

Pleistocene assemblage. Here the difference between the early and later Middle Pleistocene groups is significant, as Wolpoff also demonstrates. But when the Lower Pleistocene fossils are compared to the later sample, the mean difference is less than 150 cc. The associated *t*-value is -2.234 , and the probability of observing a difference this large if the two groups are really drawn from populations having the same mean is greater than .05. The difference is not quite significant when a two-tailed test is used.

Read in this way, the data do not reflect any "dramatic" expansion of vault size in *Homo erectus*, as claimed by Wolpoff. Late individuals do tend to have capacities which are larger than those of early specimens, but the trend is hardly marked. Current work of my own indicates that change in fact occurs only slowly during much of the Pleistocene. When brain sizes for all of the more complete African and Asian fossils are regressed against geological ages estimated for each individual, the resulting slope shows cranial capacity to be increasing at a rate of about 135 cc per 1.0 ma (Rightmire 1985). There is no evidence that this trend is statistically significant.

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Stasis in the interpretation of evolution in *Homo erectus*: a reply to Rightmire

Milford H. Wolpoff. *Department of Anthropology, University of Michigan, Ann Arbor, Michigan 48109*

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Focusing on the question of trends in *Homo erectus* cranial capacity evolution, Rightmire contends to have reanalyzed the data and demonstrated "a pattern of change . . . quite different from that described by Wolpoff." Accepting the procedures used in this earlier analysis (Wolpoff 1984), he does this by changing the composition of the *Homo erectus* sample.

In order to ascertain whether or not there were evolutionary trends within the species, *Homo*

erectus specimens were divided into early, middle, and late subsamples (Wolpoff 1984), a procedure which, although "disturbing" to Delson (1985, p. 763), realistically reflects the low resolution required by dating inaccuracies. In his response Rightmire proposes that three specimens be removed from the analysis, the two smallest specimens from the early subsample and one of the largest specimens from the late subsample.

His reasoning for removing the cranial capacities of the smallest two specimens from the early subsample is unclear. For instance, in discussing the ER 1805 vault he asserts that "there is no consensus that this individual is *Homo erectus*," in spite of the fact that the only two authors who have allocated the specimens to *any* species (Howell 1978; Wolpoff 1980) agree in considering it *Homo erectus*. Moreover, he does not respond to any of the points raised in the discussion of why ER 1805 was considered *Homo erectus* (Wolpoff 1984, pp. 391–392), nor does he refer to the fact that all of the analyses within that publication were made both with and without ER 1805 and it made no difference (p. 397).

The other small specimen, the Modjokerto child, is removed because the "lengthy note of justification is not convincing." This assertion is not surprising to me since Rightmire reads this note to mean the capacity used "is essentially uncorrected for age." Although it is the age-at-death estimate of the specimen that is criticized, the Modjokerto adult cranial capacity estimate is based both on the age and on the only direct volume determination ever made for the specimen, the clearly described (and easily repeated) water displacement volume determination for the whole vault. The omission of the adult capacity estimate from the sample is by assertion, and is not supported by a single fact. There is only the citation of Le Gros Clark's (1964) estimate of an adult capacity that may have been no larger than 1,000 cc, an estimate which if correct would imply a doubling of the fossil's actual measured endocranial volume. Following a human pattern of growth, such a doubling would only be possible if the specimen was less than a year old at death (Tobias 1971, pp. 10–11), an interpretation of age that has never been suggested by anybody who actually worked on the specimen.

In the late subsample the capacity of one of

TABLE 1. Dimensional changes in *Homo erectus* temporal subsamples. Comparison of the three *Homo erectus* subsample means for vault size and mandible size measurements. All dimensions are in millimeters. Significances for the three possible subsample comparisons are given from one-sided Student's *t*-tests. Details of the sample compositions and measurement definitions are given in table 1 of Wolpoff (1984), as modified in the text of this paper. Measurements of the Narmada cranium are given by Sonakia (1984, 1985a,b). The WT 15000 measurements were kindly provided by Dr. Alan Walker, based on an accurate cast of his reconstruction of the vault. As discussed in the text, growth curves of these measurements published by Heintz (1966) were used to estimate the adult values that are used in the analysis.

