

Human origins: Out of Africa

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Our species, *Homo sapiens*, is highly autapomorphic (uniquely derived) among hominids in the structure of its skull and postcranial skeleton. It is also sharply distinguished from other organisms by its unique symbolic mode of cognition. The fossil and archaeological records combine to show fairly clearly that our physical and cognitive attributes both first appeared in Africa, but at different times. Essentially modern bony conformation was established in that continent by the 200–150 Ka range (a dating in good agreement with dates for the origin of *H. sapiens* derived from modern molecular diversity). The event concerned was apparently short-term because it is essentially unanticipated in the fossil record. In contrast, the first convincing stirrings of symbolic behavior are not currently detectable until (possibly well) after 100 Ka. The radical reorganization of gene expression that underwrote the distinctive physical appearance of *H. sapiens* was probably also responsible for the neural substrate that permits symbolic cognition. This expensively acquired potential lay unexploited until it was “discovered” via a cultural stimulus, plausibly the invention of language. Modern humans appear to have definitively exited Africa to populate the rest of the globe only after both their physical and cognitive peculiarities had been acquired within that continent.

Homo sapiens | evolution | fossil record | symbolic cognition

Africa is in a profound sense the fount of human evolution. Not only did our zoological family Hominidae (*Homo sapiens* plus its extinct close relatives, often nowadays restricted to the subfamily Hominiinae; for the purposes of this article the difference is merely notional) originate there ca. 7 Ma (1), but over the past 2 Ma the continent has regularly pumped out new kinds of hominid into other areas of the Old World (2). The genus *Homo* evolved in Africa at some time ca. 2 Ma [all older contenders to *Homo* status are debatable (3, 4)], then rapidly spread out of its natal continent to populate Eurasia for the first time (5, 6). The first truly cosmopolitan species of *Homo*, *Homo heidelbergensis*, is first known from Africa at ca. 600 Ka (7), before appearing at sites in Europe and eastern Asia from ca. 500 Ka onward. The now-ubiquitous species *H. sapiens*, to which all living human beings belong, is initially documented in Africa as, somewhat later, is the first material evidence of the symbolic cognitive system that appears to be unique to humans.

Modern *H. sapiens* Is Highly Derived in Its Osteology

Morphologically, our living species *H. sapiens* is extremely distinctive. It is not unique among hominids in having a large brain [averaging ≈1350–1400 mL in volume (8)]; but it is unique in the proportions of the skull in which that brain is housed, and in numerous smaller-scale cranial characteristics (4, 9). Among other features not found elsewhere, *H. sapiens* possesses a short, tall and more or less globular braincase, beneath the front of which a small, anteroposteriorly short and delicately built face is distinctly retracted (10). The orbits are surmounted by indi-

vidual supraciliary ridges; although not invariably tiny, these are bipartite, with a central portion separated from a lateral plate by an oblique crease (4, 11). In the lower jaw, the *H. sapiens* chin is not simply a swelling at the external base of the symphysis [which can be found elsewhere among hominids (4, 12)]. Instead, it is a complex structure in the form of an inverted “T,” in which a vertical keel bounded by lateral depressions meets a basal transverse bar running between lateral tubercles (4, 12).

H. sapiens is equally derived in the structure of its postcranial skeleton. For example, in sharp contrast to the recently reconstructed skeleton of *Homo neanderthalensis* (13), that of modern humans is slender and delicately built; and although the Neanderthal rib cage is conical, tapering distinctly upwards from a broad base that matches the markedly flaring iliac blades of the pelvis, in *H. sapiens* the thorax is barrel-shaped. It is relatively narrow and tapers inward at the bottom and at the top, while the relatively delicate pelvis below it lacks lateral flare and has notably more vertical iliac blades. The dissimilarity between the two species is striking, and may have affected gait and external appearance (14). Nonetheless, until recently there was room for uncertainty over which thoracic/pelvic condition was derived within the genus *Homo*.

