



Clarifying distinct models of modern human origins in Africa

Brenna M Henn^{1,2}, Teresa E Steele¹ and Timothy D Weaver¹

Accumulating genomic, fossil and archaeological data from Africa have led to a renewed interest in models of modern human origins. However, such discussions are often discipline-specific, with limited integration of evidence across the different fields. Further, geneticists typically require explicit specification of parameters to test competing demographic models, but these have been poorly outlined for some scenarios. Here, we describe four possible models for the origins of *Homo sapiens* in Africa based on published literature from paleoanthropology and human genetics. We briefly outline expectations for data patterns under each model, with a special focus on genetic data. Additionally, we present schematics for each model, doing our best to qualitatively describe demographic histories for which genetic parameters can be specifically attached. Finally, it is our hope that this perspective provides context for discussions of human origins in other manuscripts presented in this special issue.

Addresses

¹ Department of Anthropology, University of California, Davis, CA, 95616, United States

² UC Davis Genome Center, University of California, Davis, CA, 95616, United States

Corresponding author: Henn, Brenna M (bmhenn@ucdavis.edu)

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Models for modern human origins

In the 1980s and 1990s, much of paleoanthropology was focused on whether modern humans originated across the Old World (Multiregionalism) or exclusively within Africa (Out of Africa). With the resolution of this question [1] — current consensus has modern humans originating in Africa — attention has now turned to discussion of what was happening *within* the continent before modern humans expanded their range globally [2,3–7]. In this context, geneticists, human paleontologists and archaeologists have all proposed scenarios related to the tempo

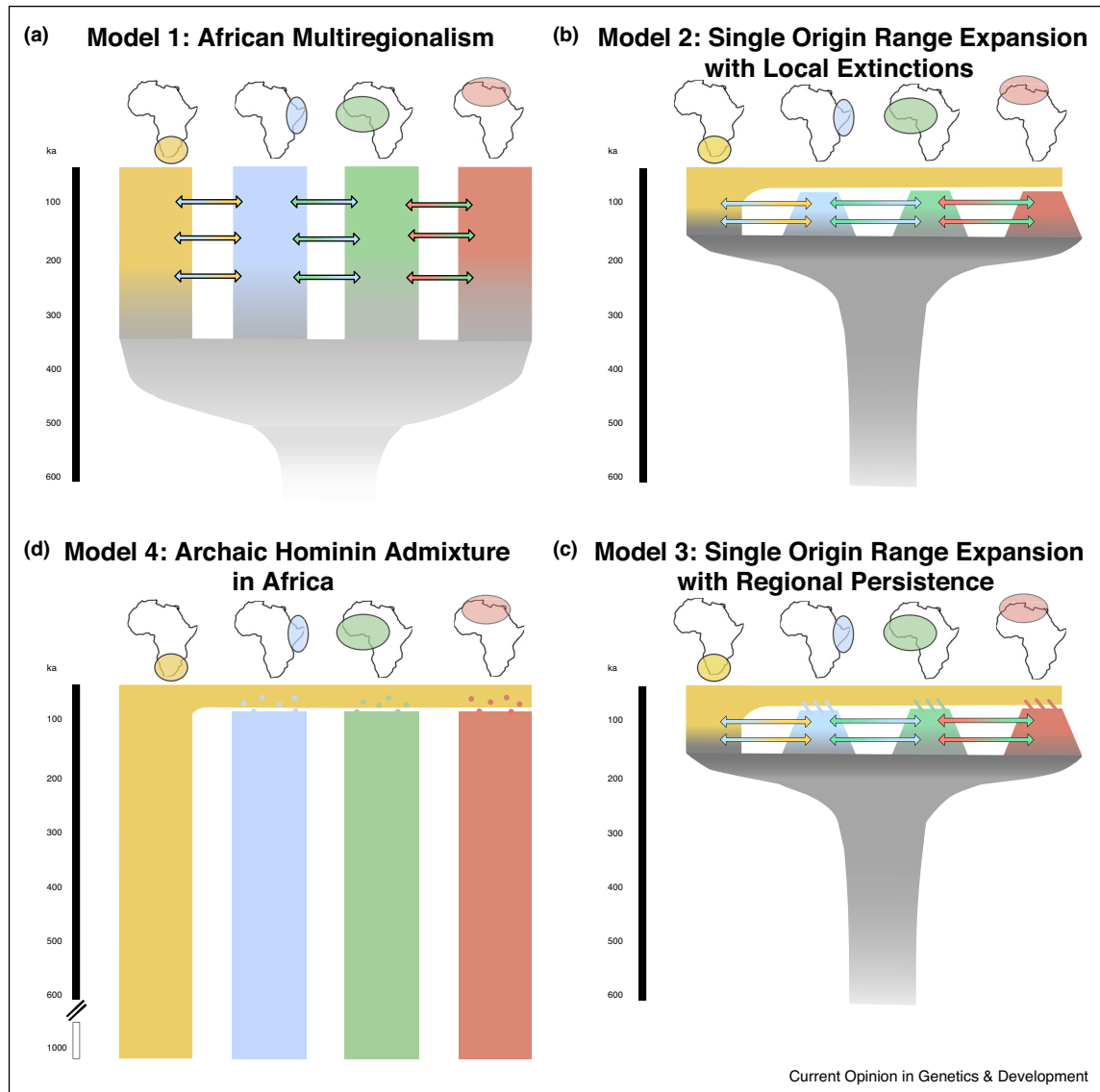
and geographic distribution of modern human origins and evolution in Africa. We attempt to delineate these ideas into four models (Figure 1), with the goal of distinguishing features of each that lend themselves to model testing.

