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The pattern of evolution in Pleistocene human brain size

Sang-Hee Lee and Milford H. Wolpoff

Abstract.—With a sample of 94 Pleistocene cranial capacities between the time period of 1.8 Ma and 50 Ka now known, we consider the evolution of cranial capacity in *Homo*, with the null hypothesis that the changes over time are a result of one process. We employ a new method that uses a resampling approach to address the limitations imposed on the methods of previous studies. To test the null hypothesis, we examine the distribution of changes in adjacent temporal samples and ask whether there are differences between earlier and later samples. Our analyses do not reject the hypothesis of a single process of brain size change, but they are incompatible with an interpretation of punctuated equilibrium during this period. The results of this paper are difficult to reconcile with the case for cladogenesis in the *Homo* lineage during the Pleistocene.

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Introduction

The end of the Pliocene and the beginning of the Pleistocene is marked with the first appearance of the *Homo* clade. Compared with the preceding hominids, the new lineage has a markedly larger brain and a markedly larger body (Hawks et al. 2000; Relethford 2000). The brain size of the new hominid clade, however, is larger than can be explained by the increase in body size. Following this, throughout the Pleistocene, brain size increases further to that seen in modern humans (Tobias 1971; Hawks et al. 2000) (also see Fig. 1). Again, this increase in brain size is not related to a mean change in body mass (Ruff et al. 1997). Brain size increase is unarguably one of the most distinct and significant evolutionary trends in Pleistocene human evolution.

Although the reality of an increase in brain size is not a topic of disagreement, there are many, often conflicting, assertions about the pattern of increase. Some have used brain size evolution as a reflection of gradualism and continuity (Henneberg 1987; Wolpoff 1995, 2000), whereas others claim that certain portions of the human lineage were characterized by stasis (Rightmire 1981). It is also contended that brain size evolution in some geographical regions has proceeded at different rates than in others (Beals et al. 1984; Leigh 1992).

Validly establishing the pattern of brain size change poses challenges because of the unique characteristics of an evolutionary sequence regarding time. In previous studies brain size evolution has been characterized by linear regression analysis using cranial capacity regressed against time as an independent variable (Lestrel and Read 1973; Lestrel 1975; Godfrey and Jacobs 1981; Rightmire 1986). However, regression analysis is not an appropriate method to examine questions of patterns in changes over time. The reasons are twofold: fossils often do not fulfill the minimum requirements that are needed for regression to be applicable, and regression as a method does not necessarily provide statistically valid information about patterns of change. Figure 2 demonstrates that although changes in cranial capacity may be plotted against time, a trend line fitted to the bivariate distribution on the basis of regression is misleading.

Regression requires that observations are independent samples, but when the data set consists of morphological changes through time potentially guided by evolution, an observation at a certain time point is not necessarily an independent sample (or this could be the point at issue, so assumptions are to be avoided). For example, from other studies we

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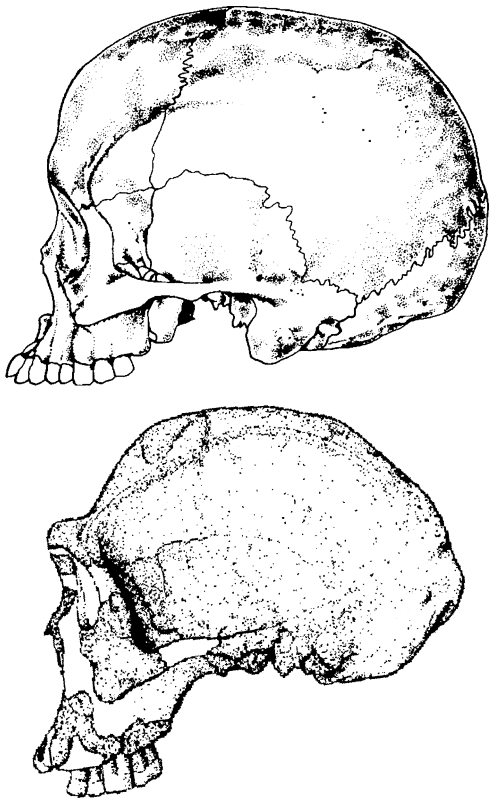

FIGURE 1. KNM-ER 3733 (below, from Rightmire 1990) is from the beginning of the Pleistocene and one of the oldest complete *Homo* crania, from the East Turkana site in Kenya, and the Masai (above, drawing by Karen Harvey) comes from the same African region today. These crania exemplify the marked change in human cranial capacity across the span of the Pleistocene. The specimens are earlier and later members of the same clade, and depending on whether or not incidents of cladogenesis are recognized between them (this is a point of some disagreement), they may be earlier and later members of the same evolutionary species.

might expect that a cranial capacity of 900 cc is more likely to be observed at certain time points and less at others.

Because of constraints on the evolutionary process each observation may be dependent on previous observations from earlier times. In some cases this may be the consequence of related populations; in others it could result from a constant process expressed over time, such as heterochrony or allometry. In any of these cases, there are constraints on each sample that come from previous samples.

