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Response: We explained the rationale behind our approach in the first paragraph of our article (1). Far from assuming the hypothesis before we started out, we feel that treating the emergence of modern *Homo sapiens* as an evolutionary event enables proper consideration of that event. Multiregional models can (and for some authors do) account for the evolution of "modern" features in geographically separate populations by parallel evolution, and it seems essential to diagnose what we mean by "modern humans" in an article which discusses the origin of modern humans. Too often other workers (including some authors of the above letter) have not made

clear and scientific presentations of what they mean by "modern human," thereby preventing tests of their preferred evolutionary models. Thus they do not provide consistency of approach or genuine testability for their ideas. Without a clear conception of what they mean by "modern human," they are unable to provide appropriate data on ranges of variation in "modern humans," to recognize the earliest appearance of "modern humans" in any given area, or to establish the existence of evolutionary intermediates or hybrids, which should be essential components of multiregional-gene flow models.

Inextricably linked with these discussions are different or confused conceptions of what is meant by the term "species." One must have a conception of what is meant by the term "modern human," as well as an awareness of the limitations of the biological species concept as applied to fossils. It is evident from recent studies that neospecies may have very high or very low levels of morphological variation. In the case of extant primates, it seems that the use of skeletal variation alone would lead to a serious underestimate of species numbers (2).

By choosing to limit the use of *Homo sapiens* to anatomically modern humans as

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diagnosed by shared, derived morphological characters, we have not precluded any process of evolutionary origin. Too often, however, paleoanthropologists have fallen into the trap of assuming that by including, say, Neanderthals in the species *Homo sapiens* (assessment based only on morphology), this therefore demonstrates that Neanderthals were able to contribute genes to the modern human gene pool (assessment based on the biological species concept). We prefer to use the known morphological differences of Neanderthals from all recent *Homo sapiens* to separate them from the unit of modern humans delineated by shared evolutionary novelties. This cladistic diagnosis of *Homo sapiens* is one which can be applied to both recent and fossil examples and, contrary to a statement by Wolpoff *et al.*, does not exclude large segments of recent populations when properly and fairly applied [that is, without arbitrarily excluding some of the proposed criteria, as was done in (3)].

Our presentation of the "predictions" of the multiregional model was based on careful reading of the relevant cited papers. Some of these predictions are evidently not welcomed by proponents of the model, but in most cases we believe that we have used the model fairly in order to generate predictions where none were spelled out. For example, it seems to us an inescapable conclusion from the universal gradualism of the multiregional model that "transitional" fossils should be widespread in time and space, and there are frequent references in the writings of proponents of the multiregional model to recognized ancestors and descendants and to fossils or samples which are "transitional" between these supposed ancestors and descendants. Indeed, Wolpoff was recently heard on BBC radio (4) asserting that "the world is full of transitional fossils." Moreover, Wolpoff *et al.* berate us for not recognizing the existence of such fossils in Europe and Israel.

Similarly, we used the multiregional notion of peripheral homogeneity (with longer term retention of primitive characters) and "central" heterogeneity to generate the prediction that combinations of "modern" features should initially be more common centrally (because of greater morphological variation and because of multidirectional gene flow through the central area). Perhaps we should have added, "subject to favorable selection." Finally, we can see no alternative but to refer to the role of parallel evolution ("together with gene flow," as stated in the caption of our figure 1) in the multiregional model. For example, if the small brow ridges characterizing modern human crania evolved separately from the distinctive larger brow ridges of different premodern popula-

tions in each inhabited area (whether or not any gene flow from other regions was involved), how else could the process be described? While we feel we did our best to lay out the predictions of the multiregional and recent African origin models as gleaned from the existing literature, it is certainly possible that we misunderstood some aspects of the multiregional model. If we have erred, it would be valuable for proponents of the multiregional model not only to point out our mistakes but also to provide alternative testable predictions.

We feel we are justified in arguing from the data that Australian aborigines are no more closely related to Indonesian *Homo erectus* than any other modern humans. Those who have repeatedly (and apparently approvingly) quoted that they uniquely show "the mark of [ancient] Java" (5-7) should perhaps be the ones to pause for thought. Regarding the figures, we chose the particular orientation of the four crania to allow simultaneous comparisons of frontal and facial morphology and shape. More figures would have been required if we had used conventional orientations, for no greater information content. Finally, regarding the study of the relevant Asian fossil material, all of us of necessity have to work with casts when studying the fundamentally important material from Zhoukoudian Upper and Lower caves. Only Chinese workers have yet had proper study access to the Dali, Hexian, and Yinkou material, but several of us have had access to the Trinil, Sangiran, and Ngandong material in European institutes. The only real advantage which one or two of the authors of the above letter might justifiably claim is that they have studied at first hand fossil material located in Java and Australia, whereas we have had to rely on original material in Europe, on casts, or on other workers' data. But it is evident that others who have studied these same original fossils in Australasia have radically different ideas from those of some of the authors of the letter (8).

Turning to specific points about the fossil record, first, we did not say that the multiregional model could not account for the loss of Indonesian-derived characters, only that it must do so. Second, with reference to Eurasian comparisons, we stated that late middle to late Pleistocene Chinese fossils more closely resembled European and African middle Pleistocene hominids, not Neanderthals. Under the multiregional model they might be expected to more closely resemble Neanderthals through gene flow or through parallel evolution, which would subsequently lead to similar modern populations in the late Pleistocene. Third, the use of "homoplasy" is certainly permissible in

the context used in our article, and we strongly question the assertion that cladistics is misapplied when used within species. Fourth, the Chinese fossils from Dali and Yinkou are morphologically distinct from their supposed local ancestors. For example, Wu Xinzhi and Wu Maolin state (9), "the morphology of the Dali cranium differs markedly from that of *H. erectus* from Zhoukoudian," while of Yinkou, Wu Rukang (10) even concludes, "if the Yinkou specimen is actually 280,000 years old as it is dated, there raises a new problem [of] whether there are two separate lineages of human evolution in China." Fifth, with reference to WLH 50, we clearly talked about morphological, not chronological, intermediacy, whereas Wolpoff (6, 7) talks with less justification of both morphological and temporal intermediacy. Sixth, we would not deny that Chinese and Indonesian middle Pleistocene fossils are morphologically distinct, but we argue that they share "Asian" features compared with "Western" samples. Last, the Narmada fossil is an interesting specimen, but its dating and affinities are as yet unclear.

In conclusion, we had hoped that the reaction to our article from supporters of the multiregional model would be based on the presentation of further data to test the models. We look forward to such a constructive response from those who signed the letter by Wolpoff *et al.*

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Erratum: The width of the shell shown on the cover of the 1 July issue was given incorrectly in the caption on page 5. The shell is approximately 2 millimeters in width, not 2 micrometers.