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*The American Naturalist*, Vol. 136, No. 6. (Dec., 1990), pp. 727-741.

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*The American Naturalist* is currently published by The University of Chicago Press.

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## THE RATE OF MORPHOLOGICAL EVOLUTION IN MAMMALS FROM THE STANDPOINT OF THE NEUTRAL EXPECTATION

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*Submitted October 13, 1988; Revised April 27, 1989; Accepted August 3, 1989*

At irregular intervals over the past four decades, a series of papers has appeared regarding the measurement of the long-term rates of morphological evolution (Haldane 1949; Lerman 1965; Cherry et al. 1978, 1982; Atchley 1980; Kunkel et al. 1980; Gingerich 1983, 1984; Wyles et al. 1983; Charlesworth 1984; Gould 1984). To say that conflicting opinions exist regarding the appropriate use of rate statistics is an understatement. There are, however, a few matters on which a consensus seems to have emerged. Many have argued, for example, that mammals have evolved at more rapid rates than other organisms (Simpson 1944, 1953; Romer 1966; Van Valen 1974, 1985; Cherry et al. 1982) and that humans have evolved extremely rapidly relative to other mammals (Haldane 1949; Wyles et al. 1983).

Wilson and colleagues (Wilson et al. 1975; Wyles et al. 1983; Larson et al. 1984; Wilson 1985) have proposed two mechanisms to account for these observations: behavioral drive (reflected by an increase in brain size) and abnormally high rates of regulatory evolution (facilitated by random genetic drift in small, socially structured demes). In order to test these hypotheses, it is necessary to know how observed rates of morphological evolution compare with the expectations under specific evolutionary scenarios. Since morphological evolution is a population-genetic process, it is difficult to accomplish this unless a rate statistic that relates to population-genetic theory is employed. It is not clear that any of the frequently used measures has such a property.

The rate statistic introduced below has a close connection with the neutral model of phenotypic evolution (Lande 1976, 1979*a*; Chakraborty and Nei 1982; Lynch and Hill 1986). This allows one to evaluate whether an observed amount of divergence is significantly lower or higher than that expected if mutation and random genetic drift were the sole evolutionary forces. An unexpectedly low rate suggests that stabilizing selection has played a predominant role in preventing phenotypic divergence, whereas an unexpectedly high rate implies an acceleration of divergence by directional selection.

Following a brief introduction of the theory, data on the cranial characters of several groups of fossil and extant mammals, including modern man, will be evaluated. These analyses lead to the conclusion that, although the rate of mor-

phological evolution in mammals may be unusually rapid relative to that in other organisms, it is actually quite low relative to its potential in the presence of diversifying selection. In addition, I consider the question of whether the rate of evolution in humans has been any faster than that in other mammalian lineages in their early stages of diversification.

#### MEASUREMENT OF THE RATE OF MORPHOLOGICAL EVOLUTION

In comparisons of evolutionary rates of different characters and/or lineages, a number of technical problems arise. Foremost among these is the need for a measure that is independent of the measurement scale. Haldane (1949) suggested the index

$$D_H = (\ln \bar{z}_1 - \ln \bar{z}_2)/t, \quad (1)$$

where  $\bar{z}_1$  and  $\bar{z}_2$  are the observed mean phenotypes of two species separated for  $t$  time units.  $D_H$  is an estimator of the mean rate of proportional change of a character. Although equation (1) provides a dimensionless measure of the evolutionary rate, the objection may be raised that it does not properly account for the variation that exists within populations for different characters. Both the statistical and the evolutionary significance of an observed amount of morphological change decline as the within-population variation increases. For that reason, evolutionary rates are often scaled to the within-population standard deviation,

$$D'_H = (\ln \bar{z}_1 - \ln \bar{z}_2)/SD(\ln z), \quad (2)$$

where  $SD(\ln z)$  is the average standard deviation of the log-transformed measures within the two populations. The use of logarithmic transformations often has the added advantage of stabilizing the within-population variance with respect to changes in the mean (Wright 1968).

For the purposes of testing hypotheses regarding evolutionary mechanisms, it is desirable to have an index for the rate of morphological evolution that relates to population-genetic theory. It is not immediately obvious that equation (1) or (2) has such a property. The neutral model of phenotypic evolution provides a useful frame of reference here, since it yields a simple prediction that is independent of population size, dominance, and epistatic and linkage relationships among loci. Provided that drift and mutation are the only important evolutionary forces, the expected between-species variance is simply  $\sigma_m^2 t$ , where  $\sigma_m^2$  is the mutational rate of input of genetic variance and  $t$  is the total number of generations separating descendant species (Lande 1976, 1979a; Chakraborty and Nei 1982; Lynch and Hill 1986). For two species derived from a common ancestor,  $t$  equals the sum of the times down both descendant branches.

