

GLOBAL JOURNAL OF HUMAN-SOCIAL SCIENCE: D HISTORY, ARCHAEOLOGY & ANTHROPOLOGY Volume 23 Issue 4 Version 1.0 Year 2023 Type: Double Blind Peer Reviewed International Research Journal Publisher: Global Journals Online ISSN: 2249-460X & Print ISSN: 0975-587X

How are Ideas about Evolution Evolving?

By Patrick Manning

University of Pittsburgh

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GJHSS-D Classification: LCC: GN281-GN289



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INTRODUCTION

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Physical remains of humans are now labeled as Homo sapiens from 300 ka. The ecological record suggests shifts in African landscapes over time, and present-day African populations continue to reflect ancient variations. Underlying these patterns, Scerri argues, were "structured" (i.e., subdivided) human populations throughout Africa, rather than an initially small, uniform, and localized population. The key to an improved interpretation of human evolution, she says, is more fully specified models of population structure.

a) Assessing the Strategy for Evolutionary Analysis

Scerri's argument on "structured" populations in Africa is an outstanding issue that points as well to further issues. The broad debate over human evolution extends to the question of the ancestors from which humans arose and, more broadly, what types of information do we need to understand such aspects of human evolution? It is remarkable how much has been learned and how much remains to be learned. This essay, in three sections, addresses the strategy of analyzing the categories of evolutionary change, an updated narrative of the phases and processes of human evolution up to the Last Glacial Maximum of 25 ka, and an exploration of more recent evolution in human social scale.

In this opening section, I review the categories of evolutionary analysis from the beginning of *Homo*

Author: University of Pittsburgh, United States. e-mail: pmanning@pitt.edu sapiens to recent times, as seen in debates since the time of Darwin. After identifying categories of information on evolution; I point to dynamics of change within each of those categories, then point to examples of discoveries in evolution. This leads to the suggestion of *unification* and *differentiation* of the human population as two broad evolutionary patterns that combine the many specific types of change. A further note focuses on the role of analytical modeling in developing specific arguments within the context of unification and differentiation. All of these models follow a *bottom-up* strategy of evolutionary analysis, in that they rely most heavily on micro-level analysis, reaching higher levels of aggregation step by step.

b) Categories of Information on Evolution

These six major categories show that early humans led complicated lives and that modern evolutionary scientists have had many issues to considern:

- 1. *Phenotype (descriptions from the 1850s):* This is the study of the physical beings of humankind, their historical remains, and their development and behavior over their life course, including the basic biological structures of household and community.
- 2. Genotype (models from the 1930s, details from the 1980s): Genomics is the study of human DNA and its genes, which evolve and produce proteins that generate all human processes and activities.
- 3. Population (models from the 1920s, regional estimates from the 1990s): Total numbers of humans and their subgroups are measured in two ways: as "census populations" of all adults and children and as "effective populations" of breeding females, estimated genetically. Population includes the "speciation" or formation of humans into a coherent and distinctive form of life. Population also includes types of human migration.
- 4. Environment (models from the 1980s, estimates from the 2000s): The environmental factors of physical geography, climatic change, plus flora and fauna—linked into ecological webs—influence human life but are also changed by human activity.
- 5. Culture 1 (models from the 1980s, data from the 2000s): This is culture as understood and studied by biologists and environmentalists, who call it "social learning." Social learning describes the ways in which individuals observe others, develop new behaviors, expand their cooperation, and influence their genome. Among humans, this process

accelerated about 300 ka and is still influential in human networks.

