DH-12 What ancient DNA reveals about the sexes

The advent of paleogenomics—the recovery, sequencing, and computational analysis of ancient DNA (aDNA) from archaeological remains—has precipitated a methodological revolution within anthropology and evolutionary biology. Prior to the widespread application of high-throughput sequencing, researchers reconstructing prehistoric social organization, mating patterns, and demographic shifts were largely restricted to inferences drawn from material culture, historical linguistics, and the genetic diversity of modern populations. Today, the direct sequencing of ancient autosomes alongside uniparental markers—specifically the maternally inherited mitochondrial DNA (mtDNA) and the paternally inherited non-recombining portion of the Y-chromosome (NRY)—permits the direct observation of population dynamics across deep time. To rigorously assess how men and women have historically organized their lives, formed familial units, and constructed societies, it is necessary to synthesize the archaeogenetic record. This report evaluates the primary literature concerning sex-biased processes in human history, examining how prehistoric migrations, extreme reproductive skew, and kinship structures shaped the genetic architecture of past and present populations.

An Analytical Framework: Physiology, Behaviour, and Culture

To accurately interpret the complex data generated by population genetics and paleogenomics, it is essential to distinguish between three distinct but continually interacting layers of human existence. The failure to separate these layers often leads to unwarranted biological determinism or the naturalistic fallacy.

The first layer is **physiology**, which comprises strictly measurable, binary, or continuous biological data. In archaeogenetics, this includes the identification of X and Y chromosomes to determine biological sex, the calculation of autosomal admixture proportions, the measurement of tract lengths of Identity-by-Descent (IBD) and Runs of Homozygosity (ROH), and the quantification of isotopic signatures (such as Strontium $^{87}Sr/^{86}Sr$ and Oxygen ^{18}O in tooth enamel versus bone collagen) to establish geographic origins. These are empirical realities of the physical record.

The second layer is **behaviour**, which represents the aggregate demographic outcomes of human actions over time. This layer is characterized by statistical distributions and overlapping averages rather than absolute binaries. It encompasses metrics such as effective population size (N_e), rates of migration, and reproductive skew. Crucially, it is necessary to distinguish what is known about averages from what can be said about individuals. While a population average might indicate a severe sex bias—such as a highly male-biased gene flow resulting in widespread Y-chromosome replacement—the overlapping distributions mean that the behaviour or reproductive success of any single individual within that population often deviates drastically from the mean. A statistical male reproductive advantage at the population level does not imply

that every individual male successfully reproduced.
The third layer is **culture**, which encompasses the highly variable, socially constructed rules and institutions that dictate human interaction. This includes systems of kinship (matrilineal vs. patrilineal descent), post-marital residence rules (matrilocality vs. patrilocality), marriage structures (monogamy, polygyny, polyandry), exogamy, and wealth inheritance. Culture is the primary variable driver that shapes behavioural statistics, which in turn leave a permanent signature on human physiology. Ancient DNA provides direct data on the physiological layer and allows for the statistical reconstruction of the behavioural layer. The cultural layer must be carefully inferred by triangulating genetic data with archaeological contexts, such as burial goods, monumental architecture, and spatial cemetery arrangements.

The Deep-Time Signal of Patrilocality and Effective Population Size

One of the most robust and consistent findings in human population genetics is the deep-time signal of male reproductive skew. On a global, long-term scale, the female effective population size (N_f) has historically exceeded the male effective population size (N_m)[1].

Effective population size (N_e) is a foundational theoretical construct in population genetics. It does not refer to the census population (the actual number of individuals alive), but rather to the size of an idealized Fisher-Wright population that would experience the exact same rate of genetic drift as the observed real population[3]. Using high-coverage sequencing from the Human Genome Diversity Panel (HGDP), Lippold et al. (2014, *Investigative Genetics*) analyzed 623 males across 51 global populations[2]. By comparing the time to the most recent common ancestor (TMRCA) of mtDNA against the NRY, they confirmed that the TMRCA for maternal lineages consistently and significantly predates the TMRCA for paternal lineages, often by a factor of two[2]. For example, in the Khoisan population of southern Africa, the NRY TMRCA was estimated at 73.6 thousand years ago (kya), whereas the mtDNA TMRCA extended back to 176.5 kya[4]. This profound discrepancy indicates that throughout deep history, fewer men than women successfully transmitted their genomes to subsequent generations. This reflects a continuous signal of mild to moderate polygyny, or serial monogamy favoring males with higher variance in reproductive success[4].
This physiological signature is driven by cultural and behavioral norms, most notably patrilocality—the practice wherein women leave their natal groups to join their husband's community. The genetic evidence for higher female migration rates was definitively outlined by Seielstad, Minch, and Cavalli-Sforza (1998, *Nature Genetics*). In an analysis of 389 individuals across ten global populations, they discovered that Y-chromosome variants were significantly more geographically localized than mtDNA variants[6]. They calculated the proportion of between-group variation (Φ_{ST}) at 0.334 for the Y-chromosome, compared to a much lower baseline for autosomes and mtDNA, indicating that diverse Y-chromosomes entered populations at a far lower rate than diverse mtDNA[6].
Remarkably, recent paleogenomic advances have pushed the evidence for patrilocality back

