Bushes and Ladders in Human Evolution

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MY FIRST TEACHER of paleontology was almost as old as some of the animals he discussed. He lectured from notes on yellow foolscap that he must have assembled during his own days in graduate school. The words changed not at all from year to year, but the paper got older and older. I sat in the first row, bathed in yellow dust, as the paper cracked and crumbled every time he turned a page.

It is a blessing that he never had to lecture on human evolution. New and significant pre-human fossils have been unearthed with such unrelenting frequency in recent years that the fate of any lecture notes can only be described with the watchword of a fundamentally irrational economy - planned obsolescence. Each year, when the topic comes up in my courses, I simply open my old folder and dump the contents into the nearest circular file. And here we go again.

A front-page headline in the *New York Times* for October 31,1975, read: "Man traced 3.75 million years by fossils found in Tanzania." Dr. Mary Leakey, unsung hero of the famous clan, had discovered the jaws and teeth of at least 11 individuals in sediments located between two layers of fossil volcanic ash dated at 3.35 and 3.75 million years, respectively. (Mary Leakey, usually described only as Louis's widow, is a famous scientist with more impressive credentials than those of her flamboyant late husband. She also discovered several of the famous fossils usually attributed to Louis, including the "nutcracker man" of Olduvai, *Australopithecus boisei,* their first important find.) Mary Leakey classified these fragments as the remains of creatures in our genus *Homo,* presumably of the East African species *Homo habilis,* first described by Louis Leakey. So what? In 1970, Harvard paleontologist Brian Patterson dated an East African jaw at 5.5 million years. True, he attributed the fragment to the genus *Australopithecus,* not to *Homo. But Australopithecus* has been widely regarded as the direct ancestor of *Homo.* While taxonomic convention requires the award of different names to stages of an evolving lineage, this custom should not obscure biological reality. If *H. habilis* is the direct descendant of *A. aficanus* (and if the two species differ little in anatomical features), then the oldest "human" might as well be the oldest *Australopithecus,* not the oldest recipient of the arbitrary designation Homo. What, then, is so exciting about some jaws and teeth a million and a half years younger than the oldest *Australopithecus?* I believe that Mary Leakey's find is the second most important discovery of the decade. To explain my excitement, I must provide some discuss a fundamental, but little appreciated, issue in evolutionary theory-the conflict between "ladders" and "bushes" as metaphors for evolutionary change. I want to argue that *Australopithecus,* as we know it, may not be the ancestor of *Homo;* and that, in any case, ladders do not represent the path of evolution. (By "ladders" I refer to the popular picture of evolution as a continuous sequence of ancestors and descendants.) Mary Leakey's jaws and teeth are the oldest "humans" we know.

The metaphor of the ladder has controlled most thinking about human evolution. We have searched for a single, progressive sequence linking some apish ancestor with modem

man by gradual and continuous transformation. The "missing link" might as well have been called the "missing rung. As the British biologist J. Z. Young recently wrote (1971) in his *Introduction to the Study of Man:* "Some interbreeding but varied population gradually changed until it reached the condition we recognize as that of *Homo sapiens."*

Ironically, the metaphor of the ladder first denied a role in human evolution to the African australopithecines. A. *africanus* walked fully erect, but had a brain less than one--third the size of ours (see essay 22). When it was discovered in the 1920s, many evolutionists believed that all traits should change in concert within evolving lineages-the doctrine of the "harmonious transformation of the type." An erect, but small-brained ape could only represent an anomalous side branch destined for early extinction (the true intermediate, I assume, would have been a semierect, half-brained brute). But, as modern evolutionary theory developed during the 1930s, this objection to *Australopithecus* disappeared. Natural selection can work independently upon adaptive traits in evolutionary sequences, changing them at different times and rates. Frequently, a suite of characters undergoes a complete transformation before other characters change at all. Paleontologists refer to this potential independence of traits as "mosaic evolution."

Secured by mosaic evolution, *A. africanus* attained the exalted status of direct ancestor. Orthodoxy became a three runged ladder: *A. africanus-H. erectus* Uava and Peking Man)*H. sapiens.*

A small problem arose during the 1930s when another species of australopithecine was discovered-'the so-called robust form, *A. robustus* (and later the more extreme "hyper--robust," *A. boisei,* found by Mary Leakey in the late 1950s). Anthropologists were forced to admit that two species of australopithecines lived contemporaneously and that the ladder contained at least one side branch. Still, the ancestral status of *A. afticanus* was not challenged; it merely acquired a second and ultimately unsuccessful descendant, the small-brained, big-jawed robust lineage.

Then, in 1964, Louis Leakey and his colleagues began a radical reassessment of human evolution by naming a new species from East Africa, *Homo habilis.* They believed that H. *habilis* was a contemporary of the two australopithecine lineages; moreover, as the name implies, they regarded it as distinctly more human than either of its contemporaries. Bad news for the ladder: three coexisting lineages of prehumans! And a potential descendant *(H. habilis)* living at the same time as its presumed ancestors. Leakey proclaimed the obvious heresy: both lineages of australopithecines are side branches with no direct role in the evolution of *Homo sapiens.*

But *H. habilis,* as Leakey defined it, was controversial for two reasons. The conventional ladder could still be defended:

1. The fossils were scrappy and came from different places and times. Many anthropologists argued that Leakey's definition had mixed two different things, neither a new species: some older material properly assigned to *A. afticanus,* and some younger fossils belonging to *H. erectus.*

