMenocal et al. 2000; Kuper 2006; Kuper and Kropelin 2006). This climatic forcing corresponds to archaeological evidence for southward pastoral dispersals into the Sahel, where early herders encountered diverse foraging populations (di Lernia 2021; Grillo et al. 2020). The ecological gradients of the Sahel shaped herd composition, mobility patterns, and dairy-based subsistence, reinforcing adaptive strategies that privileged cattle and caprines capable of thriving in increasingly arid settings (Bahbahani et al. 2018; Chritz et al. 2015; Da Silva et al. 2025; Gifford-Gonzalez 2000; Hanotte et al. 2002, 2000; Kim et al. 2020, 2017).

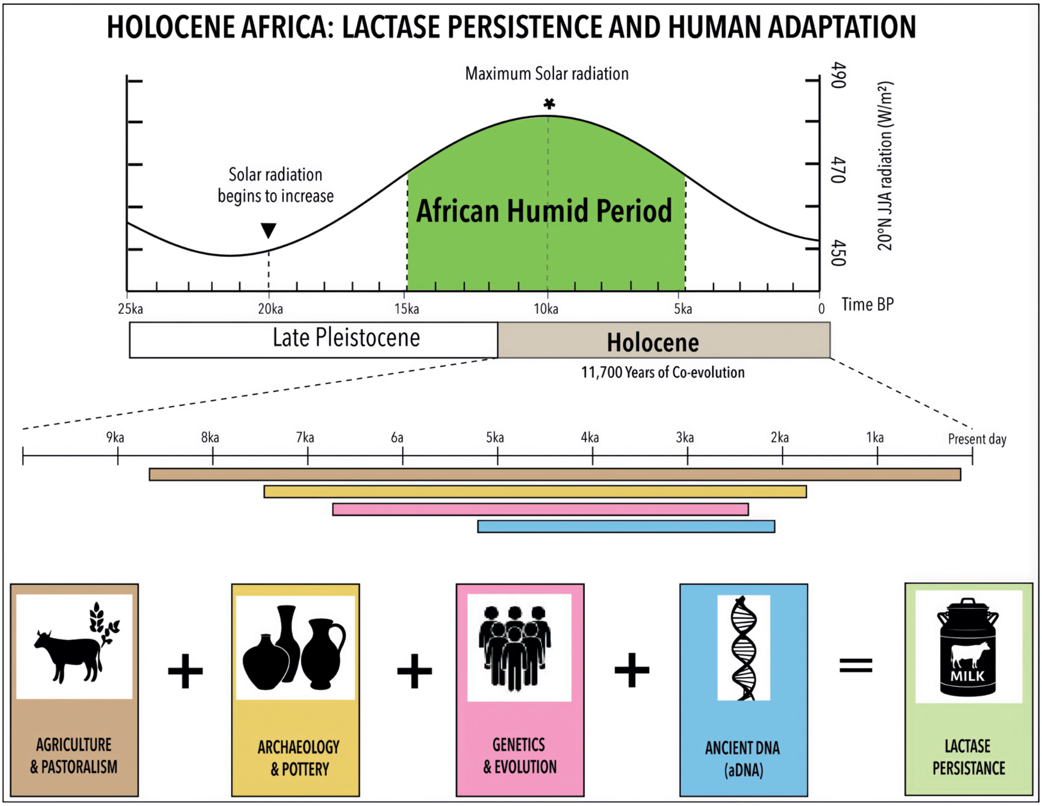

***Fig. 2** - Holocene Africa: climatic transitions, cultural change, and the emergence of lactase persistence. This figure synthesizes paleoenvironmental, archaeological, genetic, and aDNA evidence to illustrate the temporal and ecological context in which lactase persistence (LP) evolved in Africa over the Holocene (~11,700 BP). The timeline highlights key climatic phases, subsistence transitions, and genomic events associated with the emergence and spread of milk use and LP alleles.*

