

tinue to degrade, the discordance between summer and winter abundances may amplify. Contributing factors reducing the success of the monarch migration may also include sublethal effects of pesticides, road mortality, and increasing levels of disease (table S1). Planting regionally native milkweeds could buffer the monarch's population but will not alleviate migratory mortality.

Recent evidence points to a decline beginning >45 years ago in another U.S. population of monarchs, which migrates within California (14). Such long-term and broadscale negative population trends suggest continent-wide changes that transcend single explanations such as herbicide-tolerant crops.

Modeling efforts are helping to elucidate the causes of the shrinking monarch populations (13), but as is the case for most declining species, multiple stressors likely conspire. Long-term monitoring must continue but is especially important in the southern United States and northern Mexico to estimate population sizes mid-migration to and from the overwintering sites. Statistical analysis of the >25 years of monarch tagging data will likely shed light on migratory mortality and would be a boon from the hard work of citizen scientists (15). Beyond migratory mortality, latent negative effects of environmental and anthropogenic factors experienced during migration may affect overwintering itself and are in need of attention. ■

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SUPPLEMENTARY MATERIALS

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ANTHROPOLOGY

How did *Homo sapiens* evolve?

Genetic and fossil evidence challenges current models of modern human evolution

By Julia Galway-Witham and Chris Stringer

Over the past 30 years, understanding of *Homo sapiens* evolution has advanced greatly. Most research has supported the theory that modern humans had originated in Africa by about 200,000 years ago, but the latest findings reveal more complexity than anticipated. They confirm interbreeding between *H. sapiens* and other hominin species, provide evidence for *H. sapiens* in Morocco as early as 300,000 years ago, and reveal a seemingly incremental evolution of *H. sapiens* cranial shape. Although the cumulative evidence still suggests that all modern humans are descended from African *H. sapiens* populations that replaced local populations of archaic humans, models of modern human origins must now include substantial interactions with those populations before they went extinct. These recent findings illustrate why researchers must remain open to challenging the prevailing theories of modern human origins.

Although living humans vary in traits such as body size, shape, and skin color, they clearly belong to a single species, *H. sapiens*, characterized by shared features such as a narrow pelvis, a large brain housed in a globular braincase, and reduced size of the teeth and surrounding skeletal architecture. These traits distinguish modern humans from other now-extinct humans (members of the genus *Homo*), such as the Neandertals in western Eurasia (often classified as *H. neanderthalensis*) and, by inference, from the Denisovans in eastern Eurasia (a genetic sister group of Neandertals). How did *H. sapiens* relate to these other humans in evolutionary and taxonomic terms, and how do those relationships affect evolving theories of modern human origins?

By the 1980s, the human fossil record had grown considerably, but it was still insuffi-

cient to demonstrate whether *H. sapiens* had evolved from local ancestors across much of the Old World (multiregional evolution) or had originated in a single region and then dispersed from there (single origin). In 1987, a study using mitochondrial DNA from living humans (1) indicated a recent and exclusively African origin for modern humans. In the following year, one of us coauthored a review of the fossil and genetic data, expanding on that discovery and supporting a recent African origin (RAO) for our species (2).

The RAO theory posits that by 60,000 years ago, the shared features of modern humans had evolved in Africa and, via population dispersals, began to spread from there across the world. Some paleoanthro-

“...researchers must remain open to challenging the prevailing theories of modern human origins.”

pologists have resisted this single-origin view and the narrow definition of *H. sapiens* to exclude fossil humans such as the Neandertals (3). In subsequent decades, genetic and fossil evidence supporting the RAO theory continued to accumulate, such as in studies of the genetic diversity of African and non-African modern humans (4) and the geographic distribution of early *H. sapiens* fossils (5), and this model has since become dominant within mainstream paleoanthropology. In recent years, however, new fossil discoveries, the growth of ancient DNA research, and improved dating techniques have raised questions about whether the RAO theory of *H. sapiens* evolution needs to be revised or even abandoned.

