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Not peer-reviewed version

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Posted Date: 21 April 2026

doi: 10.20944/preprints202604.1479.v1

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Evolution of *H. sapiens* and Species of *Genus Homo*: Genetic Effects of Warfare

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Abstract

Ancient DNA Genomics has recently provided evidence for more than ten admixture/hybridization events within and among the three Homo species: Sapiens, Neandertals, and Denisovans, including those that, in our opinion, give rise to them as distinct species. We explore the idea that all admixtures were adversarial, governed by two behavioral instincts carried by all Homo species: group violence and constant migration. If genetically based, these instinctive behaviors of the genus Homo may explain why Homo survived as a biological lineage, while all other hominin branches perished. An evolutionary biology consideration shows how the "Rape of Sabines" instinct shared with the Pan and Homo ancestors is transformed into a hunter-gatherer predatory lifestyle in Homo. This drive progressed from Habilis to Erectus and culminated in Sapiens as the overarching planetary apex predator. The genetic mechanism in Homo species, invariably consisting of isolated tribes, ensures that warfare is the response to every intertribal encounter, resulting in minority DNA from kidnapped females being incorporated through mating into the genomes of subsequent generations of victorious tribes, populations, and species. This process allows the genetic/phenotypic gains of victims to be used as a selective advantage for future generations, instead of being lost like their lives. Warfare and ensuing gene flow between Sapiens and its minority parent, Archaics, happened for 100000 years in Africa, from Sapiens' origin to its conquest of Eurasia. This explains the patchy and puzzling paleoanthropological and archaeological record for that period. Our synthesis of the genomic history of the three Homo species covers about 800 kya and ends no later than 30 kya. After this point, biological rules no longer governed human history. Since 20kya, our species has shown the ability to create civilizations, managing the violent and migratory instincts of individuals, groups, and peoples at the cultural level.

Keywords: homo; speciation; sapiens; Neandertals; Denisovans; apex predators; intergroup violence; obligatory migration; adversarial admixtures; genome signatures

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Introduction

Based on our view of the meaning of DNA analysis results, several novel ideas about the causative processes in the deep history of our species and its Homo relatives are discussed here. The reason for the theoretical treatment is to connect disparate and complex results into a comprehensible whole. Here one can find the first answers on the questions among others: what are dominant behavioral instincts in genus Homo on the same level of biological understanding as for behaviour of elephants, lions or other social mammals; were incessant migrations necessary for survival of ancient hunter-gatherers; were admixtures/hybridizations demonstrated in humans friendly or adversarial; were origins of Sapiens, Neandertals and Denisovans saltational (hybridization) speciations; was warfare with archaics the reason for enormous time delay for modernity to take over in Africa at a dawn of our species; is it permissible for DNA scientists to push for reinterpretations of data from Paleoantrophology and Archeology on the basis of the depth and meaning of their genomic results and others. The answers our hypothesis provides are the first for these questions, but necessarily not the last. Clearly, the worth of parts or the whole of our hypothesis will be easily testable with new DNA evidence.

Our Theory of Evolution [1] proposed that new species emerge exclusively through genetic admixture/hybridization of organisms from as distant as possible interfertile populations or species. This appears to be the case in the three speciations in genus Homo for which we have genetic evidence unique in all of biology. If correct, this interpretation provides a strong boost to our Theory. In the middle of the third decade of the third millennium, the evolutionary theory is at a crossroads. On the one hand, many experimental biologists tend to think that Neodarwinian orthodoxy as taught in textbooks for nearly a century needs serious revision [2]; on the other hand, while critics are increasingly plentiful, very few of them offer a new synthesis. A special problem with those few is that they take Evolution to the most complex organisms as granted, basically accepting biological history and gene-centered determinism as told by now obviously flawed NeoDarwinism. Contrary to that, we have proposed a new evolutionary theory on the basic premises that historicity and genetic determinism must be retained and explained in a new way, because that is what molecular biology and genomics expect of the new Theory. Our proposal addresses the problem of speciation, which both Darwin and NeoDarwinists correctly recognized as the main issue in the theory of evolution. In the spirit of Punctuated Equilibrium Theory [3] and evidence, we opted for the saltatory version of speciation that species emerge in one to several generations and are selectively perfected for durable genome in a punctuated or short space of time lasting from thousands to tens of thousands of years, followed by their endurance, virtually unchanged in stasis, for much more extended time periods measured in millions of years. The mode of speciation is hybridization speciation, the union of parental genomes from lineages as distant as compatible with viability, leading to the reorganization of the genomes of offspring [1]. This serious genome scrambling, in most cases, is just lethal to the carrier, but in the rarest of the rare events, a viable genome is produced, carrying a reorganized genome composed of parts with separate histories from the distant parental lineages. This progenitor/incipient of the new species carries an innovation that distinguishes it from the parental species. In evolutionary species lineages there is an additive pattern of innovations that are produced in a series of speciations; for instance, all species of a genus have the differential function specific to the progenitor of the genus, but also each one of them has a new functionality on top of that genus specific functionality; most older species innovations are retained in the newer species on the same evolutionary branch.

The evolutionary history of species in the genus Homo over the last million years or so was selected for theoretical review, since ancient DNA and various morphological and archaeological evidence provide an opportunity unique in all of biology. The revolutionary ancient DNA results are less than 15 years old and are being produced daily. This work will hardly be repeated at this depth in any other group of animals, as it depends on two centuries of success in the search for human fossils. Human evolution is both the biggest target and the sternest test of any evolutionary theory. This work hopes to convince biologists that this unprecedented genomic evidence provides a strong argument for the validity of saltatory speciation.

To provide the generalizations required by evolutionary theory, we have found it necessary not only to survey genetic evidence, but also to offer a different biological perspective on earlier time periods in this history to which ancient DNA doesn’t extend, but paleontology and archeology do. In the spirit of molecular biology, which aims to simplify and emphasize the most important feature of any biological problem it encounters, we offer the unifying point that the evolution of the genus Homo can best be viewed as the evolution of its lineage toward becoming the apex predator in its environment. From an ecological perspective, it cannot be denied that Sapiens achieved this. The organic mass of 8 billion humans exceeds the mass of any mammalian species in nature (domestic animals excepted). Sapiens have the ability to stop or change any food chain on the planet, securing its ecological apex position. However, its predatory role is not obvious and is certainly scientifically under-recognized. The definition of a biological predator requires the killing of other organisms for survival, either as prey or as victims in conspecific group dominance bouts. With the advent of Homo, a new mode of killing, armed killing, became possible as a basis for predation. With each new Homo species, improvements in weapons increased the ecological success of hunter-gatherer life at the expense of some more or less closely related species, which were driven to extinction and/or hunted as prey.

This account contains no value judgment on the present human condition. However, it deals with the biological topic of intergroup violence in Homo genus species. Most, if not all, large (and social) mammalian species exhibit some form of violent behavior. Therefore, it is no surprise that Homo species do as well. We explore what light the new results of DNA science shed on the understanding of one of the aspects of violent behavior: intergroup violence. To our knowledge, this aspect has not been covered in the literature before for its evolutionary significance. In doing this, one must acknowledge that many scientific accounts of topics raised here hesitated to use the kind of plain language we employed, in order not to arouse instinctive sensibilities of the human audience, or due to the lack of strict proof for such assertions. To the latter colleagues, some components of our hypothesis will seem almost trivial and recognizable. However, synthesis of various kinds of evidence, like ours, does not reach the level of strictness required when data are generated. Hypothesis-driven research on the issues raised here is in the interest of science, so, in order to motivate this, a theory covering them should be understandable to all. Nevertheless, we restrict our treatment to the purely biological portion of the history of genus Homo, from roughly 2.5 million to 30,000 years ago, due to its enormous biological interest. Since that time and up to the present, its only surviving species, Homo sapiens, has shown the ability to build civilizations and thereby transcended its biological roots, ceasing to be the subject of, and to be understood by, biological evolution science alone.

Results and Discussion

Homo Genus Species: Violent Primates Aiming to be the Apex Predators

It is illustrative to see whether the instinctive, obligatory, nomadic, and violent behavior of Sapiens argued for here helps inform speculations about the 2.8-1.6 mya period, for which very few facts are available. They concern sparse fossils and stone tools. Fairly little is known about the origin of the genus Homo. For instance, it is unclear if there was an archaic Homo species before Homo habilis. However, the first recognizable species of the genus Homo was the first armed mammalian species sensu stricto. In other words, not in the use of extra-corporeal implements in daily life as chimps and crows do, but in making its survival entirely dependent on the use of lithic arms (intentionally made sharp rocks). Homo habilis is the first animal species credited with using the earliest lithic tools associated with the so-called Oldowan technology. Although stone tools had many uses in their owners' daily lives, here we focus on their use as weapons in hunting and war. There is ample evidence that many related species of the genera Australopithecus and Paranthropus lived at the same time in nearly similar ecological niches as ancestor/s of Habilis. Some of them might have been violent like their more distant chimp relatives. The new Habilis species, breaking ranks with all of them, embarked on a life on the open savanna instead of living in a more or less forested environment as they did. In the new landscape, tribes of Habilis could not rely on old ways of protecting themselves in trees; various felines, canids, and hyenas abounded in the open. The new way of life they pioneered, known as the hunter-gatherer way of life, consisted of rapid movement across the open landscape during the day and finding appropriate shelters, such as caves, ledges, or unpassable rock formations at night. Somewhat like baboons nowadays, Habilis tribes must have relayed on scaring predators of similar strength from the frontal attack by various sounds and displays, avoided stronger predator groups by appropriate scouting and evasive movement, and unlike any primate before them, attempted to kill any encountered animal group, or single individual judged to be weaker by all means possible, including using sharp stone tools prepared before hand and carried into any eventual battle, or hunt, to be decisive to the outcome. Habilis was the first habitual meat-eater among primates, but probably continued to consume some plant food as well; a tradition that was probably carried on by succeeding Homo species. There are opinions in the literature that Homo's scavenging phase preceded the ability to kill sufficient prey. In that version, sharp stone tools enabled cutting parts of animal cadavers and quickly carrying them away before the original predators returned. One can think of scavengers in two ways: one is that they lack the instinct for violence and must satisfy a craving for meat by stealing from predators; the other is that they have a sufficient instinct but are less efficient at overcoming larger prey, so, besides killing smaller prey, they scavenge from larger predators. In this work, we accept the second option, making the issue of scavenging peripheral to evolutionary considerations. This follows from the argument that the instinct for violence must have been passed along to the Homo lineage and Habilis from the primate ancestor shared with chimpanzees, which had it as well. Some ancestral species' progeny may have lost violent instincts, like the bonobos in the Pan genus, which split from chimps 2.0 mya [4]. However, such species could not practice a hunter-gatherer lifestyle, as we argue was obligatory in all Homo species we know of. This argument will be developed further in the sections that follow.