6. *Culture 2 (models from the 2010s):* This is how culture is understood and referred to in today's world. It may also be called "group culture," and its connections to biological evolution are just now being analyzed. At its most basic level, *group culture began when humans formed conscious "we-groups,"* whose decisions created syntactic language and institutions to complete tasks—a process that accelerated about 70 ka. This led later to the creation of much larger social groups such as the businesses and states of today.

c) Major Evolutionary Dynamics

Each category of evolutionary information has subcategories that change and interact with one another. For each category, here are the major *dynamics* or processes of change:

- 1. *Phenotype:* Changing physical form, steps in lifecourse development, group behavior, incorporation of new processes into the human order.
- 2. *Genotype:* DNA mutation and selection, RNA and protein creation, epigenetics and regulation of gene activity.
- 3. *Population:* Growth and decline in populations (and subpopulations), displacement of migrants, admixture among migrating groups.
- 4. *Environment:* Short-term and long-term changes in geology, climate, and flora/fauna—and how those changes influence the categories of human evolution.
- 5. *Culture 1:* Individual learning in humans and other species (known as "social learning" and "cultural evolution"), the expansion of cooperative behavior.
- 6. *Culture 2:* Group decision-making in humans, group activity in representation or modeling of the world, media of expressive culture.

Listing these dynamics is instructive, but in viewing them we must keep in mind that the human genome has only 30,000 genes—not much more than much simpler animals. Thus, it is the *interactions* among the genetic and dynamic pieces that construct the full picture of human existence.

d) Some Key Discoveries

For the categories of evolutionary analysis and the dynamics within them, I note some major discoveries and their influence.

- 1. Phenotype
- Physical remains: *Homo ergaster* skeleton of 1.5 million years ago (1984); Jebel Irhoud remains found 1961 and dated in 2017 to an age of 315 ka
- Comparing human and chimpanzee childhood skills (Tomasello).

- Identification of persistent human community and household groups (2000) through the social brain hypothesis (Dunbar 1998).
- 2. Genotype
- Mitochondrial DNA analyzed 1987; ancient DNA and human history 2015.
- Human genome initial sequencing 2003, revealing 30,000 genes.
- Merge (a genetic category) theorized (1995); Merge in the human brain 2015.
- Epigenetic processes, regulating the genome's activity through protein modifications, have now been explored in some detail.
- 3. Population
- "Effective population" of breeding females theorized in 1931; estimates of early African effective population, first made in the 1990s, have since been updated.
- Occasional migrations into Arabia from 400 ka, reported in 2017.
- 4. Environment
- Geological observations on long-term African historical climate (after 2000).
- Niche construction theory on interaction among evolutionary categories (1980s).
- 5. Culture 1
- Kin-selection theory and dual-inheritance theory (1980s); cumulative cultural evolution theory 2009.
- Initial advances in study of tool-making and culture in primates and birds were made in Japan by Kinji Imanishi during the 1950s.
- Culture 1 and Middle Stone Age (MSA) technology from 300 ka, with networked communities.
- 6. Culture 2
- Hypothesis on adolescent leadership in syntactic language and institutions (2010s).

e) Understanding Unification and Differentiation

Evolutionary science needs to know more about fluctuations in the variety within human populations. Consider this: Populations with closely similar genomes and phenotypical form and behavior are labeled as "species." Since the human genome is far more unified than that of other mammalian species, we would seem obviously to be a species. Yet fossils of human populations continue to *reveal specific characteristics for every region* and local community. Thus, in evolutionary terms, questions remain about when humans have become more similar—or more *unified*—and when they have *differentiated* over time.

You can look at the dynamics and discoveries listed above and consider which of them might lead to *unification* of the human species and which might lead to *differentiation*. For instance, migration of small and isolated groups leads to differentiation through "genetic drift." But large-scale migration from one population to another causes the two populations to become more similar. Therefore, processes of both *unification* and *differentiation* have taken place throughout human history. Another question to consider: In what situations did either *unification* or *differentiation* predominate?

f) Analytical Modeling of Past Processes

Scerri's 2018 article makes recommendations for changes in models of genetic change and population structure. To enact such changes, researchers must make explicit and sensible assumptions that define variables and their interactions. This would ensure that the resulting scientific models of unification and diversification can project detailed simulations, which can then be compared to real data.

Fortunately, the science of network analysis has greatly advanced the modeling of large and complex datasets—by including the *specific forms of networks and their links* to each other. Techniques that are now being applied in medicine, for example, might be modified and applied in the history of evolution. Whatever the application, the modeling will be complex, because it must address the various scales of human existence: those of the genome, cells, human organs, individuals, and the different types of behavior of populations, as well as the environmental influences at each scale. That is, even at enormous scales, network analysis seeks seeks to work through a bottom-up approach. It will be interesting work.

