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Evolution in *Homo erectus*: the question of stasis

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Abstract.—Using a conservative definition of the hominid taxon *Homo erectus,* the sample of specimens known at this time, 92 individuals in all, is examined to determine whether the species exhibited significant temporal trends or evolutionary stasis. The sample is divided into three low-resolution time spans, and it is shown that significant change characterizes a number of cranial, mandibular, and dental features. Rates of change are comparable to or above rates reported for other fossil vertebrate lineages sampled over a similar duration. The often repeated assertion that *Homo erectus* is an example of a species in evolutionary stasis is incorrect.

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> *Of the two claims of punctuated equilibrium—geologically rapid origins and subsequent stasis—the first has received most attention, but Eldredge and I have repeatedly emphasized that we regard the second as more important. We have, and not facetiously, taken as our motto: stasis is data.*
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> (S. J. Gould 1982, p. 85)

Introduction

Punctuational and gradualistic models of evolutionary change are not mutually exclusive, in the sense that each could account for some significant changes over the course of evolution. Thus, in ongoing discussions of these models, debate has centered on the issue of which of these processes has *predominated* over the course of biological evolution.

Perhaps because of our special interest in our own ancestors, the hominids are often brought into the discussion. In particular, the species directly ancestral to us, *Homo erectus,* has become a focus in several wide-ranging presentations supporting the punctuational model (Gould and Eldredge 1977; Stanley 1979, 1981; Eldredge and Tattersall 1982). The perception of *H. erectus* in these accounts is characterized by Stanley's statement (1981, p. 148): "there was no approach toward *Homo sapiens* in forehead development or, we may infer, in intellect . . . as far as we can tell, throughout his existence *Homo erectus* did not vary greatly in form."

Paleoanthropological positions on the issue of evolution within *H. erectus* are diverse. Some paleoanthropologists argue that the species shows continuous (although not necessarily constant) evolution over the span of its existence (Mann 1971; Tobias 1971; Bilsborough 1976; Wolpoff 1980b; Cronin et al. 1981; Allen 1982). Others claim that the species is characterized by a long period of evolutionary stasis with a clearly delineated beginning and end (Howells 1980; Delson 1981; Rightmire 1981; Day 1982; Kennedy 1983).

Both Day and Kennedy based their conclusions on the assessment of a single postcranial bone, either later (Day) or earlier (Kennedy) than *H. erectus* is traditionally considered to extend in time. Each attributes the bone in question to *H. erectus* on the basis of morphological similarity and then claims to have shown stasis for *H. erectus* because of the morphological similarity between the (earlier or later) *H. erectus* sample and the bone in question. With regard to the femur, even if this reasoning was appropriate (for a contrary argument, see Trinkaus 1984), it is far from clear that the data actually show stasis (Bridges 1984), while the innominate sample is too small to support any interpretation. Only Bilsborough (1976) and Rightmire (1981) have published quantitative analyses comparing *H. erectus* samples to support their claims.

Bilsborough (1976) examined changes in *H. erectus* using both univariate techniques and a multivariate statistic, Generalized Distance (D^2) obtained by a Q-technique applied to a number of variables. *Homo erectus* was divided into an early and late sample for the analysis, which also

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included *Australopithecus africanus* and modern *H. sapiens.* It was concluded that *H. erectus* populations are characterized by rapid evolutionary change.

Rightmire (1981) reported Bilsborough's results, but subsequently ignored them in arguing that *H. erectus* is characterized by evolutionary stasis. Rightmire chose four variables and attempted a least mean squares regression for each of these against time (geological age). He divided his total sample of 65 individuals (16 of which may not be *H. erectus*) into six groups and regressed the average dimension for each group against the average age for the group. Thus, each of his regressions had six points and five degrees of freedom. None of the slopes calculated were significant, and Rightmire therefore concluded that the species shows evolutionary stasis.

There is reason to believe that Rightmire's results are an artifact of his procedure. Allen (1982), for instance, repeated the regression analysis for Rightmire's sample but used individual "best estimate" dates for each specimen instead of dividing the sample into six groups and using their averages. She showed that all of the resulting regression slopes were significant, and concluded that there were evolutionary trends within *H. erectus.*

In one way or another all of these analyses are flawed. A number of specimens have been discovered or made available for study since Bilsborough's work, and in fact neither Bilsborough nor Rightmire included all of the *H. erectus* specimens that were known when their studies were published. Rightmire divided the sample into too few components to allow a regression analysis to show significance (there were only five degrees of freedom regardless of sample size) unless the slopes attained extraordinary magnitude (Rightmire 1982). Moreover, he included a number of specimens in his analysis that many paleoanthropologists feel do not represent *H. erectus.* This made his assertion of evolutionary stasis unexpected by any model. By including (what many regard as) late australopithecines and (what many regard as) archaic *H. sapiens,* the combined sample should have shown significant change by either a gradualistic or a punctuational model unless there was no evolutionary change from late australopithecines to early *H. sapiens.* In correcting for the problem of too few sample groups for a regression analysis, Allen's analysis becomes sensitive to the exact date estimates used for individual specimens. While some of these are established with accuracy, others have much larger error ranges (and others are little better than guesses within broad time spans). The effect of varying date estimates on the results of her regressions are unclear.

In sum, in an analysis of evolutionary change (or its absence, stasis) it is desirable to examine a sample of *H. erectus* that is more narrowly defined to minimize the possibility of spurious results. A regression approach is clearly inappropriate (Levinton 1982), and units of analysis are required that have no finer resolution than the accuracy of the dates for the fossils themselves allow. This work will focus on a conservatively and narrowly defined *H. erectus* sample, divide all of the known specimens attributable to this sample into three temporal subsets with low enough temporal resolution to be certain that the specimens can be placed accurately, and examine these subsets for evidence of evolutionary stasis.

The *Homo erectus* Sample

Homo erectus remains were first discovered in Indonesia, with subsequent early discoveries also made in Indonesia and in China. Indeed, the majority of known *H. erectus* remains are still from these east Asian regions, in spite of additional discoveries in Europe and Africa. The taxon, as it is regarded today, is a meld of older genus names that were used to reflect geographic and in some cases also temporal variation; for instance, *Sinanthropus, Pithecanthropus, Atlanthropus,* etc.

As recently as the 1950s, *H. erectus* was distinctly delineated by clear temporal boundaries. At its "beginning," the only hominid samples known to be older were the south African australopithecines, and these were not even universally regarded as hominids at the time. At its "end," the oldest of the later remains were European specimens from Steinheim, Swanscombe, and Mauer (Broken Hill was then regarded as being very late), and these showed numerous distinctions from the youngest known *H. erectus* sample from Zhoukoudian (reviewed by Howell 1960). Thus, a clear definition of the taxon and broad agreement about its contents were developed, based initially on easily delineated morphological distinctions from earlier and later hominid samples.

