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Author manuscript
Curr Opin Genet Dev. Author manuscript; available in PMC 2015 December 01.

Published in final edited form as:
Curr Opin Genet Dev. 2014 December ; 29: 120–132. doi:10.1016/j.gde.2014.09.003.

The peopling of the African continent and the diaspora into the new world

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Abstract

Africa is the birthplace of anatomically modern humans, and is the geographic origin of human migration across the globe within the last 100,000 years. The history of African populations has consisted of a number of demographic events that have influenced patterns of genetic and phenotypic variation across the continent. With the increasing amount of genomic data and corresponding developments in computational methods, researchers are able to explore long-standing evolutionary questions, expanding our understanding of human history within and outside of Africa. This review will summarize some of the recent findings regarding African demographic history, including the African Diaspora, and will briefly explore their implications for disease susceptibility in populations of African descent.

Introduction

Current paleontological and genetic evidence indicates that anatomically modern humans (AMHs) arose in Africa ~200 thousand years ago (kya) and have lived continuously on the African continent longer than in any other geographic region. African populations are characterized by higher levels of within-population and between-population genetic diversity relative to non-Africans consistent with a larger long-term effective population size of ancestral African populations [1–3]. The history of Africans has encompassed other demographic events such as population structure, admixture, long-range and short-range migration that have shaped patterns of genetic variation in modern populations [1,4]. In recent years, the resequencing of large portions of the genome and their analysis with new computational methods have increased power to infer past demographic events at an

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Conflict of interest
The authors declare no conflicts of interest.

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unprecedented resolution. Most notably, the recent finding that non-African populations share ancestry with Neanderthals, consistent with a model of archaic introgression, has provided additional insights into human evolutionary history. However, the extent of archaic admixture in diverse African populations still remains unclear. Given the central role of Africa in human evolution, characterizing extant genomic variation in diverse Africans will be important for reconstructing both ancient and recent demographic events, and for identifying variants that play a role in disease susceptibility in African populations. Here, we summarize our current knowledge of modern human origins and patterns of genetic diversity in populations of African descent, as well as explore their implications for the risk of complex disease.

The origin of anatomically modern humans in Africa

The earliest suite of derived morphological traits associated with AMHs was identified in fossils from Ethiopia dating to ~160–195 kya (Figure 1; Table 1) [5–7]. Other early AMHs displaying modern features were also found in Ethiopia, Sudan, Tanzania and South Africa dating to >100 kya and in the Middle East dating to ~100 kya (Figure 1; Table 1) [8–12]. Although eastern Africa has often been considered the geographic location of modern human origins ~200 kya, some have argued that South Africa is the site where AMHs originated. Indeed, a recent study suggested that the geographic distribution of genetic diversity in Africa, as measured by linkage disequilibrium (LD), is more consistent with a South African origin of modern humans [13]. However, this inference does not account for the possibility that the geographic location of populations in the present may have differed in the past. Furthermore, a large-scale analysis of southern African populations demonstrated the difficulty of localizing the origin of modern humans using summary statistics of diversity, such as LD [14••]. Nevertheless, regardless of the precise location of origin, paleontological and genetic evidence indicates that AMHs evolved on the African continent.

Recent archaeological data also showed that modern behavior (such as symbolic culture and complex tool production) arose at a relatively early stage of human evolution, contrary to prior studies that argued for the later development of complex cognition ~45 kya [15,16]. In particular, technological advances in the form of heat-treated microlith stone tools were found in southern Africa dating to ~71 [17•,18]. The use of pigment, art and ornamental shells, indicative of artistic expression, was also documented as early as 164 kya in South Africa [19,20] and around 87 kya in northern Africa [21]. In addition, it has been suggested that the highest levels of linguistic diversity occur in Africa and that linguistic diversity decreased as modern humans migrated across the globe from Africa ~50–70 kya [22•,23]. Thus, key behavioral and morphological traits that define modern *Homo sapiens* may have evolved fairly closely together in Africa over the last 200,000 years.

Ancient population structure in Africa

Several studies suggest that ancestral African populations were genetically differentiated before the expansion of modern humans from Africa ~50–100 kya. In particular, analyses of autosomal loci inferred divergence between the ancestors of Khoesan-speaking San hunter-

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gatherers and other African populations >100 kya [14••,24•,25–29]. This inference is in agreement with *mt*DNA and Y-chromosome studies that estimated divergence between the ancestors of Khoesan-speakers and other sub-Saharan Africans at >90 kya [14••,30–32]. Analyses have also detected substantial genetic differentiation in Central Africa, particularly between Pygmy and nonPygmy populations that are inferred to have separated ~60–70 kya (Figure 2) [30,33,34]. These estimates of divergence suggest an ancient origin of Khoesan-speaking and Pygmy hunter-gatherer genetic lineages, and provide evidence for deep genetic structure in Africa.