Part Two: Evolutionary Narrative to 25 ka

Based on this simplified summary of the strategy of evolutionary analysis and its six categories of evolutionary knowledge on humans, I turn next to combining them, proposing a narrative of some major steps in human evolution over the past half-million years, up to 25 thousand years ago. Part Two offers hypotheses on how to assemble categories of information into a current version of human evolution. I expand on the tale of human evolution, using available models of structure, dynamics, and interactions to tell a story., proposing plausible hypotheses of growth and change based on models at the levels of both phenotype and genome. As I argue, populations of Homo sapiens experienced three concentrated eras of innovation, each followed by a wave of migration and exchange. Interacting pressures of unification and differentiation, fluctuating with climate (shown in Figure 1 below), influenced successive populations in Africa. The resulting picture of human evolutionary transformations can be tested and revised based on expanding empirical observations.



Figure 1: Average temperatures over 800,000 years.

Phase 1: Homo sapiens as a Species, ca. 500 ka

Biological processes of natural selectiongenomic and epigenetic change-guided the speciation of humans. At perhaps 500 ka, in a warm and humid period (See Figure 1), there emerged ancestors of Homo sapiens whom we can call "humans." They lived especially in the highlands of eastern and southern Africa, along with other hominin lineages. Under these changing circumstances, genetic mutations and epigenetic or developmental changes led humans in several directions, bringing phenotypical changes. In a genetic mutation, the Merge capability advanced internal human logic, enabling a change in behavior in which people could lump concepts together and link them to a new concept. Phenotypical changes included expanded brain size, reduced face size, lighter skeleton, and smaller teeth. Community size also expanded, gradually reaching an average 150 members. Yet Acheulean stone technology changed little in the these

days, either among *Homo* sapiens or among other hominin.

In intimate groups, human developmental change caused the polygamous family structure to be replaced by pair-bonded households as the locus of eating, sleeping, household tasks, and the nurture of offspring. Polygamy had left females subordinated and many males without mates, but the new male-female teams supported female collaboration, so that larger numbers of offspring survived. This encouraged population growth and provided more labor for community tasks.

These community changes gave rise to the overall process of human *speciation*. Today, biological species are still defined as populations with broad similarities at both phenotypical and genetic levels. Yet details of the definition [are still updated]. For example, while Darwinian thinking initially treated species as unified populations, new evidence on genetics and environments has revealed complications. For humans, it now seems more likely that separated communities connected and exchanged innovations via migration—thus beginning as a *diverse species* derived from different ancestral communities but with growing similarities.

Phase 2: Initial diffusion, up to 300 ka

In another aspect of biological evolution, the first great migration of *Homo sapiens* began as humans moved within their highland homelands and then left for places where humans had hardly been before. Figure 2 reflects genetic movement, arguably confirming distinctive human communities in most African regions as far back as 300 ka. Migrants adapted their habits to each locale but also transformed their new homes through "niche construction." Bodies of Homo sapiens changed response aradually in to regional environments: forest dwellers became smaller, while settlers in northern Africa developed lighter skins to absorb adequate sunshine. Climate sometimes became cold and dry, forcing further migrations and even population decline. Yet overall, by 300 ka, human populations had expanded continent-wide-and their shared characteristics were far different from those of surviving erectus, heidelbergensis, or other hominin groups.



Figure 2: Principal Component Analysis of African Genomes.

(Note: Many of the genomes along PC1 resulted from later migrations.)

Phase 3: Middle Stone Age (MSA), ca. 300 ka

A process of cultural evolution gained significance among humans about 300 ka, according to models in the fields of ontogeny and dual inheritance. Kin selection and social learning facilitated tool-making; communication emerged through emulation, gesture, dance, and protolanguage (in which small vocabularies of isolated words were shared within local networks). These cultural advances accelerated epigenetic development and other processes of biological evolution.