The two best pelvic specimens reported for species of *Australopithecus* (15, 16) made it clear that a broad, flaring pelvis is primitive for Hominidae; but whether pelvic flare is also primitive for the genus *Homo* [defined as those hominids possessing essentially modern body proportions (3)] was less evident. In contrast, the best skeleton of an early

Homo (KNM-WT 15000 from West Turkana in Kenya) shows a weakly conical thorax and, as reconstructed, only a modestly wide pelvis (17). Still, it belonged to an immature and thus incompletely developed individual. At the same time, the excellently preserved and widely flaring adult pelvis (SH Pelvis 1) from the Sima de los Huesos at Atapuerca in Spain (18) is that of a Neanderthal relative, and does no more than confirm that this pelvic conformation is primitive for the Neanderthal clade. However, a recently reported adult pelvis from Gona in Ethiopia (19), dated to between 1.4 and 0.9 Ma and attributed by its describers to the same species as the Turkana specimen, joins more limited materials described earlier (20, 21) in showing great robusticity and the broadly flaring conformation. Available evidence thus now strongly suggests that the wide, flat, heavy pelvic morphology is indeed primitive for the genus *Homo*, in which case, the basic body form of *H. sapiens*, as well as that of its skull, is highly derived.

The same can also be said for the unique mode of cognition possessed by all living *H. sapiens*. Alone among organisms, as far as can be told, our species exhibits symbolic mental processes. That is to say, its members deconstruct the world around them into a huge vocabulary of mental symbols. These they combine and recombine in imagination to describe alternate worlds and situations, based on a capacity for generating a potentially infinite array of meanings

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from a finite set of elements (“discrete infinity”; see ref. 22). As a result, unlike other organisms including such cognitively sophisticated ones as chimpanzees, we live in worlds that are largely of our own making. And despite our manifold physical distinctions from our closest living relatives, it is clearly this cognitive difference that makes us *feel* so different from them.

Fossil Record of *H. sapiens*

How and where, then, were the distinctive features of *H. sapiens* acquired? The relevant fossil record is fairly thin, but it does firmly establish that as an anatomically recognizable entity our species made its first appearance in Africa (23, 24). The “Out of Africa” hypothesis of modern human origins emerged in the mid-1980s, when paleoanthropologists such as Günter Bräuer in Germany (e.g., ref. 25) and Chris Stringer in the U.K. (e.g., ref. 26) began to point out that, sparse as they were, the earliest fossils that resembled members of our species came from southern and eastern Africa. The resultant notion of a “single African origin” for modern humans stood in contrast to “multiregional” interpretations, in which the major modern geographical groups of *H. sapiens* were seen as having extremely deep roots in time (27). The single African origin notion received an enormous boost from molecular systematics when DNA comparisons (28, 29) began strongly supporting earlier conclusions based on proteins (30) that Africa had been the ultimate source of modern human populations worldwide. Over the last quarter-century, evidence on both the molecular and the fossil fronts has accumulated to the point where there can be little doubt that humankind ultimately originated in Africa.

Beyond this, however, the picture is a little hazy. To some extent, the perspective is complicated by context, for although *Homo neanderthalensis*, for example, was clearly a member of a larger clade of species united by a suite of readily identifiable characters, the distinctive *H. sapiens* is largely isolated, bereft of evident close fossil relatives. This isolation was obscured for many years by paleoanthropologists’ habit of designating as “archaic *H. sapiens*” a very motley assortment of relatively large-brained hominids that are geologically fairly recent, but that are clearly not of modern *H. sapiens* morphology. In Africa, fossils assigned at one time or another to this meaningless wastebasket taxon include the very distinctive crania from Ngaloba, Ndutu, Kabwe, Florisbad and Jebel Irhoud. In blurring the very clear morphological boundaries of our

living species the artificial construct of “archaic *H. sapiens*” served to obscure a picture of considerable morphological and presumably also taxonomic hominid complexity in the later Pleistocene, and it is fortunate that most paleoanthropologists seem now to have recognized its counterproductive nature.