In addition, a genome-wide study of a larger set of diverse Africans detected even more extensive population structure within Africa. Specifically, an analysis of 848 short tandem repeat polymorphisms (STRPs), 476 insertion-deletions (INDELs) and 3 single nucleotide polymorphisms (SNPs) genotyped in ~2400 individuals from 121 geographically diverse populations indicated 14 genetically divergent ancestral population clusters in Africa [3]. Each cluster consisted of populations that shared genetic similarity, as well as cultural and/or linguistic properties (e.g. Pygmies, Khoesan-speaking hunter-gatherers, Bantu-speakers, Cushitic-speakers). Thus, populations that speak languages belonging to the same linguistic family, for example, tend to have high levels of genetic relatedness. However, in some cases, there is discordance between linguistic and genetic affiliation due to a language shift, which can occur when the language of an expanding population is adopted by another population with little accompanying gene flow [3,35]. In addition, some linguistically-defined groups have shown evidence of fine-scale genetic differentiation, such as the northwestern and southeastern Khoesan-speakers in the Kalahari who are proposed to have separated within the last 30,000 years, as well as the Bantu and non-Bantu Niger-Kordofanian-speakers in western Africa [3,36,37•]. Overall, the observed population sub-division in Africa could have been facilitated by a number of factors, including physical barriers such as mountains and desert, as well as past climatic shifts that may have isolated sub-populations for periods of time followed by limited contact between groups [38,39].

Archaic admixture in Africa

With the recent increase in whole genome sequence data from fossil remains, a number of studies have identified regions of the genome in non-African populations that likely originated from archaic hominins, such as Neanderthals and Denisova (Figure 2) [24•,40–44,45••,46,47, 48•,49]. As more researchers explore the possibility of introgression in Africa, evidence for archaic admixture in African populations is emerging [50–53]. For example, a resequencing study of 61 autosomal intergenic regions detected longer blocks of LD than expected under a model of no admixture in western Biaka Pygmy hunter-gatherers, and suggested that these divergent haplo-types may have been introduced into the ancestors of the Biaka Pygmies by an unknown hominin species in Central Africa (Figure 2) [51]. A whole genome sequence analysis also identified overlapping regions of inferred introgression among Hadza, Sandawe, and Pygmy hunter-gatherers consistent with an admixture event with an archaic hominin in Africa predating the divergence of these populations [26••]. Additionally, a recent comparative study of African and Neanderthal genomes reported Neanderthal ancestry in East African and African American populations [47,54••,55•]. However, it was inferred that this introgression was likely due to recent

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admixture with non-Africans who could have introduced archaic DNA into these populations of African descent [47,55•]. Interestingly, a survey of Y-chromosome variation found a lineage (A00) that is highly divergent from other known lineages in an African American individual which could have an archaic origin [56]. Additional analyses are needed, however, to determine whether or not the presence of this unusual genetic lineage arose in humans through ancient population structure or archaic introgression.

Given the poor preservation of DNA in African fossils, direct comparison between modern and archaic African genomes, analogous to analyses of archaic admixture in non-Africans, is not currently feasible [1]. Therefore, until high quality archaic DNA is recovered in Africa, future studies will need to rely on robust computational methods, together with additional African genomic data, to further explore this question of ancient admixture, including the timing and location of admixture events. Intriguingly, the presence of archaic DNA in African populations also raises the possibility that the higher levels of diversity in sub-Saharan Africans compared to non-African populations could partially be the result of archaic admixture [57].

Migration and admixture

Although ancient admixture remains challenging to infer, more recent migration and admixture in Africa have become increasingly clear. One of the most significant migration events in recent history has been the expansion of Bantu-speaking agriculturalists first into the equatorial rainforests and then into eastern and southern Africa ~3–5 kya (Figure 3). Studies of autosomal and Y-chromosome loci have reported a relatively high level of shared variation among western Bantu Niger-Kordofanian-speakers as well as the presence of Bantu Niger-Kordofanian ancestry in many eastern and southern African populations [3,58], consistent with widespread migration across Africa. Furthermore, the highest frequency of the Y-chromosome lineage, E1b1a, typically associated with the Bantu expansion, occurred in western Africa and the frequency clinically decreased with geographic distance from this region, suggesting migration from an origin in western Africa [58,59]. These genetic results are congruent with linguistic data that proposed a West/West Central African origin for the spread of Bantu languages into East and South Africa [60–64]. Thus, the radiation of Bantu-speakers simultaneously involved the movement of people, language, and genes across the continent [35].

