THE CONUNDRUM OF HOMINID SYSTEMATICS

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The "Colloquium on Taxonomy and Systematics of the Human Clade," held in Palma (Balearic Islands, Spain) in February 2000, was intended to discuss what meaning and content should be given to Hominidae. As explained at the start by Camilo J. Cela Conde (University of the Balearic Islands) and Phillip Tobias (University of the Witwatersrand), the question of what extant and fossil diversity can be recognized within our own clade is most timely, because in recent years the gap between the various schools of paleoanthropologists has become increasingly unbreachable. By explicitly asking how many taxa and with what ranks should these taxa be classified within the human family tree, the goal was to elicit discussions around an issue that extends far beyond the academic research programs of the participants.

The contributions gathered in this issue of *Ludus Vitalis* form a paramount compendium of state-of-the-art paleoanthropology. This paper is intended only as an introductory overview of the Colloquium; it highlights the main points raised, as well as the sources of disagreement among scholars. Along with this survey I have included some critical remarks on issues fundamental to the goals of the meeting, and recurrent in the inspiring discussions that followed each session.

The first speaker was Jeffrey H. Schwartz (University of Pittsburgh), who made a historical review on the variety of opinions relating to the taxonomy of hominoids. It is often said that the presumed close relationship between humans and the extant African great apes was initially inferred by Huxley and later supported by Darwin. In fact, Huxley's conclusion was only that humans deserved to be placed in a separate family most closely related to another one including all of the great apes, and Darwin arrived to it only after referring to mythical beliefs about primitive African humans. On the same sort of evidence, Haeckel predicted that human evolution had gone through a speechless "man-ape" stage which he called *Pithecanthropus*. The discovery of *P. erectus* culmi-

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nated the nineteenth century's pursuit of a "missing link". However, soon after other fossils competed for this place, every single one being presented as truly intermediate between ape and man—most notably *Homo heidelbergensis*, *H. neanderthalensis*, and *Australopithecus africanus*.

The theoretical arguments of the New Synthesis affected the study of human evolution by suggesting that only one human species could have existed at any given point in time, rendering a linear view of human origins. The taxonomy of fossil apes was accordingly oversimplified, but only until a wide diversity of Miocene taxa began to be discovered (Schwartz, 1986). The relationships of all these fossil hominoids with the human lineage are far from settled. Likewise, molecular studies of living apes are based on a quite unique version of homology, and have yet to incorporate the developmental cascade of regulatory genes. Accordingly, at the dawn of the twenty-first century it is nowhere clear that a linear succession from African ape ancestors to modern humans should be seen as the only reasonable possibility (Schwartz, 2001). The current state of hominoid taxonomy emerges so puzzling that we should keep an open mind while seeking with improved tools to understand the relationships between and within the various clades.

The second talk was by Morris Goodman (Wayne State University), who presented a bold attempt to reconcile molecular studies and paleontological research into an objective time-based phylogenetic classification. Two basic tenets are needed: first, that in accepting grade taxa as artificial (and useless), only monophyletic groups should be recognized; and second, that the only way to objectively establish the rank of any supraspecific taxon appears to be attending its age of origin. Combining these two criteria it is possible to build a taxonomic scheme that should be testable, repeatable, and predictive (Goodman *et al.*, 1998; Avise and Johns, 1999). In order to apply this idea to primates, one has to consider the large amount of robust molecular studies, together with the resulting notion that we humans are not greatly different from our closest living relatives. Applying these criteria, all great apes belong within Hominidae, and the genus *Homo* is extended to include chimpanzees as a subgenus—*Homo (Pan)*. Thus, bipedal hominids are all placed within *Homo (Homo)*, and their genealogical relationships can be portrayed in an indented classification (Goodman, 2001).

Shocking as this proposal may look at first, it must be acknowledged that there are very sound reasons to subscribe to it, at least in principle. Yet, what remains unclear is whether so explicitly recognizing our closeness to chimps really compensates the loss of communicative ability caused by deleting all names for the australopithecine groups. Furthermore, the obvious risk lies in pushing even further the ratchet of diverging nomenclatures given to the same fossil specimens by different scholars.