beyond *Homo sapiens*. Skov et al. (2022, *Nature*) sequenced the remains of 11 Neanderthals from the Chagyrskaya Cave and two from the nearby Okladnikov Cave in the Altai Mountains of Siberia, dating to approximately 54,000 years ago[8]. The sample included a father and his teenage daughter, alongside several close relatives, constituting the first genetically documented Neanderthal family[8]. The researchers observed extremely low overall genetic diversity, indicative of small, isolated groups of 10 to 20 individuals[8]. Crucially, when comparing maternal and paternal markers, they found significantly more genetic diversity in the mitochondrial DNA than in the Y-chromosomes. This physiological evidence strongly implies that female Neanderthals migrated between communities to choose mates, while male Neanderthals remained in their natal groups—demonstrating that patrilocal behaviour and female exogamy predated the emergence of anatomically modern humans[8].

To capture the nuances of effective population sizes over time, modern computational methods such as the Multiple Sequentially Markovian Coalescent (MSMC), developed by Schiffels and Durbin (2014, *Nature Genetics*), analyze the observed pattern of mutations across multiple phased genomes[10]. MSMC focuses on the first coalescence between any two individuals to estimate relative cross-coalescence rates, tracking how population sizes and separations fluctuated over hundreds of thousands of years[12]. These models consistently show that the genetic separation of non-African ancestors from African ancestors was a gradual process spanning from roughly 120 kya to 40 kya[12], throughout which the discrepancy between male and female effective population sizes was maintained by the cultural ubiquity of patrilocality[13].

The Neolithic and Bronze Age Y-Chromosome Bottleneck

While a baseline reproductive skew favoring females exists throughout human evolution, this phenomenon escalated into an extreme genetic bottleneck during the mid-Holocene. Between roughly 5000 and 3000 BCE, human populations across Africa, Europe, and Asia experienced a catastrophic collapse in Y-chromosome diversity, even as mtDNA diversity and overall census populations expanded[14].

Karmin et al. (2015, *Genome Research*) sequenced 456 high-coverage Y-chromosomes from 110 diverse modern populations, establishing the sheer scale of this demographic event[15]. During this period, the male effective population size plummeted, creating a physiological landscape where the ratio of female to male effective population size reached an astonishing 17:1 in certain global regions[14]. Stated behaviorally, for every 17 women who successfully passed on their mtDNA, only one man's Y-chromosome lineage survived the bottleneck[15]. The average man alive in 4000 BCE left no paternal descendants, while a highly select group of men achieved unparalleled reproductive dominance.

Competing Models: Warfare vs. Peaceful Fission

The mechanisms driving this mid-Holocene Y-chromosome bottleneck remain one of the most intensely contested issues in evolutionary anthropology. The debate centers on how cultural systems—specifically the transition to agriculture and pastoralism—distorted behavioral statistics.

The Warfare and Cultural Hitchhiking Model: Zeng, Aw, and Feldman (2018, *Nature Communications*) proposed that the bottleneck was primarily driven by violent intergroup competition among patrilineal kin groups[17]. Following the Neolithic transition, human populations organized into corporate clans defined by shared paternal descent, where men remained in their natal villages and defended highly localized resources[17]. Under this model, the Y-chromosome "hitchhiked" on the cultural success of the clan[15]. Zeng et al. mathematically modeled a scenario of frequent, apocalyptic clan warfare resulting in the physical extinction of entire male lineages. If a victorious clan consistently wiped out the men of a defeated clan but assimilated the surviving women, the female effective population size would remain robust while the male effective population size would crater due to the systemic elimination of diverse Y-haplogroups[15].