Other major migration events in Africa include the dispersal of Nilo-Saharan-speakers from Sudan both west-ward into Lake Chad ~8000 years ago and eastward to Kenya and Tanzania ~3000 years ago (Figure 3) [2,57]. Many Nilo-Saharan-speakers in East Africa also have high levels of Cushitic Afroasiatic ancestry, implying a long history of admixture between Nilo-Saharan and Cushitic-speakers, in agreement with archaeological data [2,3,65]. Recent data have also demonstrated the presence of the East African-specific mutation (C-14010) associated with lactose tolerance in southern Africa, suggesting gene flow between these geographic regions [66,67,68••,69]. Additionally, although present-day northern Africans are genetically differentiated from sub-Saharan Africans, populations in northern Africa have low levels of ancestry from western and eastern Africa [3,57,70–76], likely reflecting

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historic migration from these geographic regions into different parts of North Africa (Figure 3).

The genetic history of Africans has also been influenced by back-migration of non-African populations into Africa (Figure 3). For example, a genome-wide analysis detected substantial Maghrebi/Near Eastern ancestry in North African populations, resulting from ancient and recent migration of non-Africans into North Africa pre-sumably within the last 40,000 years [77]. Studies have also found a high proportion of non-African ancestry in Cushitic-speakers and Semitic-speakers from East Africa attributed to admixture >7 kya [78], as well as low levels of West Eurasian ancestry (European or Middle Eastern) in Khoe–Kwadi Khoesan-speakers in southern Africa [79]. The West Eurasian component present in southern African Khoe–Kwadi-speakers could have been acquired indirectly by these populations through admixture with migrating pastoralists from East Africa who have high levels of Cushitic ancestry [3,79,80]. This hypothesis of gene flow from eastern to southern Africa is further supported by other genetic and archaeological data documenting the spread of pastoralism from East to South Africa ~2 kya [37•,68••,79,81,82]. More recently, Europeans, South and East Asians have also migrated and admixed with local populations in southern Africa, giving rise to the modern-day ‘colored’ populations within this geographic region [3,57,83,84]. Overall, these above studies demonstrate that migration with subsequent admixture occurred at different points in time and over a wide geographic range, resulting in complex patterns of genetic variation in Africa.

Origin of African hunter-gatherer populations

Human populations practiced hunting-gathering/foraging strategies for much of their evolutionary history (Lee and Hitchcock, 2001). However, little is still known about the origin of African hunter-gatherer populations. Recent genome-wide SNP data indicated shared ancestry among East (Hadza and Sandawe) and South (San) African Khoesan-speaking hunter-gatherers [37•] consistent with the results of a previous *mt*DNA and Y-chromosome study [85]. Furthermore, *mt*DNA and Y-chromosome data suggested that these Khoesan-speakers likely shared a common ancestor ~35 kya and that the East African hunter-gatherers diverged from each other ~15 kya [85]. Interestingly, studies of genome-wide variation have found that Central African Pygmy and San hunter-gatherers share common ancestry, suggesting either an ancient common origin or gene flow among these populations [3,86]. These studies are congruent with Y-chromosome data showing uniquely shared lineages between Pygmy and Khoesan-speaking populations [30]. In addition, other analyses have inferred common ancestry among San, Hadza, Sandawe and Pygmy hunter-gatherers, implying a deep link between these populations [3,26••]. However, these latter results are also consistent with the possibility that shared variation among African hunter-gatherers could have arisen through gene flow between the ancestors of the San and Pygmy populations or by the loss of shared alleles in the ancestors of the Hadza and Sandawe [26••].

Among hunter-gatherer populations, the ancestors of San Khoesan-speakers are inferred to have separated from other Africans >100 kya, representing the earliest population split in the modern human lineage (Figure 2) [25,29,88]. Furthermore, studies of African *mt*DNA and

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autosomal diversity have suggested a deep time of divergence between the ancestors of Central African Pygmy and non-Pygmy populations ~60–70 kya [30,33,34] and a later divergence between ancestral western and eastern Pygmy populations >18 kya [29,30,33,34,89]. Fine-scale substructure was also observed among western Pygmies who diversified ~ 2.8 kya, possibly due to recent geo-graphic isolation, genetic drift, and differential levels of admixture between Pygmies and neighboring Bantu-speaking agriculturalists [30,33,34,90–93]. In addition, other analyses of autosomal and *mt*DNA variation inferred a higher effective population size (N_e) for the ancestors of Bantu-speaking agriculturalists with respect to Pygmy hunter-gatherers. These differences in N_e likely reflect the recent population expansion of ancestral Bantu-speakers associated with the emergence of agriculture and strong bottleneck events, occurring as early as 20 kya, in ancestral Pygmy populations [29,30,33,92,93].