	Early	Middle	Late	E-M	M-L	E-L
Bregma-inion length	124.5	132.0	141.3		.04	.004
Sample size	4.	6.	8.			
Standard deviation	8.8	10.4	8.1			
Auricular point to bregma height	87.4	91.8	98.6		.06	.008
Sample size	5.	4.	8.			
Standard deviation	5.9	4.1	7.4			
Biparietal breadth	131.1	137.5	140.2	.09		.006
Sample size	5.	8.	9.			
Standard deviation	6.6	8.5	4.8			
Mandibular corpus height at M_1/M_2	34.5	30.6	29.6	.02		.01
Sample size	12.	9.	7.			
Standard deviation	4.4	4.1	3.4			

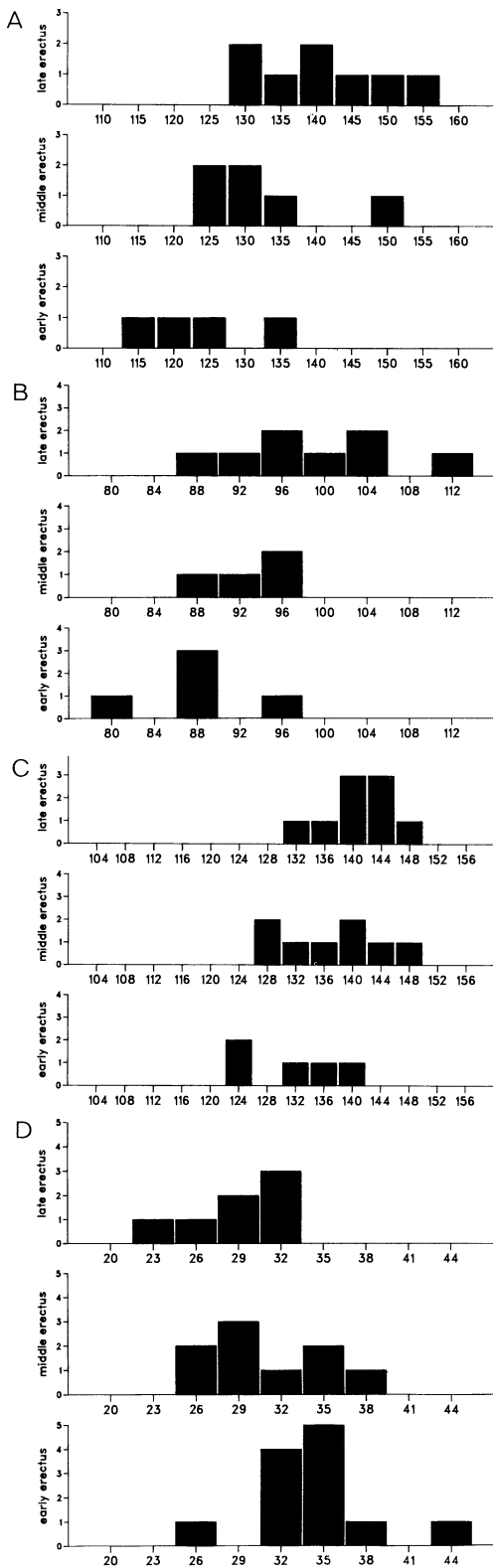
the largest specimens, Sambungmachan, is removed on Rightmire's assertion that he "knows of no accurate estimate of brain volume." It is not clear to me why the published estimate of the cranial capacity for this very complete individual (Jacob 1976) is unacceptable. Both Rightmire and I have used capacity estimates for much less complete *Homo erectus* specimens, such as OH 12. Moreover, in another similar analysis Rightmire (1985, p. 260) believes it is valid to use Weidenreich's (1943) 850-cc capacity estimate for a very much less complete specimen, Zhoukoudian cranium VI, represented by three cranial vault bone fragments of which neither the frontal nor the parietal bones are even half complete, and these cannot be fitted to each other. Rightmire positions the estimated capacity of this possibly small but definitely very fragmentary vault at the late end of his *Homo erectus* sample, hardly a procedure one would expect of an author who describe others as "measuring everything in sight." Be that as it may, any consideration of consistency dictates that if it is valid to use an estimated capacity for CKT VI, it is at least equally valid to use an estimate for the capacity of the much more complete Sambungmachan cranium.

Rather than entering into a discussion of whether Rightmire's reconstitution of the *Homo erectus* cranial capacity subsamples might reflect bias on his part, I propose dropping cranial capacity from the analysis of *Homo erectus* evolu-

tion. Moreover, I will agree to omitting ER 1805 and the Modjokerto child from the earliest subsample (there is no need to omit Sambungmachan if cranial capacity is not considered). I agree to these changes not because I believe they are valid (because I do not so believe), but because I will show that they make no difference and that stasis can still be refuted as a reasonable interpretation of *Homo erectus* evolution.

