IS THERE A PHYLOGENY OF *HOMO*?

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ABSTRACT. Hypotheses of species genealogy are poorly supported when the species are closely related, and phylogenetics cannot be justified at all below the species level both for this reason and because the parsimony principle is invalid when there is reticulation. With the transfer of the habiline species out of *Homo*, several lines of evidence suggest that this genus has only a single lineage and therefore a species throughout the Pleistocene: *Homo sapiens*. Anatomical details supporting this contention are found in the continuity of different features in different regions. The emerging pattern shows population reticulation based on gene flow and population movement that reflects a network of interrelationships allowing adaptive changes to broadly spread throughout the species range. Genetic evidence precludes a recent small population size bottleneck, and thereby makes very unlikely an explanation of Pleistocene variation and evolution based on successive species replacements. Multiregional evolution remains both well supported and not refuted by these data, and this implies that Pleistocene human evolution and relationships must be studied without a taxonomic framework.

KEY WORDS. Taxonomy, phylogeny, species, evolutionary trees, multiregional evolution.

TEMPORAL HUMAN SPECIES: *HOMO ERECTUS* AND *HOMO SAPIENS*

Homo erectus is a human species with a distinct origin, in a cladogenic event at least 2 myr ago (Hawks *et al.*, 2000). The lineage founded then has shown itself biologically and culturally adapted to an increasingly broad range of different ecologies. It was able to successfully colonize much of the world by a half-million years after its appearance. This was coincident with (Asfaw *et al.*, 1992) or perhaps even before (Gabunia *et al.*, 2000) the discovery of new adaptations and behaviors reflected in the Acheulean Industrial Complex. However, the lineage does not have a distinct fate.

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The vast majority of ways that *H. erectus* is distinct from *Australopithecus habilis,* a sister group (Wolpoff, 1999a; Wood and Collard, 1999), also characterize the descendant species on the erectus lineage, *H. sapiens*. In other words, these distinctions are shared by both of the *Homo* species, and the diagnosis of *H. erectus* relative to *A. habilis* largely characterizes *H. sapiens* as well. This means there is little difference between the phylogenetically relevant features that distinguish the earlier part of the lineage from *A. habilis* and those that distinguish the later part of the lineage from *A. habilis*. Therefore there is only minimal discrimination of taxonomic importance between the earlier and later parts of the lineage. In fact, every one of the few features that are not shared between the earlier and later parts of this *Homo* lineage appear to be changes that respond to the evolutionary trends of:

1. increasing brain size,
2. greater cultural complexity,
3. substitution of technology for biology.

Moreover, *H. erectus* is not at all a static species. It shows a number of evolutionary trends in the direction of *H. sapiens* (Wolpoff, 1984, 1986). Yet, no single definition has been found that distinguishes the *H. sapiens* descendent from *H. erectus* in all the regions where the fossils of both are found. Criteria that apply to one area of the world are demonstrably invalid for other regions. In fact, no region inhabited by both of these time successive species preserves evidence of a distinct or abrupt boundary between them. Quite different from the events at the origin of *H. erectus*, there is nothing to mark the beginning of *H. sapiens*. New combinations of features separating earlier and later populations do not appear, as they must in every inhabited area if *H. sapiens* had a single populational origin. Instead, the characteristics of *H. erectus* and *H. sapiens* are mixed in transitional samples that are found in the later Middle Pleistocene of every region where there are human remains, yet different features are mixed in different regions. These include a wide range of disparate features such as details of the midface, central maxillary incisor shoveling, frontal and maxillary sinus patterns, mandibular foramen form, and many others (Crummett, 1995; Etler, 1996; Frayer, 1993; Kramer, 1991; Lahr, 1996; Pope, 1992; Smith *et al.*, 1989; Szilvássy *et al.*, 1987; Wolpoff, 1991; Wu, 1995, 1997).