The Peaceful Fission and Variance Model: A leading critique of the warfare model was advanced by Guyon, Marchi, Heyer, and Chaix (2024, *Nature Communications*), who argued that extreme, apocalyptic violence is not mathematically required to produce a 17:1 bottleneck[19]. Drawing on deep anthropological literature regarding segmentary patrilineal systems, they demonstrated that normal variance in reproductive success between groups, combined with a cultural process known as "lineal fission," is entirely sufficient to explain the genetic data[19]. In agropastoral societies, wealth (such as land or cattle) is highly concentrated. Wealthy clans experience rapid population growth and eventually split (fission) into two or more new sub-clans. Because these sub-clans trace their descent to the same founding patriarch, they carry the exact same Y-chromosome[19]. Conversely, poorer clans gradually and peacefully die out over generations because their men lack the material resources required to attract wives or sustain large families[19]. In this model, the Y-chromosome bottleneck is a symptom of extreme economic inequality and cultural structure, rather than systemic massacres.

This peaceful variance model is powerfully supported by the economic analysis of Borgerhoff Mulder, Bowles, et al. (2009, *Science*). In a landmark study of 21 historical and contemporary societies, they calculated the intergenerational wealth transmission coefficient (β)[20]. They found that in foraging and horticultural societies, the transmission of embodied wealth (skills, physical strength) and relational wealth (social networks) is relatively low ($\beta \approx 0.13$ to 0.18)[22]. However, in pastoral and small-scale agricultural societies, the intergenerational transmission of material wealth (land, livestock) is overwhelmingly high ($\beta \approx 0.61$)[22]. This structurally persistent inequality meant that a child born into the top wealth decile of an agricultural society was 11 times more likely to remain in the top decile than a child born into the bottom[21]. The cultural invention of heritable material wealth provided the exact environment necessary for specific patrilines to monopolize reproduction over millennia, thereby driving the physiological collapse of Y-chromosome diversity without strictly necessitating warfare.

Sex-Biased Migrations and Expansions

The archaeogenetic record reveals that prehistoric migrations were rarely symmetrical movements of entire, balanced populations. Instead, demographic expansions were frequently

highly sex-biased, altering the recipient populations in profound ways.

The Pontic-Caspian Steppe Expansions

Beginning in the early third millennium BCE, nomadic pastoralists associated with the Yamnaya culture expanded westward into Europe and eastward toward Central and South Asia[24]. Originating on the Pontic-Caspian steppe, these populations utilized wheeled wagons and domesticated horses, allowing them to traverse vast distances[26].

The Central European Methodological Controversy: A fierce controversy regarding the degree of sex bias during the Steppe expansion into Central Europe emerged in 2017. Goldberg, Reich, et al. (2017, *PNAS*) sought to measure sex bias by comparing the proportion of Steppe-related ancestry on the X-chromosome versus the autosomes in Late Neolithic and Bronze Age populations (such as the Corded Ware culture)[27]. Because the X-chromosome spends two-thirds of its evolutionary time in females, a significantly lower proportion of incoming ancestry on the X-chromosome relative to the autosomes signals a male-biased migration[27]. Utilizing the clustering software ADMIXTURE, Goldberg et al. calculated that Central European Bronze Age individuals possessed 61.8% Steppe ancestry on their autosomes, but only 36.6% on their X-chromosomes. They concluded this disparity required a massive influx of 5 to 14 Steppe males for every one Steppe female[28].

This finding was immediately challenged by Lazaridis and Reich (2017, *PNAS*), who published a paper titled "Failure to replicate a genetic signal for sex bias in the steppe migration into central Europe"[28]. Lazaridis re-analyzed the identical genetic data using qpAdm, a robust statistical framework that leverages f-statistics and distant outgroups to eliminate biases caused by genetic drift[28]. The qpAdm analysis yielded an X-chromosome Steppe ancestry estimate of 67.5% ($\pm 17\%$), which was statistically indistinguishable from the autosomal estimate of 61.4% ($\pm 2.9\%$)[28]. To diagnose the discrepancy, Lazaridis simulated 1,440 pseudo-individuals with known admixture proportions and processed them through the supervised ADMIXTURE pipeline used by Goldberg[28]. They discovered a severe mathematical artifact: ADMIXTURE systematically underestimated X-chromosome ancestry at intermediate levels, imposing a definitive -19.5% downward bias that artificially created the appearance of a male-driven migration[28]. While Goldberg subsequently defended the original findings by pointing to limitations surrounding small haploid reference panels[29], the extreme 14:1 ratio is heavily contested, serving as a cautionary tale regarding the limitations of simple admixture algorithms.

