

Letters to the Editor

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A Shortage of Ph.D.s?

I ENJOYED JEFFREY MERVIS'S EXCELLENT article "Down for the count?" (News Focus, 16 May, p. 1070), which provided a very balanced perspective on scientific manpower issues. In perusing this article, I was disappointed to learn that certain university administrators and other interested parties are once again beating the drum for increased federal funds for training in science, including Ph.D. training. Don't these people ever talk to young scientists? In the fields that I am familiar with, there is no dearth of young Ph.D.s; rather, quite the opposite is the case.

I have supervised Ph.D. training programs in the biomedical sciences for over 20 years. In my experience, most new Ph.D.s have extreme difficulty in finding jobs that actually utilize the research skills that are central to Ph.D. training. More and more biomedical Ph.D.s are being shunted into managerial jobs in the pharmaceutical and biotechnology industries. These jobs require a certain degree of scientific and technical sophistication, but they really do not require the lengthy and intense training in laboratory research that is associated with a Ph.D. The current slump in biotechnology funding has limited even this avenue of employment. As a result, many young biomedical Ph.D.s are locked into long "holding patterns" at the postdoctoral level before they attain a "real" job. This situation has been discussed at length elsewhere (1-3).

If there were truly a dire shortage of new Ph.D.s (as apparently some would have us believe), then in our free market system, young scientists should be seeing rapidly rising compensation and abundant attractive job opportunities. This is certainly not the case in the biomedical arena. I believe that those who are pushing for increased funding for Ph.D. training are confusing quantity with quality. What we need is not more Ph.D.s, but rather more rigorous Ph.D. training so that young biomedical scientists will be prepared for

the rapid convergence of biology and physical science that is certain to occur during the next decades.

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Another Perspective on Hominid Diversity

IN HIS PERSPECTIVE "EARLY HOMINIDS—diversity or distortion?" (28 March, p. 1994), Tim White criticizes fellow paleoanthropologists for too often identifying as separate species, or even genera, specimens that in reality had belonged to the same species. He presents two bonobo skulls (differing in supra-orbital toral thickness, midfacial robusticity, subnasal elongation, and orbital shape) and

argues that, if they were hominid specimens, some paleoanthropologists would place them in separate taxa. Perhaps. But variability aside, these bonobos are essentially identical in toral and midfacial morphological detail. One has a

more exaggerated subnasal curvature and subovoid orbits, while the other's orbits are more rectangular. Thus, orbital shape notwithstanding, these specimens vary in ways expected of members of the same species, i.e., in degree of expression, not kind, of morphology.

Nevertheless, White's distrust of claims of hominid diversity is partly understandable. Often, type specimens lack morphological detail and taxonomic judgements are based on nonbiological criteria, e.g., time and/or geography. Unfortunately, once published, hominid taxa, and usually only the describers' interpretations of them, are perpetuated through media hype and marketing pressures for textbooks to be "up to date."

How might one propose a new taxon? Following the International Code of Zoological Nomenclature, first compare your specimens with the type specimens (holotypes) of recognized taxa to determine if they represent one of them. If not, conservatively suggest that the specimens

constitute a morph (a group of specimens united by uniquely shared morphologies) or propose a new species and/or genus.

In contrast to this taxonomic procedure, systematic analysis yields hierarchies of hypotheses. For example, first hypothesize morphs on the basis of morphologically sound specimens. With further study, you might combine some morphs and/or subdivide others. Then, theorize patterns of relationship between morphs. This may lead to taxonomic decisions (e.g., morphs as species), but you can also start addressing questions of diversity. Of course, one systematist's morph or species might be another's species or genus, but this conceit is far less important than elucidating patterns of relationship. Thus, suppose I delineate groups A, B, and C and identify them as different species, or even genera, but A and B actually belonged to the same species. If I conclude that A and B are more closely related to each other than either is to C, my conclusion remains viable. For example, if I refer White's bonobos to different taxa, specific morphologies of "being bonobo" should still lead me to conclude that they shared a common ancestor not shared with specimens of other taxa.

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RESPONSE

SCHWARTZ RAISES THE ISSUE OF METHODS by which fossil species are recognized. He provides a surprising view into the methods he uses to recognize early hominid species diversity [which presumably led to his suggestion of three contemporary *Homo* taxa from a single Dmanisi stratum and locality (1)]. Schwartz's approach is overtly typological. He contends that within-species variation is "in degree of expression, not kind, of morphology."

Biology abandoned the Platonic concept of "essences" long ago. Even in paleoanthropology, the typological approach has had rare overt application since its popularity peaked during the first half of the 1900s. Operationally, Schwartz suggests "first compare your specimens with the type specimens (holotypes) of recognized taxa to determine if they represent one of them." As Mayr noted in 1969, "Species consist of variable populations, and no single specimen can represent this variability." (2, p. 369). In a comment directly relevant to the question of *Kenyanthropus*, Simpson noted 42 years ago that the "[f]inal decision as to conspecific status depends, however, not on nearness to any one specimen, type or other, but on

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falling within or outside of ranges of variation *inferred* for the whole taxon.” [(3, p. 184), his italics]. In modern paleontology, comparison with the hypodigm (the available fossil record of a taxon) is the criterion for taxonomic recognition. Schwartz’s typology represents a different approach.