Back to morphology, David S. Strait (George Washington University, Washington, D.C.) and Frederick E. Grine (State University of New York) presented a comprehensive, expanded cladistic analysis (Strait *et al.,* 1997) aimed at testing the hypothesis that the recently described *Australopithecus garhi* is ancestral to *Homo* (Asfaw *et al.,* 1999). The theoretical framework is that a phyletic hypothesis can be tested using cladistics, by determining whether the putative ancestor is the sister species of its putative descendants (Szalay, 1977; O'Keefe and Sander, 1999). The limits to this research program are, of course, the small number and fragmentary nature of available fossils. A requirement is to have a reasonable alpha taxonomy—i.e., a sound definition of species hypodigms, together with a correct nomenclature. Following the results of the analysis, it was suggested that new generic names are needed at least for *A. garhi* and *A. anamensis* (Strait and Grine, 2001).

Nobody can seriously doubt now that cladistics is a powerful tool for phylogenetic inference. The argument is what to do with the resulting cladogram. Thus, new genus names for the already known hominid fossils are only meaningful under a strict epistemological adherence to the cladistic approach—the cladogram has to be read as depicting relationships among lineages, not as an artificially branching reflection of a linear phylogeny (which was indeed advocated at the onset). Moreover, in order to propose such names one has to apply the criterion (Wood and Collard, 1999) that genera should ideally correspond to both grades and clades, thus giving a reified consistency to those (possibly artefactual) branches. Methodological queries aside, the proliferation of genera for pigeon-holing fossil hominids may easily become too cumbersome to stay within reasonable limits.

The meaning of the genus category was the subject of the talk by Bernard Wood (George Washington University) and Mark Collard (University College London), who focused on what unique features should characterize all species allocated to *Homo.* This inquiry was triggered by realizing that simple, wide hypodigms previously accepted could be interpreted as complexes encompassing more than one species. Such diversity calls for a revision of supraspecific taxa, and hence the question of what should *Homo* be. The point is that the genus is indeed an important category, and there is an urgent need to define its content in an objective way. Previous views in the meaning of the genus emphasized its adaptive uniformity, or its monophyly. Combining both criteria, it appears reasonable to restrict our own genus to just *H. sapiens* and those fossil species most closely related to it—namely, those sharing full bipedalism, a large body mass, and an open-habitat physique (Wood and Collard, 1999).

This restricted definition of *Homo* leaves *H. habilis* and *H. rudolfensis* out, supporting their transfer to *Australopithecus*, even at the expense of increasing its reported paraphyly. Whether *rudolfensis* really belongs into the recently discovered *Kenyanthropus* is an open issue (Leakey *et al.,* 2001; Lieberman, 2001). At any rate, much work needs to be done and additional fossils are required before the australopithecines can be confidently divided into natural groups. Taxonomies, after all, are scientific hypotheses deserving evaluation as any others generated by paleontologists (Wood and Collard, 2001).

Although the theoretical grounds for defining the genus as "a single adaptive zone" are appealing, its practical application is questionable. Even obviating the caveats for an utmost application of the monophyly criterion (Mayr and Ashlock, 1991), there is no objective way to evaluate just how large a shift in inferred life style ought to deserve a separate genus. As with Hutchinson's multidimensional niche, there is no a priori way to decide what variables or adaptive features are to be measured, and there is no answer beyond the focus of a particular study. What a genus is remains a slippery question, and the lack of a truly objective frame leaves the door open for any supraspecific taxonomy of hominoids.

A radically contrasting view of human evolution was presented by Milford H. Wolpoff (University of Michigan). Acknowledging that a critical point, perhaps the most important one in phylogenetic inference is the correct diagnosis of species, an in-depth exploration of our closest fossil relatives was undertaken. The criterion applied is that of uniformitarianism—i.e., that current processes are the key to understand past events. There appears to be no clear-cut distinction between *Homo sapiens* and its immediate ancestor, *Homo erectus*; instead, a gradual, mosaic transition can be observed over a very wide geographic range. Thus, the distinct possibility exists, that there ever was only one species of *Homo*. If this is the case, then all forms of *H. erectus* are just early stages of the unbroken evolutionary lineage we belong to. In contrast, earlier remains do not fit so clearly in our genus. Thus, *H. habilis* may be best placed within *Australopithecus*.

Such synonymizing of the various species accepted by other authors within *Homo* is considered a contemporaneous reappraisal of the scientific refutation of "races" and the associated idea that biology and behavior are linked in humans. Indeed, the issue at stake in both instances is whether more than one contemporary lineage may exist differing in "humanness". For example, if Neanderthals were a separate species, how did they manage to acquire an undeniably complex and increasingly sophisticated behavior? In other words, how could they get to be "human", and then "more human"? Even assuming transfer of cultural traits only, the ability to make any sense out of them necessitated a high degree of "humanness". Thus, either different taxa became human in parallel, or their common ancestor was already human.