The diffusion of dairying into eastern Africa unfolded in similarly dynamic ecological and cultural contexts. Livestock appear in the Turkana Basin by ~5,000 BP alongside monumental mortuary complexes known as pillar sites (Hildebrand et al. 2018). The Lothagam North Pillar Site, with hundreds of burials and elaborate beadwork, reflects emergent pastoral social networks and mortuary symbolism during a period of lake-level decline and heightened mobility (Grillo et al. 2020; Hildebrand et al. 2018) (Tab. 3). Ceramic lipid analyses from Lukenya Hill, Narosura, Luxmanda, and other PN sites in Kenya and Tanzania show ruminant milk processing by ~5,000 BP, intensifying by ~3,000 BP (Bleasdale et al. 2021; Grillo et al. 2020; Janzen 2022; Warinner et al. 2014) (Tab. 3). Dairy biomarkers appear alongside evidence for plant exploitation and diversified subsistence, aligning with ethnographic models of risk-buffering in East African pastoral systems (Bleasdale et al. 2021; Grillo et al. 2020; Janzen 2022).

Stable isotope analyses from fauna, humans, and ceramics reveal flexible seasonal mobility, herd division, and exploitation of diverse ecological niches (Bleasdale et al. 2021; Chritz et al. 2015; Grillo et al. 2020; Hildebrand et al. 2018; Rotunno et al. 2023). Seasonal herding patterns documented among modern Turkana, Rendille, and Dassanetch communities provide

***Tab. 3** - Archaeological timeline of dairying in Africa. Summary of archaeological and biomolecular evidence for the emergence and spread of dairying across Africa during the Holocene. The table integrates chronological, regional, and cultural data from sites with indicators of milk use, including ceramic lipid residues, faunal remains, iconography, proteomics, and isotopic analyses. Dates are reported in years before present (BP). The timeline shows that dairying practices preceded the emergence of lactase persistence (LP) variants and were shaped by climatic change, population movements, and cultural interactions.*

REGION	SITE/ CULTURAL CONTEXT	DATE (BP)	EVIDENCE TYPE	KEY FINDINGS	CITATIONS
Central Sahara (SW Libya)	Tadrart Acacus / Takarkori	~8,300–7,000	Ceramic lipid residues; faunal remains	Earliest confirmed ruminant dairy processing; caprine introduction from NE Africa	Dunne et al. 2012; Dunne et al. 2018; di Lernia et al. 2021
Central Sahara	Messak & Acacus rock art	~8,000–6,000	Iconography	Cattle with enlarged udders; explicit milking themes	di Lernia 2021; Gifford-Gonzalez 2011
Nile Valley & Upper Nubia	Pastoral & early agriculture	~6,000–3,500	Faunal, isotopes	Mixed herding–fishing–farming systems	Marshall and Hildebrand 2002; di Lernia 2021
Eastern Sahara	Nile corridor pastoral emergence	~7,000–6,000	Faunal shifts; herder settlement	Taurine cattle arrival via Nile–Levant corridor	Hanotte 2002; Marshall and Hildebrand 2002
Sahara desert margin retreat	Wadi Howar / Central Sahara	After ~5,500	Radiocarbon synthesis; paleoenvironment	Desertification triggers southward herder dispersal	deMenocal 2000; Kuper and Kröpelin 2006
Eastern Africa Turkana Basin (Kenya)	Lothagam North pillar complex	~5,000–4,500	Monumental mortuary, beads, fauna	Early mobile pastoral networks; social complexity	Hildebrand et al. 2018
Eastern Africa Kenya/Tanzania	PN sites (Jarigole, Luxmanda, Narosura, Ngamuriak)	~5,000–3,000	Lipid residues; pottery; proteomics	Ruminant milk processing; gradual intensification	Grillo et al. 2020; Bleasdale et al. 2021; Warinner et al. 2014
Eastern Africa (Kenya/Tanzania)	Dental calculus proteomics	~3,300–3,000	Paleoproteomics	Direct detection of β-lactoglobulin; milk before LP	Bleasdale et al. 2021; Warinner et al. 2014
West Africa (Sahel / Chad Basin)	Early cattle-herding	~4,000–3,500	Fauna, settlement	Caprine + cattle herding before widespread dairying	Grillo 2020; di Lernia 2021
Southern Africa	Arrival of livestock	~2,000	Fauna; pottery	East African herder migration; limited early dairy	Smith 2009; Skoglund et al. 2017; Janzen 2022