Signatures of the trans-Atlantic movement

Africa is the geographic origin of millions of individuals of recent African descent in the United States and Caribbean whose ancestors were forcibly brought to the New World as slaves. Historical records have documented the movement of Africans into this region of the world primarily from locations along the western coast of Africa (from Senegal to Angola) (Figure 3) [94]. Subsequent to migration of indigenous Africans, there was considerable admixture with Europeans with a smaller contribution from indigenous American populations. Specifically, Afro-Caribbean populations are estimated to have ~65– 95% West African, ~4–27% European, and ~0–6% Native American ancestry [95–99]. Although pooled individuals from the Caribbean have a high proportion of African ancestry, fine-scale genetic structure has been observed within and between islands (particularly, Dominica, Grenada, St. Kitts, St. Lucia, St. Thomas, St. Vincent, Jamaica, and Trinidad) due to regional differences in levels of African and/or European ancestry [100•]. Similarly, a study of genetic admixture within Puerto Rico showed that levels of African ancestry varied geographically with the highest proportion occurring in the eastern part of the island where African slaves and their descendants historically engaged in sugar pro-duction [101]. In addition, genome-wide data have suggested that patterns of genetic ancestry in Cuba, Puerto Rico and Hispaniola (the Greater Antilles) were consistent with a model of two migration events from different regions of western Africa, implying that Afro-Caribbean populations have mixed African ancestry [102•]. These results are also congruent with a Y-chromosome study that found diverse haplotypes in Afro-Caribbeans from the Bahamas that were inferred to originate from different ethnic groups within West Central Africa [103]. Furthermore, isotope data from skeletal remains of enslaved Africans in Barbados suggested that first generation captives had different dietary histories likely due to differences in their geographic origins in Africa [104]. During the slave trade, the Caribbean has been an end-point of migration for hundreds of years, resulting in diverse genetic patterns. Because of the complexity of past migration events, additional studies across a broader geographic range of the Caribbean are needed to fully understand the extent of genetic variability and the different demographic processes that have contributed to it in Afro-Caribbean populations.

African Americans also have a high proportion of ancestry originating from western Africa, particularly Bantu and non-Bantu Niger-Kordofanian ancestry [3,36,105]. However, African

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Americans are characterized by genetic variability between populations living in different regions of the United States. An analysis of Y-chromosome loci genotyped in ~1300 individuals from Africa, the Caribbean, the District of Columbia (DC) and South Carolina (SC) detected genetic differentiation among African Americans that was largely attributed to geo-graphic differences in levels of European admixture [106•,107]. Specifically, a low proportion of European admixture was observed in individuals from SC compared to DC. These findings are in agreement with a prior study that also found low levels of European ancestry in SC, particularly among the Gullah Islanders [107,108]. Genome-wide data also demonstrated that individuals who self-identified as African American have a range of genetic ancestry with some individuals showing close to no West African ancestry, while others have almost complete West African ancestry [36]. Indeed, these studies indicate that populations of African descent have a complex history resulting in genetic heterogeneity. In the future, African Americans could potentially become more genetically diverse. Particularly, this pattern could emerge as individuals migrate from regions of Africa, not originally represented in the African Diaspora, into the United States contributing ancestry to subsequent generations of individuals who may self-identify as African Americans.

Implications of genetic structure and admixture for disease susceptibility mapping

Given the complex population history in the United States and Caribbean, it is not surprising that populations of recent African origin are genetically heterogeneous. This pattern of diversity has implications for traditional mapping studies of disease loci, which rely on accurate knowledge of population structure in cases and controls to avoid erroneous associations [1,109,110]. An alternative strategy specifically aimed at identifying variants associated with differential disease risk in admixed populations is mapping admixture by linkage disequilibrium (MALD) or ‘admixture mapping’. This approach uses admixture information to localize disease-associated polymorphisms that are divergent in frequency in the parental populations that have contributed to the population under study. MALD assumes that the genomic region containing disease-susceptibility alleles will be enriched for ancestry from the parental population in which disease risk is more prevalent [111]. Thus, MALD can be used to identify regions of the genome that potentially contain loci associated with differential disease susceptibility. Indeed, recent successes using this approach include the identification of loci underlying hypertension-attributed kidney disease [112,113] and prostate cancer [114,115], which disproportionately affect individuals of African descent.

Evolutionary history has influenced patterns of genetic variation, including the frequency and/or distribution of disease-susceptibility alleles in human populations, which could have implications for the onset of disease. For example, alleles at several genes associated with age-related macular degeneration (AMD), which is a break-down of tissue at the back of the eyes responsible for fine-scale vision, have been observed at different frequencies in human populations. In particular, the G-allele at SNP rs2230199, correlated with increased risk for AMD, is found at much higher frequency in European populations compared to African and Asian populations [116]. A number of studies have also reported higher mortality rates for

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several types of cancers, including breast, ovarian and prostate, in individuals of African ancestry compared to individuals of European or Asian descent [117–120]. Although environmental factors such as diet and access to health care play a key role in differential disease risk, genetic variation also contributes to differences in cancer susceptibility between populations. Recently, micro-RNAs (miRNAs) have been correlated with the onset, progression, and/or metastasis of cancers with known health disparities among populations. For example, the T-allele (rs12355840) within miRNA hsa-mir-202 has been shown to down-regulate expression of known cancer genes, and to be protective against breast cancer mortality [121]. A recent analysis of global miRNA variation demonstrated that African and African American populations have a lower frequency of the hsa-mir-202 T-allele compared to non-Africans [122], raising the possibility that differences in allele frequency at this locus could potentially contribute to current disparities in breast cancer mortality.