By treating  $\sigma_m^2$  as a fraction  $k$  of the within-species phenotypic variance,  $\sigma^2(\ln z)$ , the expected neutral rate of divergence can be expressed in phenotypic terms as  $k\sigma^2(\ln z)t$ . This suggests

$$\Delta = \text{var}_B(\ln z)/[t \text{var}_W(\ln z)], \quad (3)$$

where  $\text{var}_W(\ln z)$  and  $\text{var}_B(\ln z)$  are the observed within- and between-species components of phenotypic variance for log-transformed measures, as a measure of

the rate of morphological evolution. Although no measure of evolutionary rate can identify with certainty the mechanism that has caused an observed morphological change,  $\Delta$  can be used to support some hypotheses. If, for example, diversifying selection has been a predominant evolutionary force on the species under study, the expected value of  $\Delta$  should be larger than  $k$ . The opposite is expected if selection has generally opposed the divergence of independent lineages. A  $\Delta$  approximately equal to  $k$  is consistent with the neutral theory, although it is also in accord with any number of hypotheses involving selection and migration.

The within- and between-species variances in equation (3) are obtainable from the mean squares generated by an ANOVA (Snedecor and Cochran 1967) and, in the case of a two-species analysis, can be expressed in terms of phenotypic means and standard deviations:

$$\text{var}_w(\ln z) = \frac{(n_1 - 1)[\text{SD}(\ln z_1)]^2 + (n_2 - 1)[\text{SD}(\ln z_2)]^2}{n_1 + n_2 - 2}, \quad (4a)$$

$$\text{var}_B(\ln z) = \left[ \frac{n_1 n_2 (\overline{\ln z_1} - \overline{\ln z_2})^2}{n_1 + n_2} - \text{var}_w(\ln z) \right] / n_0, \quad (4b)$$

where  $n_1$  and  $n_2$  are the sample sizes for the two populations,  $n_0 = n_1 + n_2 - [(n_1^2 + n_2^2)/(n_1 + n_2)]$ , and the overbars denote means of the log-transformed data.

In estimating rates of evolution from information reported in the literature, the means and variances on the original scale of measurement are often the only available data. The following Taylor approximations permit these statistics to be converted to the logarithmic scale with little loss in accuracy, provided that the coefficient of variation of the original scale,  $\text{CV}(z)$ , is less than 0.3:

$$\overline{\ln z} \approx \ln \bar{z} - [\text{CV}(z)]^2/2; \quad (5a)$$

$$\text{var}(\ln z) \approx [\text{CV}(z)]^2. \quad (5b)$$

In the sense that both are independent of scale,  $\Delta$  is similar to  $D'_H$ , but there is a fundamental difference. Although  $\Delta$  is based on the quadratic change in  $\overline{\ln z}$ ,  $D'_H$  is a function of the proportional change in  $\bar{z}$ . The Mahalanobis (1936) distance for a single variable,  $D^2 = (\overline{\ln z_1} - \overline{\ln z_2})^2 / \text{var}_w(\ln z)$ , is also closely related to  $\Delta$ , and Turelli et al. (1988) have suggested  $D^2/2$  as a measure of the evolutionary rate. Whereas the numerator of  $\Delta$  is an unbiased estimate of the between-species variance, the expected value of  $(\overline{\ln z_1} - \overline{\ln z_2})^2/2$  is greater than the expected value of  $\text{var}_B(\ln z)$  by the amount  $E[\text{var}_w(\ln z)]/n_0$ . Thus, the biased estimator  $D^2/2$  converges on  $\Delta$  as  $n_0 \text{var}_B(\ln z) / \text{var}_w(\ln z)$  approaches infinity. For large sample sizes and/or large evolutionary distances, the estimator of Turelli et al. is quite adequate.

In order to compare estimates of  $\Delta$  with the neutral expectation, information on  $k$  is needed. A recent survey of a diversity of taxa and characters indicates that  $\sigma_m^2$  divided by the environmental variance ( $\sigma_e^2$ ) of the trait usually falls in the range of  $10^{-4}$  to  $10^{-2}$  (Lynch 1988). Since all the evolutionary rates reported in this article are low, we need consider only the lower limit to  $k$ . The environmental component is frequently as small as 50% of the total phenotypic variance but seldom much less. Thus, a global estimate for the lower limit to  $\Delta$  under the

neutral hypothesis is on the order of  $\Delta_{\min} = 5 \times 10^{-5}$ . Estimates of  $\sigma_m^2/\sigma_c^2$  for cranial, mandibular, and limb bone characters in the mouse are actually on the order of  $10^{-2}$ , ranging down to  $4 \times 10^{-3}$  (Atchley et al. 1988; Lynch 1988). Thus,  $10^{-4}$  appears a reasonable estimate of  $\Delta_{\min}$  for mammalian skeletal traits.

