

if anything to genetic influences acquired from extinct hominid species such as *H. neanderthalensis* in the process of driving them to extinction. And even if some such influence could be convincingly documented, what effective light would this throw on the history of diversification among hominids? There may be a blurry margin between the tokogenetic and the phylogenetic, but at the resolution at which we are able to examine events in the fossil record this lack of definition is unlikely often to be significant. If we regard fossil species as historically individuated entities (which, to be on the safe side, will involve accepting a fair degree of morphological variation within those we recognize), then we need not agonize unduly over whether some *Paranthropus* may or may not have hybridized occasionally with an *Australopithecus*, any more than we need worry about distinguishing *Theropithecus* from *Papio*. Each is a morphologically well-individuated entity with its own evolutionary history that needs to be acknowledged if that entity is to be properly understood.

To correct the final point made by Holliday in his thought-provoking commentary: none of the arguments made by Schwartz and me depends on any inferences about adaptiveness in traits that vary among lineages. After all, individuals (and species) succeed or fail as the sums of their parts, not as the possessors of individual characteristics.

MILFORD H. WOLPOFF

Department of Anthropology, University of Michigan, Ann Arbor, Mich. 48109-1382, U.S.A. (wolpoff@umich.edu). 10 VII 03

Phylogenetic problems are significant in paleoanthropology because it considers taxa that are very closely related and many of its key questions revolve around the level of taxonomic differences suggested by variation and its pattern. The issue of Holliday's paper is whether much of this can be avoided by recognizing that the level of taxonomic variation can be set arbitrarily, in spite of reticulation. However, as long as it is acknowledged that reticulation is possible below the species level and not possible at or above it, the species attains a special status in phylogenetic considerations because it is the lowest level of organization for which parsimony considerations are valid in hypothesizing relationships. It makes little practical difference whether fertile hybrids between species are very rare or simply impossible; they are very unlikely to be represented in the sparse fossil record and are too rare to have any significant influence on the pattern of evolution. At the same time, if fertile hybrids between species are common enough to be found in the fossil record and to influence the evolution of the species, it is reasonable to propose that they are not hybrids but the consequences of reticulation within what always was a single subdivided species; in this case the phylogenetic hypothesis, not the biological definition of species, would be invalid. The point is that reticulation is not hybridization: the former is a normal process within spe-

cies while the latter is a rare occurrence between them. This distinction reflects difference between whether or not apomorphies can be validly hypothesized and whether synapomorphies can be validly used to hypothesize relationships, because when reticulation is a credible source of similarity attempts to describe relationships with branching models yield contradictory and effectively useless results. In one study of tree modeling when there is reticulation, cited by Holliday (Xu 2000), when drift alone was assumed the genetic distance between populations (branches) was a function of how long they shared the same evolutionary pathway (prior to branching), while when mutation alone was assumed the divergence corresponded to the divergence time; selection variation for the different populations could not even be considered, and there was a requirement for identical effective population size in all of the populations modeled. This is the mother lode for a good deal of fuzzy thinking in paleoanthropology, since assuming that a phylogenetic approach is the valid way to deal with relationships is tantamount to assuming that the variation is at the species level or above, and this is almost always the very difficult question that is being asked.

We have the extremes of the 17 hominid species recognized by some (Tattersall and Schwartz 2000) and the single human species recognized by others (Goodman 2001, Henneberg and Thackeray 1995, Wolpoff 1999).<sup>1</sup> Thus, Holliday's assertion that "the genus *Homo* provides many potential examples of hybridization" cannot be taken at face value, because for a growing corpus of paleoanthropologists and geneticists there is reticulation and not hybridization between these *Homo* groups. These scientists who contend that there is only a single species of *Homo* (Aguirre 1994, Curnoe and Thorne 2003, Henneberg and Thackeray 1995, Jelínek 1981, Wildman et al. 2003, Wolpoff et al. 1994) are united by two precepts: (1) that higher-primate variation should be described at the same level and with the same criteria as that in other mammals and (2) that phylogenetic hypotheses are effectively null hypotheses of no difference and if they cannot be disproved, differences should not be named.

Multiple human species are one of the many "facts" in paleoanthropology established by repetition rather than research. There is no lack of descriptions for these "species," but studies showing that the elements in the descriptions are unique to the groups described (or even more common in these groups than in others) and that

1. This should provide a cautionary note for those who have insisted that the well-understood word "hominid" be replaced by "hominin" because this reflects the current understanding that humans and chimpanzees are sister groups. The argument is that since humans and the African apes are thereby placed in the Hominidae, it would make all of them "hominids" and humans alone would then be in the subfamily Homininae. Now that some would have humans and chimpanzees in the same genus, consistency should require yet another vernacular description. However, there is nothing wrong with "hominid," just as there is nothing wrong with "ape." They are descriptive and not taxonomic terms, and we don't need to keep on changing them every time a new taxonomic interpretation comes down the road!

the “species” have independent and diverging evolutionary pathways are not to be found. And if repetition doesn’t pour enough grist into the mill, there is always renaming taxa and even descriptions of them. Thus, while Wiley equated his evolutionary species concept with Templeton’s cohesive species concept (1981; Wiley and Mayden 2000), Holliday renames them as different concepts because of Templeton’s use of demographic exchangeability in defining species. But demographic exchangeability is essentially a description of monophyly at the individual level (every individual in a species is a potential common ancestor to all members of the species later in time) and fits well within Wiley’s framework. I have been burnt by this myself in the depiction of a “classic” multiregional evolution and now a “revised” multiregional evolution (Stringer 2001, Trinkaus 2002).