In addition, regression assumes that the dependent variable has equal variance for each value of the independent variable (homoskedacity) (Bailey 1995). However, this assumption is not met in many data sets, including the one used in this study where sample size and variance are much smaller in earlier time periods than in later time periods (see Fig. 2).

Moreover, our analysis is sensitive to another problem that prevents regression from being an adequate method to examine questions about patterns of change. Regression tests the significance of the rate of change by asking if it is different from zero. However, whether brain size increased with statistical significance is not at issue here: there is no question that brain size increased over time. What we want to know is whether there was a change in the underlying process of change, and this cannot be answered with statistical rigor by fitting a single linear model for all the data points over time. For example, regression cannot be relied on to distinguish between a pattern of punctuated equilibrium and a gradual, constant change, because both of these could produce best-fitting trend lines with similar statistical attributes. This prevents us from using a regression method to fit one line for all the data points in answer to our question about process.

Advances in statistics have brought robust regression methods that allow some deviations from the above assumptions about the population to be tolerated. For example, Model II regression techniques have been developed for cases when it cannot be assumed that the independent variable is measured without error. Several other methods of data transformation can be used if linear relationship cannot be assumed. When these methods are not applicable, or when the underlying population cannot be modeled, nonparametric regression techniques are available (for discussion of various regression methods, refer to Pedhazur and Schmelkin 1991 and Sokal and Rohlf 1995). These, however, do not address the problems of potential interdependence within data sets such as ours.

An alternative to a regression method is to adopt random walk as a null hypothesis (Bookstein 1987). This acknowledges the potential interdependence of evolutionary data in adjacent time spans. For example, Roopnarine (2001) suggested a procedure that com-

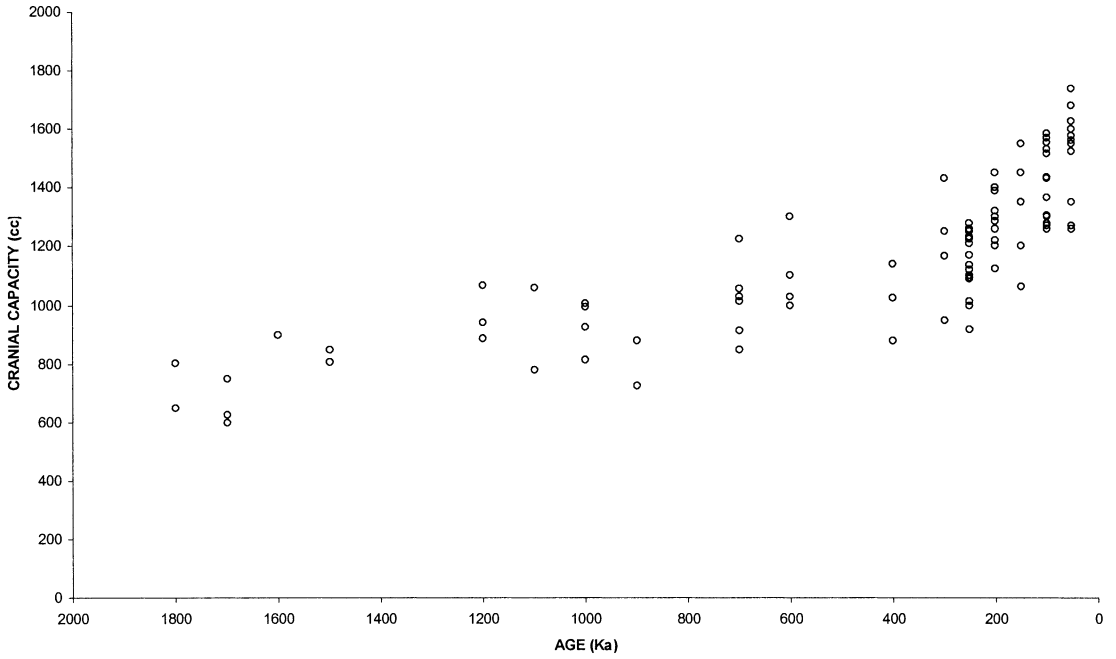

FIGURE 2. Cranial capacity (in cc) as a function of time for 94 specimens of Pleistocene *Homo*. The dates of the specimens between 1800 Ka and 300 Ka are rounded to the nearest 100 Ka, and to the nearest 50 Ka for specimens between 300 Ka and 50 Ka. The distribution has the visual appearance of curvilinearity.

bines a variant of random walk and stratophenetics (Gingerich 1974, 1993). Roopnarine generated a simulated stratophenetic series using probability parameters that are generated from various random walks and further modified by the expected effects of fossilization. The observed stratophenetic series was then compared with simulated series to test hypotheses of evolutionary patterns. However, for several reasons this approach is not well suited for our purposes. First, our data set is not adequate for a random walk analysis of comparable scale to Roopnarine's: the data set used in our study, the most comprehensive of cranial capacity data in the *Homo* lineage, consists of 17 temporal samples, as described below. This would provide 16 steps for a random walk analysis; in contrast, Roopnarine's procedure (2001) involves simulations in which an episodic ''punctuated'' change takes place in 2000 steps in a 75,000-step series. Second, the random walk approach utilizes average values for each temporal sample, but we do not believe that average values are meaningful in our data set where a time sample may comprise as few as two or three data points. In fact, regardless of sample size, we hesitate to weight any value within each time sample as more representative than other values.