Given the accepted definition of evolutionary species (Wiley, 1981) and the fact that *H. sapiens* is a widespread polytypic species, it is not surprising that the *H. erectus*-H. sapiens divisions cannot be made solely on anatomical grounds. No set of criteria can uniquely distinguish most (let alone all) members of one of these from the others. Like its descendant, *H. erectus* is a polytypic species, continuously varying but with geographic variations showing continuity in certain characteristics over time. Within the geographic range of the polytypic species, *H. sapiens* different unique combinations of morphological features appear commonly in different regions. Some of these differences are also found in the comparisons of the same geographic regions today. In other words, there are different continuities across the so-called species boundary in different parts of the world. This poses a problem, because new species can only be created by cladogenesis. This means the internal subdivisions of a species, for instance into subspecies or races, can never extend from an ancestral species to its descendant. Regional continuity across a speciation event, from one species to another involving different features in different regions, is simply impossible.

It could be that the observations of regional continuity linking geographic variants of *H. erectus* to geographic variants of *H. sapiens* are invalid, or based on unknown adaptations to conditions unique to each region and therefore have a different explanation, however, the implications of the evolutionary species concept combined with the cladogenic origin of species suggest a different solution. Evolutionary species are similar to individuals in having real beginnings and ends, and have their own evolutionary tendencies. Neither *H. erectus* nor *H. sapiens* alone fit this description, but a lineage combining both does. The meaning of these details is that there is no speciation involved in the emergence of *H. sapiens* from *H. erectus*. The absence of a branching event creating a distinct boundary at the "origin" of *H. sapiens*, together with the related patterns of polytypism in both "species," provide an explanation for the inability to develop a valid morphological definition of *H. sapiens*. No valid definition is possible because there is not a single region of origin from the preceding polytypic species. With neither clear distinctions nor a definition possible nor a distinct beginning for *H. sapiens* as narrowly defined, these reasons combine to require that the full *H. erectus-H. sapiens* lineage be regarded as a single evolutionary species: *H. sapiens* (Wolpoff *et al.*, 1984). *H. erectus* is but an early version of *H. sapiens*, and the similarities between their geographic variations can be explained by ancestry rather than parallelism (the assumption of all phylogenetic analysis is that unique resemblances are much more likely because of ancestry than because of parallel development). Regional distinctions crossing a species boundary imply that the species boundary is the illusion.

Some of my colleagues express discomfort with the idea that *H. erectus* and earlier *H. sapiens* might be the same species. For instance, Tattersall (in Flanagan, 1996) is cited as saying that merging the two reflects the bias and emotions we have in studying ourselves, and "penchant for linking everything from *Homo erectus* to *Homo sapiens* into 'one big happy family' paleontologists don't give other animals such special treatment." Perhaps this is a reflection of paleontological versus evolutionary genetics outlooks, because the highly respected evolutionist A. Templeton thinks just the opposite. He is cited in the same review as saying: "we make far too much of our anatomical differences, as our fixation on trivial racial differences so often tragically demonstrates. Biologists who study, say, fruit flies know that each population can look quite distinct ... and yet they are not tempted to hastily split them into separate species. Why must we look at ourselves any differently?"

But for the question of *H. erectus* and *H. sapiens* there is something wrong in both sets of comparisons, because this issue is not about ranges of variation *nor* about the interpretation of evolution, but rather concerns how we name species in accordance with evolutionary species criteria. The important fact is that there is no distinct beginning for *H. sapiens* as long as *H. erectus* is recognized as distinct. The earlier species can be seen merging into the later everywhere they both are found, and because each has some of the morphology of the other there is continued and unresolvable confusion about whether they overlap in time. Such a pattern would be unexpected if there was cladogenesis, with subsequent expansion of the daughter species and replacement of the mother one. The best solution that recognizes these facts is to cease distinguishing the earlier specimens on the lineage as *H. erectus*, and instead include them in *H. sapiens.*