The second argument for ancestral Homo predation is based on evidence from the next prominent Homo species to arise, Homo erectus. In its long tenure from about 2,05 million years ago to maybe even 0.4 million years ago in South Asia (see below), it spread Oldowan technology across the entire Africa, invented the next generation of stone arms, Acheulean technology, used fire, and began to populate Eurasia by 1.8 million years ago and resided there as the only human species for maybe half a millennium. The notion that it was a single, unique branch of the hominin species bush from 1.6 million to about 1.0 million years ago, for specific biological or environmental reasons, is one option. Much more likely is that Erectus successfully eliminated competing or prey species of hominines through its superior numbers, size, and weaponry. In the period from when the first stone tools were invented, about 2.5 mya, to 1.6 Mya, a bush of Homo, Paranthropus, and Australopithecus species is very evident. From 1.6-1 mya, Homo erectus was the only hominin species worldwide.[*] Similarly another species bush arose after 1 mya when stone arms carried by new post-erectus bigger-brained Homo species were being greatly improved and Erectus was in retreat, losing ground to the newcomers everywhere. The second bush trimming after Erectus occurred in genus Homo; it was accomplished by Sapiens about 40 kya, leaving it the sole hunter-gatherer species on the planet, also through force of superior arms.

Homo Genus Species: Permanent Inter-tribal Warfare

Here, we hold that all species of the genus Homo shared innate violent social behavior, other than hunting any animal they could possibly kill, to offer battle to the death when their migrating tribe encountered a weaker tribe of their own species, or one from a related species whose females were judged to be interfertile. The winning tribe killed all males from the conquered tribe and took those females captive, who were capable of extending the winning group's reproductive prowess. Occasionally, we will use "Rape of Sabines" as the short name for this behavioral phenotype. This is not to say that other instincts were not present and important for the behavior and survival of Homo species, but they are not directly identifiable and interpretable from DNA results at this point.

Let us begin with chimpanzees. Starting with Goodall's discovery:

> *In the chimpanzee, territoriality functions not only to repel intruders from the home range, but sometimes to injure or eliminate them; not only to defend the existing home range and its resources, but to enlarge it opportunistically at the expense of weaker neighbors; not only to protect the female resources of a community, but to actively and aggressively recruit new sexual partners from neighboring social groups. [5]*

Now, 40 years on, it is accepted that Pan troglodytes' stronger bands attack neighboring weaker bands, aiming to kill all males in them and append all their females to the conquering band.

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[*] Except for the cases of H. floresiensis , H. luzonensis and Dinaledi hominin. The first two might have originated from Erectus as isolated, endemic populations on small islands. The anatomical features of the third indicate an age of at least a million years older than found. It was a plant-eater and hence probably not a predator, unlike the Homo species. Due to its unresolved status, we are omitting its consideration from our generalizations about genus Homo.

For most of the time since Goodall's discovery, the discussion has been about what this chimp's behavior means for humanity: are we as bad as they, or is there hope that we are both good? For the latter view, see [6]. Inquiry into why this phenotype is advantageous to the fitness of P. troglodytes as a species is conspicuously missing in the literature. Here we are dealing with Homo, not Pan, but answering only broad-brush evolutionary questions, which are missing in research on either genus. No value judgments are offered about outcomes in nature; only partial biological answers are given about which processes contributed to those outcomes, which are being uncovered in Homo by revolutionary DNA research.

From 3100 to 2450 BCE, Europe underwent three westward population replacements. The first two were the peoples of the eastern steppes: Yamnaya and Corded Ware, and the third and final conquerors, the Bell Beakers, arose in Western Europe from a mixture of the Corded Ware front and domestic hunter-gatherers. The Yamnaya front was stopped at the Danube Basin in 2900 BCE, the Corded Ware front in what is now Central Germany around 2650 BCE, and Bell Beakers finished their expansion by running out of land on the western edges of Europe in Britain and Iberia a couple of generations after 2450 BCE [7].

Ancient DNA analysis showing the sex and genetic ancestry of precisely dated exhumed human remains uncovered an interesting pattern in these mass population replacement events. Local hunter-gatherer/farmer males, when in a path of expansion, were totally replaced by all three conquering fronts. Judging by the specific Y chromosome types, no Yamnaya males propagated their Y chromosomes to subsequent generations, or survived (see below, which of the two fates is more likely) in Corded Ware expansion, and no Corded Ware males survived Bell Beaker expansion in their former territories, which were subsequently covered by the conquerors. However this cannot be said of presumably conquered females, as they have been found to have survived conquest, had progeny and some even ended sharing the graves with the conquerors [8] The extreme case of sexual asymmetry of survivors is found in Iberia where the only migration surviving male lineage (Y chromosome) was of Bell Beaker type, but the overall steppe ancestry simultaneously stayed stable at a around 40% (Beaker males had 20% non-steppe ancestry), suggesting the total survival of local females [9]. The loss of old settler-type males in further generations was rapid locally, but moderately paced in progression over the entire Iberia [8].

Ancient DNA analysis shows demographic changes with a resolution of 1 or a few generations (50-100 years) and therefore cannot directly prove that violence caused the rapid ancestry replacement. However, we opt here to argue for the plausibility of male killing and Sabine-like rape of females as modus operandi in European population displacement from 3100 to 2450 BCE, since several additional "modern" examples of violent events changing demographics in exactly the same way exist, like the Spanish conquest of Latin America and Vanuatu male replacement in Oceania [8].

Why do these graphic examples of the violent social behavior of "Rape of Sabines" at the time extremes of at least two million years ago, from the origin of the chimpanzee species to 5000 to 500 years ago for "civilized" Sapiens, can be taken to hold for all known Homo species existing in between times? We will develop the following four arguments in detail to make our case. First, all species in question were hunter-gatherers; second, there is genomic evidence of many asymmetric admixture/ hybridization events in the three most recent species of genus Homo, which can be seen as consequence of kill-rape behaviour which allows the assumption about the same for all three; third, adversarial admixture is the only solution we can think of to offer for the paradoxical overall diversity increase in Africa, here called "archipelago" effect.

> *The whole continent of Sub-Saharan Africa, and probably Eurasia, at this time is full of thousands, tens of thousands of little groups that are communicating hardly at all with each other…… Diversity is maintained in an ensemble of rarely mixing groups… Archipelago of groups losing diversity and going extinct on some level, but together there is enough recontact to recharge diversity and create incredibly diverse populations you see today. [10].*

There is evidence of admixture from small African tribes dating back 50,000 to 5000 years. It poses a paradox to the genetics and biology of Homo in general. Reich and colleagues had the opportunity to study a collection of the oldest African aDNA genomes, reaching back up to 18000 years [11,12]. These individuals from 2-18 kya were somewhat inbred, living in small bands/tribes of a few hundred people without exchanging genes with other such tribes, even nearby ones. In this period, it appears that these tiny tribes are practicing a sedentary way of life, or at least moving within a 100 km radius, and have not exchanged genes with anyone living outside the circle for a long time, measured in thousands of years [12]. However, within each of the two regions studied, Eastern and Central Africa, the tribal genomes in the 5-20 kya period were fairly similar, attesting to prior tens of thousands of years of ancestry stability extending maximally from 50-80kya. Before that, Sapiens tribes in Africa were incessantly nomadic, migrating over long distances beyond future regional boundaries to achieve the mixing of ancestries observed later in that “frozen” period.

The question is how the overall African population, atomized into non-interacting bands, produced so many polymorphic DNA differences that we see in the genomes of present-day Africans. As mentioned, thousands of such tribes existed, but each, due to protracted isolation from mating conspecifics of even the closest other tribes for on the order of thousands of years, was inbred and thus lost diversity and eventually went extinct. However, we know that somehow the overall genetic diversity of the Sapiens main lineages in Africa did not decrease. Contrary to expectations of inbreeding, genomics has shown that diversity steadily increased over the last 100 ky. Reich’s answer is that mergers among groups must have occurred, but very rarely, maybe less than once on average over each group’s entire duration before they went extinct.