Accepting the considerable evidence that Pleistocene human cranial capacity has significantly changed, we propose a new method to examine the problem of how brain size may have changed over time in the Pleistocene. Cranial capacity is larger than brain size. However, the proportion of brain size to cranial capacity is known and highly predictable with growth and development (Tobias 1971). Because we use mostly adult crania in this study, we feel it is justified that we use brain size and cranial capacity interchangeably in this paper.

We take advantage of both a sample size for Pleistocene *Homo* specimens with known or estimated cranial capacities that has now reached 94, and the recent improvements in some of their date determinations, to test hypotheses about the pattern of human brain size evolution with a data resampling approach that compares intervals of change within the distribution of all known human cranial capacities between 50 Ka and 1.8 Ma.

Our question is whether gradualism, expressed as a single process of change, characterizes this period. We adopt this as our null hypothesis.

If this hypothesis is rejected, alternative hypotheses can be examined: whether there are different processes at different times as might be expected with punctuated equilibrium (Gould and Eldredge 1977, 1993), or punctuated anagenesis (Springer and Murphy 1994), or even an oscillating pattern of change without direction that might be considered a form of gradualism. Multiple processes of cranial capacity change may have characterized the human clade through the Pleistocene in several ways, but the single-process interpretation has only one explanation.

Materials and Methods

Our data set of 94 cranial capacities includes all available specimens dated to between approximately 50 Ka and 1.8 Ma. The dates and the cranial capacities are taken from recent literature reviews (Ruff et al. 1997; Klein 1999; Wolpoff 1999) and other publications (Swisher et al. 1994, 1996; Gabunia et al. 2000; Hawks and Wolpoff 2001; Larick et al. 2001; Márquez et al. 2001; Shen et al. 2001; Asfaw et al. 2002). Following the definition of *Homo* as proposed by Wolpoff (1999) and by Wood and Collard (1999), our data set does not include the habiline specimens. Many of these cranial capacities are direct determinations but some are estimates from regression analysis using similar specimens of known capacity. The sample of known capacities postdating 50 Ka is orders of magnitude larger than the number of earlier capacities. We were concerned that recent data points would exert significant bias in our analysis due to the disparity in sample sizes, and because for all intents and purposes cranial capacities at 50 Ka can be considered recent or modern, we did not include any data later than 50 Ka in our analysis.

It is likely that error is inherent in the dates of the specimens, with significant effects on any analysis (De Miguel and Henneberg 2001). To address the error introduced by dates, and to distribute it more evenly through the sample, we rounded date estimates to the nearest 100 Ka for specimens dated between 1.8 Ma and 300 Ka, and to the nearest 50 Ka for the specimens dated between 300 Ka and 50 Ka. We treated the younger sample differently because of the higher resolution in dating accuracy for the more recent specimens. An added benefit is that this division serves to make the time samples more equal in sample size. These divisions gave 17 time samples, all with specimens (Table 1).

We used these data to address the issue of whether a single process underlies the Pleistocene evolution of cranial capacity. If it does not, different time periods must be described in different ways. For instance, if it could be shown that early Pleistocene hominids were in stasis for cranial capacity change, and accelerated evolution began in the middle Pleistocene, as one of the authors believed (Wolpoff 1999), no single explanation could validly describe the process, and it would be important to discover what significant factors in human evolution changed.

We propose a new method to address these problems. First, we use a logarithmic transformation (natural logarithm) of the linear relationship between cranial capacity and time. A logarithmic transformation may help avoid the problem of interdependence within the data set because it can be derived from the assumption that the rate of change of cranial capacity at any particular time is proportional to the cranial capacity of the sample at that time (Huxley 1932).

Second, we use increments of change between individual observations in the logarithmically transformed data as our variable of interest. We assume that any one point in a given time sample has the same probability of changing into any one point in the next time sample, and therefore we do not give weight to the centroids in the time samples. This procedure addresses our discomfort in using a mean or median for a time sample with only a few data points.

The increment used this paper is in effect a ''rate,'' determined by choosing at random one of the observations at a particular time and subtracting one of the observations from the previous time, also chosen at random:

$$\Delta X_i = X_i - X_{i-1}.$$

TABLE 1. Data of hominid cranial capacity and date.