#### EMPIRICAL ESTIMATES OF $\Delta$ FROM MAMMALIAN SKULLS

*Large cats.*—Wayne et al. (1986) reported the means and standard deviations of 16 continuously distributed aspects of the cranium in four Felidae: leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), ocelots (*Leopardus pardalis*), and margays (*Leopardus wiedii*). The fossil record (Hemmer 1974; Savage and Russell 1983) and immunological data (Collier and O'Brien 1985) are in accord that a split between the pantherine and ocelot lineages occurred in the mid-Miocene ( $\approx 10$  million yr before the present [M.Y.B.P.]). Because the earliest appearances of *Panthera* and *Acinonyx* in the fossil record are 5 and 2.5 M.Y.B.P., 4 M.Y.B.P. is assumed to be the approximate time of their separation. The immunological distance between ocelots and margays is approximately one-third of that between *Panthera* and *Acinonyx*, suggesting a divergence time of the former of  $\sim 1$  M.Y.B.P. Mean generation times of *Panthera* and *Acinonyx* are approximately 5 and 4 yr, and for *Leopardus*, approximately 3 yr (Eisenberg 1981; Wootton 1987). Upon application of equations (4) and (5), the pairwise evolutionary rates, averaged over all characters, are found to range from  $2.2 \times 10^{-6}$  to  $1.7 \times 10^{-5}$  per generation. The average value of  $\Delta$  over the whole lineage is  $8.6 \times 10^{-6}$ , which is approximately 10% of the minimum neutral expectation.

*Cave bears.*—Kurtén (1955) recorded an evolutionary increase in the size of the first upper molar over a period of 22 million yr in a lineage of cave bears. His table 6 contains dates, means, standard deviations, and sample sizes for five samples believed to be members of a direct line of descent. If a generation time of 10 yr is assumed and the data are transformed to natural logs by equations (5), the four estimates of  $\Delta$  range from  $7.5 \times 10^{-6}$  to  $8.6 \times 10^{-5}$  with a mean of  $4.6 \times 10^{-5}$ , which is approximately half the minimum neutral rate.

*Squirrels.*—Collections from the University of Illinois Museum of Natural History were used to obtain estimates of  $\Delta$  for the Sciuridae. Nineteen metric traits, distributed over the cranium and mandible, were measured with dial calipers on approximately 10 skulls of each sex for 10 North American species: antelope squirrels (*Ammospermophilus leucurus cinnamomeus*), prairie dogs (*Cynomys ludovicianus*), woodchucks (*Marmota monax*), rock squirrels (*Spermophilus (Otospermophilus) variegatus grammurus*), chipmunks (*Eutamias minimus* and *Tamias striatus*), ground squirrels (*Spermophilus (Spermophilus) tridecemlineatus*), gray squirrels (*Tamiasciurus hudsonicus*), and flying squirrels (*Glaucomys volans*). Based on the work of Eisenberg (1981) and Wootton (1987), 1.5 yr was assumed to be the mean generation time for all species except *C. ludovicianus* (3 yr), *M. monax* (3 yr), and *T. striatus* (1 yr). The assumed between-species divergence times are based on the phylogenetic tree in figure 1. This tree is admittedly somewhat subjective, but it is a reasonable compromise of results derived from paleontological (Black 1963, 1972), electrophoretic (Hafner 1984), and immuno-



FIG. 1.—Phylogenetic tree assumed for sciurid species

logical (Ellis and Maxson 1979, 1980; Maxson et al. 1981) studies. The 45 pairwise estimates of  $\Delta$ , each an average over characters and sexes, range from  $4.1 \times 10^{-8}$  to  $2.6 \times 10^{-5}$ . The average value of  $\Delta$  over the entire lineage is  $3.0 \times 10^{-6}$ , which is 3% of the minimum neutral expectation.

*Horses*.—The well-worked data set of Simpson (1944) for the molar measurements of paracone height and ectoloph length at four stages in the presumed line of descent of the horse has been analyzed previously from the standpoint of neutrality by Lande (1976), who summarized the log-transformed data and divergence times. These lead to an average  $\Delta$  of  $1.8 \times 10^{-5}$ , approximately one-fifth of the minimum neutral rate.

*Condylarths*.—A detailed account of the fossil history of North American condylarths (an extinct group of ungulates) of the genus *Hyopsodus* was given by Gingerich (1974). His figure 1 summarizes stratigraphically the log-transformed data on size of the first lower molar for 11 species within the *Hyopsodus* lineage over a period of about 4 million yr of early Eocene deposits in Wyoming. Sample sizes for 6 of these (*H. loomisi*, *H. simplex*, *H. latidens*, *H. minor*, *H. lysitensis*, and *H. powellianus*) are quite large, and it is the largest of the samples for each of these that are focused on here. Following Lande (1976), a generation time of 2 yr is assumed. Averaging over all pairwise combinations of sample populations,  $\bar{\Delta} = 1.2 \times 10^{-5}$ .

