ISSUES

Phylogenetic Trees and Evolutionary Forests

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Hominid or hominin (here rendered hominid/n) systematics is presently in its worst shape since the 1930s. The reasons for this are diverse, but include the moral economy of taxonomic "splitting," in which everyone's fossils become very important, versus "lumping," in which fewer fossils, and fewer paleoanthropologists, hold privileged positions; the strict application of cladistic monophyly, which may be useful in some cases and inappropriate in others; and the tension between genetic and anatomical data and approaches.

The taxonomic chaos in the field of human origins that prevailed in the 1930s is generally held to have been resolved by Ernst Mayr's[1] 1950 summary and revision, although Mayr has no particular expertise in either the study of extinct forms of life or human ancestry. Mayr incorporated many of the opinions in Simpson's mammalian classification, published five years earlier, with the notable exception of this example of Simpson's frustration: "Perhaps it would be better for the zoological taxonomist to set apart the family Hominidae and to exclude its nomenclature and classification from his studies."[2]

The subsequent proliferation of species is to some extent predicated on the publication of hitherto unknown fossil forms; for example, *Homo habilis* (1964) and *Australopithecus afarensis* (1979). However, this anatomical and presumed genetic diversity does not come ready-packaged into categories; rather, we load theory and meaning into the categories we create to accommodate the animals. Classification is consequently value-laden narrative. Although this fact has been widely noted below the species level in *Homo sapiens*,[3] it is just as true above the species level. The frustration expressed by Simpson in 1945 was largely a consequence of the competing values encoded in various schemes of classification, the products of diverse training and interests on the parts of researchers.

Two theories are currently drawing anthropological systematics in opposite directions, and away from the classic association of humans and apes at the Superfamily level and elaboration of the human lineage at the Family level. The first is Morris Goodman's[4] proposal that the genetic similarity of human and chimpanzee ought to be translated into a classification that places human and chimpanzee in close proximity. This emphasis on biological similarity was adopted by Jared Diamond as the theme and title of a scientific best-seller, *The Third Chimpanzee*.[5] In practice this would place humans and chimpanzees in the same genus, *Homo*. While this is not widely accepted in its most radical form, it is compatible enough with the philosophy of cladistic classification that humans and chimpanzees are now commonly associated at a lower taxonomic level, for example, the Supertribe Hominina[6] or Subfamily Homininae.[7]

The second theory, emphasizing biological diversity, involves the application of the "phylogenetic species concept," to the effect that the discovery of any uniquely derived feature (autapomorphy) is an adequate basis for the attribution of species status.[8–10] This is also rarely followed in its strongest form (it would carry bizarre implications for, say, the autapomorphically derived depigmented peoples of EurAsia), but is compatible enough with the practice of taxonomic splitting that it readily results in a proliferation of new species.[11]

Geneticists, emphasizing continuity with the apes, call for lowering the taxonomic level at which we differentiate humans from our closest living relatives. The impact of recent paleontological discoveries, on the other hand, has been paradoxically to expand dramatically the number of species recognized at the lowest taxonomic levels, in an apparent void of genetic diversity.

When we combine these two ideas—a refusal to distinguish humans and apes at a high taxonomic level and a proliferation of fossil species at a low taxonomic level—we are left with an odd situation: lots of species and hardly any taxonomic space within which to organize them usefully. The two opposing taxonomic forces, compression from genetics and expansion from paleontology, are squeezing the taxonomic structure out of the human lineage. One makeshift solution to this situation is to see our ancestry as just a part of a highly speciose but largely unstructured and untheorized evolutionary lineage. But this utterly defeats the purpose of scientific classification, which is the meaningful organization of nature.

THE CONTRIBUTION OF CLADISTICS

The third part of the puzzle is the cladistic stricture to name only monophyletic (or holophyletic) groups, and to reject paraphyly (that is, the group "left behind" by a radical divergence). Following Mayr,[12] it is important to distinguish between cladistic analysis

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and cladistic classification. Cladistic analysis (identifying shared derived traits and establishing phylogenetic proximity on that basis) is now commonplace, although in practice even cladistic analysis runs into difficulty when levels of homoplasy (parallel evolution) are high in relation to synapomorphy. Unfortunately this does appear to be the case throughout human evolution, in the relation of humans to apes,[13] Plio-Pleistocene bipeds to one another,[14–16] and later groups of the genus *Homo*.