CONTEMPORARY HUMAN SPECIES: THE GANG OF SIX

Not all taxonomic divisions of *Homo* are temporal. Tree analysis is increasingly important in the discussions of Pleistocene human variation, and it is recognized that such trees must depict species variation because they cannot validly reflect the pattern of relationships when there is reticulation (Slatkin, 1991). Some paleoanthropologists believe that there are six or more Pleistocene species of the genus *Homo*; that is, *human* species (Tattersall and Schwartz, 2000) with multiple species even at single sites such as Dmanisi (Schwartz, 2000) and Skhul (Tattersall and Schwartz, 2000). Phylogenetic techniques are used to establish the pattern of relationships of these species, but this prejudges the main issue that is at stake: What if they actually are samples of populations *within* a species—ours? Using cladistics within our species raises the issue that there are many more sources of similarities than just homologies and homoplasies, sources that change the nature of parsimony because they leave other explanations more probable than descent for shared homologies. In this case, homologies no longer reflect necessarily the pattern of descent, because human populations are not isolated and constantly branching, like species. They are much more like the channels in a river (Moore, 1994), continuously dividing but also merging so that any population may have many ancestors. No cladistic analysis could possibly model such a process, because the parsimony principle that is the most probable cause of shared homologies descent cannot validly apply. The odds that phylogenetic analysis will not accurately reflect population histories are just too great.

One different way of using the phylogenetic approach to further examine the number of species in *Homo* is to analize the distribution of evolutionary changes for evidence of parallel evolutionary trends. If different species are compared, homoplasies are a less likely source of similarity than descent is, and if we look at evolutionary trends shared by the putative species, the likelihood of homoplastic explanations plummets significantly. Even though parallel trends are much less probable than parallel features, they seem acceptable in the interpretation of different human species (Tattersall, 1996), on the argument that similar species might be expected to evolve the same way. History repeats itself here; there is nothing new about this issue because in the last quarter of the nineteenth century, similar ideas about the nature of humanity in an evolutionary context were afoot and questions were being asked about the evolution of *humanness* that should have a ring of familiarity to us. Haeckel, the great German evolutionary biologist, contended that the human races were different species, because they can be clearly diagnosed and their differences were on the order of those between naturally occurring animal species. "The human races appear to be good species ... differences in the color of skin, nature of the hair, and build of the skull, are not less marked than those differences by which many species of animal genera in a wild state are distinguished" (1883: 78-79). To be explicit, he believed "the morphological differences between two generally recognized species—for example sheep and goats—are much less important than those ... between a Hottentot and a man of the Teutonic race" (1876: 434). The differences between these human species were the result of natural selection, caused by the competition between them.

Haeckel recognized the difference between diagnosing species and separating the individuals in them, noting "the differences ... that appear so marked in the extremes of the human race, are connected by a mass of gradations and transitional forms in such a way that it is quite impossible to separate the various races from one another" (1883: 79). Yet, "the same fact holds in regard to many animal forms that are generally looked upon as 'good species' (1883: 79)."

One of the differences with such a gradation was humanness. Certain of the human species were fully human, other less evolved were not—a description not unlike that proposed for the multiple Pleistocene species of *Homo* that some recognize today. Haeckel avoided the problem of parallel evolution with his interpretation that the human species differed by how far they had evolved, rather than by in which direction. He believed that some of the human species he recognized had evolved further away from their common ancestor, "the white man further and to greater beauty than all others" (1883: 84). The degree of humanness attained by each species could be seen in their accomplishments, which he presumed reflected their abilities. Lower species, he contended, are not fully human because they are "incapable of a true inner culture or of a higher mental development ... no woolly-haired nation has ever had an important history" (1876: 310). Make no mistake, *humanness* was the focus of these comparisons: "the lower races ... are psychologically nearer to the mammals—apes and dogs—than to the civilized European; we must therefore assign a totally different value to their lives" (1905: 390).

This is not distant from today's considerations of multiple Pleistocene species. There is a "humanity" described for them that transcends species boundaries. Although Tattersall (1994), one of those who supports the multiple species interpretation, exhorts that "humanness must be kept within reasonable grounds", and cautions against "too generous a view of it", he extends humanness to Neanderthals ("I find great difficulty in denying Neanderthals human status"), although he is "convinced that they did belong to a species distinct from our own."

But how, then, did a separate Neanderthal species get to be human? Was it through an orthogenic process, an inner drive to humanize, or perhaps a parallel evolution *à la* Coon in which competing human species became more human because of the competition, although crossing the "Human Rubicon" at different times, so while Neanderthals are human, their Upper Paleolithic European successors are *fully* human. Or perhaps humanness is the primitive condition—Neanderthals and moderns share it because of their common ancestor's humanness. Each of these mechanisms would explain different degrees of humanness by some species that evolved further than others.