One scenario that has generated recent discourse is a form of multiregionalism that is limited to Africa (i.e. **African Multiregionalism, Model 1**) (Figure 1a) [8,9,10*]. This view has been motivated by the presence of regional geographic variation in the African archaeological record by 300 000 years ago [11,12], the morphological diversity of the African fossil record between 300 000 and 100 000 years ago [10*,13,14**,15**], and the presence of modern, derived morphological features in divergent regions of Africa [14**,16–18]. Together, these findings inspired the hypothesis that populations across Africa were all connected to each other. This model states that migration across the continent is more parsimonious than independent convergence of anatomical features and archaeological innovations.

The **Single Origin Range Expansion with Local Extinctions (Model 2)** is a corollary of the better understood Out of Africa expansion and suggests that the source of modern humans was further restricted to a single region of Africa (Figure 1b). This population then expanded throughout Africa, either outcompeting remnant ‘near modern’ human groups or these other groups were extirpated due to climatic pressures. This view has been primarily motivated by genetic analyses [19–21] but also by studies of fossils [22,23] and archaeology [24]. Requisite in this family of models is an explanation of why one population of ‘near modern’ or ‘modern’ humans underwent a demographic expansion while others did not. The Single Origin Model is often implicitly assumed in visual schematics of human origins, with an arrow originating in southern or eastern Africa leading to the Out of Africa founder event.

A related but distinct member of this family of models is the **Single Origin Range Expansion with Regional Persistence (Model 3)**, which gives priority to a single geographic region of Africa but allows for limited gene flow between the source population expanding from a single region and the ‘near modern’ or ‘modern’ human populations local to the other regions (Figure 1c). To our knowledge, this possibility has not been formally described but could encompass discussions of genetic divergence [25] and the persistence of locally distinct archaeological traditions [26]. The time scale of hominin