Hominoid fossils are rare, and decades of research have shown how easy it is for trivial, normal individual variation to be confounded with a real taxonomic signal—particularly when typologists use individual fossils as the units of comparison. Compounding the problem today is the fact that limited sets of morphological data are often subjectively employed in cladistic and phenetic analyses. Here, the subjective dichotomous categorization of continuous skeletal variation combines with the lack of appreciation for intragroup variation to produce erroneous phylogenetic and taxonomic conclusions. The two bonobo crania I illustrated, beyond those features Schwartz notes, show variation in zygomatic root position and lower facial projection, “characters” used to support the purportedly new genus and species *Kenyanthropus platyops*. The apparent lack of appreciation for such degrees of normal within-species variation, compounded by

geological distortion of the fossil, led to the erection of the questionable taxon, the subject of my Perspective. Schwartz does not provide any evidence to support the hypothesis that this fossil is a species separate from *Australopithecus afarensis*.

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Chromosomal Speciation

IN THEIR REPORT “CHROMOSOMAL SPECIATION and molecular divergence—accelerated evolution in rearranged chromosomes” (11 April, p. 321), A. Navarro and N. H. Barton present strong evidence for an important role for molecular divergence in chromosomes in speciation. L. H. Rieseberg and K. Livingstone (“Chromosomal speciation in primates,” Perspectives, 11 April, p. 267) point out the importance of this work with regard to the split between the line leading

to the chimpanzee and that leading to humans (the hominid-panid split).

Rieseberg and Livingstone argue, “The most plausible interpretation of this pattern is that the chromosomal rearrangements ‘triggered’ speciation by allowing differences under selection to accumulate in genes linked to the rearrangements, despite continued interbreeding between the two lineages for up to 3 million years after their initial divergence...” (p. 267). I find such inbreeding highly unlikely. Navarro and Barton state, “Human chromosomes 1, 4, 5, 9, 12, 15, 16, 17, and 18 are separated from their chimpanzee’s [sic] homologs by pericentric inversions, and human chromosome 2 is the result of the tandem fusion of two acrocentric chromosomes common to the rest of the great apes...” (p. 322).

The authors appear to treat chromosome 2 in the same manner as the rest of the reorganized chromosomes. I doubt this is appropriate, because of the observed effects of the fusion of acrocentric chromosomes. These fusions, also known as Robertsonian translocations, result in “one large metacentric chromosome made up of the long arms of both acrocentric chromosomes and a small submetacentric chromosome made up of the short arms. The smaller chromosome is generally lost...”

without consequence...” (*I*, p. 342). An individual carrying such a large fused chromosome will produce six sorts of gametes: one normal with the two ancestral chromosomes, one with the fused chromosome, and four with unbalanced chromosome sets (*I*). Only the first two of these are likely to result in a viable offspring. One would expect that any such situation would be rapidly selected against, but here we are with 46 chromosomes, while the Great Apes have 48. This suggests strong selection for the fused chromosome and a rapid separation into two populations.

Such strong selection can be envisioned if the fusion produced a major preadaptation such as the appearance of bipedality. Bipedality is the marker trait for the hominids. It involves the sacrum forming after the sixth lumbar vertebra instead of the third (2). The shift from lumbar to sacral vertebral form is marked by the shift from HOX D9 to D10 (3). The pelvis starts to form where Hox D9 goes from high to low level (4). The HOX D sequence is on chromosome 2. If the control of these genes were to be altered, perhaps by mismatch repair duplication of a control element in the course of the fusion, the appearance of a preadaptation, which would be highly adaptive in the later savanna environment and perhaps useful on the floor of the ancestral forested environment, can be envisioned. A shift in the boundary between Hox D9 and Hox D10 would, of course, be expected to produce change not just in the vertebral column, but also in the chela, consistent with the structure observed for the proximal foot in Little Foot (5) and the new Australopithecene hand (6). Accordingly, I think that the idea that chromosomal alteration could produce peripatric speciation is perhaps plausible, but the idea of several million years worth of gene flow involving a Robertsonian translocation is not. Speciation involving a change of this sort is apt to be rapid and would be facilitated by the development of a new environment in which the new form was at a selective advantage.

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BOWERS RAISES SEVERAL ISSUES, THE FIRST three of which we agree with: that different kinds of rearrangements have different

degrees of underdominance; that, in the particular case of fusions like the one in chromosome 2, strong positive selection may have been involved in their fixation; and that several million years of gene flow are unlikely. However, none of these three issues appear to be new or relevant to the results of Navarro and Barton. First, Rieseberg and Livingstone only proposed an upper limit of hybridization time. Navarro and Barton made very clear that the size of the detected effect opens the possibility of complementary or alternative explanations, and suggested some of them. Second, there seems to be confusion regarding why we treated the reorganized chromosomes “equally.” Neither Navarro and Barton nor Rieseberg and Livingstone suggest that all 10 major autosomal rearrangements between humans and chimpanzees played identical roles in speciation. If fact, we were fully aware not only of the possibility that different chromosomes may have had very different evolutionary roles, but also that some of these roles may have been unrelated to speciation. The only reason chromosomes were pooled together in the analysis by Navarro and Barton is that the available data did not allow for a more comprehensive study, which would analyze each chromosome and, indeed, each rearranged region separately. Moreover, Navarro and Barton's data do not support the fourth issue raised by Bowers, the possibility that chromosome 2 had a particularly relevant role, because chromosome 2 has average K_a , K_s , and K_a/K_s values (K_a is the rate of nonsynonymous nucleotide substitution per nonsynonymous site, and K_s is the rate of synonymous substitution per synonymous site). Removing chromosome 2 from the analysis yields identical results.

The fifth and last issue introduced by Bowers, the possibility that the fusion in chromosome 2 produced a mutation that turned out to be a major preadaptation, such as bipedalism, might be an attractive idea, but we are not aware of any evidence that supports it. Although the HOX D cluster is in chromosome 2, it maps several tens of Mb away from the fusion breakpoints and so could not have been mutated by the rearrangement itself. In any case, it is very unlikely either that a single mutation could be responsible for changes in the complex traits that distinguish us from chimpanzees or that the Hox genes would be involved in such mutations.

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