If humanness was primitive, the question then would become: How far back humanness goes? Perhaps to the Nariokotome youth himself? Tattersall casually dismisses this possibility, suggesting that if it was true, it would mean that "members of (early *Homo sapiens* would) hardly need to be recognizably human at all." But let's look at the evidence. Early *Homo sapiens* (Tattersall's sometimes *Homo ergaster*, sometimes early African *Homo erectus*) appears just when Oldowan industries do. This association should not be taken as a species marker, as Tattersall asserts some (unnamed) paleoanthropologists do, but it does reflect a dramatic behavioral change. Why such a change then? Remember that Nariokotome is one of those rare specimens with both cranial and postcranial remains. This allows relative brain size to be established, and he is the earliest hominid to have relative brain size outside the non-human primate range (Wolpoff, 1999). Unlike all of the australopithecines and habilines with known or estimated brain and body sizes, the Nariokotome boy's brain is larger than primate allometry could account for, and this in spite of his large body size. It is difficult to ignore the implication of these two facts. The Oldowan toolmakers were not human by virtue of manufacturing the Oldowan industry, but the fact is that they were the first—and the only—hominid species to take this important step, and the first and only to have clearly expanded brain sizes.

Yet even if we conclude that humanness is a primitive feature (the most palatable of the alternative explanations of Tattersall's assertions), a central problem for all of these ruminations remains. How did Neandertals get to be *more* human (Simek, 1992) through the span of their existence? Neandertal folk, after all, were not only the Middle Paleolithic Europeans but were also the *earliest Upper Paleolithic* population of Europe. Without any change in brain size, Neandertals of the Châtelperronian at Arcy-sur-Cure (Grotte de Renne) and St. Césaire left behind all of the markers of modern behavior (Binford, 1989) found in Upper Paleolithic Europe (hut and hearth, pierced beads and carved and grooved teeth [personal adornment] and a bone and antler industry). The behaviors *expressed* in the Middle Paleolithic turned out to be poor reflections of Neandertal behavioral *capacities*.

Making species out of races, attributing reality to more species than there actually were so muddies the waters that it becomes impossible to examine hypotheses of cause and effect. Correct diagnosis of species is a critical aspect of understanding the evolutionary process, from virtually any perspective. We require very different hypotheses about the evolution of language and intelligence if we are buying the idea that Neandertals are a separate species. We become obliged to explain why this species *independently* evolved the anatomy of language abilities (Houghton, 1993; Schepartz, 1993), established a complex culture (Hayden, 1993), and perhaps developed or at least significantly contributed to the origin of the European Upper Paleolithic (Wolpoff *et al.*, 2001). Did these changes happen because Neandertals were competing with *Homo sapiens*, a species in the process of undergoing exactly the same changes? This is an unlikely explanation, and the more tangled these arguments and special pleadings become, the more convoluted and unreasonable the interpretation of multiple species appears.

In a different approach designed to avoid the burdensome taxonomic nomenclature that must result from such a multiple species scheme, it has been suggested that instead of using species units, human evolution can be depicted as the evolution of paleodemes—separate independently evolving human lineages that may or may not be described as different evolutionary subspecies or species (Howell, 1996). However, this does not avoid the problems that any branching evolutionary model (including Howell's) raises (Wolpoff, 1999b). Paleodemes are described as "evolutionary ephemera" with "patchy, even sporadic and impersistent distributions, differentiated by barriers in space and through time." This makes them just exactly what human populations are *not*, "a succession of ancient populations, morphologically distinct and exhibiting particular spatio-temporal distributions" (Howell, 1999). Make no mistake about it: they are taxa, and they evolve by branching.

The logical consequences of a branching approach include the return of Haeckel's contention that biology and behavior are linked in humans (1876). Even quite recently there continue to be phylogenies based on behavior, such as the connection postulated between a modern human species and (what are referred to as) "Mode 3 technologies" (Foley and Lahr, 1997; Lahr and Foley, 1998)*, or in the explanation that modern humans were able to replace all contemporary indigenous populations because they alone had invented human language (Klein, 1999).