In the following decades, these boundaries became increasingly blurred, and finally in the view of many paleoanthropologists indistinct (Hemmer 1967; Mann 1971; Bilsborough 1976; Wolpoff 1980b; Cronin et al. 1981; Jelínek 1981). The discovery of *H. erectus* remains from below the Okote Tuff at Lake Turkana provided an "origins" age of more than 1.7 Myr. Earlier in time, the late australopithecine sample (late *H. habilis*) is now known to include specimens such as ER 1813, OH 16, and OH 13 that vary markedly in the *H. erectus* direction (Tobias 1980; Wolpoff 1980b; Cronin et al. 1981). At the late end of the time range, a number of Middle Pleistocene specimens were discovered in Europe, beginning in the 1950s. Many of these are evidently males corresponding to previously discovered females (Wolpoff 1980a). These specimens, which are much more robust (and *erectus*-like), include Petralona, Vértesszöllös, Bilzingsleben, and the Arago males. Their discovery resurrected the question of whether some or all early Europeans represent *H. erectus*, and dramatically blurred the boundary by the very inability to resolve the problem (Wolpoff 1980a; Cronin et al. 1981; Jelínek 1981; Stringer 1981). Even in east Asia, where *H. erectus* samples are the largest and most complete, the late end of the range is extremely difficult to delineate, as evidenced by the difficulties in agreeing on whether the Ngandong sample is *H. erectus* or *H. sapiens* (Weidenreich 1943; Jacob 1976; Santa Luca 1980; Wolpoff 1980a, 1980b; Holloway 1981; Wolpoff et al. 1984).

The purpose of this short history is to explain why paleoanthropologists do not agree on which particular specimens belong in *H. erectus*, and to justify the use of a conservative definition of the taxon in this examination of whether or not it was characterized by evolutionary stasis. The conservative definition of *H. erectus* is based on the historic precedence of features characterizing the taxon as originally defined, and a reasonable estimation of the expected observed ranges and increased combinatorial possibilities for these features, because attempts at a broader morphological definition have failed when applied on a worldwide basis (Wolpoff et al. 1984). However, in this case a historic definition seems in line with normal taxonomic usage. Simpson (1961, p. 165), in discussing the implications of phyletic evolution, argues that "the lineage must be chopped into segments for purposes of classification, and this must be done arbitrarily." In practice, however, phyletic species are rarely defined in a completely arbitrary way. This is because "in most fossil sequences there are convenient breaks between horizons to permit a nonarbitrary delimitation of species" (Mayr 1969, p. 35) because of accidents of discovery, and if "one or more species are found and defined before the more extensive lineage is at hand, those species should be preserved as far as possible" (Simpson 1961, p. 166). The history of *H. erectus* discoveries reflects such a process. While various paleoanthropologists have subsequently attempted to include a wider range of specimens in the taxon (Howells 1980; Santa Luca 1980; Rightmire 1981), this would expand its range both in morphological variation and in temporal span. Thus, adhering to a definition based on the features originally ascribed to the taxon, and reasonable variants of these features, weights this analysis in favor of stasis, since the conservative definition limits the number of specimens and the range of potential variability included. In this regard, the sample used here is more limited in its morphological variation than the sample used by Rightmire (1981) in his "demonstration" of stasis.

To minimize error due to absolute age determinations and to maximize the sizes of samples for comparison, the conservative *H. erectus* sample is divided into three time spans, as detailed below. The earliest sample is from the Lower Pleistocene. The late sample is from the traditional "endpoint" of the species, and the middle sample is from the earlier Middle Pleistocene, between these in age.

Specifically (see Table 1), the early sample includes the remains attributed or attributable to *H. erectus* from the Lower Pleistocene deposits at east Turkana,[1] Olduvai Beds II and III, the

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[1] In the initial descriptions and subsequent summary of the east Turkana hominid discoveries (Leakey and Leakey 1978), species allocations for the specimens were not provided. The allocations used here are based on the author's

Lower Pleistocene Beds at Laetoli, Omo Member J and above, and the Lower Pleistocene sites from east Asia including specimens from the Putjangan Formation near and at Sangiran in Indonesia and Chinese specimens from the Dragon Bone cave at Jian Shi and from the Badong District—36 individuals. The middle sample is comprised of specimens from Olduvai Bed IV and the Masek Beds, Chad, Ternifine, Thomas, Gomboré II, Baringo Kapthurian Formation, Swartkrans Member II, the Indonesian remains from Trinil and from the Kabuh Formation at Sangiran, and from China both Lantian specimens (Gongwangling and Chenchiawo) and the remains from and attributable to Longgudong—25 individuals. The late sample is from Zhoukoudian, Hexian, the isolated teeth from south China, and the Indonesian site of Sambungmachan—31 individuals. In all, 92 *H. erectus* individuals are represented in these samples. Dates and provenances for the individuals are reviewed by Curtis (1981), Howell (1978), Jacob (1976), Matsu'ura (1982), Sartono (1982), Sartono and Djubiantono (1982), Wolpoff et al. (1984), and Zhou et al. (1982).

These samples are similar to Bilsborough's (1976) and Rightmire's (1981), and had these authors divided *H. erectus* into three time spans, sample compositions would have been almost the same for the specimens that their analyses share with this one. This analysis includes more *H. erectus* specimens than either of the previous ones, but omits certain individuals Rightmire included because these do not fit the conservative definition of the taxon; in particular OH 13, Sidi Abderrahman, Salé, Petralona, Montmaurin, and the Arago and Ngandong samples.

While this exhausts the sample that can be attributed to *H. erectus,* as conservatively defined, a number of other specimens have also been included in the taxon by some paleoanthropologists. The Ngandong remains, Petralona, Vértesszöllös, Bilzingsleben, and the Arago sample are thought by some to represent *H. erectus,* although this is by no means a universal opinion and many paleoanthropologists regard some or all of these as *H. sapiens* (Weidenreich 1943; Stringer et al. 1979; Wolpoff 1980a; Stringer 1981). It would be a mistake to include these in the *H. erectus* sample analyzed here, because it could be argued that by including specimens that may be *H. sapiens,* analysis might appear to show a lack of stasis in the sample when there actually was stasis for *H. erectus* more accurately defined. If there is error in which specimens are included in *H. erectus,* it is better to err on the conservative side. Thus, as a matter of interest, a fourth "later sample" of 13 individuals was constructed of the above specimens. However, *no statements made about* H. erectus *refer to this sample.* It is not analyzed along with the *H. erectus* remains either for the presence of evolutionary change or for the determination of its rate.

Methods

The three temporal spans within the *H. erectus* sample were compared for a number of measurements. The same comparisons were made between the late *H. erectus* sample and the even later hominid group described above. All of the linear measurements were taken by the author

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experience with the original material and reflect the application of conservative criteria in the assessments. Thus, for instance, ER 1648 and 1821 are large cranial fragments (used only for cranial thickness measures) with a temporal line that marks a distinct angulation between the superior and lateral aspects of the vault. This is a morphology not found in any of the australopithecine species, but common in *Homo erectus.* Similarly, the isolated ER 806 dentition is found within the Okote tuff, where the only hominids that can be unambiguously identified are *H. erectus* and *Australopithecus boisei.* The teeth are far too small to possibly represent the megadont australopithecine species. Finally, including the east Turkana specimen ER 1805 (Day et al. 1976) in the *H. erectus* sample, instead of describing it as a "bizarre" australopithecine with a "pongid-like" morphology, as some have suggested, is a consequence of considering the morphological details that align it with *H. erectus* and distinguish it from any of the australopithecine species. The appearance of several functional complexes supports this contention. These include the emphasis on posterior temporalis as indicated by the posterior approach of the temporal lines, the expansion of the nuchal plane to incorporate the posterior aspect of the mastoids, the marked expansion of the anterior braincase reflected in the lack of significant postorbital constriction, and the broadening of the face that is indicated by the very wide interorbital area and the notable distance between the infraorbital foramina. Other details that support this diagnosis include the deep digastric grooves and the postbregmatic depression. It is the expansion of the posterior temporalis and of the nuchal musculature on a small vault that results in the sagittal and compound temporal/nuchal crests (with the associated shelving in the region of the parietal notch) that has confused the interpretation of this individual. The small postcanine dentition indicates that these muscular expansions reflect an increasing use of the anterior dentition in horizontal loading and do not result from the pattern of molar loading that causes muscular hypertrophy in the australopithecines.