Cladistic classification, however, has more baggage. It yields the benefit of applying a single criterion, proximity of descent, to the act of scientific classification. That virtue, however, is balanced by the vice of ignoring adaptive divergence, which is arguably the central feature of evolutionary theory since 1859. One could argue that the adaptive distinction between tetrapods and (paraphyletic) fish, birds and (paraphyletic) reptiles, or anthropoids and (paraphyletic) prosimians is not as important as the branching relationships of the species, but that is an arbitrary and rather odd position. After all, the development of supportive limbs for locomotion on land (in the case of tetrapods), flight (in the case of birds), and diurnal sociality and intelligence (in the case of anthropoids) were arguably very important features in the history and ecology of life on earth.

There is consequently nothing "anthropocentric" or "creationist" about acknowledging the divergence of our own lineage from the apes, although one occasionally hears that.[17] Divergence and adaptive radiation are facts of evolution, and they leave paraphyletic categories in their wake. Indeed, it seems almost perversely creationist to deny the significantly divergent aspects, the adaptive radiations of the history of life, in a scientific classification. After all, the geographic and demographic success of humans is predicated upon the evolutionary novelties acquired since parting ways with the apes. To fail to acknowledge that fact in a scientific classification is to conceal the major features of human evolution, not to represent them.

Moreover, paraphyly is inescapable, since it is a necessary byproduct of

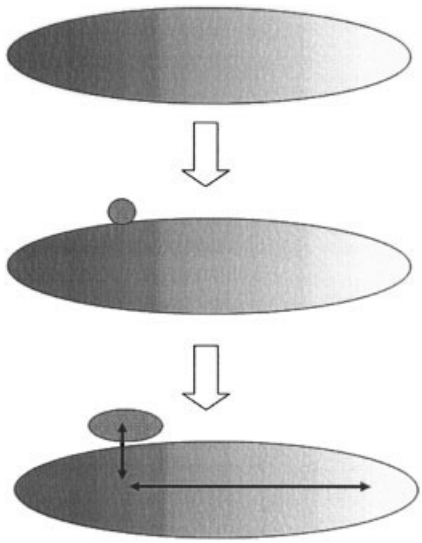

Figure 1. A diverse species (top) buds by founder effect speciation (middle). All subsequent change is autapomorphic. Regardless of reproductive compatibility, the founding parental species (bottom) now has some populations more closely related to the daughter species than to other populations of its own species, and is consequently paraphyletic.

founder-effect speciation (Fig. 1). Once a daughter population buds from a diverse parental species, all of its subsequent evolutionary divergence is autapomorphy, and thus is not phylogenetically relevant. The new daughter species is especially closely related to one part of the founder species. Thus, the founder parental species may well contain populations more closely related to the new daughter species than to populations of its own species, regardless of reproductive compatibilities.[18] One solution is simply to acknowledge and accept paraphyly, which would defeat the cladistic injunction against recognizing such groups; another is to regard the founder as a different species after the daughter species buds, which effectively disconnects the taxonomic entities from biological reality.

Thus, strict monophyly is nice, but it is probably unwise to become obsessive about it. Its classificatory products do not comprehensively represent evolutionary relationships above the species level, and it may not even exist at the species level.

Here, then, the low-level taxonomic linkage of human and chimpanzee runs into difficulty in two ways. The first is the fact that the human really is extraordinarily different from the chimpanzee ecologically. While they clearly share phylogenetic intimacy, nevertheless the adaptive divergence of the human lineage is so profound that it seems, once again, almost perversely creationist to fail to acknowledge it. When Diamond[5] rhetorically invokes the view from Mars and tells us that "a zoologist from Outer Space would immediately classify us as just a third species of chimpanzee," he is apparently not trying to tell us that cladists are extra-terrestrials in human guise. Rather, he is saying that he thinks "objective" space aliens would cast a blind eye (assuming they have eyes) to the fact that members of only one of those three species are sweating, cutting their hair, pulling their wisdom teeth, wearing clothes, speaking, walking, praying, cooking, cleaning, building, marrying, struggling through childbirth, and threatening one another by brandishing their lawyers rather than their canine teeth.