One might think that biological anthropology had finally finished off the Haeckelian precepts of separate evolutionary tracks for human taxa evolving in parallel, but this is not so (Wolpoff, 2000). The descriptions and interpretations that once applied to the human races are now applied to human ancestors (Wolpoff and Caspari, 2000). Are they any more valid in this realm? Trees of relationships continue to be drawn because they are said to *accurately* describe research results; best-fitting trees can always be determined from phylogenetic methods, the question is whether they *validly reflect* underlying process. For the Pleistocene human species, trees do not reflect this process, they fail to meet the criterion of treeness: if trees validly depict relationships, we can expect that all the endpoints on one side of a split (i.e., species, populations or races) are equally related to all the endpoints on the other side. This does *not* appear to be the case for the human taxa of the Pleistocene.

THE OTHER EXPLANATION

Multiregional evolution (Table 1) is a model of population variation and evolutionary change in the widespread, geographically diverse, internally

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*This is part of an evolutionary model that, according to its authors, does not require that the diverging taxonomic units be different species. Lahr and Foley wrote (1998:170): "in reality, whether any of these large-brained late Pleistocene hominids represented a biological species that could not interbreed with the others is questionable." Yet, it is difficult to explain either the divergence of the taxa or their associations with different behaviors without this requirement.

subdivided human species. It provides an alternative explanation of Pleistocene human variation. As Tattersall describes it (1997: 66-67):

> For the past two million years the history of our lineage has been one of a braided stream of evolving populations in all areas of the old world, each adapting to local conditions, yet all consistently linked by gene exchange. The variation we see today among the major geographic populations of humans is the latest permutation of this lengthy process.

Multiregional evolution posits that humans evolved as an interconnected polytypic species from a single origin in Africa some 2 myr ago. Small population effects during initial colonizations as humans expanded out of Africa helped establish regional differences, some of which were subsequently maintained through isolation-by-distance and others reflected adaptive variation. Advantageous changes could spread widely because of genic exchanges, promoted by exogamy and mediated by language. Also contributing was the common evolving cultural system whose elements dispersed widely, since this promoted shared adaptations expressed in behaviors and technologies. Therefore, the key elements of the model are:

- The historic and adaptive processes that created and maintained features that vary across space, contrasting the center with the edges of humanity and different peripheral populations with each other;
- The dynamics of reproduction, communication, and population movements that link local populations and provide the network for advantageous changes to diffuse throughout the species, whether these are based on new gene combinations or new ideas.

Most modernizing features arose at different times and places and diffused independently. They spread, persisting and often predominating, because of the advantages they brought, according to the multiregional model. But the spread of features is not always the spread of populations.

> Recent debates about the humanoid fossil data are based on the myth that replacement of one physical feature in a fossil series by another feature can only be created by one population replacing another (by exterminating them, for example), but such a fossil pattern could be a reflection of one genotype replacing another through gene flow and natural selection. Morphological replacement should not be equated with population replacement when one is dealing with populations that can interbreed (Templeton, 1996:1363).

This description of the pattern of human evolution and the explanation of how evolutionary processes created it assumes uniformitarianism: the present is a valid basis for interpreting the past for *H. sapiens*. The pattern of population relations created by widespread admixture was promoted by exogamy, the social rule that marriages must be with a mate from outside the group. No branching model can accurately represent it because human populations can merge as well as split apart. Weidenreich perhaps was the first to grasp this genetic insight, writing a half-century ago:

> If the Hominidae are one species in the genetical sense and an exchange of genes was possible throughout their evolution, the commonly used form to represent their lineage gives an entirely wrong idea. The tree with a common stem and more or less abundant ramifications leaves no possibility to indicate graphically an exchange of genes. The branches and sub-branches appear to evolve completely independent of each other once they have deviated. In reality, there must have been intercommunications between the branches. The graph which best fits this perception is a network. Its interconnections indicate the lines along which the exchange of genes could be effectuated (cited in Wolpoff and Caspari, 1997).