The Iberian Bell Beaker Replacement: While the sex bias of the initial Corded Ware expansion into Central Europe remains debated, the subsequent expansion of the Bell Beaker culture into Western Europe provides unequivocal evidence of extreme male bias. Olalde et al. (2019, *Science*) analyzed a transect of ancient DNA from the Iberian Peninsula, documenting the arrival of Steppe-related ancestry via Bell Beaker networks around 2500 BCE[33].

The physiological data revealed a striking asymmetry. The overall autosomal DNA of the Iberian population shifted by approximately 40%, indicating substantial admixture between incoming Steppe-descended groups and local Chalcolithic Iberians[33]. However, the Y-chromosome turnover was near absolute. The paternal lineages that had dominated Copper Age Iberia

(primarily I2a and G2a) were almost entirely eradicated from the gene pool, replaced by a single incoming Steppe-derived lineage: R1b-M269[33]. By the Middle Bronze Age, R1b-M269 accounted for nearly 100% of male lineages in the region[35]. This exact pattern of 90% to 100% Y-chromosome replacement by R1b-M269 also occurred during the Bell Beaker migration into Britain and Northern France[36]. The behavioural implication is stark: incoming Steppe-descended males, likely leveraging advanced metallurgy, pastoralist wealth, or novel social structures, were highly successful at monopolizing local reproduction, passing their Y-chromosomes forward, while local male lineages were systematically excluded from the breeding pool.

South Asia and the Origins of Caste: A parallel male-biased expansion occurred eastward. Narasimhan et al. (2019, *Science*) sequenced 523 ancient genomes spanning 8,000 years of human history in Central and South Asia[38]. They traced a gradient of Steppe pastoralist ancestry migrating south into the Indian subcontinent during the first half of the second millennium BCE, precisely overlapping the decline of the Indus Valley Civilization[38].

The genomic data revealed that Steppe ancestry in modern South Asians is primarily derived from males, pointing to asymmetric social interactions[38]. Furthermore, this ancestry is heavily skewed toward specific cultural endpoints. Groups that identify with traditional priestly status, including Brahmins and Bhumihars, carry disproportionately higher levels of Steppe ancestry compared to the general population, exceeding expectations based on standard Ancestral North Indian (ANI) and Ancestral South Indian (ASI) admixture models[26]. This indicates that incoming Steppe-related males integrated themselves into the highest echelons of a developing stratified society, marrying local women, and subsequently locking their genetic legacy into place through the rigid cultural enforcement of endogamy that characterizes the caste system[38].

The Bantu Expansion and the Americas

The phenomenon of male-biased admixture is not unique to the Eurasian Steppe. During the Bantu expansion (roughly 3000 to 1000 BCE), agricultural populations spread across Sub-Saharan Africa. Genetic analyses reveal a strong sex bias in this migration, characterized by the replacement of local Y-chromosomes (often with haplogroups E1b1a) alongside the retention of diverse local maternal lineages (L mtDNA), reflecting incoming Bantu-speaking farmers absorbing local hunter-gatherer women while outcompeting local men[40].

A well-documented modern corollary occurred during the colonization of the Americas. Bryc et al. (2015, *American Journal of Human Genetics*) analyzed the genetic ancestry of 148,789 European Americans, 5,269 African Americans, and 8,663 Latinos utilizing the 23andMe customer database[42]. They identified pervasive asymmetrical sex bias across all studied groups, observing a massive overrepresentation of European male ancestors paired with Native American and African female ancestors[43].

While subsequent sensitivity analyses (e.g., the debate surrounding Micheletti et al.) have warned that unassigned ancestry on the X-chromosome can sometimes confound the exact quantification of these biases[44], the physiological contrast remains undeniable. Throughout Latin America, the modern Y-chromosome pool is predominantly European (e.g., haplogroup R1b), while the mtDNA pool remains overwhelmingly Native American (e.g., haplogroups A, B, C, D)[46]. This genetic reality is the direct, measurable legacy of the cultural and behavioural

imbalances of colonialism, frontier demographics, and systemic enslavement[43].