	CC	Time (Ka)
Guattari	1550	50
La Chapelle	1626	50
La Ferrassie	1681	50
Forbes Quarry	1270	50
La Quina 5	1350	50
La Quina 18	1260	50
Neandertal	1525	50
Teshik Tash	1578	50
Le Moustier	1564	50
Amud	1740	50
Shanidar	1600	50
Saccopastore 1	1258	100
Saccopastore 2	1300	100
Spy 1	1305	100
Spy 2	1553	100
Jebel Irhoud 1	1305	100
Jebel Irhoud 2	1430	100
Laetoli 18	1367	100
Qafzeh 6	1569	100
Qafzeh 9	1531	100
Qafzeh 11	1280	100
Skhul 4	1554	100
Skhul 5	1518	100
Skhul 9	1587	100
Tabun 1	1271	100
Omo 1	1430	100
Omo 2	1435	100
La Chaise (Suard)	1065	150
Fontéchevade II	1350	150
Krapina(4) 2 (Cranium B)	1450	150
Krapina(4) 3 (Cranium C)	1200	150
Singa	1550	150
Eliye Springs 11693	1350	150
Vertesszöllös 2	1300	200
Jinniushan	1260	200
Atapuerca 4	1390	200
Atapuerca 5	1125	200
Atapuerca 6	1220	200
Biache	1200	200
Ganovce	1320	200
Ehringsdorf	1450	200
Eyasi	1285	200
Guombe (ER 3884)	1400	200
Solo 1	1172	250
Solo 5	1251	250
Solo 6	1013	250
Solo 9	1135	250
Solo 10	1231	250
Solo 11	1090	250
Ngawi	1000	250
Narmada	1260	250
Dali	1120	250
Kabwe	1280	250
Ndutu	1095	250
Saldanha	1225	250
Petralona	1210	250
Sambungmacan 1	1100	250
Sambungmacan 3	917	250
Reilingen	1430	300
Swanscombe	1250	300
Steinheim	950	300
Arago 21	1166	300
Choukoutien H3 (5)	1140	400
Hexian (PA 830)	1025	400
Sale	880	400
Nanjing	1000	600
Choukoutien D1 (2)	1030	600
Yunxian (9002)	1100	600
Bodo	1300	600
Choukoutien Il (6)	850	700
Choukoutien L1 (10)	1225	700
Choukoutien L2 (11)	1015	700
Choukoutien L3 (12)	1030	700
Choukoutien E1 (3)	915	700
Ceprano	1057	700
Olduvai (IV) 12	727	900
Sangiran (Kabuh) 3	880	900
Daka (BOU VP-2/66)	995	1000
Buia	925	1000
Sangiran (Kabuh) 2	813	1000
Sangiran (Kabuh) 17	1004	1000
Gongwangling (PA 105)	780	1100
Sangiran (Kabuh) 12	1059	1100
Sangiran (Kabuh) 10	885	1200
Olduvai (II) 9	1067	1200
Trinil 2	940	1200
Sangiran (Putjangan) 4	808	1500
ER KAR 3883	848	1500
Nariokotome III (WT) 15000	900	1600
Dmanisi (D2280)	750	1700
Dmanisi (D2282)	625	1700
Dmanisi (D2700)	600	1700
ER KAR 3773	804	1800
Perning	650	1800

This is then divided by the absolute value of the difference in time between the intervals:

$$\Delta T_i = |T_i - T_{i-1}| \qquad D_i = \Delta X_i / \Delta T_i.$$

To test our hypothesis, these increments are resampled many times from all 16 time intervals, defined by the 17 time samples. Thus, we apply data resampling as an alternative to regression. By assuming that the observed data adequately represent the underlying population, resampling avoids assumptions about the underlying distributional characteristics, such as its normality or whether it fits a mathematically derived model with known properties (Efron and Tibshirani 1993). To address the problem of variation in sample sizes for the different times, we resampled with replacement for equal number of times for each increment (500 times). This generated a grand

distribution of D (n = 8000) as well as a distribution for each of the 500 resampling runs.

The mean and the mode of the generated distribution of resampled increments provide information about the overall pattern of changes through time. Although there are several interpretations for punctuated equilibrium (Gould and Eldredge 1977, 1993), the model generally assumes more than one process of change: a period of no change and a period (or more) of changes. That would be reflected in the distribution of D as two or more peaks, with one strong peak around zero (no change) and one or more peaks around higher rates of changes. Gradualism implies a broader range of expectations, because gradual change is not constant change and could be compatible with single or multimodal distributions for D. One case of gradualism would be expressed as a single peak at a non-zero value in the distribution of D; this hypothesis is the one we attempt to disprove.

We test our null hypothesis with the distribution of resampled increments. If there is one underlying process of change, we expect that the increments will converge to a specific, non-zero value, and the distribution will show a unimodal shape with one peak. A distribution of resampled increments with more than one peak will therefore reject our null hypothesis, implying more than one processes of change. Moreover, a unimodal distribution with a peak at zero refutes our null hypothesis, as it implies a stasis, a period of no change.