*Oreodonts*.—Bader (1955) provided means and coefficients of variation for 23 cranial and mandibular characters for five species in the lines of descent of two subfamilies of oreodonts, a group of extinct pig-like artiodactyls. The abundant Miocene deposits from the Great Plains of North America span a period of approximately 12 million yr. The mean estimates of  $\Delta$  for the *Brachycrus* and *Merycochoerus* lines of descent, assuming generation times of 3 yr, are  $2.0 \times 10^{-6}$  and  $5.5 \times 10^{-6}$ , respectively, both substantially below the minimum neutral rate.

*Primitive primates*.—Stratigraphic data from the same geological setting as the *Hyopsodus* are available for a lineage of North American Adapidae (Gingerich 1980, his fig. 3). A continuous record of descent spans an approximately 6-million-yr period in the Eocene. The largest samples for *Pelycodus mckennai*, *Copelemur consortutus*, *Notharctus tenebrosus*, and *N. robustior* were used to compute  $\bar{\Delta} = 2.0 \times 10^{-5}$ , approximately one-fifth of the minimum neutral rate, under the assumption of a 2-yr generation time.

*Hominids*.—Wolpoff (1984) provided means, standard deviations, and sample sizes for 13 measures of the cranium, mandible, and teeth of *Homo erectus*, the putative ancestor of modern man. Since the average time between samples of early and late *H. erectus* is a million years,  $t = 50,000$  under the assumption of a generation time of 20 yr. Averaging over all 13 traits,  $\bar{\Delta} = 2.1 \times 10^{-5}$  ( $\pm 2.0 \times 10^{-5}$  SD).

*Humans*.—An exceptionally large data set on the cranium of *Homo sapiens* (Howells 1970, 1973a, 1973b) allows the estimation of rates of evolution in the modern races of man. Sample sizes for each population are on the order of 30–50 for each sex, with 61 measures on each skull. All of the sample populations were carefully selected to minimize the likelihood of interracial gene flow, although it is impossible to rule it out entirely.

The focus here is on four racial groups, each containing two or more samples: Capoids (Bushmen, Andaman Islanders), Congoids (Teitas, Zulus, Dogons), Caucasians (Medieval Norse, Medieval Hungarians, Carinthians of Austria, Gizeh Dynasties of Egypt), and Orientals (Northern Japan, Southern Japan, Hainan, Atayal, Ainu). Using the mean between-population variance as a distance measure, an analysis of the complete data set leads to a phylogenetic hypothesis with Capoids as an outgroup and the remaining three races splitting at about the same time, approximately halfway between the root of the tree and current time (Lynch 1989). These results are in only partial agreement with molecular data (Nei and Roychoudhury 1981; Cann et al. 1987), which also exhibit some inconsistencies with each other. The fossil and molecular evidence implies that modern man originated between 200,000 and 100,000 B.P. In the following, it is therefore assumed that a split occurred between Capoids and Congoids-Caucasians-Orientals 150,000 B.P., followed by a three-way split of the latter group 75,000 B.P. A generation time of 20 yr is assumed.

The mean  $\Delta$  for each interracial comparison was obtained by averaging over all 61 characters, both sexes, and all possible pairwise combinations of populations (table 1). These averages range from  $4.4 \times 10^{-5}$  for Capoids-Congoids to  $5.3 \times 10^{-4}$  for Caucasians-Orientals, with a grand mean for the entire data set of  $3.2 \times 10^{-4}$ .

TABLE 1  
 RATES OF MORPHOLOGICAL EVOLUTION OF THE CRANIUM BASED ON INTERRACIAL COMPARISONS  
 OF MODERN MAN

RACIAL COMPARISON	$\Delta$		N
	Mean	$\overline{SD}$	
Capoids-Congoids	$4.4 \times 10^{-5}$	$5.0 \times 10^{-5}$	6
Caucasians-Congoids	$5.5 \times 10^{-5}$	$7.8 \times 10^{-5}$	12
Capoids-Caucasians	$6.0 \times 10^{-5}$	$7.2 \times 10^{-5}$	8
Capoids-Orientals	$2.9 \times 10^{-4}$	$1.1 \times 10^{-3}$	10
Congoids-Orientals	$5.1 \times 10^{-4}$	$2.2 \times 10^{-3}$	15
Caucasians-Orientals	$5.3 \times 10^{-4}$	$2.3 \times 10^{-3}$	20
Weighted average	$3.2 \times 10^{-4}$	$1.3 \times 10^{-3}$	

NOTE.— $\overline{SD}$ , standard deviation of character-specific estimates of  $\Delta$  averaged over  $N$  pairwise population-by-population analyses. Because characters and populations are not independent, to an unknown degree, the standard error of each mean  $\Delta$  is between  $\overline{SD}$  and  $\overline{SD}/(61N)^{1/2}$ . Data from Howells 1973a, personal communication.