Migration Event	Primary Source	Incoming Ancestry	Y-Chromosome Replacement	Sex-Bias Indication
Central Europe (Corded Ware)	Goldberg 2017; Lazaridis 2017	Pontic-Caspian Steppe	High (R1a dominant)	Contested (Methodological debate over ADMIXTURE vs qpAdm models)
Western Europe (Bell Beaker)	Olalde 2019; Brunel 2020	Steppe / Central Europe	Near 100% (R1b-M269 replaces I2/G2)	Extremely Male-Biased, complete paternal turnover
South Asia (MLBA)	Narasimhan 2019	Central Steppe MLBA	High (R1a dominant)	Male-Biased, highly stratified by modern caste structures
Sub-Saharan Africa	Various	Bantu Agriculturalists	Moderate to High	Male-Biased (Incoming farmers reproducing with local hunter-gatherer females)
The Americas	Bryc 2015; PLOS 2009	European	High	European Male / Native American & African Female Bias

Reconstructing Prehistoric Kinship: Pedigrees in the

Cemetery

While population-level DNA traces broad demographic shifts over millennia, the recent ability to sequence multiple individuals from single cemeteries allows geneticists to reconstruct exact, multi-generational pedigrees. This bridges the gap between behavioural statistical averages and the lived cultural reality of prehistoric households.

Strict Patrilocality and Female Exogamy

Gurgy 'les Noisats', France (Middle Neolithic): Rivollat et al. (2023, *Nature*) provided an unprecedented look into early European social structures by sequencing 94 out of 128 individuals from a Middle Neolithic cemetery in France (4850–4500 BCE)[48]. Using advanced Identity-By-Descent (IBD) mapping, they reconstructed two massive family trees, the largest of which connected 63 individuals across seven consecutive generations[48].

The physiological data revealed rigid cultural rules: the pedigree was entirely patrilineal and patrilocal. Every generation was connected to the previous one strictly through the biological father[50]. Crucially, adult daughters of the core lineage were almost entirely absent from the cemetery, proving the practice of female exogamy—they left their natal village to marry into neighboring groups[50]. The adult women buried at Gurgy were mothers who had married into the clan. Strontium isotope analysis confirmed these incoming women possessed non-local childhood signatures, and autosomal DNA proved they were genetically unrelated to each other[48]. This indicates that Gurgy participated in a fluid, reciprocal network of female exchange spanning a wide geographic area[50]. The absence of half-siblings and a high number of adult full-siblings suggested stable health conditions, high fertility, and monogamous pairing within this specific farming community[51].

Elite Patriarchs and Social Stratification

Hazleton North, UK (Early Neolithic): Fowler et al. (2021, *Nature*) reconstructed a complex three-generation pedigree from 35 individuals buried in a 5,700-year-old tomb in Britain[52]. The social structure of this monumental site was organized around a single patriarch who had offspring with four different women[52]. The lineage descent was tracked exclusively through six of his sons. While this could theoretically represent serial monogamy, the temporal overlap and architectural segregation of the burials strongly hints at polygyny[52]. This cemetery provides a micro-level snapshot of the male reproductive skew that drives global population statistics: a single male achieved massive reproductive success, founding a localized clan that commanded the labor to build a monumental tomb.

The Lech Valley, Germany (Early Bronze Age): Mittnik et al. (2019, *Science*) expanded on this by studying Bronze Age farmsteads in the Lech Valley of southern Germany[53]. Reconstructing six distinct pedigrees, they again found strict patrilocality. Out of 10 parent-offspring pairs detected, the offspring was male in 9 cases; adult daughters had consistently left the farms[54]. Strontium and Oxygen isotopes revealed that the mothers of these sons had migrated from up to 350 kilometers away[53].

However, the Lech Valley data added a profound layer of social inequality. The non-local women were buried with high-status grave goods, matching the wealth of the local elite men. Yet, buried

in the exact same cemeteries were individuals who were genetically completely unrelated to the core family, and who were interred without any wealth or grave goods[55]. This constitutes the earliest direct genomic evidence of complex, socially stratified households in Europe, combining biologically related patrilineal elites with unrelated, impoverished individuals who likely served as servants or slaves[55].

Matrilineal Dynasties and Non-Biological Kinship

While patrilocality dominates the Eurasian archaeogenetic record, notable exceptions exist, proving that cultural invention can override baseline biological tendencies.

