

RATES OF EVOLUTION IN DIVERGENT SPECIES LINEAGES
AS A TEST OF CHARACTER DISPLACEMENT IN THE
FOSSIL RECORD: TOOTH SIZE IN PALEOCENE
PLESIADAPIS (MAMMALIA, PROPRIMATES)

by

Philip D. GINGERICH *

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* Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

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ABSTRACT

Two species lineages of North American late Paleocene *Plesiadapis* exhibit a pattern of size divergence from a common ancestral lineage. Time series of fossils in each of these lineages are analyzed to test the idea that size divergence represents competitive character displacement. The critical factor in a test of character divergence is showing that divergent lineages evolved directionally rather than randomly (multifactorially). Analysis of evolutionary rates and their temporal scaling in *Plesiadapis* shows that both divergent species lineages have the scaling slope expected for lineages evolving randomly rather than directionally, and size divergence in *Plesiadapis* does not represent character displacement. Rates of evolution commonly observed on a per-generation time scale are high enough to produce character displacement within a few generations. Thus character displacement is not likely to be visible on scales of time that can be studied in the fossil record.

RESUME

Deux lignées spécifiques de *Plesiadapis* du Paléocène d'Amérique du Nord montrent un schéma de divergence de leurs tailles à partir de celle de leur lignée ancestrale. Les séries temporelles de fossiles sont analysées dans chacune de ces lignées pour tester l'hypothèse que la divergence de taille pourrait résulter d'un déplacement écologique. Le facteur critique dans un test de déplacement de caractère est de montrer que les lignées divergentes ont évolué de façon directionnelle et non pas au hasard (i.e., de façon multifactorielle). L'analyse des vitesses d'évolution et de leur distribution en fonction du temps chez *Plesiadapis* montre que celles des deux lignées spécifiques divergentes sont distribuées selon une pente correspondant à des lignées évoluant aléatoirement et non directionnellement. La divergence de taille chez *Plesiadapis* ne peut pas représenter un déplacement de caractère. Les vitesses d'évolution observées couramment à l'échelle de chaque génération sont assez élevées pour provoquer un déplacement de caractères en quelques générations. De ce fait, un déplacement de caractère a peu de chances d'être visible aux échelles de temps qui peuvent être étudiées dans le registre fossile.

INTRODUCTION

Rates of evolution are important for understanding the tempo and mode of evolution. Rates are most conveniently quantified in standard deviation units per generation, and rates must be compared taking account of the time interval over which they were calculated (Gingerich 1983, 1993a). There are now a total of 29 published case studies analyzing evolutionary rates with the statistical power to yield interpretable conclusions (Gingerich 1993a, 1993b, Gingerich & Gunnell 1995). These studies are predominantly of lineages in the fossil record, but one laboratory study is also included. Twenty-nine studies are a small beginning, but these provide encouragement for further work and a baseline for comparison of new studies. Three lineages are newly quantified here.

Divergent lineages are of special interest in evolution because they exhibit a pattern of character divergence or displacement expected when interspecific competition between similar species drives the species apart. Character displacement was originally

conceived as a static geographic pattern resulting from the first post-isolation contact of newly evolved cognate species (Brown & Wilson 1956), but it was later reformulated as a process by which morphological characteristics change under natural selection due to competition from one or more ecologically and reproductively similar species present in the same place and environment (Grant 1972). Most studies of character displacement are geographic and involve static proportions or ratios of minimal similarity in sympatry that break down in allopatry (e.g., Dayan *et al.* 1989a, 1989b, 1990). Fagerstrom (1978) reviewed a number of paleontological examples claiming to represent character displacement and concluded that these are mere descriptions of character differences among similar species in various degrees of sympatry. In a contemporary study of *Plesiadapis* not mentioned by Fagerstrom, I interpreted progressive divergence in size between coexisting lineages as “size divergence to minimize competition between two sympatric, closely related, but genetically isolated populations” (Gingerich 1976, p. 67). This example is reconsidered here and analyzed in more detail to test for character displacement.

NORTH AMERICAN *PLESIADAPIS*

Late Paleocene *Plesiadapis* is one of the best known early Cenozoic genera to exhibit a divergent pattern of species lineages changing through time. This is true for North American lineages (Fig. 1), and it is also possibly true for European lineages (Gingerich 1976, p. 61). The North American case is the better documented because of its more extensively sampled stratigraphic record.

Two hundred and twelve *Plesiadapis* specimens known from the Clarks Fork Basin and adjacent northern Bighorn Basin in northwestern Wyoming (U.S.A.) preserve lower first molars that can be used to compare the sizes of individual specimens within and between samples of fossils, and to compare the mean sizes of species at different times between samples. Empirically, samples of tooth area ($\ln L \times W$ of M_1) for individual species of *Plesiadapis* from single localities and stratigraphic levels have standard deviations on the order of 0.10, corresponding to a coefficient of variation for $L \times W$ of M_1 of 10. Use of logarithms and calculation of coefficients of variation are equivalent ways of standardizing variance for differences in overall size. The average body mass of North American *Plesiadapis*, based on tooth size, is about 1.7 kg (based on scaling coefficients in Legendre 1989), and mammals of this size typically have generation times on the order of one generation per year (based on data in tables of Eisenberg 1981).