present-day analogs for ancient strategies in which lactating animals were moved strategically to maximize milk yields and minimize grazing stress (Gifford-Gonzalez 2011; Gifford-Gonzalez and Hanotte 2011; Grillo et al. 2018; Janzen 2022; Le Meillour et al. 2023; Tishkoff et al. 2007). These mobility systems established a cultural foundation for the sustained, intensive milk consumption that later drove selection on LP alleles (Hassan et al. 2016; Hollfelder et al. 2021; Ingram et al. 2007; Jones et al. 2015, 2013; Ranciaro et al. 2014; Tishkoff et al. 2007).

Further South and West, dairying trajectories differed. In West Africa, archaeological evidence for cattle keeping appears by ~4,000–3,500 BP in the inland Niger Delta and Lake Chad Basin, yet biomolecular signatures of milk are comparatively rare, suggesting delayed or variable adoption of dairy processing (Bleasdale et al. 2021; di Lernia 2021; Grillo et al. 2020). This aligns with genetic findings showing later LP allele expansion among Fulani and other Sahelian populations compared to the Horn (Cerny et al. 2009, 2021, 2023, 2007; Cizkova et al. 2017; Fortes-Lima et al. 2025; Priehodova et al. 2020; Ranciaro et al. 2014; Vicente et al. 2019; Xue 2018). In southern Africa, livestock entered the Kalahari and Western Cape around ~2,000 BP via migration of East African herders (Coelho et al. 2009; Henn et al. 2008; Macholdt et al. 2014; Ranciaro et al. 2014; Schlebusch and Jakobsson 2018; Vicente et al. 2021), yet lipid and proteomic evidence show limited milk use at early sites, reflecting ecological constraints and persistent foraging traditions (Janzen 2022; Lander et al. 2018; Le Meillour et al. 2023; Schlebusch and Jakobsson 2018; Skoglund et al. 2017; Smith 2009).

Across Africa, paleoproteomics and lipid residue studies—supported by sediment aDNA innovations—demonstrate that milk use preceded widespread LP allele expansion by millennia, reinforcing a gene–culture coevolutionary model in which cultural innovations in fermenting, storing, and processing dairy enabled exploitation of animal milk long before genetic adaptation was prevalent (Bleasdale et al. 2021; Grillo et al. 2020; Skoglund et al. 2017; Warinner et al. 2014). The archaeological record thus reveals that dairying was not merely a subsistence strategy but a transformative social and ecological practice embedding livestock into ritual, identity, mobility, and mortality in ways that shaped human biology and landscape use.

Taken together, the archaeological, biomolecular, and paleoenvironmental records provide compelling evidence that dairying became deeply embedded in northern and eastern African subsistence systems well before the widespread rise of LP alleles. Long before genetic adaptation, pastoralists in the Sahara and Horn of Africa developed sophisticated cultural and technological strategies for exploiting milk, including fermentation, herd management, and seasonal mobility, as demonstrated by lipid residues in ceramics, paleoproteomic evidence in dental calculus, specialized cattle iconography, and monumental pastoral cemeteries (Bleasdale et al. 2021; di Lernia 2021; Dunne et al. 2012; Hildebrand et al. 2018; Kasser et al. 2025; Prendergast et al. 2019; Warinner et al. 2014) (Tab. 3). These innovations illustrate that dairying was not simply a dietary supplement but part of a broader cultural complex in which cattle played nutritional, symbolic, and ritual roles central to identity, social structure, and mobility networks (Gifford-Gonzalez 2011; Hildebrand et al. 2018; Holl 2020; Marshall and Hildebrand 2002).

