# CLASSIFICATION AND PHYLOGENY IN HUMAN EVOLUTION

IAN TATTERSALL

ABSTRACT. The competing claims and requirements of classification (epistemological) and phylogeny (ontological) are briefly reviewed. Classification is a product of systematists, while phylogeny is a product of nature. For paleontologists the principal source of information about the evolutionary histories of groups of organisms is morphology, yet speciation and morphological shift are far from synonymous. This simple fact complicates everything from basic species recognition to phylogeny reconstructions involving higher taxa. It is concluded that in the interests of stability, simplicity, and effectiveness of communication, classifications should be consistent with what is known or can reasonably be inferred about phylogeny, but need not be exact transliterations of it. In the case of human beings and their close relatives it is clear that the evolutionary story has not been a simple linear process, but has instead involved extensive experimentation, with the production of numerous terminal species. These species must be accounted for in any classification that claims consistency with the fossil record.

KEY WORDS. Classification, phylogeny, monophyly, diversity, species, evolution, hominidae.

## INTRODUCTION

Phylogeny is a product of nature. It is a historical pattern that exists independently of human perceptions of it. Classifications, on the other hand, are artifacts of the human mind, made for human purposes. It is thus almost inevitable that there should be some degree of tension between these twin paleoanthropological preoccupations. Phylogeny, of course, we can do nothing about; it is simply there, and all we can do is try to decipher it as accurately as possible (never an easy task). But before even beginning to construct classifications, we have to agree on what we wish those classifications to achieve. An agreement among colleagues on such matters is more or less essential, for classifications are in one way or another intended to communicate, and the language involved should be

Department of Anthropology, American Museum of Natural History, New York, NY 10024, USA. / iant@amnh.org

one in common. Indeed, the central role of classification is to provide a sort of shorthand for reference to the taxic complexities of nature and its hierarchical organization (which I trust we can agree is empirically observed, rather than epistemologically imposed by the human mind). In an important sense, then, competing classifications are never "right" or "wrong" in principle unless they are inconsistent with the assumptions on which they were constructed. Instead, they will fail or succeed according not only to how effectively they reflect the intentions of their authors, but also to how well they meet the needs of their audience.

SPECIES RECOGNITION

In any attempt to organize the evident complexities of nature in a way that is comprehensible to humans, the first requirement is to sort out the basic entities of which natural diversity is composed. For the living world is quite evidently not a smooth continuum, however difficult it may be in practice to recognize some of the boundaries within it, especially at low taxonomic levels. And it is, I trust, possible for us to agree that species are in some sense "real," whether or not we subscribe to the compelling notion that they are "individuals" (Ghiselin, 1974). Failing consensus on this, of course, there is no hope whatever for effective communication, either among specialists or between the latter and the general public.

In paleoanthropology, unfortunately, disagreements are vast as to what constitutes a species in the fossil record. One school of thought would go as far as to allocate virtually all hominid fossils of the last two million years to the single species *Homo sapiens* (Wolpoff *et al.*, 1994), while others would recognize a minimum of seventeen species in the hominid record as a whole, with six to eight (Tattersall, 1998, 2000; Wood and Collard, 1999) within the genus *Homo*. These differences of interpretation proceed from radically different notions of how the evolutionary process works, and in terms of the analysis of the fossil record they have vastly differing implications. Taking the first approach involves including a huge range of morphological variety under the umbrella of a single species, with the attendant danger of obscuring the phylogenetic pattern within it. Taking the second introduces the practical problem of sorting out this morphological complexity, in which the phylogenetic signal may be obscured by homoplasy and similarly inconvenient phenomena. My own view, for what it is worth, has long been that if we must err in our estimates of hominid species richness, we will distort the actual phylogenetic pattern much less by overestimating than by underestimating taxic diversity in the human past (e.g., Tattersall, 1992).