The paradox is resolved mechanically by Raich, but not in any biological sense. We provide the following biological solution to the genetic paradox. What type of human behavioral process could have produced such a simple summary of the outcomes of thousands of rare mating events between individuals from different tribes? Their regularity and rarity seem incompatible with tribes having any kind of friendly relations and exchanging mates voluntarily. Suppose they met in warfare rather than friendliness, but extremely rarely, since the habitable land in Africa was enormous and human density quite low, and maybe tribes avoided meeting each other. But due to constant migration over a long period, even in semi-sedentary situations, absolute avoidance was not achievable. If in majority of these very rare encounters, stronger tribes attacked the weaker ones, how would intertribal matings take place simultaneously? Well, not simultaneously, but if the vanquished tribe’s fertile females were captured by the victors, such matings could have taken place soon enough. This behavioral mechanism ensures that, while the conquered band physically perishes, barring its fertile females, its genetic bounty safely lives on in subsequent generations through the victors’ genomes. A moment’s consideration permits a conclusion that a genetic contribution of enslaved women to the victor’s genome must have been a minority one, way down from the maximal possible 50% , to maybe no more than 10%. This results from the supposition that tribes of victors, on average, had their own fertile females and that, over several generations, Sabine females’ contribution would have been diluted, leaving only those genomic regions that had a selective advantage in the newly mixed tribe’s genome. This way of improving species and populations’ genomes is somewhat unexpected, given that such intraspecies group violence in other mammalian orders is mainly motivated by territorial disputes, but secondarily, those battles may end with the winning males acquiring female harems from the losers, to the same genetic effect. Nevertheless, the Homo species’ migratory violence ensures that surviving nomadic groups have repeated access to hybrid vigor (bursts in fertility) through admixtures and to all usable genomic improvements available in the DNA of groups they manage to conquer.

Our explanation of the “archipelago” paradox might be considered inconclusive for its rather complex logic chain, if the proven cases of chimpanzee and Yamnaya “Rape of Sabines” violence, discussed at length above, were not available. Such redundancy of examples of the behavioral background of admixture events in higher primates eliminates the possibility of any coincidence claim. Shared genetic inclination to engage in group violence affecting the demise of conquered males and adoption of conquered females into the victorious tribe not only explains the “archipelago” diversity paradox, but also seems to offer the most parsimonious generalization for all documented and even undocumented admixtures among non-reproductively isolated genus Homo lineages in the last million years.

Homo Genus Species:Incessant Tribal Migration through Unforested Lands to avoid Warfare, if Weaker Party, and to find the New Prey and Weaker Opponent groups to attack.

Here, we consider that the only reliable direct evidence of the usual or average tribe size in any species of the genus Homo is the work of Lipson et al. [12] and Sümer et al. [13], which indicates a low hundreds range. While there is indirect evidence supporting it for Sapiens, Neandertals, and Denisovans, we are not aware of any convincing evidence for a larger tribe size than that in any other Homo species. Therefore, it is more parsimonious to consider such small sizes as a requirement for the efficient nomadic hunter-gatherer life than to leave the question of tribe sizes open. The migratory nomadic prowess of Paleolithic hunter-gatherers is confirmed in at least three proven treks of the Out of Africa people :

i. Sapiens out of East Africa to West Asia trek, Skull known as 45 ky-old Zlaty kun from Chechia [14] is fully modern, giving credence to the supposition that the founder tribe of extant Non Africans from ~47kya ago was fully modern too. If this is so, then tribes originating around the Horn of Africa 58-55 kya and setting on a trek (5400 km road distance AdisAbaba- Tabriz) that gave rise to the founder tribe of NonAfricans in Western Asia (around present day Tabriz) some 10-7 ky later, might have been fully modern too.

ii. Zlaty Kyn/ Ranis Western Asia to Germany trek. We do not have any evidence about the speed of migration within Africa; however, in Eurasia, we have evidence that the Ranis-Zlaty Kun tribe of about 300 people moved from Iran to Germany in less than 2,000 (more likely 1,500) years and survived the trek as a group[13]. Add to that the requirement to adapt from the last vestiges of a mild climate akin to that of Africa in Southwestern Asia to the harsh winters of Northern Europe in such a short migration time, within less than 50 generations. However, they might have been preadapted to a degree by their recently acquired Neandertal genetic component. Using Google Maps, the land distance between Tabriz, Iran (near the presumed origin of the Eurasian founder population), and Leipzig, Germany (close to Ranis Cave), is about 4000 km. The tribe managed to cover it in 1500 years, with an average direct migration rate of 2.7 km per year. Given the meandering expected from hunter-gatherer tribes in search of food and to avoid difficult terrain, the actual migration speeds should have been much faster.

iii. West Asia to Sahul trek. New Guinea and Australia are about 11000 km from the Caucasus Mountains by a mostly coastal land route. So about 7,000 years was all the time needed, with all the necessary stops in between (and with all other humans they encountered along the way going extinct), to reach every last corner of the vast Eurasian supercontinent. Such a minimal speed of roughly 1.6 km per year doesn't seem overly fast, but on the other hand, it requires a relentless urge to follow unexplored directions for at least one Sapiens tribe to keep on the shortest 11000 km trek required to cover such a vast distance.

In summary, the last two treks covered over 4000 km over 1.5-7 thousand years at rates of 1.6-2.7 km per year.

If all Homo hunter-gatherer species before 50000 years ago shared an obligatory nomadic way of life, their migratory populations were divided into tribes not much bigger than several hundred individuals (see above). Each of these tribes didn't migrate to find an ideal place to settle; they migrated because that is the way of life: you don't stop migrating, or you will be attacked; you stop for a while, then continue moving. How can this migration problem be solved if the caves you encounter cannot accommodate all 300 or so members? Well it will certainly hold an extended family of about 30 to 50 and this is probably how these tribes were organized; they must have had from 3 to 10 bands (subpopulations, demes), which kept in touch while migrating and, of course, they would come together in the country where a larger number of hunters together is needed, or if attacked by other tribe. Probably, the new tribes formed by the generational expansion of centripetally separated bands of ancestral tribes. But for the best use of surroundings/resources as one migrates, it makes sense that the whole tribe didn't travel together. In the only case where evidence exists, the separation between bands/demes was 230 km in the Zlaty Kun/Ranis Sapiens migrating tribe [13].

Homo Genus Species: No Genetic Admixture in Homo Species and Populations was ever "Friendly" until Holocene.

If the disposition to group violence inherited from primate ancestors was selected for allowing hybridization of individuals from different lineages, raiding for female sexual partners of a conquered group achieved this biological purpose. Furthermore, this instinct precluded any friendly exchange of sexual partners, wrongly presumed to have occurred by majority opinion in some more famous and consequential hybridizations (admixtures in aDNA speak), which we will discuss next.

Since the first sequencing of the Neandertal genome in 2010, it has become widely known that all non-Africans carry a few percent of Neandertal DNA. This is interpreted as proof that all living Non-Africans are descendants of a small founding population that originated in Africa and mated with Neandertals before growing in size and spreading across Eurasia. The latest results provide evidence that the hybridization/admixture event took place 47,000 years ago in Western Asia [13]. That mating resulted in a fertility boost that enabled the small founding tribe of 800 [15], after experiencing a bottleneck, to grow enough to send seeding bands in any available direction. Some of these Sapiens seeding bands perished, but others grew and went on to replace any other humans and make Sapiens the only surviving species in Eurasia. Adding Neandertal DNA to their genomes, among other things, enabled them to survive harsher climatic conditions than they were originally adapted to in Africa.

One or more of these offshoot bands opted for a southern route, hugging ocean coasts on the way to becoming Aboriginal Australians and Oceanians. Apparently necessary to achieve this, they underwent an additional admixture with a pre-Denisovan subspecies, whose several percent of DNA they carry in their genomes today. Interestingly, the latest results indicate that different Asian Sapiens populations underwent separate admixture events with the other 2 true Denisovan subspecies in the Indian subcontinent and Siberia, respectively [16]. While southernmost Sapiens underwent a change from exclusively stone to "mostly bamboo" tool technology, presumably practiced prior to that by tropical pre-Denisovans, we do not yet know whether the other two true Denisovan subspecies conferred phenotypic advantages to Sapiens through admixture as well.

Soon after these four admixtures, within a couple of thousand years at most, Neandertals, pre-Denisovan, and two Denisovan subspecies went extinct, leaving Sapiens as the sole surviving human species in Eurasia. We know of three Sapiens tribes (Bacho Kiro, Oase, and Ust-Ishim) that underwent further hybridization with Neandertals during that period, increasing the number of known battles Sapiens won in Eurasia to 7. However, these tribes that engaged in additional hybridizations failed to survive and contribute DNA to living Sapiens populations [13].

In light of the "rape of Sabine" phenotype seen from the case of the African "archipelago" paradox, we can not avoid extending the same interpretation to the spread of Sapiens in Eurasia. All four contributing hybridizations resulted from a single battle between a few hundred Sapiens and a tribe of Eurasian humans. Those were tribes of probably a smaller size, 60-100 individuals [16]. In all four encounters, Sapiens tribes were victorious, killing males and mating with females of the losing tribes, as indicated by the minority genetic contribution of the losers to the resulting genomes. In this view, there is reason to suppose that every subsequent encounter between expanding Sapiens tribes and residential tribes was violent, and that the majority outcome was Sapiens prevailing, as was the case in the mentioned additional 3 admixture events. The extinction of all Neandertals and Denisovans in the homelands they were adapted to in such a short time could not have happened otherwise.