Archaeologists identified this era as the Middle Stone Age because of such new technology as prepared-core manufacture of stone tools, hafted spears, and intensive use of fire. Further, paleontologists have confirmed dates for skeletal remains that fit with the same era—applying the term *Homo sapiens* to two distinct skulls: from Jebel Irhoud in Morocco (315 ka) and Omo Kibish 1 in Ethiopia (230 ka). Figure 3 shows these skulls, along with those from other lineages such as the Kabwe skull in Zambia (300 ka). Meanwhile, household nurturing of offspring contributed labor that expanded community activities. Thus, hunting and toolmaking relied more on community than households.



Figure 3: Homo sapiens and others, about 300 ka.

Phase 4: Migratory exchange of innovations, 300–100 ka

The era of biological and cultural evolution, relying on technical and cultural innovations of the Middle Stone Age, brought a second great migration throughout Africa and even beyond. Households produced larger numbers of maturing offspring; larger numbers took up community labors including toolmaking, firewood collection, and participating in communication. In the exchanges of this era, the human skull became increasingly globular, and the chin emerged—though each pattern leaves evidence of human diversity.

Eras of high humidity brought not only expanded settlement in the Sahara but also periodic

settlements in Arabia. The Arabian deposits of steadily evolving stone tools since 400 ka (Figure 4) reveal migrations by humans who diffused in humid times, then withdrew to Africa as drought drove them out. Parallel migrations may have spread throughout Africa, including cases where settlers joined existing populations. The Arabian examples indicate the overall magnitude of the second great African migration, the fluctuations of drought and humidity, and the development and sharing of innovations across the continent.



Figure 4: Assemblages from Khall Amsayah and Jubbah lake sites in north Arabia. Left to right: A (ca. 400 ka); B (ca. 300 ka); C (ca.200 ka), D (ca. 100 ka), E (ca. 55 ka). Scale bar at left: 1 cm.

Phase 5: Syntactic language, 70-65 ka

A new process – social evolution – emerged as syntactic language took form in a single region and spread to all humans, taking with it the broader structures of institutions [as elements] social evolution. Social evolution was distinctive because of the new ability to form self-conscious groups, but social evolution also interconnected tightly with the ongoing processes of biological and cultural evolution.

The innovation emerged east of Lake Victoria, where archaeological studies document the finely made Later Stone Age artifacts from 65 ka, arguably the products of speaking communities. I hypothesize that "we-groups" of adolescents played and practiced until they had created and shared common words and syntax for combining them into complete sentences, not just isolated words. Their skill in categorization, based on a verbal application of their Merge capability, shaped the logic of full sentences.

The creation of language required years of devotion by bright and maturing adolescents, debating and working together to agree on common speech patterns. It spread by teaching to other adolescents and some adults—then to adolescents in other communities. Siblings and parents began to teach language to the toddlers in their households. Languages, spoken in communities of 150 people, became institutions governed by common agreement. Communication by speech led to the advance of the Later Stone Age.

Phase 6: Language in Africa; settlement in Eurasia and Oceania, 65–25 ka

Social evolution led to the third great migration of humans. The migration was distinctive in that spoken language came from a single origin (though languages, once formed, evolved further with time and in every place). Within Africa, speaking migrants settled among non-speaking human populations and introduced language-parallel to the MSA exchange of fire and hafted spears. Beyond Africa, speaking migrants settled new lands, encountering Neanderthals and Denisovans-parallel to the first wave of human migration. Both the African and Eurasian migrations can be documented through genetic, archaeological, and language-distribution evidence.

By 25 ka, structured populations of *Homo sapiens* had passed through great waves of unification and diversification, innovation and migration, expansion and transformation. Many details are not yet filled in, but this framework—relying on migration of diverse and structured populations while also anchored in households and community groups—enabled humans to undergo immense changes within half a million years.

Part Three: Growing Social Scale

Did evolution end there? Or can we link the long process of human evolution to life today? The biggest subsequent change is the expansion in the scale of the human order, which must be seen as a problem in evolution. With the Ice Age of the Last Glacial Maximum, peaking from 25 to 18 ka, a fourth set of innovations opened Phase 7 of human evolution – triggering changes that transformed *Homo sapiens* once again, leading to the human society we live in today.