Brace et al. (1987) have recorded a remarkable decline ( $\approx 30\%$ ) in the composite tooth size (their TS) of humans over the past 100,000 yr. Their figure 2 shows the regression of mean TS for 14 samples (number of skulls per sample, 13–79). No information is provided on the within-sample variation, but the coefficient of variation is probably near 0.1 (Yablokov 1974). Treating the regression estimates of the means as the population parameters, the between-sample variance is estimated by half the squared difference between the means. The average value of  $\Delta$  obtained over six discrete intervals is  $2.6 \times 10^{-4}$ , which is not greatly different from the estimate extracted from Howells's data set. Thus, both sets of data are in agreement that the average rate of morphological evolution in modern man is approximately three times the minimum neutral rate.

*The great apes.*—It is of interest to see whether the relatively high evolutionary rates estimated for human skull morphology extend to other hominoid primates. Unfortunately, although a large number of comparative studies on hominoid cranial morphology have been reported in the literature, the data are not usually reported in a form that allows a computation of  $\Delta$ . Cherry et al. (1982) provided means and sample sizes for four cranial measures in humans, chimpanzees, gorillas, and orangutans. Estimates of the between-species variance were obtained for these under the assumption that the coefficient of variation is 0.1.

Considerable debate still exists over the exact branching pattern of the hominoid phylogeny (Ferris et al. 1981; Templeton 1983; Sibley and Ahlquist 1984; Hixson and Brown 1986), but there is general agreement that the orangutan is more distant from the members of the human-chimpanzee-gorilla clade than the latter three are from each other and that the splits between humans, chimpanzees, and gorillas occurred at nearly the same times. It is assumed here that the three members of the clade separated simultaneously  $9 \times 10^6$  B.P., following an earlier separation ( $13 \times 10^6$  B.P.) from orangutans (Gingerich 1984b). Generation times of 13 yr are assumed for each of the nonhuman primates.

When pairwise rates of divergence are computed for the four great apes, it is

TABLE 2  
ESTIMATES OF EVOLUTIONARY RATE FOR CRANIAL AND POSTCRANIAL TRAITS FOR PAIRWISE  
COMBINATIONS OF HOMINOIDS

	H-C	H-G	H-O	C-G	C-O	G-O	<i>N</i>
Skull	8.2 (11.0)	9.1 (6.1)	8.2 (9.8)	1.2 (1.8)	.2 (.2)	.3 (.6)	4
Pelvis	9.5 (2.7)	9.3 (2.8)	4.2 (1.1)	2.7 (.6)	.2 (.1)	2.0 (.3)	18
Humerus	.9 (.2)	4.7 (.5)	.7 (.2)	2.0 (.2)	.1 (.1)	.9 (.1)	16
Femur	2.1 (.6)	1.1 (.2)	1.7 (.4)	2.6 (.6)	.3 (.1)	1.9 (.3)	20
Capitate	1.1 (.3)	1.9 (.6)	1.0 (.2)	.9 (.3)	.1 (.04)	.3 (.1)	11

NOTE.—Values are mean  $\Delta$  ( $\times 10^6$ ) and standard deviation (in parentheses). H, human; C, chimpanzee; G, gorilla; O, orangutan. *N*, the number of characters measured. Sources: skull, Cherry et al. 1982; pelvis, McHenry 1975; humerus, McHenry 1976; femur, McHenry 1978; capitate, McHenry 1983.

found that they are all substantially below the minimum neutral expectation (table 2). The mean  $\Delta$  among the nonhuman apes,  $6 \times 10^{-7}$ , is substantially lower than any of the values computed up to now; but the mean  $\Delta$  involving comparisons of humans to the other great apes is more than 10 times higher. These results suggest that the rate of morphological divergence among the great apes has not been unusually high except in the branch leading to modern man.

Included in table 2 are estimates of  $\Delta$  among the great apes for several groups of postcranial characters. These are also well below the neutral expectation and bear out the conclusion that the average rate of morphological evolution in man substantially exceeds that in the other apes. Relative to cranial evolution, the average rate of postcranial evolution is substantially slower in humans but approximately twice as fast in gorillas.

#### DISCUSSION

The main result that emerges from these analyses is the generalization that the mean rate of morphological evolution is well below the minimum neutral expectation in all mammals, with the possible exception of modern man (fig. 2). Because of the consistent nature of the results, no further attempt will be made to test the neutral hypothesis with rigorous parametric statistics. Lande (1976, 1977) and Turelli et al. (1988) have devised such tests, but they have limitations when applied to macroevolutionary problems. Unless the divergence times and  $\sigma_m^2/\sigma_e^2$  are known with certainty, it is difficult to construct a quantitatively reliable null hypothesis. Therefore, the remaining discussion focuses on the major qualitative aspects of the results, with attention first being given to possible sources of error in the computations of  $\Delta$ . It is of particular interest to inquire whether there is anything inherent in the analytical procedures that could have biased the estimates of  $\Delta$  downward.