Figure 1



Four models of modern human origins in Africa. In all of the panels, four regions of Africa — south (yellow), east (blue), west/central (green), and north (red) — are depicted with different colors to illustrate the salient features of the models. Horizontal arrows indicate gene flow between regions. Diagonal lines or dots indicate admixture between expanding and local populations, with lines corresponding to higher gene flow than dots. **(a)**, Model 1: African Multiregionalism (pan-African origins). Modern humans originate across Africa. No single region is the primary source of modern humans. Instead, genetic, morphological, and archaeological markers of modern humans originate in multiple regions and spread by migration between regions. Depending on the amount of gene flow between regions, the pan-African population is more or less structured. Regional structure dates back to just after the split with the evolutionary lineage leading to Neandertals. We depict a smaller population in a single region before regional structure develops, but the initial population could have been larger and spread across multiple regions. **(b)**, Model 2: Single Origin Range Expansion with Local Extinctions. A single region is the source for modern humans within (and outside of) Africa. 'Near modern' human populations are present throughout Africa after 200 000 years ago and connected by migration between regions. Subsequently, a population from a single region of Africa expands across the continent. The source region is usually thought to be south (as depicted in the figure, for illustrative purposes) or east Africa. The expanding population successfully outcompetes the other populations, for either biological or behavioral reasons; or alternatively it expands into the vacuum left by local population extinction due to climatic events. **(c)**, Model 3: Single Origin Range Expansion with Regional Persistence. Similar to Model 2, except that rather than complete replacement there is some gene flow between the expanding and local populations. Gene flow could be high or low. **(d)**, Model 4: Archaic Hominin Admixture in Africa. Modern humans evolve in Africa side by side with archaic hominins (e.g. *Homo naledi*). As modern humans expand across Africa there is gene flow between modern and archaic populations. Archaic gene flow is very low (<5%).

divergence and levels of gene flow are key to distinguishing Model 3 from Model 1.

Finally, there have been proposals that **Archaic Hominin Admixture in Africa (Model 4)** was a crucial component of modern human origins (Figure 1d). ‘Archaic’ here refers to groups that shared a distant common ancestor with modern humans (more than 500 000 years ago and assigned to a *Homo* species). This view is often discussed in concert with African multiregionalism, but it is distinct enough conceptually to warrant a fourth model. This view is motivated by discussions of archaic admixture outside of Africa, between modern humans, Neandertals, and Denisovans [27–29], patterns of variation at certain genes [30,31], and fairly recent (<25 000 years ago) African fossils that appear to show morphological similarities with archaic humans [32–35].

A complication in combining evidence across disciplines in support of one of these models is that morphological,

genetic, and archaeological definitions of modernity need not match. We expand on the different definitions of ‘modern humans’ in Box 1. A related point is that ‘modern human’ and ‘*Homo sapiens*’ are not necessarily synonyms. For example, *Homo sapiens* could include any populations more closely related to present-day modern humans than to non-modern groups, such as Neandertals, but some of these populations may not be morphologically modern, and even those that are morphologically modern may not be archaeologically modern. While these different definitions of modernity were important for identifying Africa as the source of modern humans, as we progress to more fine-grained models of origins, it is important to move from classification of ‘modern’ or ‘non-modern’ categories to predictions about what we would expect to observe in the morphological, genetic, or archaeological realms given a particular model. In addition, the morphological, genetic, and archaeological data are often sampling different populations, and therefore these lines of evidence may support different models.

Box 1 Defining ‘modern humans’ across disciplines.

Morphological definition: Morphologists have taken two related approaches to identifying (anatomically) modern humans in the fossil record. One approach is to designate fossils as modern if they exhibit a sufficient number of traits that are typically found in recent [or more ancient but uncontested] modern humans (e.g. features of the cranium, such as short, high vault) [63,64]. While this approach can make use of metric measurements to diagnose certain traits, it has tended to focus on presence or absence. Alternatively, a fossil could be considered modern if its shape, as quantified by a set of linear measurements or the x–y–z coordinates of anatomical landmarks, is close in multivariate space to modern humans (e.g. Refs. [65,66]). When the latter approach is applied in a piecemeal fashion (e.g. separate analyses are done for the face and cranial vault [14**]), it converges somewhat on the former approach, because it allows for a mixture of modern and non-modern anatomical regions. These types of analyses have shown that fossils that are morphologically modern for at least some anatomical features appear in the fossil record by ~300 000 years ago [14**,15**] or more certainly by 200 000–150 000 years ago [16–18] in Africa. However, it should be noted that fossils from 200 000 to 150 000 years ago—or even most fossils more than 20 000 years old [65,66]—are still morphologically different from present-day modern humans. That is, there has continued to be morphological evolution in modern humans after the earliest modern humans appear in the fossil record.