By accounting for anatomical variation with isolation-by-distance and adaptive variation explanations, the multiregional model provides an alternative basis for long-lasting diversity. Unlike the taxonomic explanation, by incorporating a key role for genic exchanges it also accounts for species-wide evolution. Isolation is not essential for maintaining geographic distinctions. To begin with, distance itself is an isolating mechanism, and when isolation by distance characterizes the distribution of a genetic system, it may not be under selection. However, many adaptive characteristics are found in broad gradients, responding to selection that differs over a wide geographic range, for instance skin color, that usually corresponds to the amount of solar radiation that skins are exposed to. This pattern would be typical of skeletal features that can reflect climatic adaptation such as relative limb lengths or nasal form. The interpretation of the pattern of variation shown by features such as these is complex, however, because many, perhaps most, adaptive characteristics *function in several different adaptive* systems. Therefore, the distribution of these features may respond to several different evolutionary pressures. Relative limb length, for instance, is important in both climatic adaptation and in different patterns of mobility.

Genic exchanges underlie these processes and the magnitude required to do so is not especially great (Relethford, 1999). In fact, observed magnitudes of genic exchange are more than sufficient to account for the multiregional pattern, because they exceed this required magnitude. Lasker and Crews (1996) examined data collected for 1510 Native Aboriginal Australians living in hunting/gathering populations. They determined that in an average tribe of some 500 individuals, some 6 percent could be expected to have one parent who was a member of a different tribe. For a fraction of this 6 percent, 0.4 percent of the total, the different tribe was a distant one, not an adjacent tribe as usually was the case. These are surprisingly high figures, given the low density of the occupation that was being examined, an important aspect since some authors have claimed that multiregional evolution could not work because the world was not populated densely enough for genic exchanges to connect populations. However, these observations imply the potential for any genetic variation to quickly (in terms of geologic time) spread through the entire Native Aboriginal Australian population, and explain why most genetic variation is within and not between tribal groups. This is a microcosm of the whole human species: most variation is found in and not between populations.

> The most important evidence that the genetic data have yielded so far is that humans evolved into their modern form as a single unit, despite past and current regional differentiation for some traits (Templeton, 1996: 1363).

A PHYLOGENY OF *HOMO*?

Phylogenetics is a tool for developing hypotheses of species genealogy. It depends on the principle of parsimony, an assertion about the probability of causation that varies from one circumstance to another; for instance, hypotheses of species genealogy are poorly supported when the species are closely related. Phylogenetics cannot be justified at all below the species level for this reason and because the parsimony principle is invalid when there is reticulation. With the transfer of the habiline species out of *Homo*, several lines of evidence suggest that this genus has only a single lineage and a single species throughout the Pleistocene, so the issue is whether our species, evolving through the Pleistocene as a single unit of subdivided, interconnected populations, can have an internal phylogeny with a structure that could be interpreted with phylogenetic analysis. Lacking evidence that the pattern or magnitude of past variation was much different from today (Hawks and Wolpoff, 2001), the answer must clearly be in the negative (Templeton, 1998). The differences paleoanthropologists write about were surely present, but so were the similar evolutionary trends and the shared humanness revealed by evidence of human behavior. There is only one reasonable explanation for this—multiregional evolution—and this evolutionary pattern relates populations in a species that does not even internally separate into distinct races, let alone into taxa of higher order.

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	Populational origin of modernity		**Multiple origins of modernity**	
	Selection	**Neutrality**	**Selection**	**Neutrality**
Speciation/ Replacement	A better adapted species outcompetes and replaces parent species across its range	Natural disaster or disease leads to extinction of parent species	NA	NA
Multiregional Evolution	Better-adapted (African) population spreads, outcompetes, and replaces other populations encountered while mixing with them, maintaining many or most of its genetic distinctions. Prominent features are better adapted but many features spreading widely are neutral. Some variants of this explanation are labeled as "Recent African Origin"; other variants emphasize reticulation more.	Modern populations spread into regions with low population densities or oscillating population size and eventually predominate in mixtures with local populations.	Modern traits appear independently in different regions at different times and predominate because of their advantages coalescing into a recognizable "modernity", as they become more widespread and common. Common features also promoted by widespread changes in cultural adaptation.	Modern traits appear independently in different regions at different times. Genes move from denser to sparser occupied areas and isolation by distance prevails.

TABLE 1
The key mechanisms of change distinguishing Multiregional evolution from the species replacement explanation of evolutionary change.

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