Chaco Canyon, USA (Pueblo Bonito): Kennett et al. (2017, *Nature Communications*) sequenced DNA from nine elite individuals buried in a sealed crypt (Room 33) within the massive Pueblo Bonito structure in Chaco Canyon, New Mexico, dating between 800 and 1130 CE[56]. All nine individuals shared an identical mitochondrial genome (haplogroup B2)[57]. Autosomal data from the six best-preserved samples confirmed mother-daughter and grandmother-grandson relationships[57]. This provided unprecedented evidence of an elite matrilineal dynasty that monopolized political and ritual power in a complex, pre-contact North American society for 330 years[56]. (It must be noted that this study generated significant ethical controversy, as destructive sampling was conducted on Native American remains without tribal consultation, highlighting the deep tensions between paleogenomic research and indigenous sovereignty[59]).

Fujia, China (Neolithic): Similarly, a 2023 analysis of the Fujia site (2750–2500 BCE) in eastern China revealed two distinct matrilineal clans practicing high endogamy (in-marriage)[61]. This demonstrates that early agricultural communities in East Asia experimented with diverse kinship rules that differed sharply from the European Neolithic patrilocal model[61].

Çatalhöyük, Anatolia (Neolithic): Finally, ancient DNA reveals that biological kinship is not the only mechanism by which humans organize domestic life. Yaka et al. (2021, *Current Biology*) analyzed 22 new ancient genomes from Neolithic Anatolian sites, including the dense proto-city of Çatalhöyük, bringing the regional dataset to 59 individuals[62]. They discovered that individuals co-buried beneath the floors of the same domestic buildings were frequently not closely biologically related[63]. This suggests that in some early, highly dense agricultural settlements, "kinship" was a social construct based on co-residence, practical alliances, or adoption, rather than strict biological descent[64].

Summary of Robust Findings

#	Finding	Description
1	**Female Effective Population Size**	Throughout global history, the female effective population size has consistently exceeded the male effective population size, reflecting a deep-time

		baseline of male reproductive skew.
2	**Higher Female Migration**	Due to widespread cultural patrilocality, women have historically migrated at higher rates than men, evidenced by the global geographical localization of Y-chromosomes versus widespread mtDNA.
3	**The Y-Chromosome Bottleneck**	Between 5000 and 3000 BCE, male effective population sizes crashed dramatically (up to 17 females reproducing for every 1 male), driven by the rise of agropastoral wealth and patrilineal clans.
4	**Male-Biased Admixture in Europe**	The Bronze Age Bell Beaker expansion into Western Europe (e.g., Iberia, Britain) resulted in a near-total (90-100%) replacement of local Y-chromosomes by Steppe-derived lineages (R1b).
5	**Caste and Steppe Ancestry**	In South Asia, incoming Steppe pastoralist ancestry was heavily male-biased and disproportionately integrated into the higher, priestly castes of modern populations (e.g., Brahmins).

6	**Neolithic Pedigrees Confirm Patrilocality**	Massive 7-generation family trees (e.g., Gurgy, France) definitively prove that some Neolithic communities practiced strict patrilocal residence alongside female exogamy.
7	**Early Stratified Households**	Bronze Age European households (Lech Valley, Germany) contained wealthy, biologically related patrilines co-residing with entirely unrelated, impoverished individuals (servants/slaves).
8	**Evidence of Prehistoric Polygyny**	Genomic data from monumental sites like Hazleton North (UK) document localized clans founded by a single patriarch reproducing with multiple women, driving extreme reproductive skew.
9	**Matrilineal Dynasties**	Rare but clear exceptions, such as the 330-year elite matrilineal dynasty at Chaco Canyon, prove that human kinship cultures are highly variable and not strictly bound to patriliny.
10	**Biological vs. Social Kinship**	Sites like Çatalhöyük demonstrate that early human co-residence and burial practices were sometimes based on social bonds rather than biological

		relatedness.