Genetic definition: Genetic researchers have primarily relied on paleoanthropologists and archaeologists to define modern humans as a species. However, since the initial reconstruction of the human mtDNA phylogenetic tree by Cann *et al.* [67], there has been a tendency to conflate the time to the most recent common ancestor (tMRCA) with the ‘origin’ of *Homo sapiens* [68] — even though the authors of the original article caution that ‘transformation from archaic to anatomically modern forms’ need not have happened at 140 000–290 000 years ago. The confusion stems from the difference between genetic lineages and populations; genetic lineages are contained within individuals which in turn are members of populations. These individuals are not duplicates of each other with identical mtDNA copies (at least not for humans), but rather exhibit a diversity of genetic lineages. So, even if there is only a single population existing on the landscape at a given slice of time, it will have a tMRCA that links all the genetic variants in the group together (i.e. coalesce) but this coalescent may be quite old. Indeed, the expected tMRCA is proportional to the effective population size. The tMRCA of the mtDNA and Y-chromosome may however provide a meaningful upper bound on the earliest population divergence within *Homo sapiens* [69]. If two populations diverge and remain relatively isolated from one and another, then the tMRCA will significantly pre-date the population divergence between them, as the genetic diversity in the ancestral population is randomly sorted in descendant group A or B. The discrepancy between the tMRCA upper bound and the actual population divergence can be large, again depending on the effective population sizes. There are some caveats to this description, mainly that it describes the evolution of these genetic lineages under neutrality.

Archaeological definition: Consolidating what had been suggested in earlier publications, McBrearty and Brooks [11] converged on a definition of modern humans based on the archaeological (i.e. behavioral) record; modern humans show evidence of abstract thinking, sequential planning, innovativeness, and symbolic behavior. Throughout their paper, they discuss how these behaviors may be and have been identified in the archaeological record. Subsequent authors have elevated symbolic thinking, most readily identified through art and personal ornamentation, as the most indicative evidence of culturally modern behavior [70–72]. Others focus on innovativeness (e.g. Refs. [73,74]), language (e.g. Ref. [75]), and cumulative culture [76,77]), which can manifest as technological complexity (e.g. Ref. [78]), but the archaeological proxies of these behaviors are not always clearly defined [2*]. When considering the appearance of these behaviors, archaeologists tend to focus on mode and tempo. The mode or mechanism for the stimulus of their development could be demographic (e.g. an increase or decrease in human population sizes or densities), environmental (e.g. an increase or decrease in the carrying capacity or complexity of the landscape), or biological (e.g. genetic changes that support the capacity for full language). The tempo could be gradual through the Middle and Late Pleistocene (781 000–126 000 and 126 000–11 700 years ago), or more abrupt with the transition from the Acheulean stone tool industries to the Middle Stone Age industries (~300 000 years ago) in the mid-Middle Pleistocene, within the Middle Stone Age, or at the end of the Middle Stone Age (~40 000 years ago).

Predictions and evidence for the respective models

We briefly summarize evidence for Models 1–4, and discipline-specific predictions. This is not an exhaustive list of predictions, but rather examples of how existing data, or data that may be available soon, could be used to support or refute the different models.

African multiregionalism

Morphology

Consistent with African multiregionalism, African fossils from 300 000 to 100 000 years ago are quite variable in their morphology [13,14**]. Fossils exhibiting at least some diagnostic modern traits are found in multiple regions in Africa [14**,15**,16–18]. The presence of modern traits in multiple regions is to be expected if multiple localities were involved in modern human origins. Substantial variation would be expected if modern human origins occurred across a wide geographic area. However, two key components of the original, global multiregionalism model are: first, morphological variation is geographically patterned, and second, there is temporal continuity in morphology *within* geographic regions [36,37]. Neither of these components have been demonstrated for the African fossil record, although the fossil record is limited enough that these patterns may simply not be apparent. As later occurred with updated versions of global multiregionalism [38], one could posit a weaker form of multiregionalism: simply that multiple regions contributed to modern human origins through a series of population expansions and contractions with reticulation [9,39*]. However, this ‘weak multiregionalism’ interpretation could span Model 1, Model 3 and Model 4, depending on the timing and amount of gene flow (i.e. anything except Model 2). Hence, because it is currently underparameterized, ‘weak multiregionalism’ does not delineate a specific pattern of human evolution.