TABLE 1. Composition of the hominid samples, by specimen and measurement or measurements represented.

	Cranial capacity	Bregma-inion length	Maximum cranial breadth	Biparietal breadth	Biasterionic breadth	Biauricular breadth	Auricular-bregma height	Midorbit supraorbital height	Central parietal thickness	Mandibular P_3–M_2 chord	Corpus breadth at M_1	Corpus height at M_1/M_2	Breadth of M_1
Lower Pleistocene *H. erectus* sample													
ER 727											X	X	
730										X	X	X	X
731												X	
806													X
820													X
992										X	X	X	X
1593									X			X	
1648									X				
1805	X	X	X	X	X	X	X		X	X	X	X	
1808								X	X	X	X	X	
1821									X				
3733	X	X	X	X	X	X	X	X	X				
3883	X	X	X	X	X	X	X	X					
OH 9	X		X	X	X	X	X	X	X				
EM 550									X				
EM 551									X				
51											X	X	
Laetoli 29B											X	X	
Omo K7-19													X
Modjokerto	X												
Sangiran 1										X	X	X	X
4	X	X	X	X	X	X	X		X				
5											X	X	
6											X	X	X
9										X	X	X	X
27								X					
P 12													X
S 14													X
S 33													X
S 51													X
S 52													X
S 53													X
S 72													X
S 98													X
Jian Shi PA 504													X
Badong District PA 507													X
Early Middle Pleistocene *H. erectus* sample													
OH 12	X				X			X	X				
22										X	X	X	X
SK 15											X	X	X
Baringo										X	X	X	X
Gombde II									X				
Chad								X					
Ternifine 1										X	X	X	X
2										X	X	X	X
3										X	X	X	X
4				X					X				

Table 1. Continued.

	Cranial capacity	Bregma-inion length	Maximum cranial breadth	Biparietal breadth	Biasterionic breadth	Biauricular breadth	Auricular-bregma height	Midorbit supraorbital height	Central parietal thickness	Mandibular P_3–M_2 chord	Corpus breadth at M_1	Corpus height at M_1/M_2	Breadth of M_1
Thomas 1										X	X	X	X
3								X					
Trinil 2	X	X		X	X			X					
Sangirin 2	X	X	X	X	X	X	X	X	X				
3	X	X		X	X				X				
10	X	X	X	X	X	X	X	X	X				
12	X	X	X	X	X	X	X		X				
13A									X				
17	X	X	X	X	X	X	X	X	X				
18A								X					
20									X				
22											X	X	X
Lantian PA 102										X	X	X	X
PA 105	X			X				X	X				
Longgudong PA 531													X
Later Middle Pleistocene *H. erectus* sample													
Sambungmachan	X	X	X	X	X	X	X	X					
CKT A1													X
A2										X	X		X
A3													X
B1													X
B2													X
B3													X
B4													X
C1													X
C3													X
D1	X	X	X	X	X	X	X	X	X				
E1	X	X	X	X	X	X	X	X	X				
F1													X
G1										X	X	X	X
G2									X				
H1										X	X	X	
H3	X	X	X	X	X	X	X	X					
H4											X		X
I1									X				X
K1										X	X	X	X
L1	X	X	X	X	X	X	X	X	X				
L2	X	X	X	X	X	X	X	X	X				
L3	X	X	X	X	X	X	X	X	X				
L4													X
M2										X	X	X	
O2													X
PA 86										X	X	X	
PA 69/70													X
Hexian PA 830	X		X	X	X	X	X	X			X		
831											X	X	X
834													X
S. Officinalis 3													X

Table 1. Continued.

	Cranial capacity	Bregma-inion length	Maximum cranial breadth	Biparietal breadth	Biasterionic breadth	Biauricular breadth	Auricular-bregma height	Midorbit supraorbital height	Central parietal thickness	Mandibular P_3–M_2 chord	Corpus breadth at M_1	Corpus height at M_1/M_2	Breadth of M_1
Latest sample													
Ngandong 1	X	X	X	X	X	X	X	X	X				
3			X	X	X	X	X		X				
4				X	X			X	X				
5	X	X	X	X	X	X	X	X	X				
6	X	X	X	X	X	X	X	X					
8				X	X				X				
9	X	X	X	X	X	X	X	X	X				
10	X	X	X	X	X	X	X	X	X				
11	X	X	X	X	X	X	X	X	X				
15								X					
Petralona	X	X	X	X	X	X	X	X	X				
Arago 21	X		X	X			X	X	X				
Vertesszollos	X				X								

on original specimens, with the exception of those for the Hexian cranium which are from published sources (Wu and Dong 1982; Wu 1983). Cranial capacities have been reported by Weidenreich (1943, 1945), Chiu et al. (1973), Wolpoff (1977), Riscutia (1975), Holloway (1978, 1980, 1981, 1982, 1983), Stringer et al. (1979).

Measurements were chosen to reflect different parts of the cranium and mandible and, as far as possible, these represent metrics with the largest sample sizes. Moreover, the four measurements used by Rightmire (1981) are also included.

Cranial capacity is an absolutely critical measure, reflecting the size of an organ that changes more over the course of human evolution than does any other. It was also used by Rightmire (1981).

The cranial length measure chosen was the bregma to inion chord. The sample size for this measure is much larger than for the more traditional length measure from glabella to opisthocranion (which for this sample is the same as to bregma). For instance, in the middle sample there are only two specimens that allow the length from glabella to be taken, while the sample size for the length from inion is six.

Four cranial breadth measurements were used. The maximum cranial breadth and the biparietal (i.e., braincase) breadth describe somewhat different aspects of the cranium because of the marked basal pneumatization in *H. erectus.* Biasterionic breadth estimates the breadth of the nuchal plane, an area that expands dramatically with the appearance of *H. erectus* and markedly changes again in *H. sapiens* in response to the changing function of the nuchal musculature (Wolpoff 1980b). Biauricular breadth was included because Rightmire (1981) used it.

The only cranial height measure with sufficient sample sizes was the sagittal projection of the chord from the auricular point to bregma.

Two other structures that are independent of the gross size of the vault were included. The height (thickness) of the supraorbital torus over the middle of the orbit provided a measurement of brow ridge size. Thickness of the cranial vault walls was measured by the parietal thickness at its approximate center.

For the mandible three dimensions were used. The length of the tooth row between the most mesial point on the P_3 root where it enters the alveolus and the most distal point on the M_2 root where it enters the alveolus provides a measure of the room that the postcanine tooth row takes up. This particular measurement can be made on the alveolar rim of the mandibular corpus, whether or not the crowns of the teeth are preserved. The maximum breadth of the cor-

TABLE 2. Comparison of sample statistics for *Homo erectus* divided into three time spans, and a sample of later hominids attributed to *H. erectus* by some authors, but to *H. sapiens* by others. The average rate of evolutionary change for the three *H. erectus* samples is given in darwins, and the significance of various comparisons of the means at the 0.05 level using a single sided student's *t*-test is indicated. The three possible comparisons are made within the *H. erectus* sample, and the late *erectus* group is compared with the sample of later hominids (L–LL). Details of the samples and of the measurements examined are in Table 1 and the text. Specific frequency distributions for most of the measurements are given in Figs. 1–12.