Environmental pressures associated with the end of the AHP, particularly increasing aridification and ecological instability after ~5,500 BP, further intensified the reliance on livestock and milk as reliable, transportable, and drought-buffering resources (Chritz et al. 2015; deMenocal et al. 2000; Kuper 2006; Phelps et al. 2020). The spread of pastoralism into the Sahel and subsequently eastern Africa created ecological and cultural niches in which sustained milk consumption became advantageous. In these contexts, milk offered critical calories, hydration, fats, and micronutrients, especially under the seasonal uncertainties of transhumant herding systems (Bleasdale et al. 2021; di Lernia 2021; Janzen 2022; Warinner et al. 2014). This long-standing cultural reliance on dairy products set the selective stage for lactase-persistence alleles to rise rapidly once fresh-milk consumption intensified and became stable across generations.

The chronological offset between the archaeological evidence for dairying and the later expansion of LP alleles strongly supports a cultural-first, genetic-later model of human adaptation, in which the widespread practice of milk use created persistent selective pressures on lactase regulatory variants (Bersaglieri et al. 2004; Bleasdale et al. 2021; Prendergast 2023; Prendergast et al. 2019; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007; Vicente and Schlebusch 2020) (Fig. 2). Genomic signatures—including extended haplotype homozygosity around LP alleles in East African pastoralists—confirm that once milk became central to subsistence in arid regions, natural selection acted with exceptional intensity, driving some of the strongest documented selective sweeps in the human genome (Fan et al. 2023; Jones et al. 2013; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007).

Overall, the archaeological, environmental, and biomolecular record demonstrates that dairying was a foundational element of early African pastoralism, predating genetic adaptation by millennia. The temporal and geographic distribution of milk use across the Sahara, Sahel, and eastern Africa underscores the combined influence of cultural innovation, climatic forcing, and long-distance interaction networks in shaping patterns of human adaptation on the continent (Bleasdale et al. 2021; di Lernia 2021; Dunne et al. 2013, 2012; Fortes-Lima et al. 2024; Fregel et al. 2018; Prendergast et al. 2019; Schlebusch and Jakobsson 2018; Skoglund et al. 2017). The African LP case thus exemplifies gene-culture coevolution, where enduring cultural practices created a selective landscape that profoundly reshaped human biology.

Gene-culture coevolution and African pastoralists

The evolution of LP across Africa is a classic case of gene–culture coevolution in which a culturally transmitted subsistence practice — dairying— altered the selective environment in favor of genotypes enabling adult lactose digestion, and the spread of those genotypes, in turn, reinforced the cultural tradition (Feldman and Laland 1996; Holden and Mace 2009; Laland et al. 2001, 2010). In this framework, cultural behaviors reshape selection pressures, while genetic change stabilizes and amplifies cultural systems, generating feedback loops characteristic of human evolution (Feldman and Laland 1996; Laland et al. 2001, 2010).

Dairying operates as a form of cultural niche construction (Gerbault et al. 2011; Laland et al. 2010). By investing in livestock economies and incorporating milk into dietary systems, early herding societies created a nutritional ecology where the ability to digest fresh milk provided substantial fitness advantages—calories, fats, protein, micronutrients—and, critically, hydration in arid environments (Feldman and Laland 1996; Holden et al. 1997; Holden and Mace 2009; Phelps et al. 2020). These ecological and energetic advantages were magnified in settings of climatic unpredictability, mobility, and seasonal drought, particularly in the Horn of Africa and the Sahel (Gifford-Gonzalez 2000; Phelps et al. 2020). Precisely in these regions, genomic data reveal exceptionally strong and recent selection on LP alleles, with estimates of selection coefficients between approximately 0.04 and 0.097 for variants such as −14010C (Jones et al. 2015, 2013; Ranciaro et al. 2014; Schlebusch et al. 2013; Segurel and Bon 2017; Tishkoff et al. 2007) .