These aliens would have to be either very narrow-minded or very unobservant. If we assume them instead to be mindful and judicious, then far from classifying humans as just another chimpanzee, they might instead acknowledge that one of the species had demographically and ecologically flourished, by virtue of having evolved a radically different manner of adaptation, and should most profitably be considered separately.

The second problem with a cladistic classification of the apes is the instability of classifications based solely on phylogeny. In a notable recent example, Goodman and colleagues[19] placed humans and chimpanzees (and all known ancestors and collaterals) in the genus *Homo* and invoked a slightly higher category, the subtribe Hominina, to include gorillas. They believe that humans and chimpanzees are closest relatives, adduce evidence to support it, and incorporate that inference into the classification. And yet the data aren't quite that clear, for of the 60 phylogenetically informative DNA sequences they examined, only 22 actually gave the human-chimp result. The plurality (26 sequences) actually showed no resolution, which might be expected if the phylogenetic

event were more like a three-way-split; and the clear majority (38 sequences) simply did not dictate the phylogenetic conclusion they drew.

Of course, that conclusion may be right. The point is simply that it is a bad idea to predicate a classification on the unstable and possibly tenuous phylogenetic interpretation of data. The bio-history of these taxa is likely to have been more complex than simple successive bifurcations.[20–22] Unfortunately, the phylogenetic instability makes even a discussion of the real evolutionary issues difficult by confounding the language of comparison, the classification.

THE FOSSIL RECORD

Classificatory issues are even more difficult when we include the fragmentary and diachronic material of paleoanthropology. Nevertheless, the act of classifying still loads the science with theory, and consequently must be considered as part of a larger narrative of evolution. The classic approach was to differentiate humans and apes at the family level, recognizing the paraphyletic nature of the Family Pongidae, as the plesiomorphic sister group of Hominidae, whose members had entered a new "adaptive zone" (Fig. 2).[23] Thus, paleoanthropologists studied the "hominid" fossil record.

The paraphyly of the Pongidae becomes a problem if we consider paraphyletic taxa (such as fish minus tetrapods, reptiles minus birds, and whales minus dolphins) to be unacceptable *a priori*. That is, of course, the central tenet of cladistic classification. We could keep the traditional Hominidae and still maintain strict monophyly if we raised all of the extant ape genera to the family level and recognized the families Hominidae, Panidae, Gorillidae, Pongidae, and Hylobatidae within the Superfamily Hominoidea. But, as Peter Andrews notes, "it creates an imbalance with the other major Catarrhine group, the Cercopithecoidea . . . [where] only one family is recognized, and the diverse species and genera, which are more numerous than those of the hominoids, are divided between two subfamilies."[24]

The simultaneous resolution of these two problems (being true to cladistic classificatory principles and being fair to the monkeys) involves extending Family Hominidae to include all the living great apes. To maintain strict monophyly in the new Hominidae, we segregate (Asian) orangutans from (African) chimpanzees, gorillas, and humans at the subfamily level, that is, Ponginae and Homininae. And finally, among the hominines in the same subfamily, we identify the human lineage at a (formerly very arcane) level, the Tribe Hominini[25]: thus, hominin evolution (Fig. 3). Other levels are introduced in between to comprehend other clades.

This has several far-reaching consequences. Not only does it obscure the adaptive divergence of humans—like Jared Diamond's deaf, dumb, and blind systematist from Outer Space would have—but it also obliterates the australopithecines, who can no longer be a subfamily, and are, in any event, not a clade, but comprise yet another paraphyletic category.

I think a good case can be made for the solution being worse than the problem. First, using only the strict branching sequence does not yield categories that are necessarily any more "natural" than classifying primates on the basis of any other natural attribute, like pelage or penile morphology. All are singular biological properties, and none encompasses the scope of evolution. We may choose to privilege common ancestry above all other natural properties, but we mislead ourselves if we hold that ancestry is all there is. We may dispute the importance of adaptation and ecology as aspects of evolution, but to ignore them categorically is both arbitrary and non-Darwinian. Second, the evolutionary history and phylogenetic structure of the Cercopithecoidea is quite different from that of the Hominoidea, and there is no necessary reason why the classification of one should constrain the classification of the other. Third, in practice the new classification trades the separateness of the human lineage for the separateness of the orangutan lineage (by virtue of having branched off earliest), an emphasis that, for all the interest that orangutans certainly merit, seems, at best, misplaced. And fourth, it dramatically condenses the space available for taxonomic structure and theory in dealing with our Plio-Pleistocene fossil ancestors and collaterals.