	Homo erectus			Rate of change (darwins)	*Homo erectus* or *sapiens*	Significance at 5% level			
	Early	Middle	Late		Latest	E–M	M–L	E–L	L–LL
Cranial capacity	810	886	1,060	(.27)	1,155		X	X	X
n	6	8	8		9				
σ	175.9	112.5	93.6		75.5				
Bregma-inion length	123.2	132.0	139.1	(.12)	149.4			X	X
n	4	6	6		7				
σ	11.0	10.4	6.9		7.0				
Maximum cranial breadth	142.4	148.5	151.1	(.06)	151.9			X	
n	5	4	7		9				
σ	7.5	8.7	5.8		7.4				
Biparietal breadth	127.5	137.5	139.9	(.09)	144.3			X	X
n	5	8	8		11				
σ	13.3	8.5	5.1		4.7				
Biasterionic breadth	113.9	112.5	119.0	(.04)	125.2				X
n	5	7	8		11				
σ	13.3	9.4	11.1		4.6				
Biauricular breadth	135.4	137.0	145.0	(.07)	143.2			X	
n	4	4	7		8				
σ	4.2	10.0	3.5		7.6				
Auricular-bregma height	86.2	91.8	96.8	(.12)	102.0			X	X
n	5	4	7		9				
σ	6.6	4.1	5.9		5.1				
Midorbit supraorbital height	13.8	13.8	13.3	(−.04)	13.3				
n	5	8	8		9				
σ	3.7	3.5	1.9		2.6				
Central parietal thickness	9.2	10.8	10.7	(.15)	9.6	X		X	
n	10	11	7		9				
σ	1.4	2.1	0.9		2.0				
Mandibular P_3–M_2 chord	43.6	42.8	38.9	(−.11)			X	X	
n	6	7	6						
σ	2.0	1.7	1.8						
Corpus breadth at M_1	20.4	17.5	17.3	(−.16)		X		X	
n	11	9	9						
σ	2.6	1.9	2.5						
Corpus height at M_1/M_2	34.2	30.6	29.8	(−.14)		X		X	
n	13	9	6						
σ	4.3	4.1	3.8						
Breadth of M_1	12.4	12.1	11.8	(−.05)				X	
n	18	10	20						
σ	1.0	0.7	0.8						

pus at the M_1 position and the vertical height of the corpus between M_1 and M_2 were chosen to reflect the gross corpus dimensions.

Finally, the breadth of M_1 was reported to reflect the changes in posterior tooth size, one of the most dramatically changing features in human evolution. M_1 is used because its sample size is best, it has the highest heritability of the molars, and it was used by Rightmire (1981). The breadth dimension (rather than length or area) is reported because it is unaffected by interproximal attrition and thereby is independent of age at death.

Means and other summary statistics for these measurements are reported in Table 2, and frequency distributions for a number of them are shown in figures. The means are compared with a single-sided Student's *t*-test, with significance reported at the .05 level.

Comparisons are made between the temporally adjacent *H. erectus* samples, between the early and the late erectus samples, and between the late erectus sample and the sample of later hominids described above for all but the masticatory-related measurements—these have too small a sample size to report for the latest hominid sample and thus the last of the comparisons shown in Table 2 is not made for them (for details of dental variation during this time span, see Wolpoff 1982).

An average evolutionary rate in darwins was determined for the *H. erectus* sample, as conservatively defined, by comparing the means for the early and late *H. erectus* samples. In almost all cases the mean value for the middle *H. erectus* sample is between the earlier and the later sample means, and for the two exceptions the mean of the middle sample is virtually identical to the early (for biasterionic breadth) or the late (for central parietal thickness) sample means. Thus, comparing the early and late samples is a reasonable basis for an average estimate of rate. The duration for the rate calculation was determined by comparing the mean age of the crania in the late sample with the mean age for the early specimens. This was found to be almost exactly 1 Myr (1.4 Myr for the early sample average and 0.4 Myr for the late sample average). Fortunately, these mean dates could be determined with reasonable accuracy. It is mainly in the middle sample that many of the date determinations are less accurate and specimens can only be placed within a broad temporal span. It is likely that the probable error in the average rates does not exceed 10%.

Results

With only a few exceptions, the differences between the early and late *H. erectus* samples are marked and significant (Table 2).[2] In only two of the variables (midorbit supraorbital thickness and biasterionic breadth) does this comparison of means not attain significance. Between the adjacent temporal samples the magnitudes of the differences are somewhat less; the differences between the early and middle samples are significant in three cases (two of these are mandibular), and significance between the middle and late samples is only attained in the cranial capacity and the posterior dental chord length of the mandible.

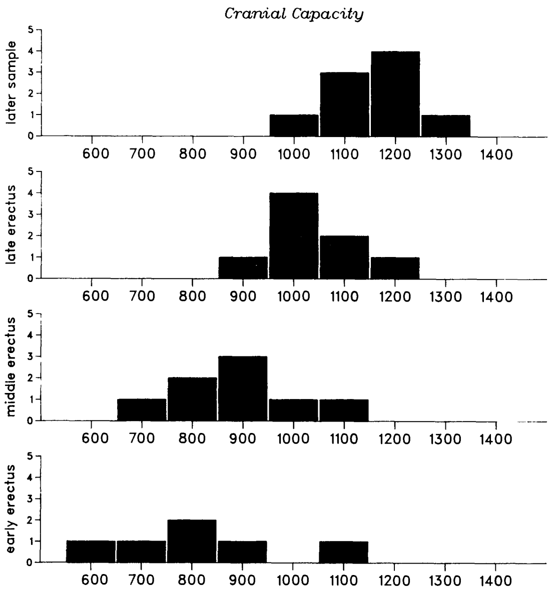

FIGURE 1. Distribution of cranial capacity in cubic centimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

In the comparison of the late *H. erectus* sample with the even later Middle Pleistocene specimens, significance is attained in 5 of the 7 cranial measures. *In almost every instance the change between late* erectus *and this latest sample is in the same direction as the change within* H. erectus.

One of the most dramatic changes is in cranial capacity (Fig. 1).[3] Changes in the mean, mode,

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[2] If ER 1805 were to be omitted from the analysis, some of the means for the early group would change. However, the only loss of significance, as indicated on table 2, is the significance of the difference in cranial capacity between the early and middle *H. erectus* samples. *In all other cases, the significances indicated in table 2 are retained,* and the relations of magnitudes of the means also remain the same. While the author does not believe that this specimen should be omitted from the sample, the fact is that analysis of evolutionary trends within an *H. erectus* sample not including ER 1805 has exactly the same results. Similarly, excluding the several cranial fragments from the analysis of cranial thickness (the only place they appear) does not significantly change the mean for the early sample. While larger samples would be desirable, the present sample sizes are large enough to shield the analysis from extreme sensitivity to single specimens. Thus, it must be concluded that an even more narrowly defined *H. erectus* sample also shows the same pattern of significant evolutionary change!