The principal problem that systematists face in species recognition is that speciation and morphological shift appear to be largely unrelated phenomena. They are at least for the greater part underlain by different

mechanisms, and in contradistinction to received wisdom, the former is not simply a passive consequence of the latter (Tattersall, 1994). There is thus no readily definable degree of morphological distinctiveness that will infallibly help us recognize separate species status among fossil samples. In terms of the bony and dental records, which are all paleontologists have to work with, even a cursory appraisal of the extant mammal fauna is sufficient to show that while some species show substantial internal variability, others are relatively uniform and may not be distinguishable from their closest relatives. What, then, to do? Since neither time nor geography has a clear bearing on phylogenetic relationships (Eldredge and Tattersall, 1975), the hapless paleontologist is left with morphology alone, and often, as I have noted, the historical signal in morphology is difficult to decipher. Yet what choice do we have other than to try to make sense of this signal? It is certainly possible to argue with some force that homoplasy and like phenomena make certainty elusive—especially at low levels of taxonomic distinction. Less plausibly, it may be argued that in consequence cosmetic solutions such as broadening the working notion of species beyond all reason are to be preferred. This, though, is ultimately a counsel of despair. Certainly, there is much work to be done in characterizing the typical extent of morphological difference among closely related species (particularly in the postcranial skeleton) as a guideline for species recognition. And not much progress will be made until we make more explicit distinctions between within-species variation and that which occurs among species. Meanwhile, however, it remains true that hard-tissue distinctions among closely related species (i.e., species in the same genus) in the living fauna are typically rather small (Tattersall, 1986). In the light of which we should have relatively little difficulty in acknowledging that, for example, Neanderthals and modern humans, both highly autapomorphic, must indeed belong to separate species. Certain other cases are, of course, less clearcut.

PHYLOGENY

Only once we have settled on the species diversity before us (and really only then), can we proceed to questions of phylogeny—a very different matter from species recognition, but one with equally vexed implications. To begin with, species are grouped into genera. And while all can presumably agree that genera should be monophyletic—indeed, holophyletic—in terms of their species content, there is no equivalent agreement about the maximum species diversity that any given genus may embrace. Fortunately, from a practical point of view it seems that it is genera (rather than species) that have a gestalt reality among primates (Tattersall, 1992), and it seems reasonable (as well as practical) to extend this analogy to

fossil forms. Thus, even in the absence of the definitive morphological appraisal that can only follow upon convincing resolution of diversity at the species level, one has little problem in assigning the species *ergaster*, *erectus*, *antecessor*, *heidelbergensis* and *neanderthalensis* to the genus *Homo* in addition to *sapiens*. As Wood and Collard (1999) have pointed out, however, the somewhat shakily-based species *Homo rudolfensis* and *H. habilis* fit rather poorly with these other species; they have thus suggested, very reasonably, that they be excluded from the genus *Homo*. The problem here is that there exists only one alternative genus to which they could be allocated even with minimal plausibility: *Australopithecus*. And such transfer is accomplished only at the expense of making *Australopithecus* even more of a wastebasket than it was already. Only once we acknowledge that early hominid diversity is substantially greater than can reasonably be accommodated by one or two genera alone (or maybe three, if *Ardipithecus* is properly thus classified) will we be able to provide a rational phylogenetic schema.

The practical difficulties of recognizing genera aside, at least we nowadays have a methodology of phylogeny reconstruction that is not only theoretically consistent but that is gradually gaining currency in paleoanthropology. This is cladistics (see Eldredge and Tattersall, 1975; Tattersall and Eldredge, 1977; Delson *et al.*, 1977), whereby phylogenetic relationships are determined on the basis of the common retention of apomorphies (evolutionary novelties). The distributions of such characters are used to reconstruct relative recencies of common ancestry that are expressed in branching diagrams (cladograms). Although it has taken some time to become established in paleoanthropology, cladistics (or at least its vocabulary) is now widely employed in the field, certainly to the extent that it is unnecessary to rehearse its principles further here. It may even by now be the dominant methodology in paleoanthropological phylogeny reconstruction, thereby conforming to the Kuhnian notion of paradigm change in science. It is notable, however, that many of the hominid phylogenies on offer are still largely intuitive, simultaneously combining such considerations as time, morphology, adaptation and geography in ways that render the resulting scenarios largely non-comparable with one another.