This coevolutionary dynamic unfolded in concert with the biological and historical trajectories of cattle. Zooarchaeological, genomic, and aDNA research demonstrate multiple domestication events: taurine cattle (*Bos taurus*) domesticated in the Near East and zebu cattle (*Bos indicus*) independently domesticated in South Asia (Ajmone-Marsan et al. 2010; Caramelli 2006; Chen et al. 2010; Frantz et al. 2020; Loftus et al. 1994; McHugo et al. 2019) . Early taurine lineages likely entered northeastern Africa via the Nile–Levant corridor, while indicine cattle arrived later through Arabian and Indian Ocean routes, this producing the characteristic "Sanga" and mosaic African cattle genomes through admixture (Bradley et al. 1994; Hanotte et al. 2002, 2000; Kim et al. 2020, 2017; Koch 2020; Magee et al. 2014; Stock et al. 2013; Utsunomiya et al. 2019). These African cattle genomes reflect not simply hybrid ancestry but an adaptive bio-cultural synthesis in which heat, drought, and parasite tolerance from indicine cattle combined with taurine traits associated with milk production, generating herds capable of thriving in challenging environments (Gifford-Gonzalez 2000; Hanotte et al. 2000; Kim et al. 2020, 2017; Koch 2020; Stock and Gifford-Gonzalez 2013). Morphological studies of early African cattle—such as horn core geometry and limb slenderness—similarly illustrate regional adaptation and raise long-standing debates about the relative contributions of introduced vs. locally managed wild aurochs, arguments enriched by both genetic evidence and classic archaeological assessments (Ajmone-Marsan et al. 2010; Marshall and Weissbrod 2011; Stock and Gifford-Gonzalez 2013; Zeder et al. 2006).

Ancient genomics reinforces that domestication was not a single punctuated event but a long, regionally variable process involving management, mobility, introgression, and repeated intercontinental contacts (Frantz et al. 2020; MacHugh et al. 2017; Magee et al. 2014; McHugo et al. 2019). Within Africa, the sequential arrival of taurine and indicine cattle and their subsequent admixture expanded pastoral possibilities into hotter and drier landscapes, enabling sustained milk production and intensifying selection for LP where fresh-milk consumption became reliable (Chen et al. 2010; Hanotte et al. 2002; Kim et al. 2020; Koch 2020; Utsunomiya et al. 2019). Reviews emphasizing the "mosaic genome" of African cattle highlight how bovine adaptation shaped human selective environments, facilitating the spread of pastoralism and strengthening the niche in which LP alleles underwent rapid, strong positive selection (Kim et al. 2020; Magee et al. 2014; Stock and Gifford-Gonzalez 2013).

The cultural precedes the genetic: archaeological and biomolecular records show early dairying long before widespread LP. Lipid residues, proteins, and ancient genomes indicate dairy use in the Sahara and East Africa by ~5,000–7,000 BP, even as early herders carried few LP alleles—consistent with fermentation, dietary mixing, and social feeding practices buffering lactose intolerance (Hildebrand et al. 2018; Prendergast 2023; Skoglund et al. 2017; Vicente and Schlebusch 2020; Wang et al. 2020). This "cultural-first, gene-second" pathway is precisely what gene–culture coevolution theory predicts when cultural innovation generates new fitness payoffs (Feldman and Laland 1996; Zeder et al. 2006).

Ecology, disease, and pastoral infrastructure further shaped this dynamic. In the Sahel and Horn, where mobility and aridity favored milk economies, selection for LP was strong; in humid or tsetse-infested regions of Central Africa, where cattle were difficult to maintain and fresh milk less central, selection was weaker (Chritz et al. 2015; Gifford-Gonzalez 2000; Phelps et al. 2020). Adaptive cattle admixture itself facilitated herding in marginal zones, extending the dairy niche and accelerating LP expansion as fresh milk became a staple food (Hanotte et al. 2002; Kim et al. 2020; Kim et al. 2017).

Potential mechanistic pathways reinforce these patterns. Fresh milk elevates IGF-I more than fermented dairy, with implications for growth, skeletal mineralization, reproductive success, and maternal health—fitness dimensions amplified under nutritional stress (Waring and Wood 2021; Wiley 2018). These advantages help explain the unusually strong selection coefficients inferred for African LP alleles (Schlebusch and Jakobsson 2018; Schlebusch et al. 2013; Tishkoff et al. 2007).