[3] The Modjokerto child is included in the cranial capacity analysis (this is the only comparison where this specimen appears). While widely regarded as an infant, or at the most

and range all reflect the continuous expansion of vault size within *H. erectus,* while the samples overlap in range, following a pattern one might expect under a model of shifting allele frequencies for this polygenic feature. The magnitude of average change contradicts the assertion that if there is any gradual evolution in a chronospecies, it is of very low magnitude and "a typical chronospecies does not exhibit a great deal more total variability, from end to end, than is found among the living populations of a similar species" (Stanley 1981, p. 14). Late *H. erectus* cranial capacity is 31% greater than the early sample's mean. In contrast, the largest mean capacity for a living human population is barely 10% greater than the smallest populational mean, according to data reported by Tobias (1971). Thus, *H. erectus* provides a valid basis for rejecting the claim that "no gradualism has been detected within any hominid taxon . . . the trend to larger brains arises from differential success of essentially static taxa" (Gould and Eldredge 1977, p. 115).

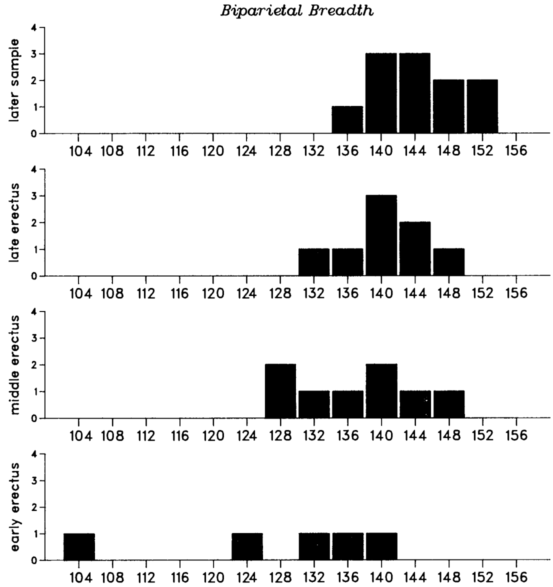

FIGURE 2. Distribution of the biparietal breadth in millimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

With a significant trend in cranial capacity increase, as expected the linear dimensions of the vault also increase, in most cases significantly. Moreover, the *pattern* of dimensional increase for vault measurements is of some interest (apart from the *fact* of increase) because of the disproportionate rates of change, many of which continue through the Upper Pleistocene and in some cases continue through modern populations. For instance, within *H. erectus* the increase in biparietal breadth (Fig. 2) is of greater magnitude

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2–3 years in age (Grimm 1941; Boule and Valois 1957; Coon 1962), there are contradictions in its morphology that have always suggested that so young an age may be incorrect (Piveteau 1957; LeGros Clark 1964). The young age was thought to be indicated by an open bregmatic fontanelle (this is actually broken bone), the relatively high vault (actually the auricular-bregmatic height is the lowest of the Indonesian sample, and relative to the bregma-inion length it is at the sample's mean), and the elongated parietal relative to the other vault bones (the parietal/occipital length ratio is also at the Indonesian sample's mean, and, while the ratio with frontal length is long, this probably reflects the lack of glabellar swelling). What does suggest a young age is the thinness of the vault and of the supraorbital torus. On the other hand, several features indicate that the specimen is far from being an infant. These include the ossified tympanic region, the depth of the glenoid fossa, the development of the mastoid process (similar to Sangiran 2), the development of the nuchal torus with a distinct although not projecting triangular inion prominence below it, the postorbital constriction, the low frontal inclination, and the marked projection of the supraorbital region anterior to the frontal squama with the consequent supratoral sulcus. The lack of cranial remains for other *Homo erectus* children makes an exact age estimation difficult, but comparison of these features with those of the few other children known in the hominid fossil record indicates the specimen is almost certainly older than Taung and Gibraltar and younger than Teshik Tash. This would bracket it between 6 and 9 years in age, and indeed taking the differences in adult morphology into account the Modjokerto child most closely resembles La Quina 18 (about 7 years in age) in the development of the features enumerated above. At this age, it is unlikely that the adult capacity would be more than 8% greater if one assumes that a human growth curve was followed (Ashton and Spence 1978; Schultz 1965), and it would be less if the growth rate in *H. erectus* were more rapid.

As to the capacity of the specimen, the liquid capacity of the *outside* of the vault determined by Riscutia (1975) by immersing it in water and measuring the displacement was 673 cc, not markedly different from the endocranial capacity estimate suggested by Dubois (1936)—650 cc—and by Boule and Vallois (1957)—not more than 700 cc. Clearly, the brain size cannot be larger than this figure. However, Riscutia's estimate was for the outside of the vault. He then attempted to determine how much smaller the endocranial capacity actually was. Using a spherical model he determined the effects on the endocranial volume of average vault thicknesses of 1, 2, and 3 mm. These were, respectively, 637 cc, 601 cc, and 568 cc. From my measurements of vault thicknesses where the specimen is broken, 3 mm would be a *minimum* average for the braincase. If an actual endocranial estimate of 568 cc (or even 601 cc) follows from this work, the adult estimate of 650 cc that I used in the analysis is quite reasonable, if not an overestimate of the likely adult volume. Given the capacity estimates for OH 12 and ER 1805, this figure is not outside the known (or excluding ER 1805 the reasonably expected) range for *H. erectus.*

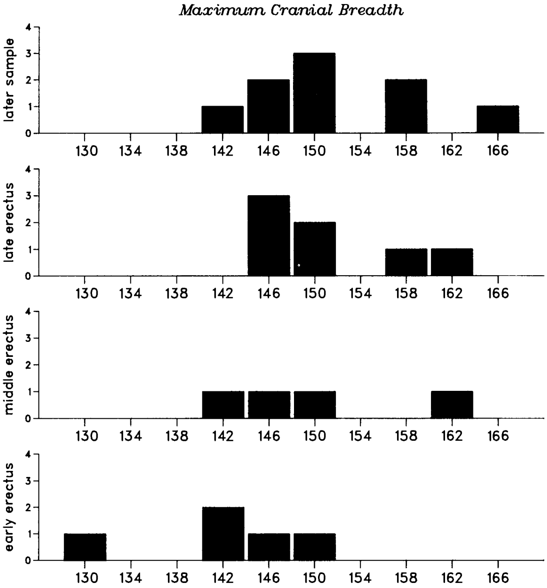

FIGURE 3. Distribution of the maximum breadth of the cranium in millimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