Although most of the time intervals in our data are 100 Ka (8 out of 16 intervals), the time intervals vary in length; some are 50 Ka (5), 200 Ka (2), or 300 Ka (1). The variation among the time intervals may introduce an effect on the results: a trend may be detected that is a product of the time interval (Sheets and Mitchell 2001). To address this potential problem, we performed two analyses: first, we exclusively sampled pairs that have time intervals of 100 Ka; second, we sampled every other time sample.

In a second test we gathered information about the underlying processes of change for the data by examining the likelihood that the pattern of change later than any specific time period was unexpected from the pattern of change earlier than the time period. If we could reject the hypothesis that the same process generated changes in both earlier and later time periods, any attempt to characterize the distribution with a single process of change would be invalid. To examine this question we divided the data set into pairs of subseries, older and younger than division points at 1.5 Ma, 1.2 Ma, 1.1 Ma, 1.0 Ma, 900 Ka, 700 Ka, 600 Ka, 400 Ka, 300 Ka, 250 Ka, 200 Ka, and 150 Ka. Increments (D) were resampled within each subseries, as described above. The distribution generated from the increments in the earlier subseries was then used to test how unlikely it is to yield a distribution like the increments in the later subseries. This was done by tallying the middle 50% of the distribution of D (25^{th} percentile to 75^{th} percentile) from the earlier subseries, which functions as a confidence interval; the mean D from the later subseries was in turn compared with the confidence interval. If the mean D from the later subseries was within the confidence interval, we concluded that there is no significant difference between the processes of earlier and later time subseries. Because the mid-50% is a narrower range than mean $\pm$ standard deviation that would encompass a 64.7% in a normal distribution, this is a conservative test of difference.

Results

Is There a Single Process?—We examined the overall pattern of evolution by generating the distribution of increments (D) for the logarithm-transformed cranial capacity data (Fig. 3), resampling as described above. Figure 4 shows the generated distribution of the increments. The distribution is strongly unimodal, with a single peak around the mean [0.21 ln(cc)/ln(Kyr), with a standard error of the mean of 0.02]. The shape of the distribution and the mean are both incompatible with punctuated pattern.

We addressed concerns about the inaccuracy in dating for some of the specimens by lowering the resolutions of the dates and examining the effect on D. Our approach was to calculate D a second time, between every other interval. This effectively halved the resolution assumed for the dates. The mean D of the re-

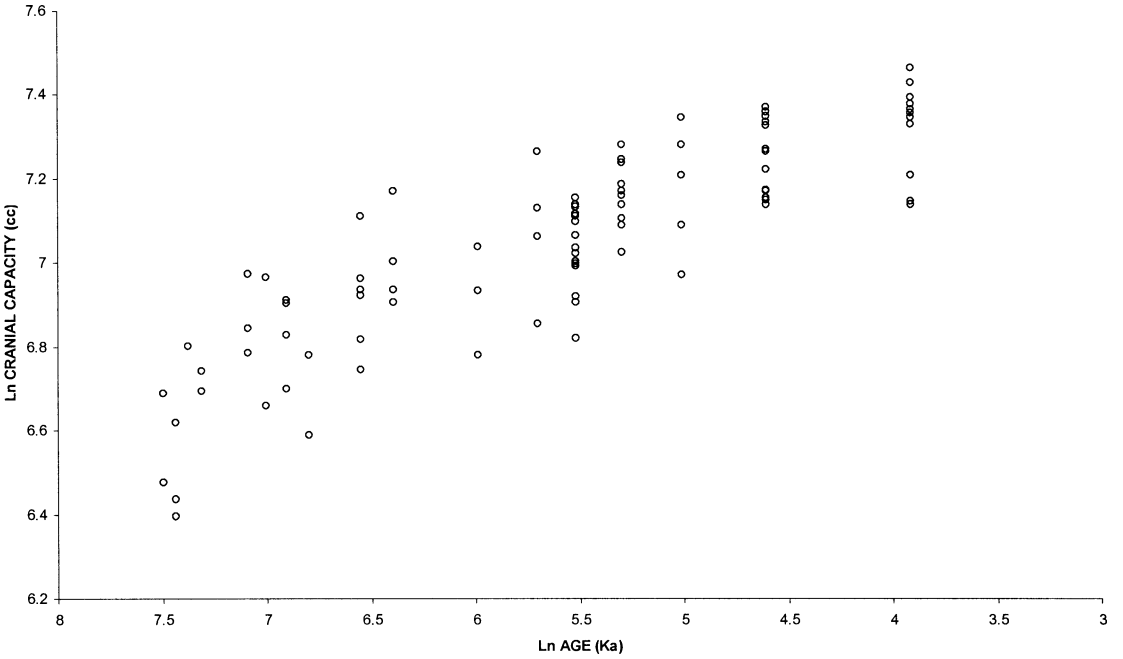

FIGURE 3. Logarithmically transformed data from Figure 2. The distribution has the visual appearance of linearity.