Finally, demography and social structure intersected with selection. Transhumant networks, endogamy among pastoral clans, sex-biased mobility, and linguistic boundaries shaped both cultural transmission and gene flow (Choudhury et al. 2018; Henn et al. 2008; Secher et al. 2014; Vicente et al. 2021). In southern Africa, the distribution of −14010C among Nama and other

***Fig. 3** - Pastoralism and cattle diffusion in Africa. Images illustrating cattle diversity and pastoral practices across African ecological zones. Traditional calabashes used for milk storage and processing highlight long-standing dairying technologies (A). The cattle shown originate from Tanzania and Ethiopia and are presented to illustrate the broad diversity of cattle types present in East Africa (B–D). Together, these images provide context for pastoral mobility and the gene–culture coevolution underlying lactase persistence. Image credit: Dr. Sarah Tishkoff's laboratory.*

Khoe communities reflects ancient East African pastoral inputs, consistent with genetic, linguistic, and archaeological evidence for the introduction of livestock prior to agriculture (Breton et al. 2014; Coelho et al. 2009; Macholdt et al. 2014). These patterns exemplify how dairying, livestock movement, and LP evolution unfolded within social systems structured by kinship, mobility, and cultural inheritance.

Taken together, cattle domestication's multi-origin history, Africa's composite bovine genomes, and the climatic and epidemiological geography of pastoral niches set the evolutionary stage on which dairying took root. Strong selection on human LP variants subsequently reshaped genetic landscapes wherever fresh milk became central to subsistence—an enduring testament to the depth and power of gene–culture feedbacks in African history (Ajmone-Marsan et al. 2010; Campbell et al. 2021; Kim et al. 2020; Phelps et al. 2020) (Fig. 3).

Lactase persistence is just one example, although a striking one of how gene–culture coevolution has shaped human biology. Similar dynamics are implicated in adaptations related to digesting starch-rich agricultural diets, including variation in salivary amylase gene copy number associated with increased starch consumption in agricultural populations (Perry et al. 2007). Another well-supported example involves alcohol metabolism, where variants in *ADH1B* rose in frequency alongside the development of rice agriculture and fermentation technologies in East Asia and Ethiopia (McQuillan et al. 2022; Peng et al. 2010; Wang et al. 2016). Beyond metabolism, cultural transitions have also reshaped pathogen landscapes. The rise of sedentism, agriculture, and dense settlements altered exposure to vector-borne and zoonotic diseases, contributing to strong selection on immune loci such as *APOL1*, and *HLA* in regions with high malaria and trypanosomiasis burden (Beckerman et al. 2018; Cooper et al. 2017; Ko et al. 2013; Norman et al. 2013). While these immune adaptations reflect host–pathogen coevolution, they were indirectly influenced by cultural practices that transformed ecological and epidemiological regimes (Cooper et al. 2017; McManus et al. 2017) . There is growing interest in the possibility that cultural evolution may have influenced cognitive and neural traits, where long-term changes in literacy and symbolic systems may have reshaped neural architecture and genetic pathways involved in neurodevelopment (Lala 2017; Laland et al. 2010), though this remains an active area of research. In essence, the African LP story powerfully illustrates the reciprocal relationship between human culture and biology, where cultural innovations create new selective landscapes that drive genetic evolution, fundamentally shaping human diversity (Feldman and Laland 1996; Laland et al. 2010; Richerson and Boyd 2004).

Conclusion: how pastoralism reshaped African genomes

Understanding the origins, spread, and evolutionary impact of LP in Africa requires an interdisciplinary synthesis that bridges genomics, archaeology, biomolecular science, linguistics, and computational modeling. Together, these approaches reveal LP as one of the most compelling examples of gene–culture coevolution in human history, where cultural innovations in dairying reshaped selective landscapes, and biological adaptation reinforced and expanded cultural practices (Feldman and Laland 1996; Kasser et al. 2025; Kuper and Kropelin 2006; Laland et al. 2001; Richerson and Boyd 2004; Stock et al. 2023; Waring and Wood 2021; Whiten et al. 2011).