A CASE FOR GENERA

Anyone familiar with the recent literature in biological anthropology is also familiar with the taxonomic chaos. Rob Foley[26] recognizes nine species within the genus *Homo;* Bernard Wood[27] puts two of them into *Australopithecus* but still comes out with seven; Tim White[28] lumps *H. ergaster* into *H. erectus;* Milford Wolpoff[29] lumps *H. erectus* into *H. sapiens*. Jeff Schwartz[30] and Tim White[31] trade lumps. Solomonic Glenn Conroy[32] wishes neither to split nor lump. (And all prior to the report of the Indonesian dwarf species, *Homo floresiensis*.)

On one hand, this is a sign of intellectual vigor and health—scholarly discourse, calling basic assumptions and theories of diversity into question. On the other hand, it pre-empts more interesting evolutionary questions, such as the fundamental evolutionary specializations and trajectories of the hominid/ns, in favor of shuffling one mandibular fragment or another into one pile or another, a rather more sterile activity.

I would like to suggest that although we all recognize that species are the basic units of systematics, it might be productive to try and sort things out at the genus level. After all, species are somewhat natural units synchronically, but they can only be approximated by paleospecies. A genus, on the other hand, is acknowledged to be a basically arbitrary group of species, but ones that share a common adaptation—variations on a single theme, so to speak, "an ecological unit consisting of species adapted for a particular mode of life"[33] (p. 93). This is in principle just as detectable in a fossil genus as in a living genus, which is why a genus is generally less controversial and a "more usable and reliable unit"[34] (p. 199).

Obviously the genus has not been altogether ignored of late,[27,35] but I think there has tended to be a focus on the issues of inclusion and speciosity,

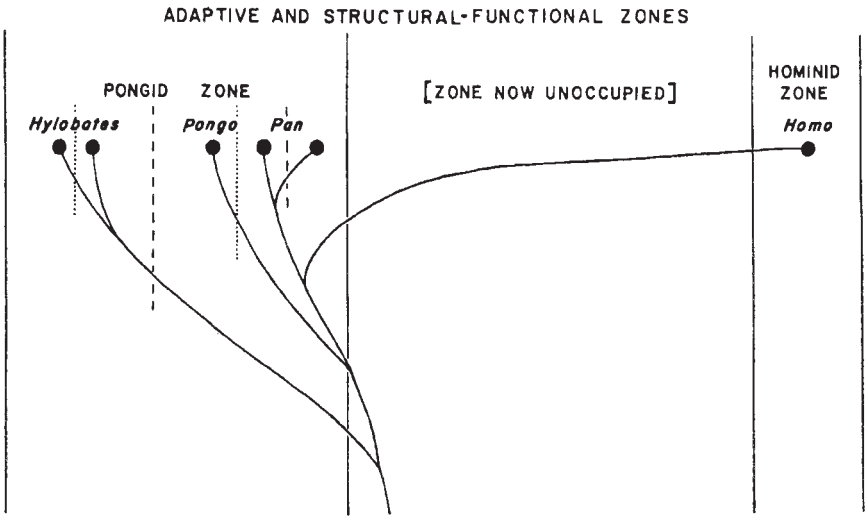

Figure 2. Simpson's (1963) depiction of the ecological divergence of hominids, leaving a paraphyletic taxonomic space for the Pongidae. (This figure also incorporates Simpson's transient synonymy of *Pan* and *Gorilla*.)

the phylogenetic trees at the expense of the evolutionary forest. For all the merits inherent in the rigors of cladistic formalism, it is accompanied by an inevitable emphasis on traits and ancestry. This, in turn, tends to push divergence and adaptation to the periphery.

ADAPTATIONS OF THE HOMINID/NS

Three basic adaptations of the exapes can be identified. The first is locomotory, and reflects a shift from quadrupedalism or quadrumanualism to principally bipedalism. This is deduced from the structure and inferred for the ecology of the genus *Australopithecus*. Begging the question of the late Miocene ancestry of this genus, we regard it as the lineage that successfully used a bipedal habit in exploiting the environments it encountered in Pliocene Africa.

Australopithecus is also a paraphyletic stem group, with descendants that secondarily specialized in divergently euphonious directions: dentally and mentally. From ancestral populations or species of the genus *Australopithecus*, then, the genus *Paranthropus* took the dental route; the genus *Homo* took the mental route.