As a unique species with their own name, Neandertals are the gold standard for a sympatric hominid species (Tattersall and Schwartz 1999), but naming a Neandertal species confuses the questions of whether Neandertals are different from living people (they are) with whether they are evolving in the same direction as other Late Pleistocene human populations (they are) and whether Neandertal features can be found in subsequent Europeans (they can). These are testable contentions (see Frayer 1997, Hawks and Wolpoff 2001b, Wolpoff et al. 2001), and tests do not reveal Neandertals to be a separate species by the evolutionary species criterion.

Why does the level of the variation we describe matter? Even if there were no theoretical reason for it, the practical fact is that how we treat variation in the past cannot be isolated from how we treat it today. Is human variation today truly nonracial while the same variation in the past is at the species level? Can race and human evolution be divorced? I think not.

## Reply

TRENTON W. HOLLIDAY  
New Orleans, La., U.S.A. 25 VII 03

I thank the commentators for their thoughtful responses to my paper. All have raised stimulating questions with regard to species concepts, reticulate evolution, and hybridization, in part because they approach these issues from a diverse set of backgrounds and perspectives. I will here expand on some of the key issues they raise.

The first concerns the arbitrariness of the species category. I agree with Lenstra and Lieberman that no one species concept is sufficient for all aspects of biology and that in many cases the species concept one uses depends on the questions one is asking. Field mammalogists and ornithologists tend to find the biological species concept the most useful for handling the kinds of ecological and geographic issues they tackle, while modern-day systematists generally shun it (and paleontologists cannot use it). Lenstra is perhaps a little tongue-in-cheek when he

puts forward a “subjective species concept,” but with Henneberg I would argue that all species concepts are subjective, even the presumably nonsubjective “gold standard” (apologies to Jolly) of the biological species concept, for reasons I have discussed at some length.

A second pivotal issue, one raised by Gauthier, Jolly, and Wolpoff, involves the recognition of species taxa in the fossil record. This is paleoanthropology’s Achilles’ heel, as is evident from the wide disagreement among researchers over the number of fossil hominin species that should be recognized. Wolpoff points out that various experts count from 1 to 17 hominin species (interestingly, each extreme is here represented by at least one commentator). In my opinion, the pragmatic approach to paleospecies circumscription is to create morphospecies that exhibit ranges of variation similar to those of contemporary hominoid species and differ from other such morphospecies in heritable characters that are unlikely to be due to sexual dimorphism, ontogenetic change, or ecogeographical clines within a widespread population (cf. Kimbel and Rak 1993). This is generally a phenetic approach, although using apomorphies to help circumscribe taxa may be desirable (albeit not always possible at low taxonomic levels such as within the Hominini). How successful we are in this endeavor is impossible to test, but Jolly (1993) paints a rather grim picture. He maintains that future paleontologists would recognize two nonoverlapping species of modern-day *Papio*. The larger species would be the present-day “Kinda” baboons, a western subpopulation of yellow baboons (*P. hamadryas cynocephalus* under the single-species taxonomy, *P. cynocephalus* under the five-species taxonomy); the smaller species would be all other *Papio*, including non-Kinda yellow baboons. Thus, if we cannot always reliably recognize species from skeletal data, then Gauthier’s and Lieberman’s questions regarding the recognition of hybrids from skeletal data are even more critical. Determining midparental means (as Lieberman suggests) for small fossil samples is a tall order indeed. Gauthier’s hybrid detection index certainly sounds promising, although I tend to share Jolly’s and Wolpoff’s pessimism regarding the utility of cladistics at low taxonomic levels.

Both Gauthier and Wolpoff raise the point that groups that interbreed over large portions of their ranges would not likely be considered separate species by any of the species concepts discussed. One problem with this statement is that some hybridizing species overlap considerably in range (coyotes and wolves, for example) and yet are considered separate species under all but the biological species concept. A second problem is that a narrow hybrid zone is not necessarily an insignificant hybrid zone, since fit hybrid genotypes may escape a hybrid zone even if most hybrids themselves exhibit reduced fitness (Barton 2001). As a potential hominin example, most paleoanthropologists recognize *Australopithecus* (“Paranthropus”) *boisei* and *A. robustus* as separate species. Few believe that these two species overlapped for most of their respective ranges, yet a narrow hybrid zone between them makes a hypothesis of separate South Af-

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