Genetics

Under an African Multiregional model (Figure 1a), we would expect deep population divergence estimates between groups found in different African geographic regions, accompanied by relatively high migration rates between proximate regions. If the populations at Jebel Irhoud (Morocco), Herto (Ethiopia) and Florisbad (South Africa) all belong to a single species distributed across the continent, then by 300 000 years ago the ancestral population must have already splintered. Substantial gene flow is requisite to connect all of these populations and transmit derived characteristics originating in one group to the others, in order to obtain shared derived traits common to all modern humans. In principle, estimates of population divergence and migration are easily obtained under population genetic theory. Presently, no estimates of the earliest population divergence significantly pre-date 300 000 years ago (Table 1). Indeed, most are much younger, on the order of approximately 150 000–

100 000 years ago with the exception of Schlebusch *et al.* [40]. One possibility is that the level of migration between the ancestors of present-day western Africans (i.e. Yoruba) and southern Africans (i.e. KhoeSan) was sufficiently high that a very old population divergence with frequent migration will have a model likelihood similar to a recent population divergence with low migration. This idea finds some support in multiple sequential Markovian coalescent (MSMC) approaches to estimating gene flow and divergence, where the earliest divergence as measured by the cross-coalescence rate begins 200 000–150 000 years ago (Table 1). However, related work has found support for a reduction in migration among demes beginning ~200 000 years ago [41**]. To our knowledge, the only paper to test the fragmentation versus single origin hypothesis found that the pan-African origin model had significantly lower support than a single origin model [21].

Furthermore, under an African Multiregional model, estimates of the ancestral effective population size of humans would be extremely large. Subpopulations scattered across the continent would need to be sufficiently widespread to contribute and absorb migrants across ecological boundaries (limited population structure), and a pan-African origin would inherently have a large N_e as it incorporates ancestral lineages across all of the subpopulations. Estimates of the ancestral human population size remain relatively small (typically a range of 9000–30 000) [20,21,42,43]. As discussed by Sjodin *et al.* [21], using an assumption that N_e reflects 10% of the census size, the maximum estimate of 32,500 would result

Table 1

Genetic estimates of the earliest population divergence among humans

Date (years)	Populations	Citation
110 000	San versus Pygmy & West Africans	Veeramah <i>et al.</i> [60]
110 000–150 000 ^{a,b}	San versus Yoruba	Gronau <i>et al.</i> [20]
130 000	San versus Eurasians	Mallick <i>et al.</i> [46]
100 000	KhoeSan versus other Africans	Schlebusch <i>et al.</i> [61]
150 000–20 000	Yoruba versus Europeans	Schiffels and Durbin [50]
120 000–140 000	San versus Mbuti	Song <i>et al.</i> [58**]
87 000	San versus Yoruba	Mallick <i>et al.</i> [46]
160 000	Central Pygmy versus West Africans	Hsieh <i>et al.</i> [55]
130 000–140 000	Central Africans versus Europeans	Lopez <i>et al.</i> [62]
260 000–350 000	ancient San versus East Africans	Schlebusch <i>et al.</i> [40]

^a Ranges here do not represent confidence intervals, but variation either in the initial versus midpoint estimate of the cross-coalescence rate; or variation between demographic inference methods.

^b Dates do not incorporate uncertainty in mutation rate except for Ref. [20].

in a population density of 1.4 individuals per 100 km² which is lower even than population densities estimated for African hunter-gatherers who have among the lowest population densities today (e.g. Dobe !Kung $\sim 6.6 \times 100$ km², Hadza $\sim 30 \times 100$ km² [44]). Densities could be increased by assuming that only a fraction of the African continent is habitable; however, this then suggests that strong ecological/physical barriers exist. Hence, a model of pan-African prehistoric migration is unlikely, especially during MIS 6 ($\sim 190\,000$ – $130\,000$) when climatic deterioration resulted in xeric conditions in the Sahara [45] and likely the contraction of the central rainforest.

Archaeology

To support this model, ‘modern’ behaviors such as ornaments and other innovations will appear in the archaeological record as ‘modern’ morphology appears. Like the fossil morphology, the items will be variable. McBrearty and Brooks [11] argue for a continent-wide, piece-meal appearance of modern behaviors, which could support this model. Perhaps more definitively, shells that are argued to have been ornaments begin appearing in the record 120 000–115 000 years ago (Steele *et al.* *in review*). These shells show some similarities and some regional patterning and variation, potentially in support of Model 1; however, the geographic patterning may be the result of ecological constraints as opposed to population structure.