Contested or Open Questions

Question / Controversy	Description and Leading Critics
The Nature of the Y-Bottleneck	Did male lineages collapse due to apocalyptic warfare and mass killings between clans (Zeng et al., 2018), or through peaceful variance in reproductive success and the fission of wealthy patrilines (Guyon/Marchi et al., 2024)?
Methodological Limits of Admixture	To what extent do computational models (like ADMIXTURE) systematically miscalculate sex-bias by misinterpreting unassigned ancestry on the X-chromosome versus autosomes, as argued by Lazaridis against Goldberg?
The Origin of Haplogroup R1b	The exact geographical and cultural mechanism by which the R1b Y-haplogroup achieved near-total dominance in Western Europe, while R1a dominated Eastern Europe and South Asia, remains partially obscured.
Fate of the Local Males	During the Iberian Bell Beaker transition, how exactly were local Chalcolithic males excluded from the gene pool? Was the mechanism violent replacement, economic marginalization, or disease?
Ethics of Paleogenomics	How should the scientific community balance the pursuit of archaeogenetic knowledge with the ethical rights of descendant communities, particularly in light of the unconsented destructive sampling seen in the Chaco Canyon study (Cortez et

	al.)?

Key Literature for Further Reading

Author(s) & Year	Journal	Significance
Rivollat et al. (2023)	*Nature*	The most complete prehistoric pedigree to date, proving patrilocality and female exogamy across 7 generations at Gurgy, France.
Karmin et al. (2015)	*Genome Research*	The foundational paper identifying the massive 17:1 Neolithic Y-chromosome bottleneck globally.
Olalde et al. (2019)	*Science*	Documents the near 100% replacement of Iberian Y-chromosomes by Steppe-related males during the Bell Beaker expansion.
Guyon, Marchi, et al. (2024)	*Nature Communications*	Provides the leading anthropological and mathematical counter-argument to the warfare hypothesis of the Y-bottleneck.
Mittnik et al. (2019)	*Science*	First genomic proof of socially stratified households containing elite patrilines living alongside unrelated servants/slaves.

Borgerhoff Mulder, Bowles, et al. (2009)	*Science*	Essential non-genetic context on how material wealth in agropastoral societies drives structural intergenerational inequality.
Lazaridis & Reich (2017)	*PNAS*	A vital methodological lesson on the limits of ADMIXTURE software in detecting sex bias, refuting Goldberg et al.
Narasimhan et al. (2019)	*Science*	A massive 523-genome study linking male-biased steppe migration to the formation of the Indian caste system.
Fowler et al. (2021)	*Nature*	Evidence of prehistoric polygyny and patriarch-focused clan structures in a Neolithic British tomb.
Kennett et al. (2017)	*Nature Communications*	Crucial evidence that complex prehistoric societies could organize political power through strictly matrilineal descent (Chaco Canyon).

Implications for Living Together

The archaeogenetic record forces a confrontation with the reality of human behavior across deep time, unclouded by romanticized notions of the past. For couples, families, organizations, and societies attempting to optimize how they live together today, several vital implications emerge.

First, we must stringently avoid the *naturalistic fallacy*—the philosophical assumption that because a behavior is "natural" or historically ubiquitous, it is therefore "good," moral, or desirable. The DNA record explicitly shows that extreme male reproductive skew, high-status

polygyny, and the exclusion of lower-status individuals from reproduction and resources are recurring themes in our history. The Y-chromosome bottleneck and the Steppe expansions demonstrate that when material wealth (such as land or cattle) becomes highly transmissible across generations, societies naturally default toward immense structural inequality. This suggests that modern egalitarianism is not our default historical state; rather, it is an active, ongoing cultural achievement. It requires continuous institutional maintenance to counteract deep-seated biological and behavioral tendencies toward wealth hoarding and reproductive monopoly.

Second, the data regarding patrilocality and female exogamy (spanning from Neanderthals to the Neolithic farmers of Gurgy) reveals that human families have long relied on expansive regional networks for survival. The modern concept of the completely isolated nuclear family is a historical anomaly. Prehistoric communities survived by continually integrating non-local individuals to build wide-ranging alliances, exchanging people to ensure genetic health, resource sharing, and mutual defense. Modern couples and families thrive best when embedded in larger, cooperative social networks.

Finally, the variability of the genetic record—from the strictly patrilineal clans of Bronze Age Europe to the matrilineal dynasties of Chaco Canyon and the socially-constructed, non-biological households of Çatalhöyük—demonstrates the immense plasticity of human culture. Biology sets a baseline and influences statistical behaviours, but cultural rules ultimately dictate how we organize. Societies possess the agency to consciously structure their institutions (whether marriages, corporations, or governments) to mitigate historical inequalities and foster cooperative, inclusive environments, regardless of our turbulent evolutionary past.

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