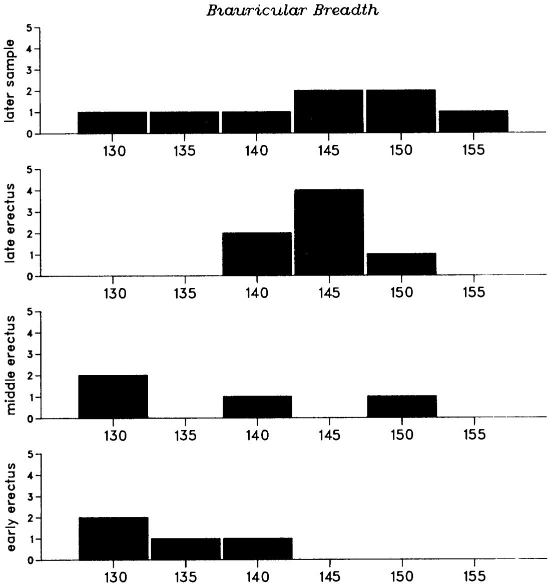

FIGURE 4. Distribution of biauricular breadth in millimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

than the increase in maximum cranial breadth (Fig. 3), and the biparietal breadth increase attains significance for more comparisons within the sample. Moreover, the *rate* of maximum cranial breadth change decreases, the greatest difference in average maximum cranial breadths is between the early and middle samples. Throughout *H. erectus,* even in the latest *erectus* sample, the maximum cranial breadth remains much greater than the biparietal breadth, but by the Upper Pleistocene the continuation of these two trends results in the maximum cranial breadth *becoming* the biparietal breadth. What happens is a combination of continued parietal expansion (reflecting larger braincases) combined with a much lower rate of expansion (and ultimately a reduction) for the pneumatization of the cranial base. The altered relationship between these measures of breadth is only expressed in Upper Pleistocene hominids, but the evolutionary trends leading to this altered relationship are clearly evident within *H. erectus.*

The pattern of expansion in biasterionic and biauricular breadths is somewhat different. The expansion of biauricular (Fig. 4) breadth is almost as rapid as the biparietal expansion. Biasterionic breadth expands more slowly within *H. erectus*; there is no significant change (actually a very slight decrease) between the early and middle samples, and the difference between early and late samples does not attain statistical significance. Interestingly, there is a jump in the expansion of biasterionic breadth between the late *H. erectus* sample and the sample of later hominids, and this difference is significant. Thus, biasterionic breadth begins its expansion only in the late *H. erectus* sample, and this is a continuing trend in the later hominids. Biasterionic breadth is the only cranial dimension examined that responds significantly to something that can be independent of vault size; in this case, the width of the nuchal plane, which is a function of the size of the nuchal musculature. The hypothesis that the size of the nuchal musculature in hominids reflects the magnitude of anterior tooth loading suggests an explanation for this pattern of change because the hominid remains from the early Upper Pleistocene have the largest anterior teeth of any Pleistocene hominid sample. The expansion of the nuchal plane accelerates after *H. erectus,* coincidently with the expansion of the incisors in the Upper Pleistocene.

The other two measures of vault size, length as measured from bregma to inion (Fig. 5) and height as measured by the projection of the au-

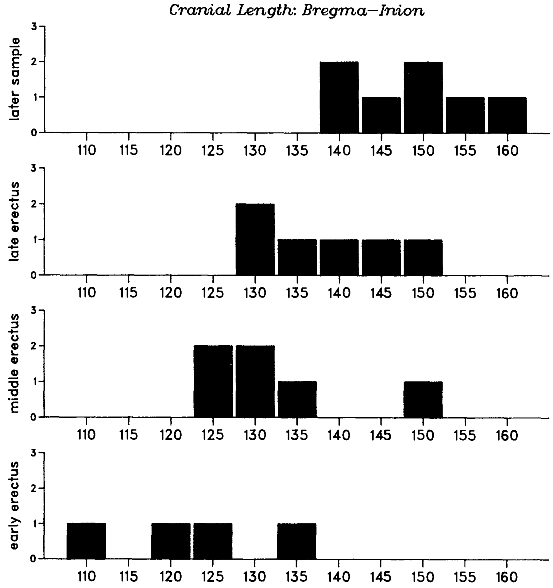

FIGURE 5. Distribution of the bregma–inion length in millimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

ricular-bregma distance into the sagittal plane (Fig. 6), both increase more rapidly than any of the breadth dimensions and both attain statistical significance for the *H. erectus* span.

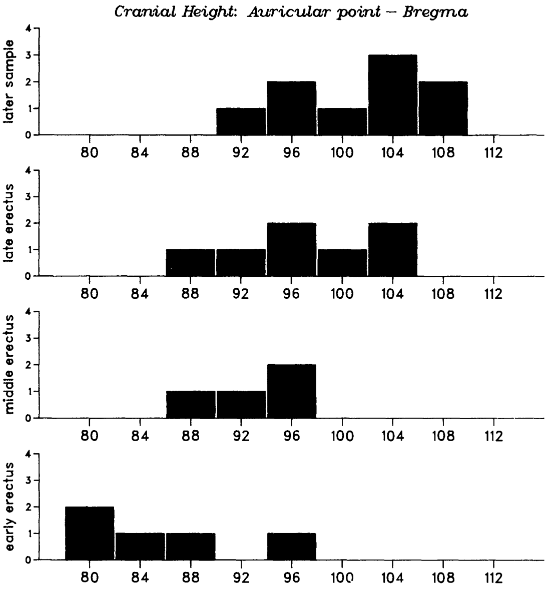

FIGURE 6. Distribution of the auricular–bregma height projected into the sagittal plane, in millimeters, for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

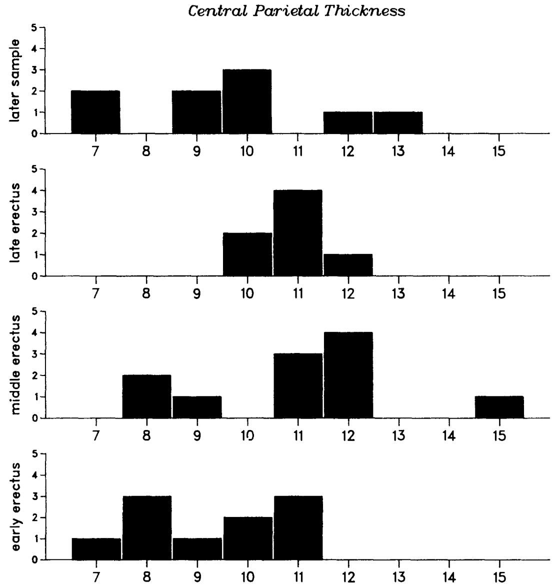

FIGURE 7. Distribution of the thickness of the parietal at its center in millimeters for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

The additional morphological features examined are independent of vault size, at least in principle. The thickness of the parietal bone at its center (Fig. 7) increases significantly within *H. erectus,* and at a much faster rate than the rate of change in darwins reported would suggest, since all of the increase is between the early and middle *H. erectus* samples. This thickness decreases between the late *H. erectus* sample and the sample of later hominids. While the difference is not significant, it is tempting to suggest that a continuation of this trend results in the much thinner vaults of modern populations. However, in this case there is no evidence of this trend within *H. erectus.*

Thickness (height) of the supraorbital torus (Fig. 8) reduces between the middle and late *H. erectus* samples but does not change at all between the late *H. erectus* and later hominid samples. The difference between middle and late *H. erectus* is not significant.