The alternative to the hypothesis that there were separate taxa within the human lineage is simply that there has always been only one. Gene flow among small populations subject to founder events and local adaptation should have been sufficient to keep all of humankind as a single evolving unit (Templeton, 1996). This multiregional model states that, on the basis of present genetic data and shared traits among fossils, humans have evolved as a single evolutionary unit during the last two million years (Wolpoff *et al.,* 1994). A compromise solution may be to depict Pleistocene hominids as belonging to "paleodemes", which may or may not be described as different evolutionary subspecies or even species (Howell, 1996). Nevertheless, this view involves a branching human tree, which is precisely the arguable point (Wolpoff , 2001).

To test these contrasting models with the data available today seems premature at best. Morphology, or rather osteology alone may not provide enough resolution, basically because there is no simple relationship between morphological shift and speciation (Mayr and Ashlock, 1991). Likewise, genetic data are limited, because the phylogeny of closely related species is surely not coincident with gene trees (Wakeley, 2000). In addition, the study of living humans, although highly relevant, cannot account for possible extinct branches—even if there really was one widespread species, was there place for offshoots stemming from it?

Part of the answer probably lies in the partitioning of morphological variation within and among species. Leslie Aiello (University College London) presented a cautionary tale on the limitation of our data. Discrimination of bone remains on the basis of single metric variables is plagued with problems. The analyses become increasingly powerful and sophisticated considering additional variables together. Thus, it is no simple task to extract character-state data from unidimensional measurements.

Morphological variation was also the subject of the talk by Ian Tattersall (American Museum of Natural History, New York), in whose opinion overestimating taxic diversity will distort the actual phylogenetic pattern much less than underestimating it. Thus, based on a perceived general low degree of differences in bony tissues among conspecific mammals, Neanderthals might be considered a separate species. This yardstick can then be applied to older fossils, yielding at least seventeen species of hominids, with up to eight belonging to *Homo* (Tattersall, 2000). Some of these, of course, may not have been distinct biological species, but under the premise of distorting phylogeny the least (obviously assuming there is a branching phylogeny within *Homo*) they may be useful taxonomic devices.

The translation of phylogenetic inference into a classification poses two main problems. First, one has to decide how much emphasis should be given to stability in nomenclature, at the expense of adequately expressing the results of novel analyses. And second, whether an ancestor should be placed in the same taxon as its descendants. A solution to the former will depend upon finding an equilibrium between scientific accuracy and ease of communication. The latter remains an open question, a partial solution to which consists in placing any putative ancestor as a "plesion". At any rate, a useful classification can only arise from an accurate phylogenetic hypothesis, and this in turn must be based on a correct delimitation of species. Genera can then be reasonably defined to have a magnitude comparable to extant Primate genera (Tattersall, 2001). However, as explored above, there is still no clear, objective way to establish how wide a genus, or any supraspecific taxon should be.

A bold proposal to establish taxonomic ranks was presented by Colin Groves (Australian National University). The starting point is the realization that recency of common ancestry is directly proportional to genetic relatedness, supporting the contention that only in a phylogenetic system can the interrelationships between organisms be measured. Thus, strict adherence to monophyletic (indeed, holophyletic) taxa allows predictions to be made about traits not observed in a given species. In such a taxonomic system, there are relevant advantages to keep the Linnean ranks. Yet, these should not be left—as is now the case—out of the goal of building an objective, unbiased and repeatable classification of all life forms. The only possible way to achieve such goal is to link taxonomic rank to age; i.e., assigning categories to taxa according only to time since divergence from sister taxa (Goodman *et al,* 1998). Cladistic nodes between named categories may be left unranked, adhering to the principle of least violence against widely used classifications (Groves, 2001).

From a neontologist's point of view, this proposal is not only reasonable, but can also be implemented—taking care to consider all evidence in estimating the age of taxa. A paleontologist, however, must confront the problem that early representatives of any clade may exhibit few of the defining apomorphies. The treatment of such fossils is still an open issue, as shown by the various opinions expressed about where to place *Homo habilis*. If we think *Homo* is special in some sense, we may find relevant to ask whether it began with a conspicuous shift in morphology and associated resource use, independently of age. Otherwise, we may consider there is nothing peculiar in our genus that could prevent assuming it started in concordance with all other taxa of equivalent rank.