Whether these between-population differences in the frequency of alleles associated with disease susceptibility are due to demographic history or natural selection requires more detailed analyses. However, it is clear that differences in the frequency of alleles correlated with disease exist among human populations. A recent con-sequence of this finding has been the emergence of ‘racialized medicine’ to treat diseases that disproportionately affect a given population. This strategy assumes that the frequencies of genetic variants influencing drug metabolism and/or the onset of disease are different between ‘races’ (i.e. the categorization of individuals into discrete groups based on shared physical and/or cultural characteristics) but similar among individuals within the same ‘race’ [123]. However, members of a self-identified ‘race’ may not necessarily be genetically homogenous as previously discussed for populations of recent African descent. For admixed populations, like African Americans, it may be more beneficial to determine individual ancestry and to devise treatments based on personalized genomic variation.

Conclusions and future directions

Over the last several years, genetic analyses of ever-increasing numbers of genomes have provided significant insight into human evolutionary history. However, a continued challenge has been the inclusion of diverse African populations in studies aimed at investigating fine-scale population structure and ancient demographic pat-terns, including archaic admixture in Africa. Given the complex human population history in Africa, putative evidence for archaic admixture will need to be weighed against alternative scenarios, such as ancient population structure, that could give rise to similar patterns. To date, the genomes of a small fraction of the 2000 ethno-linguistic groups in Africa have been sequenced. As the cost of whole genome sequencing decreases, it will become feasible to conduct large-scale genomic sequencing of ethnically and geographically diverse Africans for the more detailed study of human population history. Furthermore, the integration of genomic information with phenotypic data, including health-related traits and tissue-specific gene expression, will be beneficial for identifying novel variation underlying complex disease in populations of African descent. Overall, these studies will shed light on modern human origins, African population history, and the genetic basis of complex traits, including disease susceptibility.

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Acknowledgements

We thank Alessia Ranciaro and Renata Rawlings-Goss for crucial review of the manuscript and/or figures. The authors are funded by the US National Institutes of Health grant 5DP1ES022577 05 to S.A.T.

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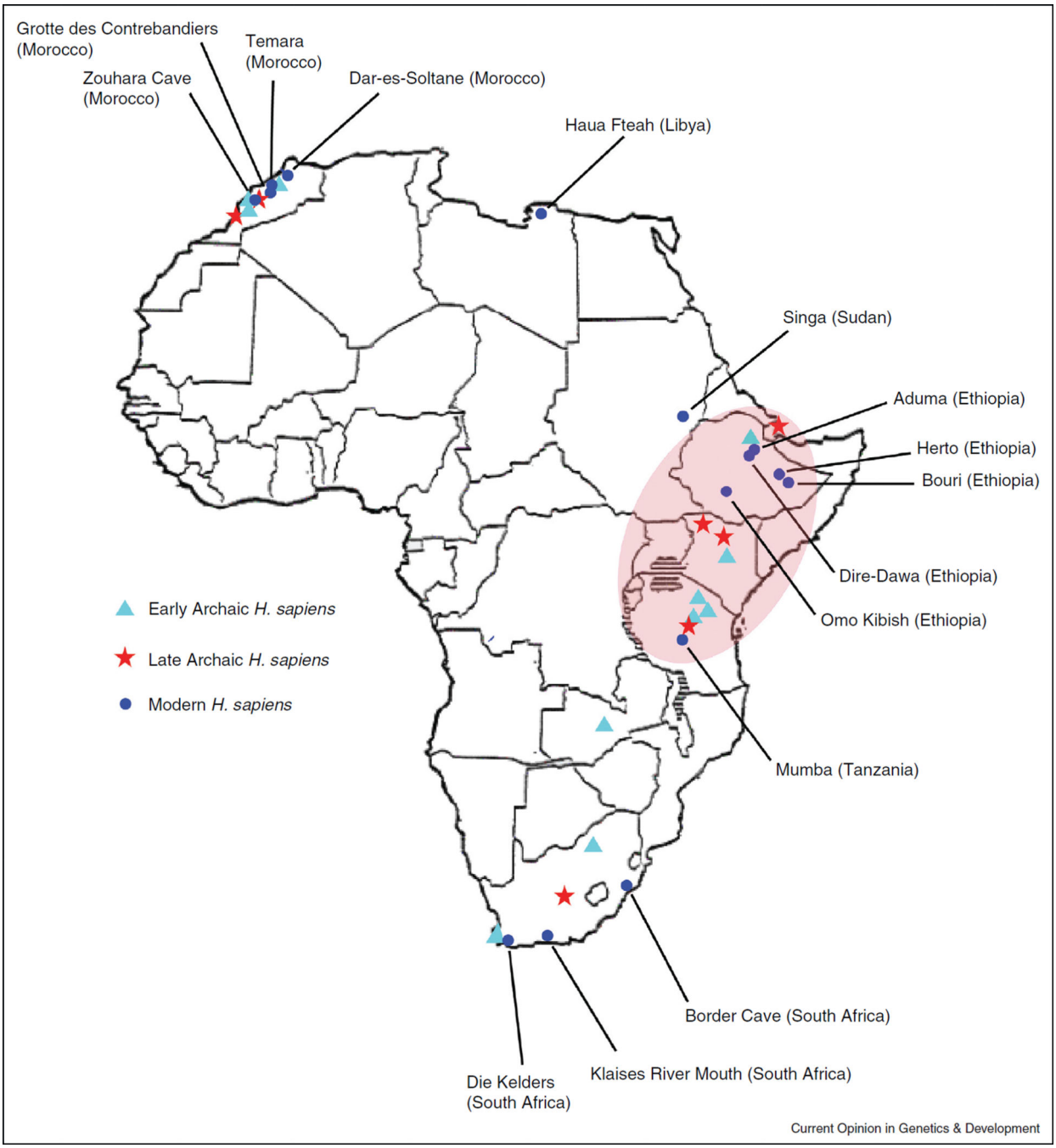