Species of Homo: A hypothesis that the three most recently occurring speciations in the genus, that of Neandertals, Denisovans, and Sapiens, resulted from "Rape of Sabine" admixtures of tribes from different species or subspecies .

Here, we argue that admixtures that result in the formation of new species differ from population-level admixtures described above. After each admixture event, many hybrids are born and have roughly equal chances to contribute to the new population's genome. However we believe that in speciations admixtures, besides those, a single hybrid, or very few hybrids, are born carrying an innovation coded in genetically dominant way They are incipients of a new species since some of their offspring obtained in backcrossing with either other hybrids of populational type or organisms of paternal or maternal lineages can carry the innovation too, meaning that they are also members of the new species. In other words, the growth of a new species is through a separate genealogy. Initially, the resulting tribe is mixed, and new species members are in the minority until, eventually, motivated by phenotypic differences, a band of a pure new breeds splits off from the parental tribe.

To pinpoint the last three speciations in the genus Homo, one needs a clear picture of the phylogenetic tree's chronology of branchings and joints, and of the broad geographical locations of participating lineages over the last million years or so. Here, we follow the latest version of such a tree from Swante Paabo's group, resulting from the analysis of the second complete Denisovan genome [16], and extend it to include branches leading to, and their joining at, the speciation of Sapiens, and to identify two of their reported Eurasian admixtures as speciations. The simple graphic model we follow for splits and admixtures in genus Homo from 1-2 million years ago to about 30 kya is shown as the main model in Figure 2 of Rogers et al. [17].

Who gave rise to the new Homo species lineage in Africa that led to Sapiens is still debated. In order of decreasing probability, it could have been H antecessor, H. rhodesiensis, or H. ergaster, as the just-described 773 ky-old Moroccan fossils seem to indicate [18]. Anyway, a new branch of pre-Sapiens split from its ancestor about 0.9-1.1 mya. There were two lineages in Africa: one of pre-Sapiens and the other of Archaics. Archaics could be a population of H. antecessor or H. rhodensiensis, or the lineage that split in Africa from pre-Sapiens soon after the latter split from its ancestor. Here, we follow the latest estimate of 695–825 kya [16] for a time when the lineage leading to Neandertals and Denisovans, which we consider to be H. heidelbergensis, split off from the pre-Sapiens lineage, inferring a probable split location either near the Gibraltar Strait or in the Levant. From 0.75 mya to at least 0.5 mya, we have a single lineage of H. heidelbergensis evolving in Eurasia. Heidelbergiensis split into pre-Neandertals in Europe and pre-Denisovans in Asia 0.5-0.6 mya [16], probably in the equidistant Levant.

Our hypothesis is that the three Homo genus admixture/hybridization speciations we are interested in occurred: Neandertals in the wider Levant 250000-275000 years ago, Denisovans in Western Asia 251000-266000 years ago, and Sapiens in Eastern Africa 150000-180000 years ago. We propose that the consequence of the two Eurasian speciations was the transmission of African-origin genetic material for larger brains and skulls from lineage to lineage through admixture, so that all three species ended up with similar larger brain sizes (1250-1700 cc). However, because their respective majority ancestors contributed differently to the genomes of the new species, the evolution of big brains led to quite different behavioral and cultural phenotypes across the three species.

Neandertal Speciation

It might be surprising to learn that the oldest fossils of Neandertals described in the literature are rather young, the Italian Altamura and Greek Apidima skulls from 170000-175000 years ago. According to the recent opinion of paleontologist Devianenko, Neandertals arose about 200,000 years ago in the Levant [19]. Well-known crania from Sima de los Huesos (430 kya) [20] and fossils from Biache (France) (240 kya) [21] are classified as pre-Neandertals because of their smaller brains and more primitive teeth than those of genuine Neandertals, respectively. The Sima de los Huesos age leaves them off the main pre-Neandertal branch leading to Neandertals, since the mtDNA tree indicates the influx of pre-Sapiens mtDNA into the Neanderthal lineage at 439 kya, and the Y-chromosome DNA tree indicates inflow from the same source at 387 kya [16]. It has been known for several years that Sima individuals and Denisovans share common ancestral mtDNA, while

doi:10.20944/preprints202604.1479.v1

Neandertals have both mtDNA and the Y chromosome DNA of the pre-Sapiens type, interpreted as a replacement through admixture from African sources [22]. However, analysis of 3 Neandertal genomes paints a different picture for nuclear DNA (excluding Y chromosome DNA). Total pre-Sapiens inflow into the recipient Neandertal genome is about 5%, far outmassing sex-specific DNAs, and is estimated to have occurred around 200-250 kya [23–25]. Further, a 190-200 ky-old Apidima 1 skull from the southernmost tip of Greece provides evidence of the appearance of pre-Sapiens in the Levant at times close to the Neandertal speciation date [26]. We can propose a tentative scenario of Neandertal speciation that incorporates three additional lines of evidence. First, the Neandertal mt DNA tree shows its first split at 270 kya [16]. Second, there was a minority Neandertal admixture with pre-Denisovans 251-266 kya, indicating that the former already existed then [16]. Third, the first Eurasian Mousterian tools, dated to 250-270kya, specific to Neandertals (and Africans but not to Denisovans), were found in Tabun cave in Israel [27]. Also, Peyrégne et al. [24] mention a possible admixture time of 256 kya, obtained with a method different from the one that yielded 200 kya. Following this, we opt for the 250-275 kya date for a 5% admixture between an enslaved pre-Sapiens female and a rare pre-Neandertal male, whose family/band carried both sex-specific pre-Sapiens DNA introgressions, introduced about 150ky before that into pre-Neandertals. Pre-Sapiens females' younger mtDNA was diluted out in backcrosses, leaving the older version of mtDNA in all subsequent Neandertals. We do not expect that either the pre-Sapiens type mtDNA or the Y chromosome was the only sex-specific haplotype present in pre-Neandertal populations during the 275-439 kya interval. All true Neandertals stem from that single union that occurred somewhere in wider Levant attesting to the hybrid vigor of their progeny which exhibited increased cranial capacity from 1200 to 1450 ml, the full robustness specific to to their species, use of Mousterian style stone tools without exception until their extinction, and the ability to replace all other hominins in Europe for the next 200000 years.

Denisovan Speciation

Denisovans are the third human species discovered by aDNA, found in a about 80 ky old finger bone from Denisova cave in the Siberian Altai Mountains about 15 years ago [28]. After a long wait, it was learned that they looked only last year, when a 146-ky-old Harbin skull was identified as belonging to a Denisovan [29]. A number of large hominin fossil skulls similar to the Harbin one, younger than about 200 ky, are known from China but have been attributed to various other lineages. We will follow an informal interpretation by French paleontologists, as presented in a popular book, that all those fossils should be considered Denisovan [30]. Further, we postulate that, similarly to Neandertals, Asian human fossils 500-600ky to about 50 ky old and with intermediate brain capacity skulls, if found, should be considered pre-Denisovans, or Asian Heidelbergensis. The pre-Denisovan lineage underwent two significant events during the 550-250 kya period: an admixture with Erectus at 550-400 kya, and a split of the tropical pre-Denisovans from the pre-Denisovan stem at 350-400 kya. This is highly speculative interpretation of the known facts that Denisovans received superarchaic inflow at 300-550 kya [16], and that the rest of Denisovans split at 350-450 kya from the tropical "Denisovan" branch that admixed with ancestors of Oceanians and Australians 40-50 kya [16,31,32][**]

[**] The paleontological literature claims puzzling survival of Erectus from 0.4 to 0.1 Mya in China and Southeast Island Asia, whereas no such evidence exists for Europe and Africa. However, Javan Ngandong at 118 kya [35,36] and Chinese Dali at 267 kya [37] fossils, besides exhibiting some similarities to Erectus, have an intermediate cranial capacity of 1150 and 1120 ml , respectively, more similar to pre-Neandertals/European Heidelbergensis and exceeding the expected 900-1000 cc of true Erectus, and may be tropical pre-Denisovans/Asian Heidelbergensists that survived to 40kya to admix with Sapiens there. If superarchaics were Erectus, due to the temporal distance from the admixture, more of their cranial features would have passed to intermediate brain-sized tropical pre-Denisovans at 350-400kya and less to the Denisovan species proper proposed here, which arose 100-150 ky later and are big-brained fossils like Harbin, found after 250 kya

doi:10.20944/preprints202604.1479.v1

A second Denisovan genome was recently obtained from a 205-ky-old tooth found in Denisova Cave [16]. The main finding from our point of view, based on the new Denisovan genome, was that it contained about 5% Neandertal DNA, resulting from an admixture of pre-Denisovans with Neandertals 46-61 thousand years prior to Denisovan life. Here, we propose that Denisovans as a species arose from that admixture event at 251 to 266 kya.