This section addresses the expansion of human societies after 25 ka as a *new phase* in evolution. For the previous two million years, human communities gradually expanded from the 40 members that were typical of primate species to 150 members for *Homo sapiens*. The latter were by far the largest persistent communities of large animals, putting humans at the top of the food chain. Yet there was no clear precedent for the accelerating expansion in human social scale that took over around 25 ka. Multiplication in the size of human groups was neither a natural nor an inevitable process; it broke the deep, existing constraints of hominin social structures.

What aspects of evolutionary dynamics enabled human groups to expand from groups of 150 members to more than a million times larger today?

Phase 7: The Problem of Expanding Human Scale

Laying the groundwork to explore the dynamics of biological, cultural, and social evolution, the preceding essays [Parts One and Two] have reviewed six categories of evolutionary analysis:

- Phenotype
- Genotype
- Population
- Environment
- Culture 1, or "social learning"
- Culture 2, or "group culture"

Since none of them give obvious explanations of expanding human scale, I will now dig deeper to identify specific mechanisms that may help explain the whys and hows of expanding social scales.

a) Five Possible Mechanisms for Scale Expansion

For each mechanism below, I provide a key question and a brief explanation for the mechanism's influence on expanding social scales:

1. Anthropological description

Key question: As anthropologists have argued, did community decisions cause the emergence of new social scales? If so, were these choices based on social visions and a changing environment?

The anthropological description implies that foraging groups expanded worldwide by a factor of 10 (up to 1,500 members within 10,000 years), reaching the scale at which surviving foraging groups are known today. Agricultural societies are argued to have expanded by another factor of three (30 times larger than the ancestral community). Anthropologist Harvey Whitehouse links the rituals of the early Holocene some more complex and demanding than others—to the formation of larger-scale social groups. While this link of ritual behavior and social scale is plausible for the early Holocene, it is not yet clear how to extent a ritualbased analysis to more recent and larger-scale social structures.

Drawing from anthropologists, I hypothesize three scales of groups that may have arisen:

- "Confederations" (at 20 ka: 500 members or three communities): Communities allied and ultimately integrated with the cold and drought of the Glacial Maximum.
- *"Ethnicities" (at 12 ka: 1,500 members or three confederations):* Intensive food gathering of fish, grains, or animals as the climate became warm and humid.
- "Societies" (at 9 ka: 5,000 members or three ethnicities): Agriculture and expanded labor; as at Çatalhöyük with 3,500–8,000 persons in the era 7500–6400 BCE.
- 2. Genetics or epigenetics

Key question: Was there change in the human genome or in epigenetics and its relations among proteins, so that individual behavior developed in new ways to facilitate larger social groups?

At the time of language expansion, genetic changes might have spread worldwide via migration; at other times, genetic change would have spread more slowly. *Epigenetic* change is best known as development in child behavior, but developmental processes also continue for adolescents and young adults. Thus, shifts in protein interactions might have been provoked through global environment change, leading to development of adolescent and adult readiness to articulate language or to work in larger groups.

3. Fractals

Key question: Were there inherent scales for human group size, awaiting the expansion of human population to each level?

Fractals reflect self-organizational of elements in ways that are parallel at multiple scales, thus yielding inherent group sizes. Perhaps the phenotypical scales of human life—simplified into the individual, the household, and the community—underwent subtle changes that enabled larger social groupings to become feasible and valuable. Robin Dunbar [led in showing] that self-organization of groups among all primate species created a hierarchy of group sizes, expanding from scale to scale by factors of just over three. He then combined empirical data and fractal theory to propose "grades" or stable sizes of human groups up to 50, 150 (communities), 500, and 1500 (tribes). Such grades might be extended, in certain circumstances, to create lager-scale grades such as those for humans after the Ice Age.

4. Phase transitions

Key question: In the same way that physical phase transitions yield sharp phase changes at crucial points—for example, water turning from ice to liquid to vapor—were there also types of *social* relations that changed greatly because of environmental influences, ultimately creating different overall human patterns and scales?