Figure 1.

The geography of major *Homo* sapiens (*H. sapiens*) fossil sites. This map, adapted from [8], illustrates the geographic distribution of sites in Africa where early archaic, late archaic and modern *H. sapiens* have been found. The labeled sites are the names of fossil remains that have been designated as modern *H. sapiens*. A more detailed description of the 'modern' features of these fossils is given in Table 1.

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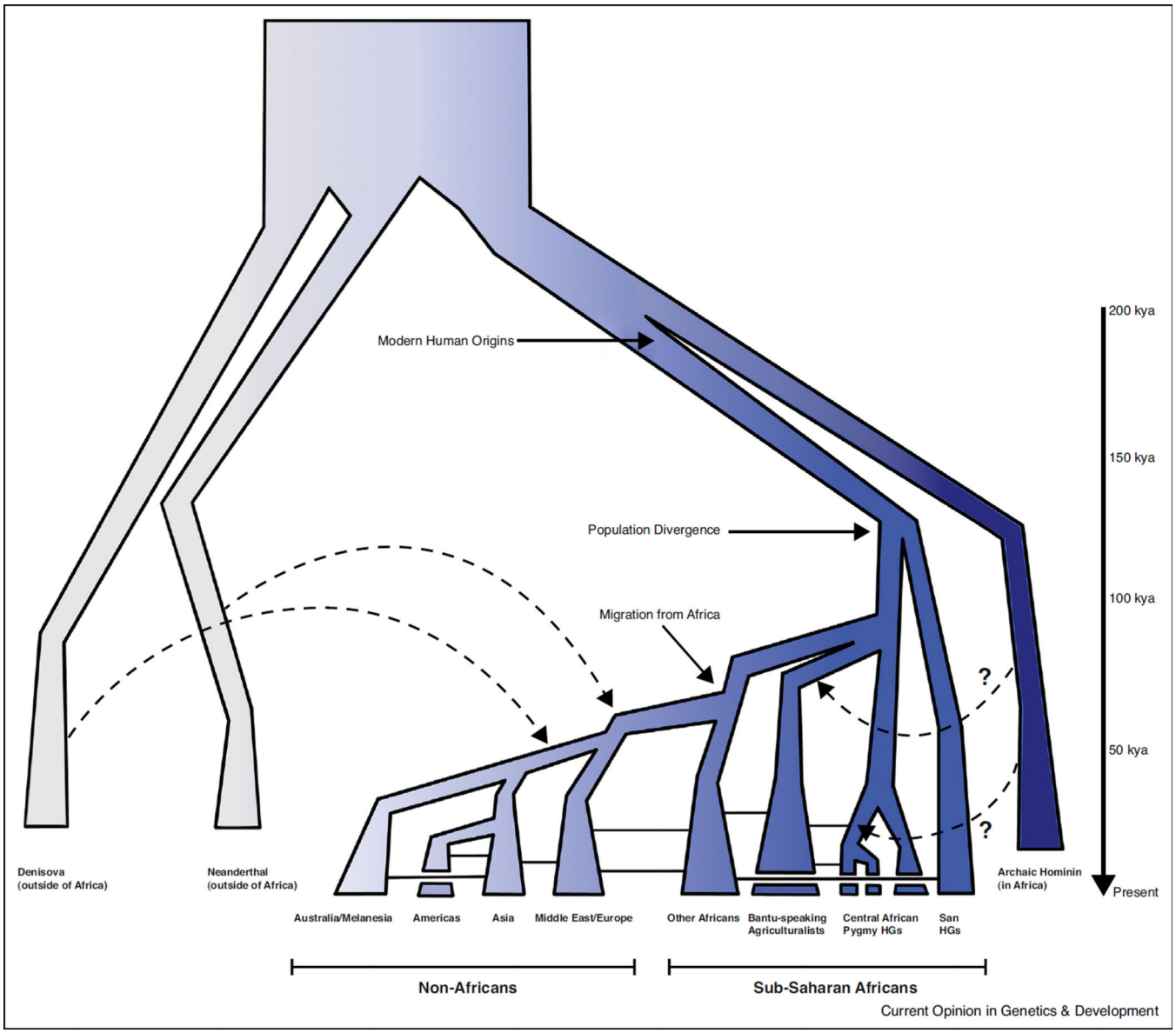