The measures of mandibular size show marked reduction, and this is surely related to posterior dental reduction. The breadth of the M_1 (Fig. 9) reduces significantly within *H. erectus,* a trend that continues through the whole span of the Pleistocene. Similarly, the mandibular measure directly reflecting the size of the dentition, the alveolar length from P_3 to M_2 (Fig. 10) also

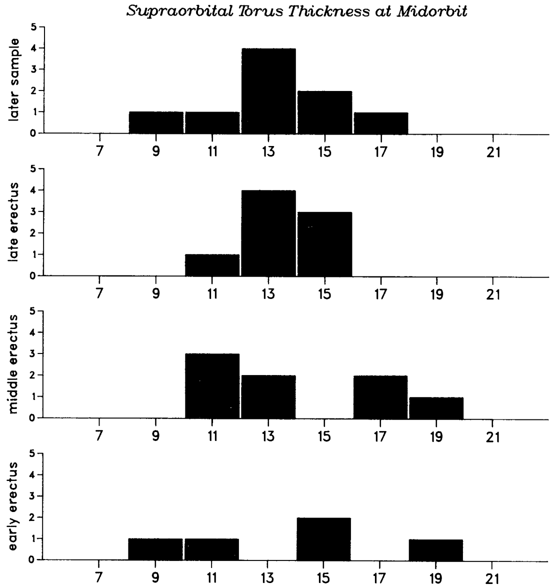

FIGURE 8. Distribution of the height (thickness) of the supraorbital torus at the mid-orbit position, in millimeters, for three *Homo erectus* samples and a sample of later hominids. See Table 2 for the means and other statistics.

reduces significantly. This reduction is of greater magnitude because it includes the size of two teeth which show even more reduction than M_1 within *H. erectus*; these are the M_2 and the P_4.

The mandibular corpus height (Fig. 11) and breadth (Fig. 12) dimensions change significantly and dramatically through the *H. erectus* span, at a much higher rate than the M_1 reduces, and indeed at a higher rate than the change in any of the cranial dimensions except for central parietal thickness. Moreover, the rate determination is an underestimate of the actual rate, since the bulk of the mandibular corpus reduction is between the early and middle *H. erectus* samples. Breadth of the corpus reduces more rapidly than height, reflecting a trend that results in the relatively thin mandibles of modern populations. It is possible that the posterior dental reduction is a consequence of the more rapid changes in the mandibular corpus dimensions, leading to crowding and insufficient room for the developing tooth crowns. The corpus dimensions may more directly reflect the decreasing use of the posterior dentition.

These reductions of masticatory structures contrast with the expanding cranial vault. If the expansion in brain size and in the vault dimensions related to it were "explained" by a hypothetical increase in body size alone, this would make the reducing masticatory structures even more significant. Similarly, an attempt to "explain" the reducing masticatory structures by a hypothetical decrease in body size would throw the increasing vault sizes into even greater contrast. Actually, what little evidence there is for

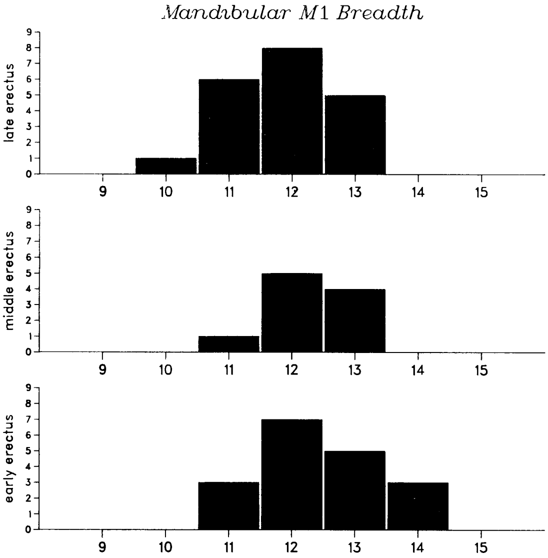

FIGURE 9. Distribution of the transverse breadth of the M_1 in millimeters for three *Homo erectus* samples. See Table 2 for the means and other statistics.

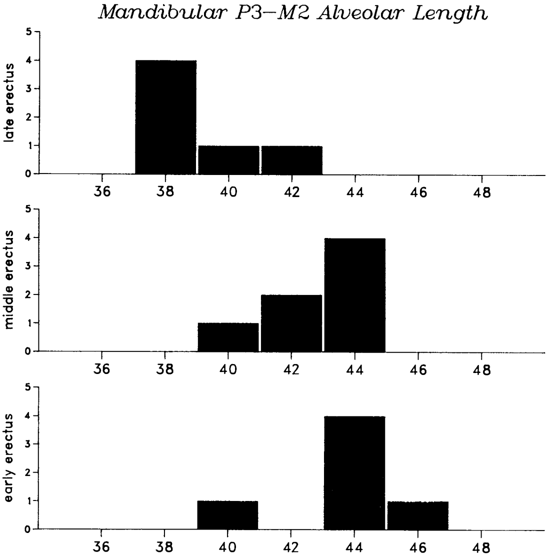

FIGURE 10. Distribution of the alveolar distance on the mandible from the P_3 to the M_2, in millimeters, for three *Homo erectus* samples. See Table 2 for the means and other statistics.

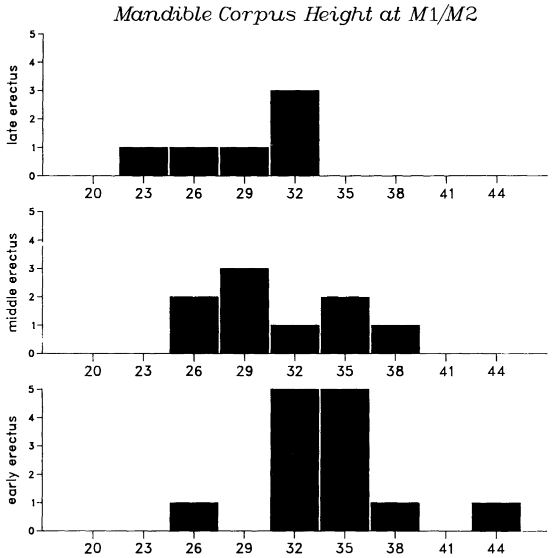

Figure 11. Distribution of the height of the mandible in millimeters, taken between the first and second molar positions, for three *Homo erectus* samples. See Table 2 for the means and other statistics.

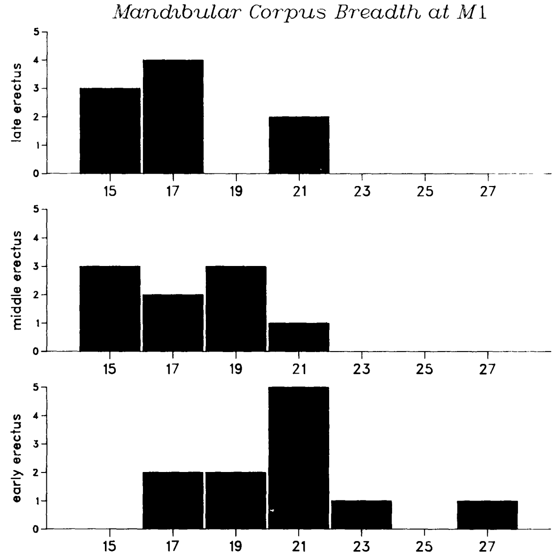

Figure 12. Distribution of the breadth of the mandible in millimeters, taken at the M_1 position, for three *Homo erectus* samples. See Table 2 for the means and other statistics.

body sizes within *H. erectus* indicates no significant change at all (Wolpoff 1980b). The minimal interpretation of these data, if the body size information is discounted, is that at least one adaptive complex changes significantly within *H. erectus*. The likely interpretation is that both adaptive systems change significantly.

Discussion

It would appear that there are significant evolutionary changes within a conservatively defined sample of *H. erectus*. Of course, all of the measurements examined do not change, but punctuationalism and stasis are contentions about the evolution of *lineages*, and not about individual measurements. The changes documented within *H. erectus* involve certainly one and most probably two adaptive systems, the two which change the most over the full course of Plio-Pleistocene hominid evolution.