Instead of cranial capacity let us consider three linear dimensions of the vault that describe its size: bregma to inion length, biparietal breadth, and auricular point to bregma height. To represent the changes in the masticatory system in this altered sample I will use the height of the mandibular corpus. The definitions of these measurements, and the rationale for their use, are given in Wolpoff (1984, pp. 395-396).

The samples used here are the same as those described in 1984 but for a few new measurements that have since become available for the Hexian vault and mandibles, and data resulting from the discovery of two new *Homo erectus* specimens. These are the Narmada cranium from central India (Sonakia 1984), part of the late sample, and the very early juvenile from Nariokotome III, west of Lake Turkana (Brown et al. 1985). Because this early male (WT 15000) was only 12 at death, growth curves for modern Europeans comparing individuals with the second molar just erupted with adults could be used in estimating adult cranial dimensions. For-



Unfortunately, these have been published for the cranial dimensions used here (Heintz 1966). The data in the analysis are the estimated adult dimensions for WT 15000. Since a European growth curve was used the estimates are too large if growth in *Homo erectus* was either faster or for a shorter period. Thus, if anything the WT 15000 estimates weight the sample in favor of stasis.

With these few additions to update the sample and the deletions to bring its composition into agreement with Rightmire, I have reanalyzed the evolutionary trends in the three vault dimensions and the mandibular dimension discussed above (Table 1, Fig. 1,A-D). The consequent patterns and magnitudes of change closely resemble those published previously (Wolpoff 1984).

Thus, the three vault dimensions show very significant increase between the early and late subsamples, $P(d\bar{x} = 0) < .01$, and in all three cases the middle subsample is intermediate in magnitude. In biparietal breadth the most significant magnitude of increase is between the early and middle subsamples, while in the cranial length and height measures the most significant magnitudes of increase are between the middle and late subsamples. Only in the case of cranial length are these differences between adjacent subsamples significant at the .05 level, using a one-sided student's *t*-test (because the direction of change is known).

The height of the mandibular corpus decreases significantly between early and late samples, $P(d\bar{x} = 0) = .01$. Moreover, there is a significant decrease between the early and middle samples. While this significant decrease, reflecting a change in the size of the masticatory system, was not challenged by Rightmire, its demonstration does contradict both his earlier

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FIGURE 1. A. Distribution of cranial length as measured from bregma toinion, in millimeters, for three *Homo erectus* subsamples. B. Distribution of cranial vault height as measured by the sagittal projection from the auricular point to bregma, in millimeters, for three *Homo erectus* subsamples. C. Distribution of biparietal breadth of the cranial vault in millimeters for three *Homo erectus* subsamples. D. Distribution of height of the mandibular corpus measured in millimeters between M_1 and M_2 for three *Homo erectus* subsamples. See Table 1 for the means and other statistics, and for the significance of the differences between the subsamples.

statements (1981) and claims made by punctuationalists such as Delson (1983).

In sum, these data comparing subsamples constructed as Rightmire suggests still show significant changes in opposite directions for measurements reflecting two adaptive systems in *Homo erectus*; cranial size increases, while the size of the masticatory structures decreases. The patterns of these changes are also quite different; mandibular dimensions decrease mostly between early and middle samples, the biparietal breadth pattern of increase agrees with this, but for the other two vault dimensions more of the increase occurs between middle and late subsamples. I believe that the analysis in my previous paper is thereby confirmed.

I am puzzled by why Rightmire's response is thought to contradict my analysis and show a "quite different pattern of change." According to Rightmire's conclusions, even after removing the smallest two specimens from the early subsample and one of the largest specimens from the late subsample the observed pattern of change in *Homo erectus* is still one in which "late individuals do tend to have capacities which are larger than those of earlier specimens, but the trend is hardly marked." Yet avoiding the problem of how marked is marked enough (how high is up?), this is exactly what my own data showed and still show; the bulk of the change in vault size occurs between the middle and late subsamples (we differ only in the extent to which we contend that this is true). Rightmire (1985) links this pattern to a general trend of accelerating cranial capacity change in the later portion of the middle Pleistocene. I have no objection to this interpretation; gradualism, after all, is not uniformity. What makes the *Homo erectus* problem interesting is that at the same time the mandibles (and more generally all elements of the masticatory system) decrease in size, and the bulk of the change occurs between the early and middle subsamples, just where cranial capacity, and the vault measurements that reflect it, generally change least. These dramatically different directions and patterns of change are within the same species, making the explanation of species replacement as a cause of these changes even more unlikely.

In sum, I believe that the *Homo erectus* data still provide no support for the punctuational model and moreover can be used to reject this model as an accurate interpretation of *Homo erectus* evolution. Surely there must be better arguments than these to support so elegant and interesting a hypothesis.

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