Convergent evolution and the cultural-first sequence

The African case is particularly illuminating: multiple regulatory mutations associated with LP arose independently in different geographic regions, each embedded within its own cultural and ecological context (Enattah et al. 2007; Ingram et al. 2007; Ingram et al. 2009; Jones et al. 2015; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007; Vicente et al. 2019). Across Africa, LP evolution consistently followed a cultural-first trajectory: dairy pastoralism and milk use emerged before the spread of the genetic variants that enable adult lactose digestion (Prendergast et al. 2019). This temporal order, now strongly supported by both ancient and modern genomic data, provides a robust framework for understanding how cultural innovations restructure the selective landscape (Gifford-Gonzalez and Hanotte 2011; Marshall and Hildebrand 2002; Prendergast et al. 2019; Skoglund et al. 2017; Vicente and Schlebusch 2020; Wang et al. 2020; Waring and Wood 2021). Archaeology and biomolecular science confirm as well that dairying came first. In fact, ceramic lipid residues from the early Sahara, milk proteins preserved in dental calculus, and faunal evidence from herding sites all point to widespread milk use millennia before LP alleles became common (Bleasdale et al. 2021; di Lernia 2021; Dunne et al. 2012; Grillo et al. 2020; Hildebrand et al. 2018; Janzen 2022; Le Meillour et al. 2023; MacHugh et al. 2017; Warinner et al. 2014).

Diverse adaptive landscapes across Africa

Although the cultural basis for dairying was widespread, the selective pressures operating on LP alleles varied markedly across regions. In the eastern African, strong selection coincided with the intensification of pastoralism and the increasing nutritional and social importance of milk (Jones et al. 2013; Ranciaro et al. 2014; Schlebusch et al. 2013; Tishkoff et al. 2007; Vicente et al. 2019). In contrast, Sahelian pastoralists experienced distinct ecological constraints linked to drought cycles and mobility, which shaped both the tempo and the geographical spread of LP-associated haplotypes (Cerny et al. 2009, 2023; Cizkova et al. 2017; Fortes-Lima et al. 2022; Hollfelder et al. 2021; Priehodova et al. 2020; Vicente et al. 2019). Meanwhile, in parts of Central and Southern Africa where fresh milk consumption remained limited or culturally restricted, LP frequencies stayed low, consistent with weaker selective pressures (Breton et al. 2014; Coelho et al. 2009; Macholdt et al. 2014, 2015; Ranciaro et al. 2014; Torniainen et al. 2009). Such regionally variable adaptive landscapes illustrate how a single cultural practice—dairying—can generate diverse evolutionary trajectories depending on subsistence systems, ecological risk, and patterns of gene flow. Furthermore, linguistic reconstructions add further depth. Proto-terms in Afroasiatic languages for cattle, milking, and dairy products imply long-standing dairy traditions predating genetic adaptation (Blench 1997, 2006; Ehret 1967, 2019; Mous 2020). These cultural, ecological, and linguistic contexts help explain why LP alleles rose rapidly in some regions but remained absent or rare in others.

What current evidence strongly supports

Taken together, the available evidence robustly supports three central insights. First, LP evolution is a classic case of repeated, independent adaptation to a shared cultural niche, with each LP variant tracing its own evolutionary history across distinctive haplotype backgrounds (Feldman and Laland 1996; Gerbault et al. 2011; Kasser et al. 2025; Laland et al. 2001; Odling-Smee et al. 2003; Phelps et al. 2020; Priehodova et al. 2020; Richerson and Boyd 2004; Tishkoff et al. 2007; Vicente et al. 2019). Second, ancient DNA has now confirmed that in Africa, as elsewhere, genetic adaptation emerged subsequent to cultural change, reinforcing models of gene–culture coevolution in which subsistence shifts create new selective environments (Fregel et al. 2018; MacHugh et al. 2017; Prendergast et al. 2019; Salem et al. 2025; Vicente and Schlebusch 2020; Wang et al. 2020). Third, the magnitude and timing of selection on LP alleles cannot be understood without accounting for the ecological and social heterogeneity that shaped pastoralist lifeways across the continent (deMenocal et al. 2000; di Lernia 2021; Dunne et al. 2018, 2013, 2012; Gifford-Gonzalez 2000, 2011; Jones et al. 2013; Smith 1992; Tishkoff et al. 2007).