Morphological delineation of *H. sapiens* is more legitimately complicated by a group of hominid fossils, mostly from South Africa, that possess all or nearly all of the diagnostic skull characters of *H. sapiens*, except for the bipartite brow and/or the chin. Among such specimens are Border Cave 5, Boskop, Fish Hoek, Klasies River Mouth (except for AP 6222), and maybe Cave of Hearths (4, 31). Most of these hominids are poorly dated; but some, at least, are probably quite recent, and all have traditionally been accepted as modern *H. sapiens*. More broadly, this group also includes some very early fossils, such as the Omo Kibish 1 specimen from southern Ethiopia recently redated to 195 Ka (23), and most likely also the <160 Ka adult cranium from the northern Ethiopian site of Herto (24) and the >130 Ka Singa partial cranium from Sudan (32). None of these fossils fulfills all of the most stringent morphological criteria applicable to living *H. sapiens*, but the Herto and Kibish fossils in particular demonstrate quite clearly that the unusual basic morphology evident in our species was established in Africa in the period following 200 Ka. If there is any justification at all for recognizing a form we might call “archaic *H. sapiens*,” this is where we find it.

Given the radical departure in cranial anatomy of these early African *H. sapiens* from other hominids known in the same time range, from the same continent (there is very little relevant postcranial record, if any), one reasonable conclusion is that the new morphology already exemplified at Herto and Kibish arose in a single change in gene regulation, with cascading developmental effects throughout the body. Significantly, there is no reason to suppose that the ramifications of this event were limited to the bony modifications observable in the fossils themselves.

Evidence of Behavior

Outside Africa there are no convincing claimants to *H. sapiens* status before ca. 93 Ka, the date of a clearly modern human skeleton (Qafzeh 9) from the Levantine site of Jebel Qafzeh (33). This find significantly predates any equivalent evidence from eastern Asia and Europe, and molecular dating supports the suggestion that the Qafzeh occurrence represents an initial foray of anatomical *H.*

sapiens out of Africa that was ultimately foiled by climatic vicissitudes (34). What makes the Qafzeh fossil particularly relevant to the origin of modern human behavior and cognition is that, despite its modern morphology, it is associated with Middle Paleolithic stone tools more or less identical with those manufactured by penecontemporaneous Neanderthals in the same region (35).

A recurrent pattern in hominid history has been a temporal disconnect between innovation in the anatomical and behavioral realms. Thus, stone tool making was apparently invented by australopiths, whereas the achievement of modern body form was not accompanied by any detectable advance in material culture (36). The same pattern seems to have held in the case of *H. sapiens*: Modern human anatomy appears in the record significantly earlier than any evidence of symbolic behaviors. Of course, because behavior does not itself fossilize it has to be inferred from material proxies, many of which are very arguable. Based on various technological and economic indicators (blade production, use of grindstones, pigment processing, hafting) it has been proposed that hints of “modern” human behaviors can be detected as far back as several hundred thousand years ago, and that a sequential accumulation of such indicators reflects a slow, gradual attainment of “modern” behavior patterns over the past 300 to 500 Ka (37, 38). There is no doubt that in such indicators we are seeing evidence of increasing behavioral complexity (even as average hominid brain sizes were tending to increase, albeit not demonstrably in a linear fashion); but it can also convincingly be argued that no strictly technological aspect of Paleolithic behavior can be taken by itself as *prima facie* evidence of symbolic (as opposed to more generally cognitively complex) behaviors. In this perspective it is legitimate to conclude that symbolic cognitive processes, and their correlates, can be reliably inferred only from the production of overtly symbolic objects (as opposed to those that are merely technologically complex).

Even if we do not adopt the more stringent requirement for inferring the appearance of human symbolic cognition, we can nonetheless remark on the remarkably crude technological contexts in which the first anatomical *H. sapiens* are found. The few stone tools reported along with the Omo Kibish 1 cranium have been described as “unremarkable” (39), whereas those from the same deposits as the Herto cranium are notably archaic, consisting of some of the latest recorded African handaxes, plus some Middle Stone Age elements, approxi-

mately equivalent to the productions of Neanderthals (40). It is only very much later in time that we begin to pick up any artifacts whatever that may convincingly be interpreted as the products of symbolic minds. Earlier potential indicators such as the pigment processing and shellfishing recently reported from the site of Pinnacle Point on the southern African coast at *ca.* 160 Ka (41) are somewhat wishful markers for “modern” behavior patterns, especially given that both activities are documented for the almost certainly nonsymbolic *Homo neanderthalensis* (42). And the “symbolic” organization of the living space reported for the \approx 100 Ka sites of Klasies River Mouth in South Africa (43) is necessarily inferential.