The lithic industry of Denisovans in the lower cultural horizons of Denisova Cave shows technical and typological parallels with the Acheulo-Yabrudian complex of the Levant Archaeology [33]

Densiovans from the Altai never used Mousterian tools; their tools were more primitive and of the specific Acheulo-Yabrudian stone tool type, found earlier only in 350-250 ky-old strata at many well-studied paleontological sites in Israel [34]. Since no trace of Neandertals or their tools was found in western Siberia and the Altai prior to 130kya, one can suppose that the location of the admixture event between pre-Denisovans and Neandertals must have been much closer to the Levant, where Neandertals originated, and maybe Asian Heidelbergensis radiated eastward from there, carrying Achuelo-Yabrudian tools. While Mousterian tool-wielding humans, probably just emerged Neandertals, abruptly and totally replaced Acheulo-Yabrudian culture about 250 kya in the Levant, at the battle/admixture site, pre-Denisovan stock was victorious over Neandertals to produce Densiovans from the minority genetic input of one of the enslaved Neandertal females with a special pre-Denisovan male. As an interesting aside, there is a strong preponderance of Neandertal females over males. out of more than ten their fossils found in Denisova cave, younger than about 130ky, to justify the idea that Denisovans beat Neandertals, capturing their females in that later period as well. If correct, this would resolve the interpretation impasse of collaborators from Leipzig and Novosibirsk over Neandertals in the cave [19]***. Maybe the arms advantage never came into play if Neandertal tribes/bands in Western Asia were always 50% or more smaller than the Denisovan ones [16]. Regarding the Densovan admixture date, an alternative approach is to equate it with the time of the split of mitochondrial DNA and the Y chromosome into Denisovan-specific haplotypes. Their split times are 286 kya and about 270 kya, respectively [16]. These times cast doubt on the Denisovan speciation hypothesis, as it occurred too close to, or even before, the Neandertal one. We opted to trust the nuclear DNA age estimates as more precise, given their narrower confidence intervals, whereas mt DNA gave 218 kya and nuclear DNA 205 kya for Denisova 25, whose genome was sequenced. The latter measurement was chosen for reporting its true age [16]. Nevertheless, the Denisovan speciation date is the most speculative of the three discussed here.

Sapiens Speciation

The issue of Homo sapiens speciation is the most complex of the three, as no aDNA exists for the so-called Dark Ages of Sapiens History (50-150 kya) in Africa. The starting and ending dates of the period are derived from DNA analysis of extant individuals. For the first time here, it is considered that all three types of human DNA, nuclear and two sex specific ones, might have originated simultaneously. The inferred date of origin of the Sapiens genome is around 155 kya, as explained in detail below. Mitochondrial Eve and Y-chromosome Adam appeared in Africa 132-155kya and 148kya (AOO Y haplotype excluded****) respectively, according to the recent estimates

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elsewhere in Asia. Therefore, we propose that pre-Denisovan admixture winners soon replaced their minority parent, Erectus, everywhere in Asia by 0.4 mya. If any big-brained fossil younger than that , but older than 50 kya, were to be found in Southeast Asia in the future, our hypothesis would be shown to be in error.

[***] The recent sequencing of a ~105 ky-old male Neandertal from Denisova cave revealed that the ancestors of both him and the 120 ky-old Altai female Neandertal received a minority admixture flow from Denisovans [38], showing that, in at least one battle, Neandertals beat Denisovans and mated with their females.

[****] A00 Y chromosome haplotype is found only in a small Cameroon Mbo tribe among living humans and in aDNA from up to 8kya old genome from the vicinity, at Shum Laka [11]. It is the oldest of the Y haplotypes, appearing to be around 250-350 ky old [16,41,42]. Due to a lack of other A haplotypes of intermediate age up to 148 ky old and the extremely low dispersal of A00 among Africans, the most parsimonious explanation is the

[39–42]. This period ended around 50 kya, when a small tribe of African emigrants gave rise to all presently living non-Africans after mating with Neandertals in Eastern Asia [13]. Also, archaeological evidence of material culture and morphological evidence of human fossils for the period is sparse for the vastness of the continent and contradictory in answering the most basic questions.

Here, a novel interpretation of human genetic results is offered, which does not accept the notions that our species' nuclear genome is twice as old as mitochondrial Eve and that we, for the first half of our presumed 300ky existence, did not improve at all in our material culture over our ancestral species/es.

Archaics are here argued to have coexisted with pre-Sapiens and Sapiens for the last almost million years, up to 5-10 kya in Africa, exchanging genes throughout the period.

All the genetic answers we have for the period come from analyses of DNA differences among the genomes of living people, both African and non-African, and from ancient DNA from Africans dating from 18 kya to the present. Genetic diversity among Africans compared to non-Africans is vastly greater, attesting to their much earlier dates of origin and to their dominance in the number of lineages formed. Statistical inference from complete genome sequences is a complex affair. involving several competing software packages and various educated guesses, restricting models and outputs. Nonspecialist reader of the six major papers answering two main questions, i) when and how Sapiens originated, and ii) when the oldest human lineage of Khoisan branched from the Sapiens stem, will go away with the impression that there is no agreement when and what took place whatsoever [11,17,43–46]. But after quite a bit of nonspecialist immersion, we are reporting that a strong majority provides data for a consensus. In truth, that is not what most consensus authors presented as their main conclusions, and hence, they may oppose this proposal.

However, they cannot deny that they also presented alternative models, extended data figures, and results in their papers, which are surprisingly similar and convergent. One can not think of an explanation for how the outputs in complicated computations can be so unified, unless reacting to the true signal present in the data. Thus, the preponderance of evidence indicates that the speciation of Sapiens was an admixture event, making it the most well-supported of the three speciations considered here.

The summary of consensus on African human genetic history is as follows: an ancestral lineage split into what we call the Archaic and ancestral Sapiens lineages around 1 (0.9-1.1) mya, both of which lived independently, occasionally exchanging genes, until they rejoined to give rise to Sapiens 135-180 kya. Archaics contributed a minority of 16-20% to the newly emerged Sapiens genome, and ancestral Sapiens the remaining 80-84%. However, the minority contribution consisted of genes that could have improved the overall brain function of emerging Sapiens [46]. Apart from consensus, we believe that Sapiens, as a species lineage, emerged from a single hybrid among many produced in this union of lineages, similarly to the two others described above. Her/his progeny, through dominance breeding over many generations, formed a Sapiens population able to separate from the lineages of her/his parents.

Back to consensus, Ancestral Sapiens split off the branch of Neandertal-Denisovan ancestor, here called H. heidelbergensis, and had a severe bottleneck in the period prior to the union. Presumably, shortly after Sapiens' origin/join, the ancestral pre-Sapiens lineage was subsumed into Sapiens or perished, but we do not know that for certain. Arhaics persisted as an independent lineage that occasionally engaged in gene flow with various African lineages until going extinct, possibly very recently (5-10 kya). Arhaics are either explicitly shown or referred to as ghost/unsampled lineages in the consensus papers. Finally, shortly after its origin, the Sapiens stem generated three lineages, in single or two closely timed splits, two of which were Khoisan and Rainforest Hunter-Gatherers (RHG, e.g., Mbuti). The stem disappeared then, or was soon thereafter transformed into Basal Eastern Africans (e.g., Mota or Gumuz). Khoisan split and other major splits occurred 110-190 kya, according

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horizontal transfer of A00 from an Archaic lineage to the Mbo and Shum Laka ancestors sometime after 100 kya. The horizontal transfer of A00 is also mentioned as a possibility earlier [42].

to the papers, and not later than 135 kya in our opinion. Later, in the last 100ky, not necessarily covered in the consensus papers, massive mixing and splitting processes gave rise to numerous genetically distinct tribes existing today in Africa, each with its own mixture of ancestries from three basic lineages, interaction with neighbors, and also some with the recent Eurasian input from 12-17 kya to the colonial era. Back to consensus, the Basal Eastern African lineage split off the ancestral tribe of all Non-Africans in a 50-60 kya time frame, which subsequently migrated to South Western Asia to mix with Neandertals by 47 kya and seed the Sapiens rest-of-world diaspora. The evidence for the consensus is enumerated and explained in the Appendix.

Homo Genus Species: Genomic History of Sapiens: Hunter-Gatherer Niche of Permanent Intertribal Warfare and Extinction of other Species

Let us assume that Sapiens emerged from a mixing event of two archaic lineages. The pre-Sapiens one contributed 80% of the genome, and the Archaics proper contributed 20% of the genome and additional neural functions [46]. Shortly after this event, the first band composed solely of Sapiens individuals was formed (from bands with minority Sapiens members). Although the band's members had intelligence equal to ours and a kernel of a language, they were not alone in the land. There were neighboring bands of humans, consisting of individuals from their ancestral lineages, all around them. For them to be caught in a conflict with any of the others was a losing proposition, since their higher mental capabilities did not translate into any immediate advantages in a war. Using identical arms as archaic arms, they needed time to develop new types of arms and ways of fighting to win bouts against opponents who were more numerous and of higher, or, in the best case, equal, physical strength. They followed the instinct of their forebears and fled in search of uninhabited land where they could be safe and multiply enough to have a chance of surviving the inevitable war. This urge in every band of humans, Sapiens included, to offer war to every encountered band or to flee is a root cause of all human migrations prior to the Holocene. One needs to assume purely demographic reasons for the Sapiens "meta population" puzzle in Africa (see below). There were simultaneously two population clines, one of archaics slowly diminishing in numbers until total extinction 5-20 ky ago, and of Sapiens slowly gaining in numbers after several cycles of near extinction due to archaics' starting superiority in numbers, and, of course, later internecine war among Sapiens tribes indicated by the "archipelago" phenomenon.