Different views on the amount of genetic and skeletal shape variation that is reasonably subsumed within a species definition directly affect developing models of human origins. For many researchers, the anatomical distinctiveness of modern humans and Neandertals has been sufficient to place them in separate species; for example, variation in traits such as cranial shape and the anatomy of the middle and inner ears are greater between Neandertals and *H. sapiens* than between well-recognized species of apes (6). Yet, Neandertal genome sequences and the discovery of past interbreeding between Neandertals and *H. sapiens* (7) provide support for their belonging to the same species

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under the biological species concept, and this finding has revived multiregionalism (8). The recent recognition of Neandertal art (9) further narrows—or for some researchers removes—the perceived behavioral gap between the two supposed species.

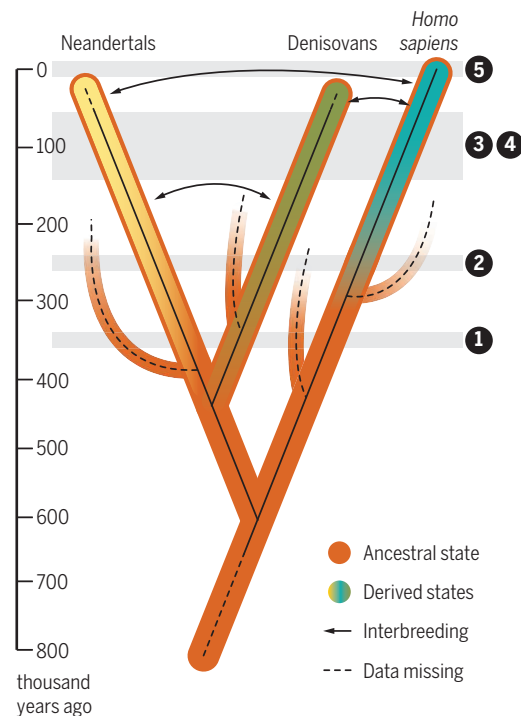
These challenges to the uniqueness of *H. sapiens* were a surprise to many and question assignments of hominin species in the fossil record. However, the limitations of the biological species concept have long been recognized (10). If it were to be implemented rigorously, many taxa within mammals—such as those in *Equus*, a genus that includes horses, donkeys, and zebras—would have to be merged into a single species. Nevertheless, in our view, species concepts need to have a basis in biology. Hence, the sophisticated abilities of Neandertals, however interesting, are not indicative of their belonging to *H. sapiens*. The recently recognized interbreeding between the late Pleistocene lineages of *H. sapiens*, Neandertals, and Denisovans is nonetheless important, and the discovery of even more compelling evidence to support Neandertals and modern humans belonging to the same species would have a profound effect on models of the evolution of *H. sapiens* (8).

Until recently, the oldest known fossils of *H. sapiens* came from east Africa, dated to 150,000 to 200,000 years ago (5); these specimens display most of the features that we associate with members of our lineage. Many researchers interpreted the emergence of this suite of traits in Africa, before *H. sapiens* dispersals into Eurasia, as important evidence in favor of RAO. However, recent research suggests that the derived traits of modern humans did not evolve together; rather, a modern-looking face appeared first, with a globular braincase evolving later (11). This pattern is exemplified by the cranial fossils from Jebel Irhoud, Morocco, which were recently redated to ~300,000 years old and which many researchers consider to be the oldest known examples of the *H. sapiens* lineage (12). The Jebel Irhoud specimens appear to represent an early iteration of the species in which some traits (such as a less-projecting face) were already present, but the typical braincase shape of modern humans had yet to evolve.

The apparently prolonged evolution of *H. sapiens* has raised questions about the extent of anatomical modernity that is necessary or sufficient for classifications of early *H. sapiens*. This has led to suggestions that ancient hominin populations in China (represented by the Dali fossil, which is roughly contemporaneous with those from Jebel Irhoud) could have been involved in modern human origins. If this is the case, it challenges the exclusivity of Africa in the evolution of the derived traits of *H. sapiens*, providing sup-

Recent African origin, with modifications

Recent discoveries provide insight into scenarios of how *H. sapiens* spread around the world.