In light of all this, the most ancient objects that many observers would accept as clearly symbolic come from the younger site of Blombos Cave, also on the southern African coast (44). Recovered from Middle Stone Age layers dated to *ca.* 77 Ka, they consist of two small ochre plaques bearing engraved geometric designs. The same deposits also yielded small gastropod shells that were apparently pierced for stringing (45). Body ornamentation is widely considered a reliable proxy for symbolic behavior patterns, and the Blombos evidence is supported by similar “beads” found at other African Middle Stone Age sites, including the 82 Ka Grotte des Pigeons in Morocco (46). Interestingly, a possible occurrence of similar kind has been reported outside Africa at the >100 Ka Israeli site of Skhūl (47). This adds a potential hint of complexity to the picture, although biogeographers have generally considered the Levant an extension of the African continent (48). Still, in the record as currently known, the first fully mature expressions of the human capacity do not appear until *ca.* 35 Ka (49–51) in Europe, when an ex-

traordinary artistic flowering testifies to lives that were drenched in symbol. However, there is no reason to expect that all of the dimensions of the new human symbolic capacity should have been exploited at once, and it is at the very least plausible that what we are witnessing in the African Middle Stone Age are the first stirrings of a long process of cognitive discovery that is still continuing today.

It is worth noting that shortly after Blombos times southern Africa experienced an episode of aridification that may have largely or entirely depopulated the area for an extended period (43), implying that early symbolic expression in this region may not have been linearly ancestral to later such expressions elsewhere. Nonetheless, whatever the details of the evidently complex acquisition of symbolic cognition in our species might have been, it seems clear that the Africa provided the stage on which this radically new mode of processing information initially evolved.

Conclusions

Evidently, then, “becoming human” took place in two separate stages. First, the distinctive modern human morphology became established, very clearly in Africa, and probably shortly after 200 Ka. This event involved a radical departure from the primitive *Homo* body form. Only *ca.* 100 Ka later, again in Africa, and in a Middle Stone Age industrial context, did modern symbolic behaviors begin to be expressed, underwritten by a new capacity that had most plausibly been present but unexploited in the first anatomical *H. sapiens*. In evolutionary terms this disconnect was entirely routine, for every new behavior has to be permitted by a structure that already exists: Birds, for example, had feathers for millions of years before coopting them for

flight, and tetrapods acquired their limbs in an aquatic context (52).

Symbolic reasoning appears to be qualitatively different from all other forms of cognition, including its own immediate precursor. Its neural substrate continues to be strenuously debated (53, 54); but, whatever it was, that structural innovation was most plausibly acquired as part and parcel of the radical biological reorganization that gave birth to *H. sapiens* as an anatomically distinctive entity. In which case (like those feathers and limbs) it remained unexploited, at least in the cognitive context, for a very substantial length of time, until its new use was “discovered” by its possessor. How this discovery was made remains a matter for conjecture, but a leading candidate for the necessarily cultural stimulus to symbolic processing of information is the invention of language (55). Language is perhaps the ultimate symbolic activity; and, in contrast to theory of mind, the other leading candidate for the role of releaser (56), it has the advantage of being a communal rather than an internalized attribute. The ability to use language depended, of course, on the presence of the vocal structures required to produce speech; but clearly these had already been exaptively acquired by the earliest anatomical *H. sapiens*.

Current evidence thus indicates that *H. sapiens* as we know it today had a dual origin: first as an anatomical entity, and only subsequently as a cognitive one. The clear signal of both the fossil and archaeological records is that both innovations occurred in Africa, from which the first fully modern humans expanded relatively recently to populate the rest of the world.

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