Three sampling problems could lead to biased estimates of  $\Delta$ . First, if there were a tendency to over- or underestimate divergence times, the resulting estimates of  $\Delta$  would tend to be biased downward or upward. The estimates of divergence times and generation times employed in this article are by no means

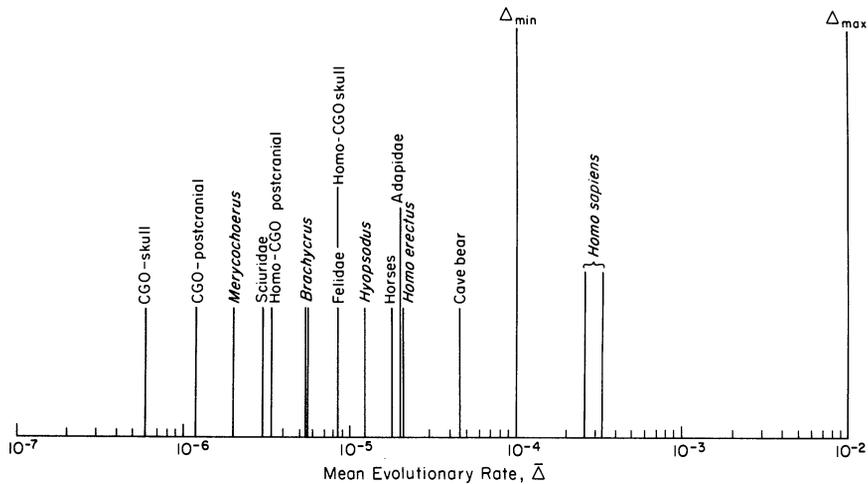


FIG. 2.—Summary of the estimates of average  $\Delta$ . CGO denotes chimpanzee, gorilla, and orangutan; Homo-CGO also includes modern man. All analyses are for cranial data unless denoted as postcranial.

free of error, but there is no obvious reason for the estimates of  $t$  to be biased upward. If anything, estimates of branch depths based on extrapolations from an incomplete fossil record are likely to be too low.

A second problem that could lead to a downward bias in estimates of  $\Delta$  is an inflation in the estimates of the within-population variance caused by the mixing of samples. This problem is most likely to be serious in studies of fossil lineages, in which samples often consist of remains from deposits spanning as many as several hundreds of generations. Any evolutionary changes or environmentally induced changes occurring within such composite samples would cause an inflation of the within-population variance relative to that expected in any single generation. Since the estimates of  $\Delta$  derived from fossil lineages (cave bears, horses, condylarths, oreodonts, primitive primates, and hominids) are all within the range of estimates obtained from contemporary populations, there is no indication that this is a serious problem for the investigations included in this study.

Finally, the existence of substantial between-population variance caused by environmental effects could result in an upward bias to estimates of  $\Delta$  by an amount that is inversely proportional to the divergence time. For simplicity, let us assume that a typical species pair that has an expected genetic divergence of  $\sigma_m^2 t$  also has an expected divergence from environmental causes equal to  $\sigma_E^2$ . The expected value of  $\Delta$  is then  $(\sigma_m^2 + \sigma_E^2/t)/\sigma^2(\ln z)$ . This model is, of course, not in quantitative agreement with the data, since almost all estimates of  $\Delta$  are less than the minimum expected value of  $\sigma_m^2/\sigma^2(\ln z)$ . However, the qualitative nature of the relationship is of special concern when considering the exceptionally high values of  $\Delta$  obtained for modern man, since the values of  $t$  used in the computations were much lower than those for any other lineage analyzed.

If environmental modification is an important source of apparent morphological

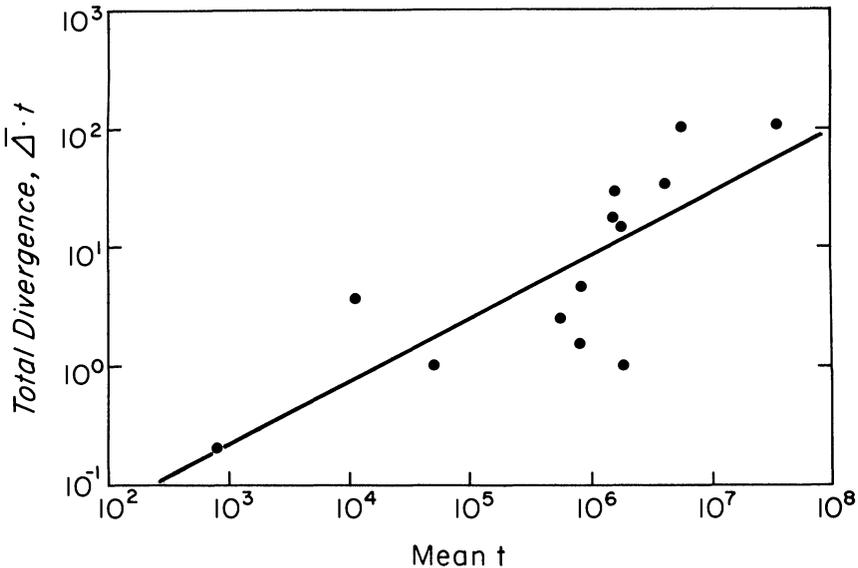


FIG. 3.—Least-squares fit for total mean divergence vs. the average number of generations involved in the computation of  $\bar{\Delta}$  for the data in fig. 2. The two leftmost points are for the data from Brace et al. 1987 and Howells 1973a.