Single origin range expansion with local extinctions

Morphology

Depending on the rates of morphological evolution, a single source model might predict modern morphology of multiple traits to appear earlier in one region of Africa. Additionally, later modern humans (from within and outside of Africa) might be expected to be morphologically closer to early modern fossils from one region of Africa. To date, none of these predictions have been systematically tested—in part because of the small number of early modern human fossils from Africa but also because, until recently, morphologists have prioritized demonstrating that modern humans appeared earlier in Africa than other parts of the world rather than distinguishing among regions within Africa.

Genetics

Model 2 predicts that patterns of genetic variation should decline with distance from a single source population in one region of Africa. Furthermore, it predicts that the vast majority of genetic lineages should stem from the single ancestral population; although, due to incomplete lineage sorting, other regions may have some basal lineages—especially under circumstances of balancing selection or differential patterns of positive selection. Model 2 is supported by evidence that the ancestral human population has a relatively small N_e , estimates of population divergence systematically find that the southern African

KhoeSan are the most divergent human population, and estimates of the time of population divergence remain relatively young (Table 1). The KhoeSan retain the largest effective population size of all human groups, despite the fact that they continued to practice a hunter-gatherer subsistence lifestyle until the historical era (with the exception of pastoralism adopted by the KhoeKhoe ~ 2000 years ago) [46–49]. This model also predicts strong population expansion in Africa before the Out of Africa bottleneck. Evidence for ancient population growth is observed in Africans, most often exemplified by PSMC curves [43]. However, the PSMC method was initially tested under relatively simple demographic models and recent coalescent analysis demonstrates that the cessation of migration among multiple demes can also create increases in N_e similar to upticks observed in PSMC [41,50].

Archaeology

Archaeologically, we would expect the earliest appearances of modern behaviors to occur in a single region alongside the earliest appearances of modern morphology and along with genetic lineages considered ancestral to all contemporary humans. Furthermore, modern behaviors associated with these modern human lineages should expand in geographic range as the human population expands. The appearance of these modern behaviors should represent a sharp break with any local behaviors, which go locally extinct. If we take ornaments as the most reliable indicator of modern behavior, arguably these appear earliest and most consistently in North Africa, starting about 120 000 years ago and persisting until about 80 000 years ago (Steele *et al.* *in review*). However, currently there is no evidence that this idea expanded out of North Africa. Similar ornaments appear, presumably independently, in South Africa by 75 000 years ago [51].

Single origin range expansion with regional persistence

Morphology

Distinguishing Model 3 from Model 2 based on morphology will depend on how morphologically divergent the source region population and the remaining regions had become, before the source population expanded. The expected degree of divergence could be determined with simulations of morphological evolution.

Genetics

Under Model 3, we would expect to see clinal patterns of genetic diversity and coalescence radiating from a singular region of Africa. However, the phylogeographic patterns will contain topologies that reflect deep coalescent events in regions outside of the immediate source. The fraction of these ‘inconsistent’ topologies will reflect the amount of gene flow from the previously isolated human populations into the expanding source. For example, if the source population expanded from southern Africa

100 000 years ago into western/central Africa and absorbed an isolated population there, we might expect to find divergent lineages specific to western/central Africa that are basal to all African/non-African lineages. However, the scale of their coalescence should be relatively recent if all modern humans spring from a common ancestral population that diverged $\sim 250\,000$ years ago (in contrast to Model 4). One example that might support Model 3 is the recent observation of $\sim 10\%$ divergent ancestry in western Africans which does not fit a monophyletic branching model of population divergence from a southern African source (represented by the ancestors of the KhoeSan) [40,52**]. Additionally, the highly divergent A00 Y-chromosome is basal to the remainder of human Y-chromosomes and has an estimated tMRCA of 250 000 years ago. Its distribution is circumscribed to Cameroon (and African-American descendants) — and the lack of diversity on the background of A00 suggests an extremely small population or very low gene flow into the modern human population [53]. We caution that these observations have not been well parameterized, especially under more complex models with ancient gene flow among geographic regions 250 000–100 000 years ago (Figure 1c) and that the tMRCA does not equal population divergence.