One has to consider that Sapiens tribes escaping the African melting pot under war pressure to the Levant at various times were among the most advanced in their time. Sure enough, they survived the long trek through several climatic zones from their place of origin in Sub-Saharan Africa. For instance, the Schull and Qafzeh people in the Levant were the first Sapiens lineage to practice interment, some 90-120 ky ago [47]. Many Sapiens tribes from Africa moved through the Levant on their way elsewhere 60-40 ky ago. One ended in the Rhone region of France 54 kya [48]. Others gave rise to Uluzzian culture at Grotta del Cavallo (Italy) [49] and, probably, to Chatelperonian culture [50], respectively, around 45-40 ky. They all went extinct. The aDNA of Sapiens we have for this period indicates that the event at 47ky from which current Non-Africans originated branches of at least three tribes in Europe: Ranis/Zlaty Kun, Bacho Kiro and Oase I, and one in Siberia, Ust-ishim, which went extinct without contributing their DNA to to modern people and two branches that did, one for Europe and one for Asia [13]

Three Sapiens peoples from Europe and Siberia, Bacho-Kiro in Bulgaria [51], Oase in Romania [52], and Ust'Ishim [53], in Siberia, also had additional Neandertal DNA in their genomes in excess of the initial amount provided by the founding event/s 47kya, unlike the earliest European, 45ky old group in Remis/Zlaty Kun [13]. This means that at least three battles of advancing Sapiens with Neandertals took place in the very own ecological territories of the latter in Europe and Siberia

All in all, there is evidence for 3 mixing events between generalized pre-Sapiens or Sapiens, and Neandertals at 200, 100, and 47 ky [23]. (Note, there is evidence for two more earlier gene inflows of pre-Sapiens into pre-Neandertals, resulting in the latter acquiring mtDNA and Y chromosomal DNA of the former). In the first two events prior to 50kya, Neandertals received a Sapiens minority-DNA contribution to their genome. However, the last time asymmetry went the other way, with a minority

Neandertal DNA contribution. Add to this the same asymmetry in the Oase, Ust-Ishim, and Bacho-Kiro people, resulting from separate mixing events at very similar but later times (40-45 ky). The majority source of DNA in the genome indicates the winner in a battle that resulted in the mixing of the winner's genomes with those of conquered females; out of six bouts, the two earliest were won by Neandertals, but in the last 4 documented cases, Neandertals lost. Winning was easy for Neandertals 275-100 ky ago in the Levant, as pre-Sapiens and Sapiens had neither an advantage in arms nor in tribal size then. However, the situation radically changed 40 ky later. Consequently, if any new Sapiens DNA were found in the genomes of Neandertals younger than 60ky, it would indicate that, in other unrecorded battles/mixing events, they were victorious. None were found. Many authors commented on this asymmetry and found it puzzling if, as currently supposed, encounters among the two peoples were friendly (cf. 56). If Neandertals weakened by inbreeding and losses of population sizes (tribes of not more than 60-90 individuals [16]) could not avoid and were forced into battling with their thrusting spears, the projectile-armed and more numerous Sapiens, then due to the almost certainty of their loss, it is obvious why their numbers dwindled over short time and they finally went extinct over their former European and West Asian territory. At the same time frame, additional admixtures occurred among both pre-Denisovans and Denisovans on the one hand, and the eastward-expanding branches of the founders of Non-Africans on the other. The Denisovan stock contributed to at least three admixture events, leaving up to 6% minority contribution to the genomes of the ancestors of Australians and Papuans, and ~1% on average for other East Asians. Neandertals, Denisovans, and all other unknown human lineages, if they existed, were simply overrun by the expanding, superior-in-war descendants of the founding tribe. After that process ended after a couple of thousand years, at 40kya, the only war in Eurasia after that time took place between bands of Sapiens sharing founder ancestry. Apparently, prior to the Holocene, there was no such thing as race/lineage discrimination, as conquered fertile females were included in the winning tribe, regardless of how different they looked, because they were from other human species. Taking the fossil evidence for the first hominin bush trimming by Erectus and genomic evidence of the seven one-sided admixtures in Sapiens' conquest of Eurasia, there is ground for generalizing that the Homo genus species drove to extinction all susceptible hominin species, including its own minority ancestors.

Homo species: Genomic Hypothesis of Sapiens Origin requires setting aside Earlier Genomic Views as well as a Reinterpretation of the African Paleontological and Archaeological Record

DNA evidence has previously been shown to improve on biological and historical interpretations based on evidence generated by older methods. It is better to maintain this stance rather than use DNA results to confirm beliefs based on trust in approaches established before its availability. In other words, the argument presented here is that while hominin paleoanthropology interpretations may be perfectly valid for older time periods for which aDNA or analysis of extant genome DNAs is unavailable, they might be in error when it comes to Sapiens anthropology. covering the last 300ky for which even DNA of extant humans has much to say in far finer detail, notwithstanding the genomes of extinct Neanderhals and Denisovans. In that light, it is natural that evidence for the explanation of Sapiens speciation considered here is entirely genomic. For this reason, we confront earlier interpretations from both Genomics itself and non-DNA sciences of Paleoanthropology and Archeology, which seem incompatible with the recent evidence and the synthesis argued for here.

For reasons explained in the preceding sections, in this view, Sapiens originated from the merger of two human lineages, here called Archaics and pre-Sapiens.It was an unequal union in which Archaics contributed only 16-20% and ancestral Sapiens contributed the remaining 80-84% to the newly emerged Sapiens genome, enabling its carriers to exhibit all biological characteristics and capacities of modern man, except for inessential cranial and dental ones. Of course, the instant emergence of modernity at speciation is an assumption of punctuated evolution, contrary to the NeoDarwinian gradual one, which would argue for the slow, piecemeal emergence of the modern human phenotype over the entire deep time, from undetectable beginnings to 50kya. We see the lineage of Archaics continuing to exist in Africa in parallel to Sapiens until going extinct, possibly quite recently, 5 to 10 kya. Soon after its origin, the Sapiens lineage split into the Khoisan lineage, and one or two additional lineages (either basal East African/Mota-Gumuz and RHG/Mbuti, or both) 135-100kya, and those events gave rise to all other African lineages.

The long-standing aim of Biology has been to understand the molecular basis of Sapiens' intelligence and language abilities. Geneticists analyzing human genome sequences agree that the answer cannot be found in their science alone, but they point to the old Neo-Darwinian recipe for the origin of biological innovations as the only remaining solution [55,56]. Obviously, here we offer a hybridization speciation as an alternative [1]. It is a mode of speciation known to occur in nature and, therefore, is more likely than the theoretical anagenetic speciation they propose [2].

The problem of Dark Age history, besides the flickering of modernity (see below), seems to be why modernity arose so late after the splitting of the three main branches of Africans (Southern Khoisan, Eastern, and Central-Western Africans), considerable time before it. The paradox is noted in the majority of thinking about human origins from at least 2000 onwards, and especially from 2017, when a 315-ky-old Jebel Irhoud human skull was taken to mean that Sapiens arose before that date [57]. The obvious facet of the problem, as understood prior to this work, was that if Sapiens arose 300 kya, genetics had to explain the inheritance basis of human modernity, which appeared about 200 ky later. To solve this paradox, some genome scientists have tried to separate the genetic and phenotypic sides, saying mutations for those characters might have emerged before the split, but the phenotypes lagged for tens of thousands of years, waiting for the right environmental conditions to emerge worldwide in all lineages simultaneously. In his account for the supposed long delay of the appearance of modernity after the origin of Sapiens, Reich proposed that natural selection favored individuals with an increasing number of alleles needed for modern human behavior over a long time from Sapiens origin to the first appearance of modernity equally, and in all separate lineages ([56] see below). After the 100-200ky-long process of selection and in the right environmental conditions, the necessary allele combination was achieved in surviving individuals and, presumably, after other individuals with insufficient alleles were selected against, modernity appeared simultaneously in all Sapiens lineages.

"Our study .., like most others ..., found that separation [of Khoisan from other Sapiens lineages, RC] *had begun by around two hundred thousand years ago and was mostly complete by more than one hundred thousand years ago" [56], p 17.*

More recent literature in the field treats the matter(RNCR plots) differently (see Appendix), There is a date for origin of Sapiens defined as a time when extant Sapiens genomes began to diversify and a later date for split of Khiosan lineage from either stem, or other Sapiens lineages, different from the Neodarwinian concept of splitting of populations as a gradual process taking a half of species duration. These dates converge on the dates mentioned in the above quote [56] (see Appendix)

"Expanding our analysis to the whole genome, we could not find any location –apart from mitochondrial DNA and Y chromosome – where all people living today share a common ancestor less than about 320,000 years ago."[56], p 18

This should not be understood to mean that the origin of Sapiens diversity occurred earlier than 320 kya, as historian Theroux interpreted it in his book [58]. It simply means that, after 320 kya, to the present, no single mutation at a single or a few locations in the genome has risen to fixation in a selective sweep and is present in all extant genomes. The origin of diversification time is not constrained by these results. It could have been either before or after 320 kya.

…., the genetic formula that may have been necessary to drive the striking advances in human behaviour…… .is not particularly mysterious. The mutations necessary to facilitate modern human behaviour were already in place, and many alternative combinations of these mutations could have increased in frequency together due to natural selection in response to changing needs imposed by the development of conceptual language or new environmental conditions. [56], p21

This is a statement that the solution offered is a standard textbook population-genetics explanation of evolution as a change in mutation frequencies. However, it is complicated by the total lack of usual plausible stories on specific selection conditions needed to impose such unique feats,"striking advances", the most complex in all biology, as the single species -Sapiens- achieved them in the entire evolutionary history of the planet.

The further complicating factor is the undisputed separation of Khoisan and Mbuti from other Sapiens lineages for up to 100,000 years. We are asked to believe that selection conditions imposed by the environment for such a long time were exactly the same across at least three populations living far apart in Africa, producing modernity (intelligence, language) at exactly the same time. This exceeds the envisioned capacity of population-genetics evolutionary formulas tested in simulations, as their models pertain to changes in gene frequencies within a single population. It also implies that Sapiens, as a species, emerged from this process only immediately prior to 50kya, contrary to most paleontological and archaeological evidence.