divergence, a plot of total divergence,  $\Delta t$ , against  $t$  should exhibit an intercept that is significantly greater than zero. Unfortunately, the extreme skewness in the distribution of  $t$  among the data sets precludes any meaningful statistical analysis of the untransformed data. However, on a logarithmic scale, a good approximation is provided by the least-squares regression  $\Delta t = 0.0067t^{0.52}$  ( $r = 0.80$ ; fig. 3). Thus, the relationship between total divergence and divergence time is clearly nonlinear, but no evidence for a nonzero intercept can be derived from the existing data. Since the point for humans falls directly on the regression line, it does not seem unduly influenced by environmental modification.

In summary, there is no compelling evidence that the estimates of  $\Delta$  are biased in the downward direction. Thus, on the basis of the distribution of  $\Delta$  (fig. 2) and the nonlinear relation between  $\Delta t$  and  $t$  (fig. 3), there is reason to be confident that the diversification of mammalian morphology was not caused solely by the interaction of polygenic mutation and random genetic drift. It is too slow for that, except in the case of modern man. Although there may have been periods in any one of the lineages analyzed during which strong directional selection elevated the divergence rate well beyond the neutral expectation, stabilizing selection has predominated in the long term, preventing a potentially much greater diversification of mammals than we see today.

The results in figure 3 indicate that the cumulative divergence of cranial morphology in mammalian lineages is proportional to the square root of divergence time (in generations). Thus, morphological diversification within lineages is most rapid in the early phases of isolation and becomes progressively slower. The

regression equation for total divergence on total divergence time implies that the rate of divergence in the  $i$ th generation of isolation is approximately  $0.0034i^{-1/2}$  (Gingerich [1983] reported a slope of  $-0.83$  for a logarithmic regression of  $D_H$  on  $t$  for diverse morphological traits in fossil vertebrates, including nonmammals. Since  $D_H$  is only roughly proportional to  $\Delta^{1/2}$ , the most that can be said is that our results are qualitatively consistent.) This suggests that the rate of morphological divergence between mammalian lineages may often proceed at a pace consistent with the neutral hypothesis for the first thousand or so generations of isolation. It also suggests the the apparently rapid rate of evolution in modern man may be an artifact of temporal scaling. It is conceivable that other mammalian lineages, in their early stages of isolation, evolved as rapidly as *Homo sapiens*.

The decline in the average rate of divergence with increasing divergence time is consistent with the hypothesis that most mammalian cranial characters (or characters genetically correlated with them) are under stabilizing selection. Consider the simple situation in which reproductively isolated populations remain subject to the same Gaussian stabilizing selective pressures, leading to an optimum phenotype  $\theta$ . During the initial phases of isolation, sampling error resulting from finite population size causes the population means to drift apart. Provided that the mean phenotype of the ancestral population was near the optimum, the initial divergence would be relatively rapid because of the flatness of the fitness function in the neighborhood of the optimum. However, as the means drift farther from the optimum, the selection gradient becomes steeper and the rate of divergence must decline. Eventually, a balance is struck between the diversifying forces of drift and mutation and the stabilizing forces of selection, such that the expected between-population variance no longer increases (Lande 1976). Probably all natural populations are under multivariate, rather than univariate, selection, and the adaptive landscape may often contain multiple peaks. The preceding logic is readily extended to such circumstances, although the dynamics of phenotypic divergence become much more complex (Lande 1976, 1985, 1986; Kirkpatrick 1982; Barton and Rouhani 1987).

Cherry et al. (1978, 1982) and Wyles et al. (1983) have argued that morphological evolution has proceeded at an exceptionally rapid pace in mammals relative to other vertebrates (amphibians in particular), that hominoids are rapid evolvers relative to other mammals, and that the rate of evolution in the genus *Homo* is unparalleled even by other hominoids. The analyses given above put these claims into perspective. Since the long-term divergence within all of the lineages analyzed in this study is less than or equal to the neutral expectation, it is clear that there is nothing remarkable about the rate of evolution in mammals from the standpoint of well-understood microevolutionary processes. Moreover, the apparently slow rate of morphological divergence in the Amphibia, which has deep splits, is quite consistent with expectations when the temporal-scaling argument in the preceding paragraph is extended to the whole vertebrate phylogeny.