What seems firmly established is that phylogenetic trees must be the basis for an objective classification of organisms. Confronted with the difficulties encountered in their construction, Camilo J. Cela Conde examined two alternative approaches to acquire the data matrix (assigning character states to the taxa under study). A straightforward means to do so might be to ignore any untested functional interpretations of characters, restricting the examination of specimens to a mere geometric comparison. The homoplasies detected through a cladistic analysis of this data base will suggest revisions that could eventually lead to the correct coding of homologies (Kluge, 1997). Such strict bottom-up approach, even if corrected with a cyclical revision of incongruencies, has no guarantee to recover the historical pattern of relationships.

Almost always taxonomists benefit from the complementary top-down approach of using tested functional inferences, in order to eliminate functionally linked (and thus informationally redundant) characters, establish character polarity, and assess homology. Accepting any source of evidence and using both bottom-up and top-down approaches appears logically inescapable. Yet, revised cladism holds that ancestors cannot be identified in the resulting tree. If this were truly so, then it would even be impossible to say whether a fossil actually belongs to an extant species. The point, however, is that the biological species concept may not be applicable to fossils, because in most cases it is most unlikely to be tested directly. Instead, it could be more useful to accept that fossil species are distinct adaptive solutions expressed in morphology. In this way, it could be feasible to reach a consensus on the general pattern of human evolution (Cela Conde, 2001).

The risk in this procedure, obviously, would be to forget that only through the study of living species can we infer anything about extinct ones. If the delineating of fossil species were to become methodologically detached from it, then any perceived traits of fossils could give rise to a plethora of nominal species whose only use would be to label different stages of a lineage, no matter how close to each other. Some degree of functional criteria must be accepted, in order to limit such species taxa within a reasonable scheme. But where exactly should that proliferation be halted? What can we do with species taxa such as *Homo antecessor*, placed in between previously known stages, and characterized only by its intermediacy? This is just what makes so interesting the proposal of finding a common ground for defining fossil species.

The case for including a top-down analysis was made even more consistent by Frederick S. Szalay (City University of New York), dwelling into the problems posed by species taxa in the hominid fossil record. A fundamental issue is that species are lineages not equitable to morphospecies. Therefore, they cannot be directly recovered from cladograms involving various stages of the same lineage. Indeed, a biological species is essentially the same as its particular antecedent lineage. Thus, species recognized by taxonomy can be seen as more or less reasonably delineated segments of lineages (Szalay and Bock, 1991). Just how large such chunks should be, and whether there was more than one lineage of hominids depends on a correct diagnosis of species hypodigms. The yardstick to be used is a critical choice—but a complex one in fact, because humans are unique in their bizarre biology. In addition, molecular approaches (or even numerical algorithms) may not be valid for calibrating the span of hypodigms.

Pliocene hominids probably lived in small demes, forming along time a bushy, sometimes anastomosing history. Yet, whether anyone of those demes can be considered a separate species remains this far from clear (Miller, 2000). Moreover, the goal of a holophyletic classification is impossible to attain at the species level. Pushing imagination perhaps a bit, one may wonder if extant chimpanzees are our own paraphyletic ancestors. Whatever the real evolutionary pattern may be, there is an urgent need for theoretically rigorous and audience-independent evaluation of fossils (Szalay, 2001). If a cladogram is to be regarded as a scheme previous to a realistic phylogeny, perhaps we need a theory linking cladograms with any species concept applicable to extant organisms.

The reality of lineages was forcefully defended by Emiliano Aguirre (Museo Nacional de Ciencias Naturales, Madrid). A careful examination of hominid fossil remains shows that the entities subject to phylogenetic analyses follow indeed a continuous evolution. Such continuity in time may not be recoverable from population genetics of extant humans, and appears to span across the full geographic range of Pleistocene *Homo*. Therefore, taxa delineated within it could be regarded as artificial categories, being largely a product of nowadays mental abstractions (Aguirre, 2001). However, an unsolved problem is how to discern gene (or character) trees from the enclosing species phylogeny—if there is any.

At the closing of the meeting, Francisco Ayala (University of California, Irvine), who had often contributed with clear explanations on population genetics, was now in charge of coordinating the formidable task of trying to reach a written consensus. Summaries of the three sessions were presented by Phillip Tobias, Emiliano Aguirre, and Daniel Turbón (University of Barcelona). And then, the improbable took place—a statement was agreed upon by everyone, showing that open dialogue can be fruitful. The spirit of *concordia* was also evident when, as a side-product corollary, and prompted by racist violence in the news, all participating experts subscribed a public declaration stressing that debates on fossil taxa notwithstanding, there is no doubt whatsoever on the fact that all living humans belong to a single cohesive entity. It was also clear, nevertheless, that we are a peculiar species particularly prone to discuss at length, and especially so when the topic is our own family.

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