Archaeology

Initially, the archaeological predictions for Model 3 are similar to those for Model 2. However, if some amount of gene flow occurred when the demographically expanding modern human populations encountered other local modern populations, then we would expect some local regionally distinctive indicators of modern behavior to persist alongside the appearance of the indicators carried by the demographically expanding modern human population, at least briefly. This pattern is not apparent in the archaeological record; however, the current record may not be robust enough to test this.

Archaic hominin admixture in Africa

Morphology

Consistent with this model, some quite recent fossils (<20 000 years ago) have been argued to be morphologically similar to archaic humans [32–35]. However, it is not clear what barriers (geographic, behavioral) allowed modern and archaic evolutionary lineages to remain distinct for hundreds of thousands of years before there was recent admixture. If the barriers were geographic, this model would predict archaic morphology to persist quite late in some regions, similar to the situation in Eurasia with Neandertals, but just within Africa. The expectations for this model will also depend on whether there was enough gene flow and whether the genetic architecture of the morphological traits was such that admixed individuals will be different morphologically than individuals who derive all of their ancestry from the region. Ongoing research [54] should give us a better understanding of

how admixture impacts morphology, which is crucial for distinguishing between Model 4 and Model 1,3.

Genetics

There are no ‘archaic’ ancient genomes comparable to Neanderthal and Denisovan sequences. Alternatively, a few geneticists have taken the approach of looking for regions of the genome that are statistical outliers in contemporary African populations which may represent introgression between divergent hominin species [30]. For example, Hsieh *et al.* consider the top 1% of S* outliers in central African Pygmy genomes [55]; they find evidence for a single pulse of gene flow into central Africans ~ 9000 years ago. These genetic regions tend to have very old coalescent ages, approximately 1 million years old. Rather than supporting evidence for extensive gene flow (i.e. Model 1), these data rather would support strong population structure for tens of thousands of years between hominin species — followed by a one pulse or a two-pulse admixture event with low migration rates. However, caution is warranted in the interpretation of such approaches as every statistic will have a set of observations in the tail, the observed ‘introgressed’ segments do not fit any of the simulated demographic models in the paper [55], and the authors stress that their approach is significantly biased in estimated introgression timing.

Archaeology

Like Models 2 and 3, we would expect the earliest appearances of modern behaviors to occur alongside the earliest appearances of modern morphology in a single region. These modern behaviors would expand as the morphologically modern and genetically distinct population expands. However, admixture with archaic populations may be difficult to detect archaeologically, because the archaic populations may lack distinctive behavioral markers.

Conclusions

We have laid out four distinct models of early modern human origins, which we hope provide a starting point for prospective prediction and model-testing. For example, in Models 2–4 we would expect a clear clinal trend of morphology and behavior expanding together. This pattern would refute Model 1. For Model 1, we might expect regional patterns of modern morphology and behavior, but they would not necessarily spread together; morphology and behavior could be geographically and temporally asynchronous. Unfortunately, little genetic work has been done to explicitly ask which genetic patterns are expected under each model, or whether geneticists can even distinguish among them. The challenge confronting the community now is embellishing these models with additional parameter details. For example, laying out whether migration is asymmetric between regions under Model 1, or whether all geographic regions contribute equally.

Especially pertinent to geneticists are priors on population divergence. The human mutation rate has been under multiple rounds of revision over the past 10 years, and there is by no means consensus yet on the final estimate [56,57] (Ragsdale, Moreau and Gravel, this issue), or on the application of these rates to dating demographic events. This variation is reflected in the range of dates in Table 1. Further, there are also significant discrepancies among genomic dating methods even using similar population datasets [58^{**},59^{*}]. We expect that genomic data will continue to accumulate at an increasing rate, while fossil and archaeological data will also accumulate at a slower rate. New data will certainly allow us to ask more fine-grained questions. However, to make real progress in understanding modern human origins, we must precisely define and parameterize possible models.

Conflict of interest statement

Nothing declared.

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