The punctuated assumption of Sapiens speciation by consensus groups elegantly removes the need to solve the problem addressed by Raich entirely, as Sapiens lineages inherited the modern phenotype from the common ancestor stem they shared. We argue here for the much later emergence and splitting of basal African lineages, which are coincident with the rise of modernity at 145-130kya and may be its cause. This scenario requires Sapiens origin to be focal -at a single geographical area- as for most, if not all, biological species. More likely than not, the location is somewhere on the eastern side of the equatorial belt, from which emerging human lineages radiated into other regions of Africa, (cf. [11], Figure 4) The upshot of technical discussion in section on speciations and Appendix is that human genomics offers a reasonable case, that needs to strengthened further, that Sapiens originated maximally only a few 10ky before his material culture artefacts in the archaeological record started to show an indication of intellectual and language ability. While demographic scenarios can cover that time span, they cannot do so on the assumption that Sapiens was mute and nonintelligent for the full first half of its genetic existence from 300-150 kya.

Current synthetic thinking about the Dark Age in Africa seeks to explain the totality of findings. For instance, Scerri and colleagues have advocated the "metapopulation concept," seemingly also abandoning the usefulness of the human fossil record for understanding African deep history:

> *[…]archaeological record bears no direct relation to a simplistic shift in the human brain but rather reflects similar cognitive capacities that are variably manifested. The interaction of multiple causal factors constitutes the most parsimonious explanation driving the variable expression of complex behaviors, with demographic processes such as population structure, size, and connectivity playing a key role.[…]we are confronted with humanity's deep, variegated roots in Africa, and a dynamic metapopulation that took many millennia to reach the critical mass capable of producing the ratchet effect commonly used to define contemporary human culture [59]*

This concept does not make sense genetically or biologically, as it advocates the reappearance (or disappearance) of major phenotypic traits (intelligence, language) in organisms of the same genetic lineage/background in various places at various times over the period of 100000 years. However, the authors had to take into account the genetic interpretation discussed above, which we argue should be replaced.

Finally, in light of Genomics results, we offer a short, bird's-eye-view critique of some interpretations of other sciences basic to understanding human history. Anthropology has a serious problem in failing to address the nomadic life of Homo lineages. It is accepted that Homo species were nomadic generally, but the error lies in not describing the nature of the nomadic life of our genus Homo ancestors and Sapiens itself. There are three possibilities of nomadic behavior: mostly sedentary with nomadic episodes; locally nomadic in certain geographical areas, however large; and finally obligatory nomadic, moving in any survivable direction without regard for retracing their former steps. The first two possibilities are types of Sapiens behavior that have occurred in the Holocene and among the extant nomadic hunter-gatherers. Based on this data, anthropologists did not consider the third possibility seriously, which, on the other hand, explains much about the deeper past of genus Homo from its origin at around 3 million years ago to 50 Kya . If obligatory nomadic living and group violence are genetically based, instinctive behaviors of the genus Homo, then they both provide the reasons for Homo's biological survival as a lineage, while all other branches of hominins perished worldwide, and the puzzling aspects of Sapiens archaeology can be totally reinterpreted. The Dark Age in Africa lasted so long because of warfare delays, since for a long while, Archaics were as capable as Sapiens. Above, we explored these exciting possibilities, but we have to acknowledge again that our species has the behavioral capacity to overcome these genetically based instincts. It did so in Africa after 50 kya, when, due to a rapid increase in population, obligatory nomads became both localized in fixed areas and less frequently bellicose, and at the dawn of agriculture, when some former hunter-gatherers became totally sedentary in the first cities.

Also, taking the Neandertal cranium as a baseline, Paleoanthropology can not provide a clear progressive picture of African fossil skulls through time. Variously claimed as the first Sapiens, skulls from 315, 220, and 160 kya are still not gracile and globular, and do not have chins. The first such African skull is just 38 ky old Hoffmeyer one [60]. Even more puzzling is the appearance of very archaic skulls at 22 kya in Eastern Africa and 13 kya in Western Africa at Ishango and Iwo Eleru, respectively [61,62]. Both extremes of skull anatomy have occurred much later than 50 ky, when the African Dark Age ended. At best, from this one can conclude that at least one or more archaic lineages of Homo existed alongside Sapiens throughout the African Dark Age, some of which must have been ancestors of fully anatomically modern Sapiens, and that all other parallel groups went extinct without leaving any issue. Genetic results from above show a continuous presence of, maybe numerous, Archaic lineage within Africa from 1000 kya up to 5-10 kya, in addition to Sapiens, thus accounting for at least half of the archaic features of African human fossils from the last 300ky and the late robust skulls mentioned above. However, the basic premise of recent Paleontology so far is that the Sapiens lineage is the only source of human fossil skulls found in Africa.

Following Brace [63], one can speculate that the remaining half of archaic cranial and dental features in pre-Sapiens and Sapiens lineages are plastic, and a direct consequence of degree of decrease in use of insufficiently cooked food in childhood, and degree of increasing use of projectile weapons, both processes reducing muscular and skeletal strength requirements for survival, thus accounting for a nonlinear decrease of robustness (increase of gracilization) with time. In Europe, from 47 kya all the way to Gravettian at 30kya, Sapiens skulls of Cromagnons and some others (Dolní Věstonice, Mladec) are still retaining archaic features similar to Neandertals in cranium, like shape and oversized brains [64], and large jaws and teeth, so the lack of fully modern examples earlier in Africa is not too surprising. In other words, morphology, one of the three legs of evidence deemed necessary for understanding Sapiens' origins during the African Dark Age [65], is here deemed uninformative and in need of reinterpretation.

Archeology, taking Neandertal and African Mousterian culture as baseline, finds the first possible Sapiens improvement consisting of Aterian shafted spear points as early as 150 kya in Northern Africa, and new types of stone tools and pierced shell beads signaling the beginnings of personal adornment appear 145 kya in Aterian culture and after 130 kya in Southern and Eastern Africa. Surely, after 100 kya, modern Sapiens intelligence is in full view. However, everything is highly ephemeral. Intelligent flame from one place disappears for a time or entirely, while appearing at other places with the same irregularity; some stages of improvement are repeated anew in the same or different locations, with West and Central Africa being the least modernized.

Migratory wanderings within Africa can be only indirectly gleaned from such analysis of archaeological findings, but documented long range African excursions into Levant are occurring in many waves started from at least 439 ky by either lineages ancestral to Sapiens or Sapiens itself after 155kya and culminating 49-47 ky ago with the single Sapiens tribe that gave rise to all now living non Africans after undergoing the mating event with Neandertals. This Levant evidence can be most simply generalized to indicate incessant migration in Africa proper as well.

Maybe from 150 kya, but surely from 100ky to 50ky, African material culture is more modern than anywhere else, including the use of bows and even poisoned arrows [68], but then the progress stalled from 5-50 kya. The widespread Initial Upper Pleistocene, characterized by the obligatory use of projectiles (bow and arrow, spear-throwers), was 10-15ky later than in Europe or Asia. The Holocene, similarly, was later in Africa than elsewhere in the world.

But if, for the best use of resources, as one migrates, it makes sense for the whole tribe not to travel together, why is this important? Because it might shed light on possible interpretations of archaeological results. The main information about material culture of humans in Africa was obtained by digging floors of the caves that are mostly not big enough to hold more than 50 people at one time, also from a migration point of view caves are temporary shelters so at any given time tribe needed several such shelters to use if it is to stop for extended time measured in months or years in some vicinity. However, eventually the tribes moved, and the caves were ready for a new wave of humans to settle there. Archaeologists have considered the layers of artifacts dug into cave floors as the result of permanent settlement, so if a given layer contains certain stone tools, it was assumed that the layer, for instance, of a thousand-year resolution, was produced by a single population of humans living there for a thousand years. For example, the assumption is that 30 generations of humans in the same cave produced what is found, but that's not what our obligate migration requirement introduces. So any such layer could contain stone tools from various migrating populations living in caves in a temporal sequence. However, tools are not in a physical sequence because of the layer resolution. Mixing within the layer is such that there is no resolution of 10 years, or hundred years, or 500 years. Simply put, it's impossible to determine who left what within a single archaeological stratum if the cave was visited and lived in by several tribes during that period.

Regarding the "flickering" innovation pattern characteristic of the Dark Age in Africa. The material culture that appears in one place by rule disappears and may appear in another place at another time, somewhat later, but then, in that place too, it disappears. For example, take the Howiesons Poort industry in South Africa. Its innovative tools are present during 51-74 kya, but at different times in tens of caves across a large area within that period, and the industry disappears after that [67]. This pattern is easily explained if the tribe or tribes responsible for it moved around within the general vicinity of South African sites characterized by that culture during those 23,000 years. The "Flickering pattern" is fully explained by incessant migration under the threat of warfare.