Figure 2.

A model of divergence and admixture in Africa. This figure illustrates some of the proposed divergence events in Africa, for example the divergence of San Khoesan-speaking hunter-gatherers (HGs) ancestors >100 kya [25,29], and the differentiation of the ancestor of Pygmy HGs from a non-Pygmy population ~60–70 kya [30,33,34]. Genetic substructure has also been detected among western Pygmies who also show evidence for admixture with Central African Bantu-speaking agriculturalists [30,33,34,90–93]. Solid lines indicate gene flow between the ancestors of modern populations, and the dashed arrows indicate archaic introgression. Studies have reported evidence for archaic introgression from an unknown archaic species into several populations including the Biaka Pygmy and the Yoruba [46,51,53] shown here by the dashed arrows and question marks (which indicate that additional studies of African populations are needed to understand the extent and timing of archaic admixture in Africa). Lastly, the decreasing intensity of the blue color within the

modern human lineage represents the loss of diversity as AMHs migrated across the globe from Africa within the last 100,000 years.

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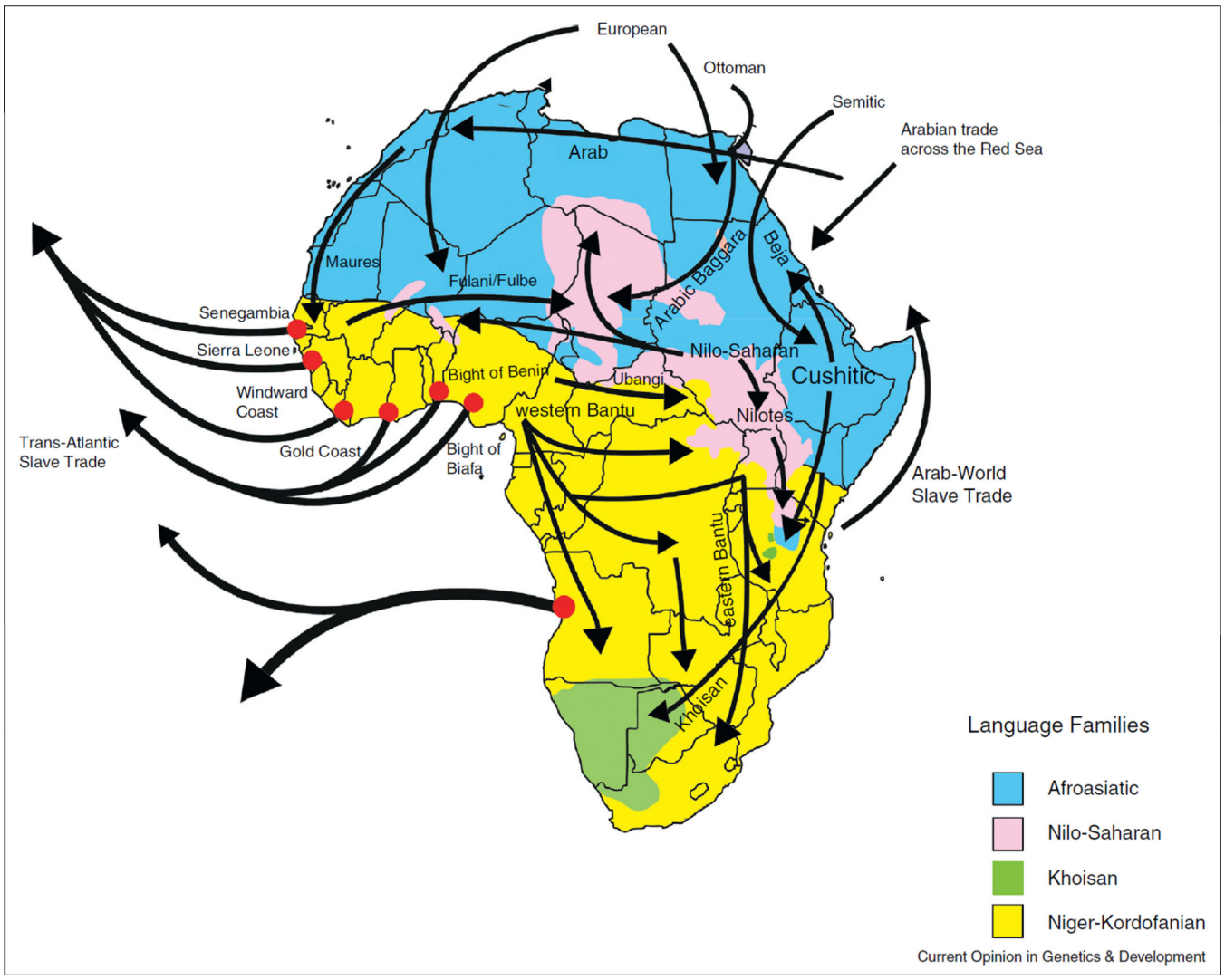