2. The dating was insecure. Even if *H. habilis* represented a valid species, it might be younger than most or all of the known australopithecines. Orthodoxy could become a four-runged ladder: *A. afiicanus-H. habilis-H. erectus-H. sapiens.*

But, as a new consensus began to coalesce about the expanded ladder, Louis and Mary Leakey's son Richard reported the find of the decade in 1973 . He had unearthed a nearly complete skull with a cranial capacity near 800 cc, almost twice that of anya. af7icanu-s specimen. Moreover,

and this is the crucial point, he dated the skull at between 2 and 3 million years, with a preference for something near the older figure-that is, older than most australopithecine fossils, and not far from the oldest, 5.5-m'liion-year date. H. *habilis* was no longer a chimera of Louis's imagination. (Richard Leakey's specimen is often cautiously designated only by its field number, ER-1470. But whether or not we choose to use the name *Homo habilis,* it is surely a member of our genus, and it is just as surely a contemporary of *Australopithecus*.)

Mary Leakey has now extended the range of *H. habilis* back another million years (perhaps closer to 2 million years, if 1470 is closer to 2 than to 3 million years old, as many experts now believe). *H. habilis* is not the direct descendant of known *A. africanus;* the new finds are, in fact, older than almost all specimens of *A. africanus* (and the taxonomic status of all fragmentary specimens older than Mary Leakey's H. *habilis* is in doubt). Based on the fossils as we know them, *Homo* is as old as *Australopithecus.* (One can still argue that Homo evolved from an older, as yet undiscovered *Australopithecus.* But no evidence supports such a claim, and I could speculate with equal 'ustice that *Australopithecus* evolved from an unknown Homo.)

Chicago anthropologist Charles Oxnard has dealt *Australopithecus* another blow from a different source. He studied the shoulder, pelvis, and foot of australopithecines, modern primates (great apes and some monkeys), and *Homo* with the rigorous techniques of multivariate analysis (the simultaneous statistical consideration of large numbers of measures). He concludes-though many anthropologists disagree-that the australopithecines were "uniquely different" from either apes or humans, and argues for "the removal of the different members of this relatively small-brained, curiously unique genus *Australopithecus* into one or more parallel side lines away from a direct link with man."

What has become of our ladder if we must recognize three coexisting lineages of hominids *(A. africanus,* the robust australopithecines, and *H. habilis),* none clearly derived from another? Moreover, none of the three display any evolutionary trends during their tenure on earth: none become brainier or more erect as they approach the present day.

At this point, I confess, I cringe, knowing full well what all the creationists who deluge me with letters must be thinking. "So Gould admits that we can trace no evolutionary ladder among early African hominids; species appear and later disappear, looking no different from their great-grandfathers. Sounds like special creation to me." (Although one might ask why the Lord saw fit to make so many kinds of hominids, and why some of his later productions, *H. erectus* in particular look so much more human than the earlier models.) I suggest that the fault is not with evolution itself, but with a false picture of its operation that most of us hold-namely the ladder; which brings me to the subject to bushes.

I want to argue that the "sudden" appearance of species in the fossil record and our failure to note subsequent evolutionary change within them is the proper prediction of evolutionary theory as we understand it. Evolution usually proceeds by "speciation"-the splitting of one lineage from a parental stock-not by the slow and steady transformation of these large parental stocks. Repeated episodes of speciation produce a bush. Evolutionary "sequences" are not rungs on a ladder, but our retrospective reconstruction of a circuitous path running like a labyrinth, branch to branch, from the base of the bush to a lineage now surviving at its top.

How does speciation occur? This is a perennial hot topic in evolutionary theory, but most biologists would subscribe to the "allopatric theory" (the debate centers on the admissibility of other modes; nearly everyone agrees that allopatric

speciation is the most common mode). Allopatric means "in another place." In the allopatric theory, popularized by Ernst Mayr, new species arise in *very* small populations that become isolated from their parental group at the *periphery* of the ancestral range. Speciation in these small isolates is *very rapid* by evolutionary standards-hundreds or thousands of years (a geological microsecond).

Major evolutionary change may occur in these small, isolated populations. Favorable genetic variation can quickly spread through them. Moreover, natural selection tends to be intense in geographically marginal areas where the species barely maintains a foothold. In large central populations, on the other hand, favorable variations spread very slowly, and most change is steadfastly resisted by the well-adapted population. Small changes occur to meet the requirements of slowly altering climates, but major genetic reorganizations almost always take place in the small, peripherally isolated populations that form new species.

If evolution almost always occurs by rapid speciation in small, peripheral isolates-rather than by slow change in large, central populations-then what should the fossil record took like? We are not likely to detect the event of speciation itself It happens too fast, in too small a group, isolated too far from the ancestral range. We will first meet the new species as a fossil when it reinvades the ancestral range and becomes a large central population in its own right. During its recorded history in the fossil record, we should expect no major change; for we know it only as a successful, central population. It will participate in the process of organic change only when some of its peripheral isolates speciate to become new branches on the evolutionary bush. But it, itself, will appear "suddenly" in the fossil record and become extinct later with equal speed and little perceptible change in form.

The fossil hominids of Africa fully meet these expectations. We know about three coexisting branches of the human bush. I will be surprised if twice as many more are not discovered before the end of the century. The branches do not change during their recorded history, and if we understand evolution aright, they should not-for evolution is concentrated in rapid events of speciation, the production of new branches.

Homo sapiens is not the foreordained product of a ladder that was reaching toward our exalted estate from the start. We are merely the surviving branch of a once luxuriant bush.