The second point concerns so-called "generic MSA (Middle Stone Age) tools". It's a term that describes a persistent, simple but useful set of stone tools, mixed in some places and periods with innovative tools, in layers where the latter could later be found, but also present at various sites where no innovative tools are found throughout that long period [68]. We would like to propose that, about 150,000 years ago in North Africa, when Aterian tanged tools first appeared, the tool signature of archaic populations, also known as "unsampled" or "ghost" populations, became apparent. In other words before that all three lineages, namely pre-Sapiens, Sapiens and archaics could have produced generic MSA tools, but after that modern Sapiens was using such simple tools only occasionally and less and less, pre-Sapiens went extinct, but that archaics, due to their genetic stasis, had to use them for the next hundred and twenty thousand years while continuing to share African continent with modern Sapiens. The Sapiens and Archaics probably fought over females, or alternated in using land resources when one group moved into an area previously occupied by the other. In either case, the cave layers would contain a mixture of tools and other material artifacts from both groups. For example, such a tool mixture, consisting of generalized MSA tools and increasingly advanced modern Sapiens ones, can be seen in all 10 recognizable consecutive layers accumulated over 10000 years spanning the 34-44 kya period in the Kisese II rock shelter in East Africa [69].

Use of AI: Grammarly for Windows was used to edit text and improve English grammar. Sentences suggested by Grammarly were reviewed by the author and accepted only if they improved the text and retained the meaning of the initial version. AI was not used in any other aspect of the work.

Abbreviations

BCE -before the common era, mya - million years ago, kya -thousand years ago. mtDNA – mitochondrial DNA, aDNA - -ancient DNA

Appendix

Evidence for points of consensus

[1]. Split of the ancestral lineage into Ancestral pre-Sapiens and Archaics around a million years ago.

This is first explicitly shown by [43] and later by [44–46] in their main models of human demographic history. [43] places the split at 500 kya, [46] at 1.5 million ya, [45] at 2 million ya, and [17] at 1.3 million ya. However, in [45], alternative models B and A, which we argue below are more reasonable, the time of the split is at 1.2 million kya

[2] Rejoin admixture of Ancestral Sapiens and Archaics-Origin of Sapiens. This result is shown in the main models of [17,44–46]. In addition, [11] in their extended Figure 7 shows their second alternative admixture graph model, with the “ghost modern 1” lineage diverging from the Sapiens stem shortly before Sapiens gave rise to the three main African lineages. We interpret this split as indicating the rejoin of “ghost archaic” lineage (not present in the model of extended Figure 7) with the stem as a logical prerequisite for the immediately following split of Sapiens and ghost modern 1 shown. In their main and first alternative admixture graphs, their “ghost archaic” lineage splits from the stem prior to Neandertals, i.e., in the deep past, as also found above in [1].

[3]. The origin of Sapiens was the minority admixture of the Archaics. Three papers addressed this question on the nature of the join. [17] found archaics contributed 20% to the Sapiens genome, [46] found 19 %, and [45] came up with 16.5%. The similarity of those numbers is striking, suggesting that the true fractional contribution to the majority of the pre-Sapiens genome is well represented. However, the 16.5% figure comes from the second- and third-best models in [45], whereas their chosen model has it at only 4.4%. In the next topic below, the assessment is given that their second- and third-best models are more accurate.

[4]. When did the Origin of Sapiens take place? At first glance, each of the 3 papers addressing the rejoin time provided estimates that differed roughly by 100kya. [44] has the youngest date of 98-119 kya, [45] slightly more than 200kya, and [46] came at 300 kya. However, the papers provide grounds for alternative, more similar estimates. The footnote gives reasons for taking [46] results to indicate origin time as around180kya[*****]. In short, they used twice as many non-African genomes as African

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[*****] We now believe data of [46] show not 300 but 170-180 kya for time of rejoining of the two long split lineages of Archaics and pre-Sapiens to produce Sapiens. which nicely aligns with 132-155 kya for mt DNA and ~148 kya for the Y chromosome, respectively. There are issues with their Figs 4 and extended data Fig 2 that may call into question their time estimate for rejoining at the origin of Sapiens at 290 kya. Of course, the authors did not read the admixture time from the graphs. They used an algorithm to iteratively search for the maximal positive difference in probability between cobraa and PSMC. Results were presented in (the extended data Fig. 2). That iteration was indicated in a matrix of 11 split times and 12 rejoin times for each human population [132 cells]. The maximal result cell was labeled yellow. Again, in the 6 African matrices, yellow cells were significantly younger on average (-180K rejoin, 1.1 million split) than the 19 non-African ones, which were closer to the reported 290K rejoin and 1.5 million split. Thus, the lack of homogeneity in the calculation of split and rejoin times across the two human groups is a fact that the authors even admit in the sentence of their disscusion section refering to extended data Fig.2.

There is a recent parallel in the literature that explains why RNCR analysis, as used for dating divergences in [46], can yield earlier dates than the true ones, and not due to ghost populations, as the authors imply. Long-standing claim that (Australians and) New Guinea Papuans show the wrong earliest split of all other Out of Africa lineages due to 1-2% presence of 120ky-old ancestral lineage DNA in their genomes [70] is explained away as an artifact of demographics, since this lineage had both a strong bottleneck and a very slow population growth [15]. Similarly, if all Non-African samples show earlier divergences than African samples here, this may genomes in their analysis. For reasons that are not clear, Africans only give time around 180kya, and results for NonAfricans clustered at over 300kya (their extended data Figure 2). As indicated above, we chose to trust the second and third models over the main model of [45] for four reasons, even though they had slightly lower likelihoods. First, these models have their 16.5% archaic contribution closer to that of [17,46] as indicated above. Second, both models place the origin of Sapiens closer to the present day, around 150 kya. Third, they separate the origin of Sapiens from its later split into Khoisan and one or two other main African lineages. Fourth, they double the contribution of unsampled (read: archaic/ghost) lineage(s) to reticulating African lineages post their main split, as described in [3] above. In the consensus statement above, the lower bound for Sapiens' origin was stated at 135 kya. Here we explain why. 96-119 kya dates of [44] should be replaced with their own lower bound of 135kya. They offer two models. The one showing the preferred likelihood has the rejoin at the Sapiens origin at the latest date, around 100 kya, while the alternative does not. However, the former argues for a biological impossibility: that archaics had two rejoin events, one with the Khoisan stem at 119 kya and the other with the stem of all other Africans at 98 kya. In other words, their preferred model requires that events 10kya apart produced identical Sapiens intelligence and language ability in two different lineages, which is contrary to expectations of both Genomics and Cladistics. Additionally, it requires that the Khoisan stem and one for other Africans arose from a split of the ancestral Sapiens lineage at 479 kya, and that they remained in complete genetic isolation from each other and the Archaics for 350 ky before the rejoining events. Less importantly, archaic lineage persists after rejoining events and then merges into the West African lineage around 15 kya. On the other hand, their alternative model, although lacking the rejoin, is reasonable in every other aspect, including gene flow between archaics and the three original African lineages, which split at 135 ky into Khoisan and others, which then split into East and West Africans at 60kya. Also, this model shows the extinction of the archaic lineage around 5-10 kya. Since the split producing Khoisan at 135 kya is believable, the origin of the Sapiens join, fuzzily indicated by their first model, must have occurred fairly shortly before 135 kya. This is how one comes to the lower bound for Sapiens origin, which is set at 155 kya, the average for the date of origin of Sapiens (average of more than 135, 150, and 180 kya dates)

[5] When did the Khoisan split from other Africans? From the graphics of the models of [43,46], one can discern dates of 190 Kya and 170 Kya for this event, respectively. Above in [3] and [4] arguments are offered that the best dates for [44,45] in their alternative models are 110 and 135 Kya, respectively… This gives an average of around 150kya

[6] What are the other main lineages of Africans, and what is the evidence that they split simultaneously with Khoisan or shortly after ? Unfortunately, some consensus papers, such as (43,46), have too few African samples to answer these questions. Others are uninformative on some finer points due to particular sample choices. The most complete answer is provided by [11,12], who, in addition to a sufficient number of extant African samples, have the benefit of using all available African aDNA samples, the oldest of which is from 18kya. For simplicity's sake, only colored graphs of admixture analysis [11,12] will be discussed. The Sapiens stem is split into three sub-stems: Khoisan, Central Africa HGs (Baka, Mbuti), and Basal East African. Others leave the origin of sub-stems unresolved: [44] the alternative model, [45] alternative model B, and [46] agree that Khoisan split first (for the timing of this event, see [5]). Yet differing in what was left, [45] saw the rest of the African sub-stem, which split shortly after (~100kya) into Central African RHG and Basal Eastern sub-stems (Hadza). [44]- their alternative model proposes the first split yielded Khoisan and Basal Eastern lineage, which, much later , around 60 kya, split off Western Africans, and 1-5 kya later the branch of future Eurasians, before continuing to present in Gumuz. [46]- see that after the Khoisan split, the original Sapiens lineage continues to present West Africans, with just the splitting of the Eurasian lineage at ~60kya. [44] lack Central Africa RHG samples, and [46] both those and any East

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be because their Out of Africa ancestor lineage underwent a strong bottleneck before emerging in Eurasia with a tiny effective population of around 800 [15].

African ones as well. [11,12]-show only one of three branches created after the initial split/s as splitting later into major stems. It is a basal East African lineage that ends with a 4ky-old Mota genome [71]. The two lineages split off in the approximately 60-80kya range. First lineage that will soon split of into East African agro-pastoralists and lineage of Western Africans, and not long after it the lineage of future Europeans Complex Western African lineage consecutively splits of North African lineage/s (Taforalt), Basal West Africans, Mende-Yoruba stem and Bantu associated lineage before ending in present Lemande This picture of genealogy of Africans suggests basic events of origin of Sapiens, origin of future Eurasians and origin of Western Africans including Bantu took place in or around Horn of Africa ([11], Figure 4). Papers with estimated divergence times mentioned above bracket this period of human history at approximately 60-150 kya.

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