Because of the complexity of the evolutionary process, there exists a great deal of morphological continuity among these three genera. This continuity is attributable to three sources: lineal descent, homoplasy or parallel evolution, and paraphyly in the stem genus *Australopithecus*.

By focusing on lineage and adaptation, we might also be able to make more sense of the species-level dynamic within the genus *Homo*. It could be argued, for example, that one lineage (*H. ergaster*) specialized in exploiting a mental niche with even greater success, and consequently exhibits strong continuity with a descendant species, *H. erectus*, and that another stem paraphyletic group (*H. habilis*) did not. A parallel argument could, of course, be made within *Paranthropus*.

CONCLUSIONS

It has been known since the work of Emile Durkheim[36] that cultures inscribe their social forms onto nature, and replicate aspects of their social relations in their natural taxonomies. The culture of science is no different. It is probably not merely a coincidence that we are currently stressing the position of humans within a great-ape clade at a time when creationists are having success taking over local school boards. But of course our classification is for evolutionists to work with, not to evangelize creationists with. In fact, the genetic data are far less transparently meaningful than it often seems;[37] after all, human DNA is invoked in contradictory fashions at the species level, both to embrace our close relatives, the chimpanzees, and to segregate our much closer relatives, the neandertals.

In sum, then, I have tried to argue for three things in this essay. First, a return to traditional taxonomic practice, separating Family Hominidae from a paraphyletic Family Pongidae, which has merit from both a theoretical and pragmatic standpoint. Second, a renewed emphasis on the eco-

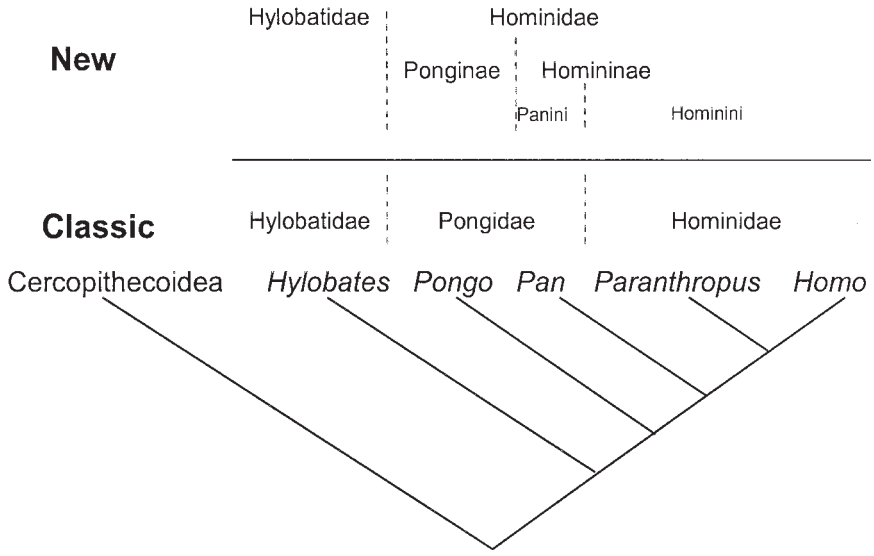

Figure 3. Cladogram with representative taxa, showing the classic evolutionary classification and, above that, the new cladistic classification. Taxa whose phylogenetic positions or status are unclear, such as *Australopithecus, Gorilla,* and everything that lived in the Miocene, are not shown.

logical specialization and adaptive divergence of our lineage, usefully encoded in the separation of humans from apes at that taxonomic level.[38] And third, reintroducing taxonomic structure (even if the taxa are paraphyletic), as opposed to species lists, into human evolutionary discourse.

If I sound like I have fossilized prematurely, that may possibly be true, but to me the newer classificatory scheme lacks a comprehensive view of evolution, an intuitive framework for discussing natural patterns of diversity, and the philosophical rigor and consistency it promises. Further, it introduces arbitrary biases—privileging genetically based narratives of relatedness, ignoring or dismissing adaptation, multiplying species in our genetically depauperate lineage and subtracting the taxonomic space they can occupy, and consequently undermining the purpose of taxonomy in the first place (which is to facilitate informed thought and discussion about the products of evolution). This is not an improvement.

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