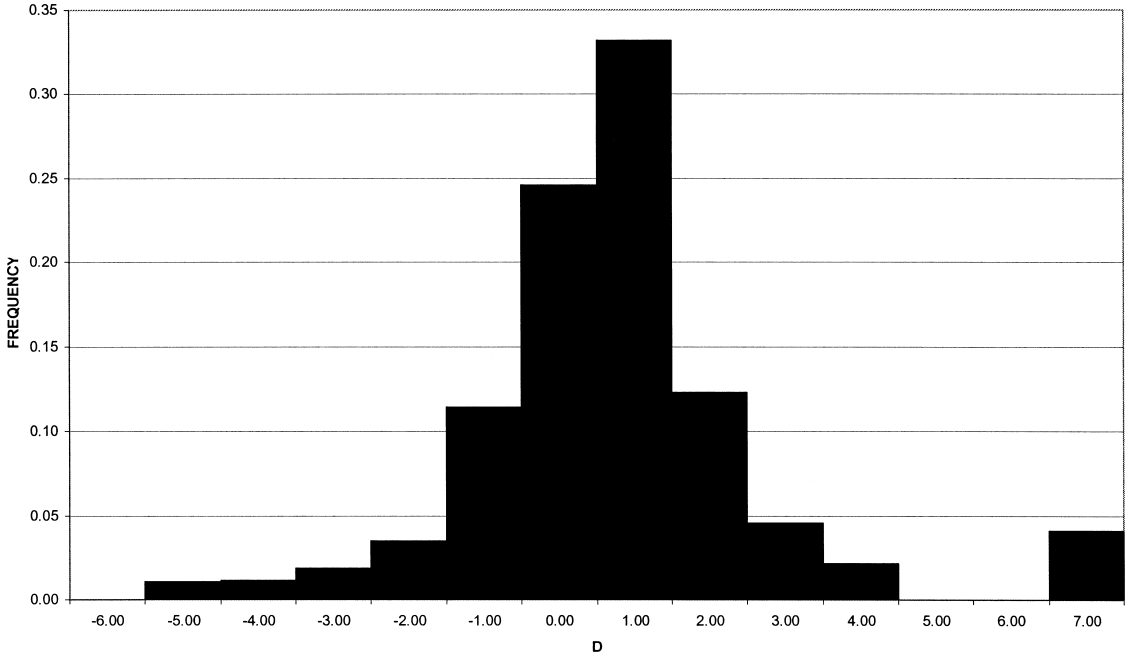

FIGURE 4. Distribution of resampled differences for the ln-transformed data, D, shown as a percentage of the total number of trials (n = 8000). The distribution is unimodal and the great majority of increments were small. Although many of the other differences are negative, the distribution on the whole is asymmetrically positive. The mean value for D is 0.21 ln(cc)/ln(Kyr), and SE = 0.02.