Of all the analyses in this article, that for modern man is most subject to the criticism that the apparent divergence is largely due to environmental, rather than genetic, differences. I have chosen to include these data for three reasons. First, the modern-man data are quite consistent with the temporal scaling relationship

in figure 3 (lower left point). Second, the modern-man data are qualitatively consistent with the neutral hypothesis, since Congoids, Caucasians, and Orientals are all approximately equidistant from the Capoid outgroup with respect to skull morphology (Lynch 1989). Third, the comparison of modern man with the other three great apes corroborates the conclusion that only the human lineage has an abnormally high average evolutionary rate, with respect to both cranial and postcranial characters. This interspecific comparison is less subject to bias from environmental modification.

Wilson and colleagues (Wilson et al. 1975; Wyles et al. 1983; Larson et al. 1984; Wilson 1985) have suggested two independent reasons for the elevated rate of morphological evolution in man: enhanced regulatory evolution and behavioral drive. Regulatory evolution includes events such as chromosomal rearrangements. Such changes have occurred often in mammals, but they do not appear to be responsible for morphological evolution of the nature discussed in this article (Lande 1979*b*). Since the rate of morphological evolution in man is by no means in excess of expectations based on empirical studies of the rate of polygenic mutation in mice, invertebrates, and plants, we need not invoke extraordinary mutational changes of any kind to account for man's rapid evolution.

Behavioral drive refers to the idea that the cultural shift of a species to a new environment can propel the process of morphological evolution by subjecting the species to new selective pressures. There are some questionable features of this argument. First, the change in the rate of morphological evolution upon the "discovery" of a new niche depends on many things, including the position of the initial mean phenotype relative to the new and old optima, the extent of gene flow between the two niches, the nature of population regulation, and the degree to which the two optima shift in time. Second, it may be questioned whether species make cultural shifts into new habitats where the selective load is intensified. Quite the contrary, sophisticated behavior such as habitat selection may often decrease the strength of stabilizing selection on morphology, since it allows different phenotypes to sort into environments that maximize their respective fitnesses (Lande 1986). Even if a cultural innovation leads to a major shift in optimal morphology, the response to selection may be weak if the fitness function is simultaneously flattened. This argument, along with the observation that the divergence rate of *Homo* is in the neutral range, leads to the alternative hypothesis that the development of cultural inheritance may have released many morphological traits in humans from stabilizing selection rather than intensifying directional selection.

In principle, most of the ideas presented above can be subjected to further scrutiny by studying additional lineages, particularly those with longer and shorter divergence times than those examined. It will be interesting to extend this sort of work to other phylogenetic groups, although few have as detailed a fossil record as is available for mammals. Many of the studies cited here are of a cross-sectional nature, involving only contemporary species. Such data are relatively easy to acquire but have the disadvantage of averaging over the entire period of divergence. This makes it difficult to test any explicit models of selection, although some general conclusions can still be reached. Studies such as those of Bader (1955), Kurtén (1955), and Gingerich (1974, 1980), but with larger

sample sizes at more-frequent intervals, are needed to further advance our understanding of the long-term dynamics of phenotypic evolution (Charlesworth 1984).

#### SUMMARY

A comparison of the evolutionary rates of cranial morphology in mammals with the neutral expectation suggests that stabilizing selection is a predominant evolutionary force keeping the long-term diversification of lineages well below its potential. The rate of morphological divergence of almost all lineages, including the great apes, is substantially below the minimum neutral expectation. The divergence of the modern races of man is slightly above the minimum neutral rate but well below the maximum rate. Therefore, there is no need to invoke extraordinary mutational mechanisms, such as regulatory gene evolution, to explain what has been perceived as rapid morphological evolution in mammals. Nor does it appear that behavioral drive needs to be invoked to explain rapid morphological evolution in hominoids. Outside of man, the long-term rate of phenotypic evolution in the great apes is actually lower than that for other mammals. The data suggest that, immediately after reproductive isolation, most lineages diverge morphologically at approximately the neutral rate and that this rate declines over evolutionary time. Such a pattern is consistent with a broad class of phenotypic evolutionary models that invoke an interaction between the forces of random genetic drift, polygenic mutation, and stabilizing selection. This pattern also suggests that the apparently rapid rates of morphological evolution in modern man relative to other mammals and in mammals relative to other vertebrates are artifacts of temporal scaling.

#### ACKNOWLEDGMENTS

Many thanks to O. Bell and M. Hussaini for assistance with data collection, G. Wagner for inspiring conversation, W. Atchley and R. Lande for helpful comments, W. W. Howells for access to unpublished data, and H. McHenry for calling his work to my attention. Financial support was provided by National Science Foundation grant BSR 86-00487 and National Institutes of Health grant 1 R01 GM36827-01A1.

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