The rate of change in these systems is of interest. The estimations of evolutionary rates are influenced by how well the group in question has been studied (Williams 1957) and by the duration over which the estimate is obtained (Gingerich 1983). In this case, sample sizes for *H. erectus* are hardly overwhelming (tending to result in an *under*estimation of rates), although evidently large enough to show significant differences within the sample. As to their magnitude, the rates calculated are for a 1-Myr span, which should make them comparable to the average (geometric mean) observed fossil vertebrate rate of 0.08 darwins reported by Gingerich (1983), since this average rate was determined for an average time span of 1.6 Myr. Such a comparison reveals that the changes within *H. erectus* are generally at or above the fossil vertebrate average. The rate of change for cranial capacity (0.09 darwins, the reported rate of 0.27 darwins divided by three to make the volumetric rate comparable to the linear rates) is more rapid than the average fossil vertebrate rate. Of the vault dimensions, only the expansion of biasterionic breadth and the reduction of supraorbital thickness fall markedly below this average, and both of these are at least in part independent of gross vault size. The rate of reduction for M_1 breadth falls below the fossil vertebrate average, but this is the slowest reducing of the posterior teeth and as detailed above its reduction is significant for *H. erectus*. The other mastication-related structures of the mandible reduce at a rate markedly above the fossil vertebrate average. The average absolute rate of change for all the dimensions examined is 0.10 darwins.[4]

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[4] Without ER 1805 the average rate of change is slightly less, 0.08 darwins.

Thus, one must conclude not only that there are significant evolutionary trends within *H. erectus* but also that the rate of change within the taxon is at or above the fossil vertebrate average. One could hardly regard these data as *supporting* the interpretation of evolutionary stasis!

However, supporting a model of evolutionary change is one thing and disproving it is another, and we may legitimately ask whether these data disprove the interpretation of stasis for *H. erectus.* Gould and Eldredge (1977, p. 133) have argued that even when a lineage *appears* to show gradual change it actually reflects stasis because the rates of change "are only sufficient to cast a superficial molding upon the pattern of evolutionary change." This argument presupposes that the rates of phyletic change are *constant* and that average rates for long durations apply to a species at all times and over all durations, an unlikely and unsupportable assumption (Charlesworth et al. 1982; Gingerich 1983). Moreover, there is something suspicious about a "superficial molding" interpretation for the changes within *H. erectus.* This is because the main patterns of change are bidirectional, *expansion* of the cranial vault and *reduction* of the masticatory apparatus, and are in exactly the directions revealed by comparing the preceding and subsequent species. Even the details of change (greater expansion of biparietal breadth than of maximum cranial breadth, greater reduction of mandibular corpus thickness than of corpus height) adhere to the macroevolutionary patterns revealed by comparing the three Pleistocene species of the genus *Homo.* Thus, most of the specific differences characterizing the comparison of *H. habilis* with *H. sapiens* are reflected in the progressive changes *within* the *H. erectus* sample. While serendipity undoubtedly plays a role in the evolutionary process, it is asking too much to invoke it as an explanation here. In this case the rates of change within *H. erectus* are neither an obvious reflection of stasis nor the "fundamental mystery" that Gould and Eldredge (1977, p. 134) suggest.

The fact is that the criteria required to adequately disprove gradual change in the fossil record are very difficult to meet (Levinton and Simon 1980; Charlesworth et al. 1982; Schopf and Hoffman 1983), as are the criteria required to validly reject the punctuated equilibrium interpretation (Gould and Eldredge 1977). Yet the ready acceptance of the *H. erectus* analysis published by Rightmire (1981) as a valid disproof of gradualism for the taxon suggests that the sample size and the geographic and temporal distribution of this species were considered sufficient to disprove gradualism and thereby to establish stasis validly. Unless more stringent criteria are required to disprove gradualism than are required to disprove stasis, the present study meets or exceeds the same criteria of sample size and geographic range, and it should be concluded that stasis for *H. erectus* can be rejected.

There are two other reasons why the *H. erectus* sample does not fit the predictions of the punctuational model. One of these involves the late or continued survival of ancestral species (a prediction of the model). Gould (1976) raised this for *H. erectus* through his contention that early specimens overlapped in time with late surviving ancestral forms in east Africa. He may have (and Stanley, 1979, definitely has) derived this idea from publications by Leakey and Walker (1976, expanded in Walker and Leakey 1978, and argued more recently in Leakey and Walker 1980). Leakey and Walker based their argument for temporal overlap on ER 1805 and on ER 1813 as well as other specimens from area 123 which were then placed "provisionally" in the Upper Member of the Koobi Fora Formation at east Turkana. However, ER 1805 is not widely regarded as an australopithecine[1] (Howell 1978; Wolpoff 1980b; Thorne and Wolpoff 1981), and area 123 is now recognized to be in the Lower Member so that the specimens in it are earlier than the known remains of *H. erectus* from east Turkana. Thus, at the moment *there are no sites where* H. erectus *remains are stratigraphically interdigitated with remains clearly attributed to (non-boisei) australopithecines.* While it has been argued that the comparison of radiometric or faunal dates for *different* sites shows (non-boisei) australopithecines at some sites to have the same age as *H. erectus* at others, all of these dates have probable error ranges that exceed the date differences between the sites. The fact that no evidence from a *single* site with both *H. erectus* and *H. habilis* shows these species overlapping in stratigraphic position indicates strongly that *H. habilis* and *H.*

erectus are neither narrowly nor broadly contemporary.

The other reason concerns the boundaries of *H. erectus*. Here, too, predictions of the punctuational model are not clearly met. In punctuational theory, species are distinct entities with a "real" beginning and end (Gould and Eldredge 1977; Vrba 1980). However, as discussed above, for *H. erectus* these terminal boundaries seem to be indistinct (Mann 1971; Wolpoff 1980a; Cronin et al. 1981; Jelínek 1981; Wolpoff et al. 1984). Indeed, because the *erectus/sapiens* boundary is so difficult to delineate on morphological grounds alone, a number of authors have discussed whether *H. erectus* should be distinguished from *H. sapiens* (Weidenreich 1943; Wolpoff et al. 1984), and some have suggested that *H. erectus* be formally sunk (Hemmer 1967; Jelínek 1981).

While this research provides some interesting and perhaps important information about *H. erectus,* it is *not* a general disproof of the punctuated equilibrium model. Indeed, this model has proven to be excruciatingly difficult to test in the fossil record (Levinton and Simon 1980; Schopf 1981, 1982; Charlesworth et al. 1982; Schopf and Hoffman 1983). Moreover, it is possible that nothing can totally disprove this model because there surely are *some* species that are characterized by periods of stasis followed by speciation with rapid change and subsequent species replacement. The issue addressed here is not whether the model is generally valid or invalid, but the often repeated claim that punctuated equilibrium is the most probable (common) source of evolutionary change. Analysis of a single species cannot resolve this either, but the fact is that *H. erectus* has been repeatedly promoted as one of the best examples of stasis in the fossil record, and the claim that stasis is common can only be addressed through specific analyses of the species that are said to show it (cf. Bookstein et al. 1978; Malmgren and Kennet 1981; Raup and Crick 1981). If "stasis is data," *H. erectus* is clearly one species providing evidence that stasis is less common than thought.

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