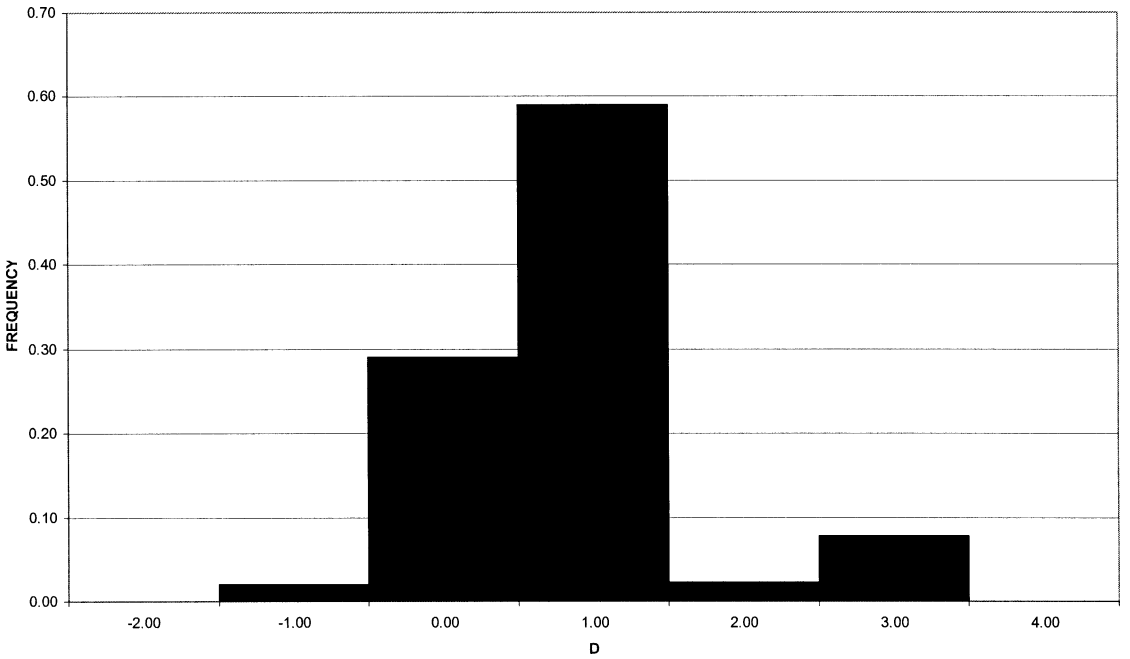

FIGURE 5. Distribution of resampled differences for the ln-transformed data, D, shown as a percentage of the total number of trials (n = 7500). This analysis differs from the analysis in Figure 4 in that D is based on comparisons for every other interval instead of for adjacent intervals. The distribution is unimodal and the great majority of increments were small. Many of the other differences are negative, but the distribution on the whole is asymmetrically positive. The mean value for D is 0.38 ln(cc)/ln(Kyr), and SE = 0.01.

sulting distribution [0.38 ln(cc)/ln(Kyr), with a standard error of 0.01] is also a positive nonzero number, and its shape (Fig. 5) is also strongly unimodal. When only the pairs that have 100-Kyr intervals are sampled, the results are the same (data not shown). We conclude that the basic results can be supported despite uncertainties in dating some of the specimens.

Figure 6 shows the distribution of D for the data set that is not logarithmically transformed. The results are consistent with that based on the logarithmically transformed data, with different mean D of 0.62 cc/Kyr and standard error of 0.03.

Do Early and Later Samples Demonstrate Different Processes?—Figure 7 addresses the question of whether a single process of change is sufficient to account for the observed pattern of variation. Results show that for all division points, the average D of later time subseries is within the middle 50% of the distribution of D of earlier time subseries. These results imply that the process for the later period cannot be said to be different from the process for the earlier period, regardless of where the data are divided into later and earlier periods. We cannot reject the hypothesis that a single process underlies the evolution of cranial capacity.

Discussion and Conclusion

The results of this study may have some relevance to the debate surrounding gradualism and punctuated equilibrium. The hypothesis we examined is whether the pattern of changes in cranial capacity during Pleistocene can result from one process. We modeled the process as a distribution of observed changes and interpreted a single process as the case where the changes predominantly converge onto a single value, resulting in a distribution shape with one peak. The value might be zero, ''no-change,'' which would imply ''stasis,'' or positive or negative, implying an increase or decrease. We proposed that if the distribution of changes had more than one peak, or a peak at zero, the null hypothesis would be rejected. Failure to reject the null hypothesis of one process is not compatible with a punctuated equi-

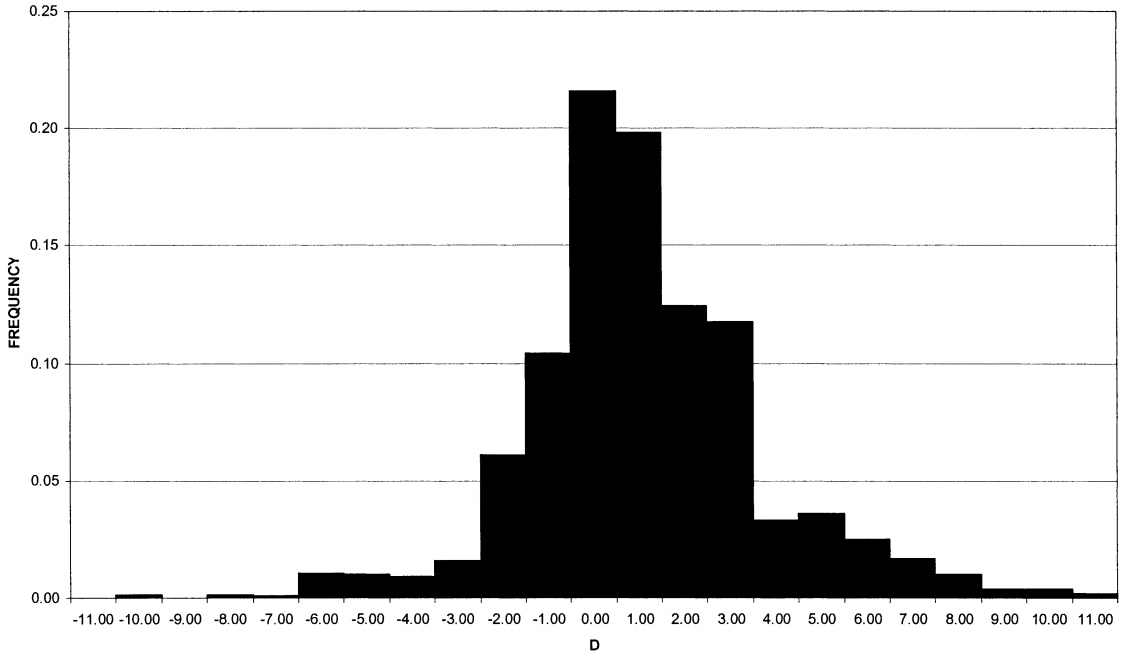

FIGURE 6. Distribution of resampled differences for the data, D, which have not been ln transformed. Data are shown as a percentage of the total number of trials (n = 8000). This analysis is otherwise similar to the analysis in Figure 4. The distribution is unimodal and the great majority of increments were small. Although many of the other differences are negative, the distribution on the whole is asymmetrically positive. The mean value for D is 0.62 cc/Kyr, and SE = 0.03.

librium model of evolutionary change and is difficult to reconcile with a speciation event.