The physics model of phase transitions helpfully suggests that changes in individual social interactions may bring global changes in social scale. This assumes that molecules within a container have patterns of interaction with each other which may change in response to external shifts in temperature or pressure. However, molecules of the physics model appear much more uniform than human individuals or their scales of individual, household, and community.

5. Scale-free networks

Key question: Were human communities linked to distant others, so that "hubs" of closely related communities formed and, later, expanded?

Among large networks, a "diameter" may be calculated to establish the number of links one must follow to get from one point to another point in the network. The diameter of biochemical cell networks, for example, is about three; this suggests tight connections. The diameter of the World Wide Web is about 19, while the diameter of U.S. society is estimated at six. Although global linkage is relatively easy today, we must consider whether long-distance links among networks were possible in the early Holocene era—and whether such early expansions required thousands of years [of gestation] before accelerating with time.

b) Summarizing the Possibilities

Studying the possible mechanisms of changing human social scale reveals intriguing links and comparisons across times from early Homo sapiens up to today. Epigenetic change, if it provokes the creation of new scales, raises the question of whether changes around the world occur at the same time. Fractals, on the other hand, are inherently about replication at multiple stages of growth. Phase transitions show that small-scale dynamics may bring large-scale results, when accompanied by the right sort of environmental change. And the hubs of scale-free networks point toward great urban centers or earlier commercial crossroads; each hub expansion tends to bring about the next.

Whatever the influence each mechanism has had, the human order has expanded over recent

millennia by a factor of about a million or 12 powers of three from the size of the original hominid community to a group of 150 million. One may then ask: What were the results and the benefits of expanded scale? Were these benefits shared widely, or were they limited to certain parts of the population or areas of the world?

c) Scale Expansion in Human Context

Which categories of information on evolution tell us most about the expansion in scale? To start, expanded scale is a phenotypical description, focusing on the behavioral groupings of humans rather than individual characteristics. Scale expansion surely brought many genetic changes in its wake. Can one argue the reverse and hypothesize a genetic change that launched the whole process?

Epigenetic change is a more likely causal candidate, as recurring environmental change might have brought new behaviors that facilitated group expansion for children and young adults. (Population has been defined in this essay as including numbers, speciation, and migration, but one can now see that it must also include scale of groups.) Environmental factors surely also influenced scale—for instance, as certain types of regions encouraged growth in scale or as the long warming of the early Holocene brought added resources to humans. (But did other species expand their social scales in the Holocene?)

Culture 1 (social learning), while it facilitated interaction at a local scale, seems to have functioned for 200 millennia without increasing the scale of the human order. Culture 2 (group culture, which began with language development, visual arts, and accelerated invention), is associated with the *initiation* of scale expansion, though no detailed mechanism is yet agreed upon.

The above mechanisms, arguments, and hypotheses show that there is much to be discovered when it comes to understanding the precise evolutionary processes responsible for the expanding scale of social organization. This question may loom largest: will these and future ideas ultimately reveal a clear and simple explanation of expansion in human scale? Or will they tell a tale of multipronged transformation?

What's Next in Understanding Evolution?

Having stepped here into the big question of expanding scale in the human order – as it is posed here – one can see that it may be related to smallerscale issues: types of group behavior, types of social institutions, and degrees of cultural differentiation. That is, a bottom-up approach, including biological analysis, remains central to study of social scale.

Nevertheless, for the Holocene era this bottomup approach to human evolution encounters a longestablished literature on social evolution that relies equally heavily on top-down approaches. Studies of social evolution in fields of anthropology (summarized by Robert Carneiro and Bruce Trigger) and worldsystems analysis (led by Christopher Chase-Dunn in publications of 1997 and 2013) begin by assuming the existence of human groups without explicit links to their biological origins. The encounter of the two approaches may lead to lively discussions, for instance over the broad pattern of unification and differentiation that appears to show up in biological evolution - and which are echoed, if less explicitly, in the anthropological and world-systems literatures. As a closing example of the unity and diversity in human society, one may note today how often young people are able to move from one social setting to another that appears entirely different – from rural to urban or vice versa – and learn to thrive in the new environment.