Where uncertainties remain

Despite major advances, several uncertainties limit our ability to reconstruct LP evolution with precision. The archaeological and aDNA records remain sparse across large parts of the Sahara, Horn, and interior East Africa, leaving critical gaps in our understanding of how early pastoralism spread and diversified (Fregel et al. 2018; Gretzinger et al. 2024; Jakobsson et al. 2025; Prendergast et al. 2019; Salem et al. 2025; Vicente and Schlebusch 2020; Wang et al. 2020). Chronologies of cattle domestication, herd management strategies, and the cultural meanings of milk are still unevenly documented, complicating efforts to align genetic timelines with behavioral change (Dunne et al. 2018, 2013, 2012; Gerbault et al. 2011; Gifford-Gonzalez 2011; Gifford-Gonzalez and Hanotte 2011; Grillo et al. 2018). Moreover, estimating selection coefficients for LP alleles remains challenging, especially in populations with complex histories of admixture, bottlenecks, and recent demographic expansions. Finally, although nutritional buffers, pathogen exposure, and hydric stress have been proposed as contributors to LP's fitness advantage, their relative importance remains unresolved (Chritz et al. 2015; Lokki et al. 2011; Stock and Wells 2023; Wells et al. 2021).

Future methodological developments

The next breakthroughs will likely emerge from tighter integration of genomic time series, high-resolution archaeological data, and ecological modeling. Expanding aDNA sampling across underrepresented African regions is essential for refining allele age estimates, clarifying the tempo of pastoral expansions, and distinguishing between demographic and selective signals. Advances in computational modeling, including methods for inferring selection in structured populations and for reconstructing genealogies through time, offer promising avenues for addressing longstanding uncertainties (Speidel et al. 2021). Equally important will be interdisciplinary work—linking isotopic analyses, zooarchaeology, and ethnographic studies—that can situate LP evolution within the broader spectrum of human adaptive strategies in variable and often challenging environments.

Concluding perspectives

Africa provides the clearest framework for understanding how lactase persistence evolved. Unlike other regions, Africa shows several independently derived LP alleles, different haplotype backgrounds, and region-specific patterns of selection acting at different times. This diversity makes Africa especially informative for studying convergent evolution driven by the same cultural practice—dairying—but shaped by different demographic and ecological contexts.

New methodological advances are strongly improving this picture. The increasing availability of aDNA from African sites (Jakobsson et al. 2025), together with lipid residue analysis and paleoproteomics, now allows us to directly link milk use, pastoral practices, and genetic adaptation through time. These data clearly show that milk consumption and dairy processing were already widespread long before LP alleles became common. As these datasets grow, they will allow more accurate estimates of when LP alleles emerged, how strong selection was in different regions, and how these alleles spread across populations.

Importantly, the African evidence shows that selection on LP cannot be explained by diet alone. The strongest signals of selection are found in arid and semi-arid regions, where pastoral mobility was high and environmental conditions were unstable. In these contexts, fresh milk was not only a food source but also an important source of fluids and energy. LP should therefore be seen as an adaptation shaped by both cultural practices and environmental constraints, rather than as a simple response to milk consumption.

More broadly, the African LP story is not only about milk, but about human adaptability. It shows our ability to reshape landscapes, technologies, diets, and genomes together. It reflects the flexibility and creativity that characterize our species and highlights how cultural innovation and biological evolution remain closely linked in shaping human diversity. Continued interdisciplinary collaboration will be essential to resolve remaining uncertainties and to build a more complete, time-resolved understanding of one of the clearest examples of recent human evolution.

Conflict of interest statement

The author declares no conflicts of interest.

Acknowledgments

I thank all the African participants who generously donated DNA and phenotypic information, enabling us to learn more about the genetic basis of lactase persistence and the spread of pastoralism in Africa. I thank Dr. S.A. Tishkoff for granting permission to use photographs from her laboratory for scientific work–related purposes only. The use and reproduction of these images without the permission of Dr. Tishkoff are prohibited.

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Editor, Giovanni Destro Bisol