1 Neandertal and Denisovan traits are beginning to emerge in Eurasia.

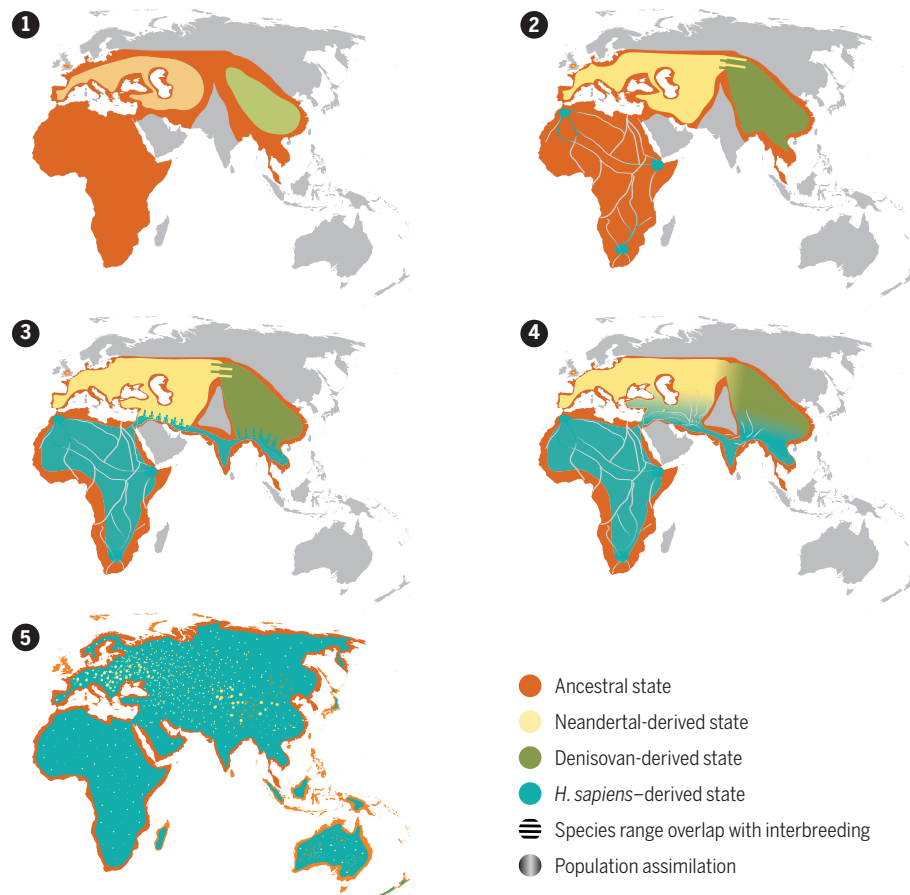
2 Neandertal and Denisovan traits continue to develop and spread; traits associated with *H. sapiens* begin to emerge across Africa; Africa and Eurasia remain isolated.

3 Novel *H. sapiens* traits evolve in Africa; *H. sapiens* disperse into Eurasia, with areas of interbreeding at the overlapping ranges with Neandertals and Denisovans (RAOWH).

4 Alternatively, *H. sapiens* traits spread into Eurasia, with more extensive blending between *H. sapiens*, Neandertals, and Denisovans; novel *H. sapiens* traits evolve in Africa, but the interbreeding between the various species may catalyze the evolution of new traits (AM).

5 Portions of Neandertal and Denisovan genes are distributed across populations of *H. sapiens* today.

Maps showing schematic slices through phylogeny



- Ancestral state
- Neandertal-derived state
- Denisovan-derived state
- *H. sapiens*-derived state
- ▨ Species range overlap with interbreeding
- Population assimilation

port for multiregionalism. However, resemblances between the Dali and Jebel Irhoud crania seem to be mainly based on primitive retentions rather than evolutionary novelties. The supposedly derived facial shape of early members of *H. sapiens*, such as those at Jebel Irhoud, may actually be more ancient, possibly tracing back to the common ancestor with Neandertals (5) (see the figure).

The apparently more deeply rooted origin of *H. sapiens* adds to the problem of how scientists can delineate *H. sapiens* from other species in an evolutionarily meaningful way and suggests that the species did not evolve as recently as previously envisaged. However, evidence of evolutionary novelty in the fossil record of putative *H. sapiens* still appears relatively recently in Africa, compared to a multiregional view of human evolution (in which *H. sapiens* began to evolve at least 1.8 million years ago). Within Africa, it is currently unclear whether the origin of *H. sapiens* was localized, as in some early RAO formulations, or involved a process similar to multiregional evolution, but operating purely within the continent (5, 13).