Figure 3.

The geography of major linguistic families and of historic migration events in Africa. Africa not only has the highest levels of genetic diversity, but a considerable amount of linguistic diversity is also found across the continent. Currently, more than 2000 distinct languages exist in Africa, representing about a third of the world's languages, which can be classified into four major linguistic families: (1) Niger-Kordofanian is a family of languages (including Bantu) spoken primarily by agriculturalists across a wide geographic region in Africa; (2) Nilo-Saharan languages are spoken predominantly by pastoralists in Central and East Africa; (3) Afroasiatic languages are spoken mainly by pastoralists and agropastoralists in East and North Africa; (4) Khoesan, which consists of languages with click consonants, is spoken primarily by hunter-gatherer populations in East and South Africa. This map, adapted from [1,2], also shows a number of key migration events, most notably the geographic expansion of Bantu Niger-Kordofanian-speakers across Africa from a homeland near the Nigeria/Cameroon border, as well as the general geographic regions (shown here by

the red circles) where enslaved Africans were transported from Africa to the New World based on historical records.

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Table 1

Description of modern human fossils in Africa. Here we outline some of the major morphological features identified in anatomically modern humans found in Africa, along with the remains recovered from each site, and the inferred age. This description corresponds to the fossils/geographic sites listed in Figure 1.

Specimen	Recovered remains	Major anatomical features	Age (in years)
Omo 1 Omo2	Partial cranium and mandible (Omo 1) Partial cranium (Omo 2)	The cranial vault of Omo 1 is high and globular, with a nearly vertical frontal profile, rounded occipital, and pronounced parietal bosses. The mandible has a slight chin. The postcranium is human-like in overall morphology [7] Omo 2 has a mosaic of modern (high vault) and archaic traits (strong sagittal keeling and angled occipital) [7].	195,000
Herto	Crania	High cranial vault with a cranial capacity of 1450 cm^3, at the high end of the human range. Some archaic morphology includes projecting supraorbital and flexed occipital tori [6,7].	154,000–160,000
Singa	Partial cranium	Vaulted forehead and reduced supraorbital morphology; cranial capacity estimated to be 1340 cm^3 [124].	>133,000
Mumba	Teeth	Size and shape of molars are consistent with AMHs	130,000
Klasies	Partial cranium, mandible	Maxilla and mandible are metrically within the range of modern humans; overall, there is a reduction in tooth size consistent with AMH morphology [8].	120,000
Border Cave	Partial cranium, mandible	Cranium has a high curved frontal bone and the supraorbital bone is slightly protrusive [8].	90,000
Aduma/Bouri	Cranial fragments	Characterized by a high vault profile, well-curved parietals and the absence of an occipital torus. Cranial dimensions cluster with AMHs [11].	79,000–105,000
Dire-Dawa	Partial mandible	Size and shape of mandible are consistent with AMH [124].	61,000–77,000
Die Kelders Cave	Isolated teeth	There is an overall reduction in the size of the crowns compared to archaic populations and overall morphological features resemble modern sub-Saharan Africans [125].	60,000–80,000
Zouhra Cave at El Harhoura	Teeth	Size of the upper and lower molars, and enamel thickness are similar to AMH [126].	Poorly dated
Haua Fteah	Partial mandibles	Absence of derived Neanderthal traits [124,127].	65,00–73,000
Temara	Cranial and mandibular fragments	Morphology and metrics of occipital are similar to AMH; no discernible presence of a supraorbital torus [128].	Poorly dated
Grotte des Contrebandiers	Teeth and mandibular fragments Reduced	Reduced anterior dentition relative to molars and reduced bucco-linguial expansion of front teeth contrary to Neanderthal specimens [126].	Poorly dated
Dar es-Soltane	Partial cranium and mandible	A flattened mid-face and presence of a chin consistent with AMHs [8].	Poorly dated