CLASSIFICATION

Fortunately, most paleoanthropologists would by now agree that classifications should somehow reflect phylogeny. But what kind of phylogeny and, literally, how? It is, of course, easy enough construct a classification that reflects all the branchings in a cladogram (and systems of rules have been proposed for doing so, e.g., Farris, 1976); but as numerous colleagues have pointed out, the number of ranks involved in a group of any size is

impossibly unwieldy. Further, the inherent instability of a classification of this kind would by itself render it impractical, since with every phylogenetic revision or addition of a species to the schema, a fundamental reorganization would be necessary. If the main point of classifications is to communicate, i.e., to allow us to refer to species in the collective, then it is imperative that everyone know the species content of each genus, family and major taxon involved. Stability, in other words, is essential if classifications are to play their communicative role. This is especially true because not only specialists but also all others need to understand their content. It may well be that those professionally interested in the systematics of a particular group find it satisfying, even a source of pride, that their classifications should be state-of-the-art and in line with the latest developments in phylogenetic understanding. But this does little to promote wider communication.

One solution to the problem is to make classifications consistent with phylogeny, but not to make them transliterations. Several nodes in a cladogram can then be incorporated into a single taxon, and as long as the group is monophyletic the needs of both phylogeny and (relative) stability can be simultaneously served. Again, the primary necessity here is agreement on the taxic content of the major ranks recognized; and this problem is, alas, as much sociological as it is scientific. But as paleontologists we have only sidestepped the scientific problem rather than resolved it, since the difficulty remains of deciding whether or not ancestors should be classified in the same taxa as their descendents. However, since ancestors are operationally unrecognizable on the basis of apomorphies (they must, after all, be uniformly primitive with regard to all their putative descendants), this is not a problem that will generally arise (Schwartz *et al.*, 1978). Those truly concerned by the theoretical lacuna here can always, of course, resort to the device of the plesion, as advocated by Patterson and Rosen (1977). This seems preferable to the alternative, which is to promote stability by explicitly allowing paraphyletic groups in classifications.

CONCLUSION

The considerations I have raised demonstrate fairly clearly that there is a sort of cascade effect involved in broaching the systematics of any group of organisms. Thus achieving a useful classification depends on having an accurate phylogeny that is, in turn, critically dependent on appropriate species recognition. Higher orders of hypothesis, in other words, cannot be properly formulated without prior agreement at lower levels. It is critical that we bear this in mind when debating our systematic priorities.

REFERENCES

Delson, E., N. Eldredge and I. Tattersall (1977), "Reconstruction of hominid phylogeny: a testable framework based on a cladistic analysis," *J. Hum. Evol.* 6: 263-278.

Eldredge, N. and I. Tattersall (1975), "Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny," in Szalay, F. S. (ed.), *Approaches to Primate Paleobiology*. Basel: S. Karger, pp. 218-243.

Farris, J. S. (1976), "Phylogenetic classification of fossils with recent species," *Syst. Zool.* 25: 271-282.

Patterson, C. and D. E. Rosen (1977), "Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils," *Bull. Amer. Mus. Nat. Hist.* 158: 81-172.

Ghiselin, M. T. (1974), "A radical solution to the species problem," *Syst. Zool.* 23: 536-544.

Schwartz, J. H., I. Tattersall and N. Eldredge (1978), "Phylogeny and classification of the primates revisited," *Yrbk. Phys. Anthropol.* 21: 95-133.

Tattersall, I. (1986), "Species recognition in human paleontology," *Jour. Hum. Evol.* 15: 165-175.

Tattersall, I. (1992), "Species concepts and species identification in human evolution," *Jour. Hum. Evol.* 22: 341-349.

Tattersall, I. (1994), "How does evolution work?" *Evolutionary Anthropology* 3 (1): 2-3.

Tattersall, I. (1998), *Becoming Human: Evolution and Human Uniqueness*. New York: Harcourt Brace.

Tattersall, I. (2000), "Once we were not alone," *Scientific American* 282 (1): 56-62.

Tattersall, I. and N. Eldredge (1977), "Fact, theory and fantasy in human paleontology," *Amer. Scientist* 65 (2): 204-211.

Wolpoff, M. H., A. G. Thorne, J. Jelinek and Y. Zhang (1994), "The case for sinking *Homo erectus*: 100 years of *Pithecanthropus* is enough!" *Courier Forsch-Inst Senckenberg* 171: 341-361.

Wood, B. and M. Collard (1999), "The human genus," *Science* 284: 65-69.