Although the untransformed cranial capacity data (Fig. 2) gives the visual impression of curvilinearity, it could also be interpreted to show a period of stasis followed by a period of significant change, and indeed one of us (M.H.W.) interpreted an earlier distribution based on a smaller sample size this way (Wolpoff 1995, 1999, 2000). For this to be a valid expectation, we expect multiple peaks for the distribution of D calculated as we describe above for the untransformed cranial capacity data. However, this distribution is strongly unimodal and does not support the interpretation of two different patterns of change in cranial capacity.

Gradual change in cranial capacity, in the sense of temporal variation responding to a single underlying process, is compatible with the single lineage interpretation of Pleistocene *Homo* and more difficult to reconcile with current speciose interpretations of Pleistocene human evolution (Howell 1999; Tattersall and Schwartz 2000). It is unlikely that there are demonstrable cases of human cladogenesis resulting from punctuated changes during the Pleistocene that are reflected in other anatomical features but not in cranial capacity—in contrast, competing australopithecine species had quite different patterns of brain size change (Elton et al. 2001). Given the importance of brain size in human adaptation and behavioral evolution, this would not be the most parsimonious interpretation of past human variation. We believe it is more reasonable to seek alternative explanations for the geographic distribution of certain human characteristics, and the persistence of some of them over significant lengths of time, while other obviously adaptive features such as cranial capacity change throughout the human range. Multiregional evolution provides such an explanation and remains the best-supported, unrefuted explanation of this observation.

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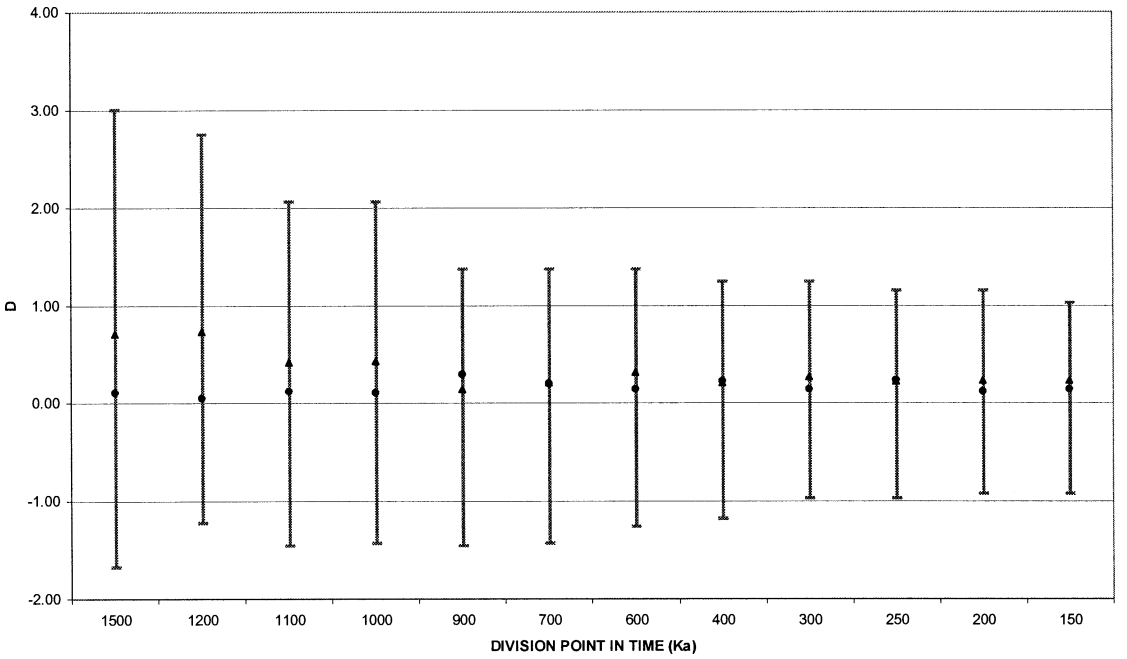

FIGURE 7. Comparison of the D values between two temporally divided subseries of cranial capacity. The total data set is divided into two subseries with division points of 1500 Ka, 1200 Ka, 1100 Ka, 1000 Ka, 900 Ka, 700 Ka, 600 Ka, 400 Ka, 300 Ka, 250 Ka, 200 Ka, and 150 Ka. For each subseries, distribution of D was generated by resampling. Solid triangles are the mean D increment for the period before each division; solid circles are the mean D increment for the period after the division. Vertical lines represent the range that includes central 50% of the generated distribution of D for the subseries earlier than the dividing point.

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