With only a few dissenters, the strictest versions of both RAO (which denies interbreeding with other lineages or species) and multiregionalism (which argues for an interbreeding network of one species over the past ~1.8 million years) are now generally regarded as falsified. Instead, two intermediate theories best accommodate the complex interactions between hominin taxa ~40,000 to 100,000 years ago (8, 14): RAO with hybridization (RAOWH) and the assimilation model (AM) (see the figure).

The two theories differ in their reconstructions of the processes by which the DNA of dispersing *H. sapiens* populations mixed with those of other populations outside of Africa. AM emphasizes demic diffusion, in which populations of African-derived *H. sapiens* and Eurasian Neandertals and Denisovans would have mixed over wide areas. Genes would have flowed gradually between these regional populations, catalyzing genetic and anatomical changes and leading to the spread of modern traits. In contrast, RAOWH envisages *H. sapiens* genes as largely entering and traversing Eurasia within the bodies of dispersing humans of African origin. Along the way there were successful hybridization events with indigenous populations, but these were effectively absorbing fragmented populations of indigenes in a relatively rapid replacement process, where they overlapped.

“...evidence of evolutionary novelty in the fossil record of putative *H. sapiens* still appears relatively recently in Africa...”

Debate continues over what constitutes necessary or sufficient evidence for either theory.

The low percentage of surviving Neandertal DNA in the human genome seems to reflect a replacement process, but the much greater amount (~6%) of Neandertal plus Denisovan-like DNA persisting in some extant Oceanian populations (7) may indicate more extensive interactions. In addition, growing evidence for a longer-term coexistence of *H. sapiens* and other lineages outside of Africa extends the potential for interactions in both time and space, consistent with AM (15). It may be that at the scale of human generations, the processes resembled assimilation, whereas viewed through the lens of deeper time, they look more like the replacement envisaged in RAOWH.

RAO has required modifications in light of new data over the past 30 years, but the accumulation of evidence still points to the evolution of the shared anatomical features of *H. sapiens* as an African phenomenon.

How the ancestral populations interacted within Africa now looks unclear (5, 13). Genomes have not been successfully reconstructed from African fossils older than about 15,000 years, but if such data become available, they will hopefully clarify many of the remaining uncertainties. With the growing influx of new

analytical techniques and discoveries within and outside Africa, it is imperative that researchers continue to rigorously challenge our theories and that they remain aware of their limitations. ■

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NEUROSCIENCE

Aberrant choice behavior in alcoholism

Impaired neurotransmitter clearance in the amygdala is implicated in alcoholism

By Rainer Spanagel

More than 2 billion people worldwide regularly drink alcohol. Alcohol is a component cause of more than 200 diseases and causes ~3.3 million deaths per year globally (1). The major disease burden comes from harmful alcohol consumption and alcohol dependence. Not everyone who regularly consumes alcohol becomes dependent: ~15% become engaged in harmful and compulsive alcohol drinking (2). Patients suffering from alcohol dependence no longer have the freedom to choose between alternative rewards because alcohol drinking dictates what should be done next, namely, shaping activities for the next drink. On page 1321 of this issue, Augier *et al.* (3) demonstrate that aberrant choice behavior—that is, choosing alcohol over an alternative reward—is a key driver for the transition from controlled to compulsive alcohol use. They also provide a mechanistic understanding of this aberrant choice behavior that could lead to new treatment opportunities.

Why do only a subset of individuals exhibit this aberrant choice behavior and become dependent on alcohol? Alcoholism is the result of cumulative responses to alcohol exposure, the genetic makeup of an individual, and environmental perturbations over time. This complex gene-environment interaction leads to heterogeneity in disease course (4). There are several key processes that drive the progression to alcoholism: the formation of habits (5), the development of increased craving for alcohol in response to conditioned cues and stress (6), and increasingly impaired behavioral control (7). Augier *et al.* introduce aberrant choice behavior—

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