The 212 specimens studied here come from 22 different stratigraphic levels that are either in the measured Clarks Fork Basin – Polecat Bench stratigraphic section (solid circles in Fig. 1) or can be correlated directly to this (open circles in Fig. 1; Gingerich 1976). Most specimens analyzed here are listed in Gingerich (1976), but new University of Michigan specimens collected during the past twenty years are included as well. These come from a 1500 m thick stratigraphic section in which the *Plesiadapis*-bearing part is calculated to have accumulated at an average rate of 370 m per million

CLARKS FORK BASIN PLESIADAPIS

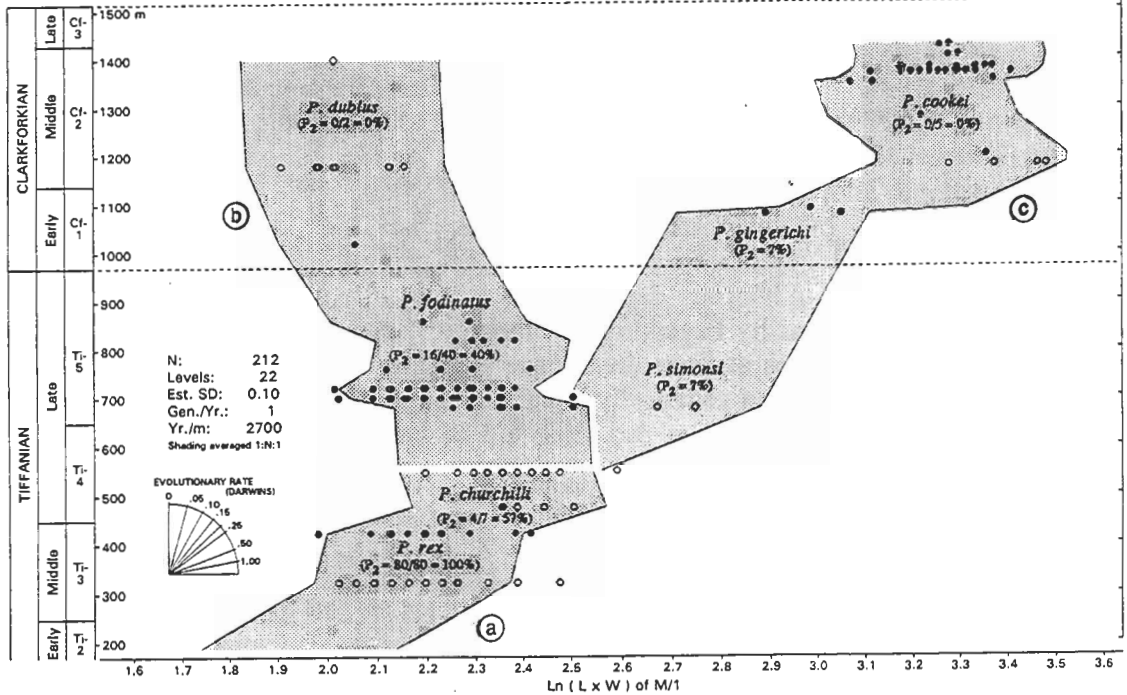


Figure 1.— Pattern of character divergence in tooth size and, by inference, body size in North American *Plesiadapis*. Abscissa is molar crown area, on a proportional \log_e scale. Within-sample variability is about 0.4 units (shaded; empirical standard deviation is 0.1 \log_e units). Ordinate is stratigraphic meter level in late Paleocene Clarks Fork Basin – Polecat Bench stratigraphic section, where one meter of sediment represents 2700 years of geological time and 2700 generations of evolutionary time. Three lineage segments are shown: (a) one preceding divergence and including five samples from ancestral middle Paleocene *Pronothodectes jepi* at 60 m (not shown) through late Paleocene *Plesiadapis churchilli* at 550 m, (b) a second lineage following divergence and including ten samples from late Paleocene *P. churchilli* at 550, through *P. fodinatus* from 680 to 860 m, and *P. dubius* from 1020 to 1400 m, and (c) a third lineage following divergence and including 13 samples from late Paleocene *P. simonsi* at 680 m, *P. gingerichi* from 1080 to 1090, and *P. cookei* from 1180 to 1425 m. Proportion of specimens retaining P_2 is shown in parentheses for species where this is known. Rates of change in tooth size, quantified as shown in figure 2, are summarized in table 1.

years (Gingerich 1982), making one meter of accumulated sediment equivalent to about 2700 years of geological time and thus equivalent to 2700 generations of evolutionary time.

Taken together, all of the specimens of *Plesiadapis* known from the Clarks Fork Basin – Polecat Bench section form a Y-shaped pattern when tooth size is plotted against stratigraphic level (Fig. 1). The earliest species in this pattern, *Plesiadapis rex* with a lower dental formula of 1.0.3.3, is from middle Tiffanian levels 325 and 425 m. The next species, *P. churchilli* with a lower dental formula of 1.0.2-3.3, is from late Tiffanian levels 480 and 550 m. Two species, *P. fodinatus* with a lower dental formula of 1.0.2-3.3 and *P. simonsi* with an incompletely known lower dental formula come from levels 680 through 860 m. The next species after *P. fodinatus* is *P. dubius* with a lower dental formula of 2.0.2.3, from levels 1020 through 1400 m. The next species

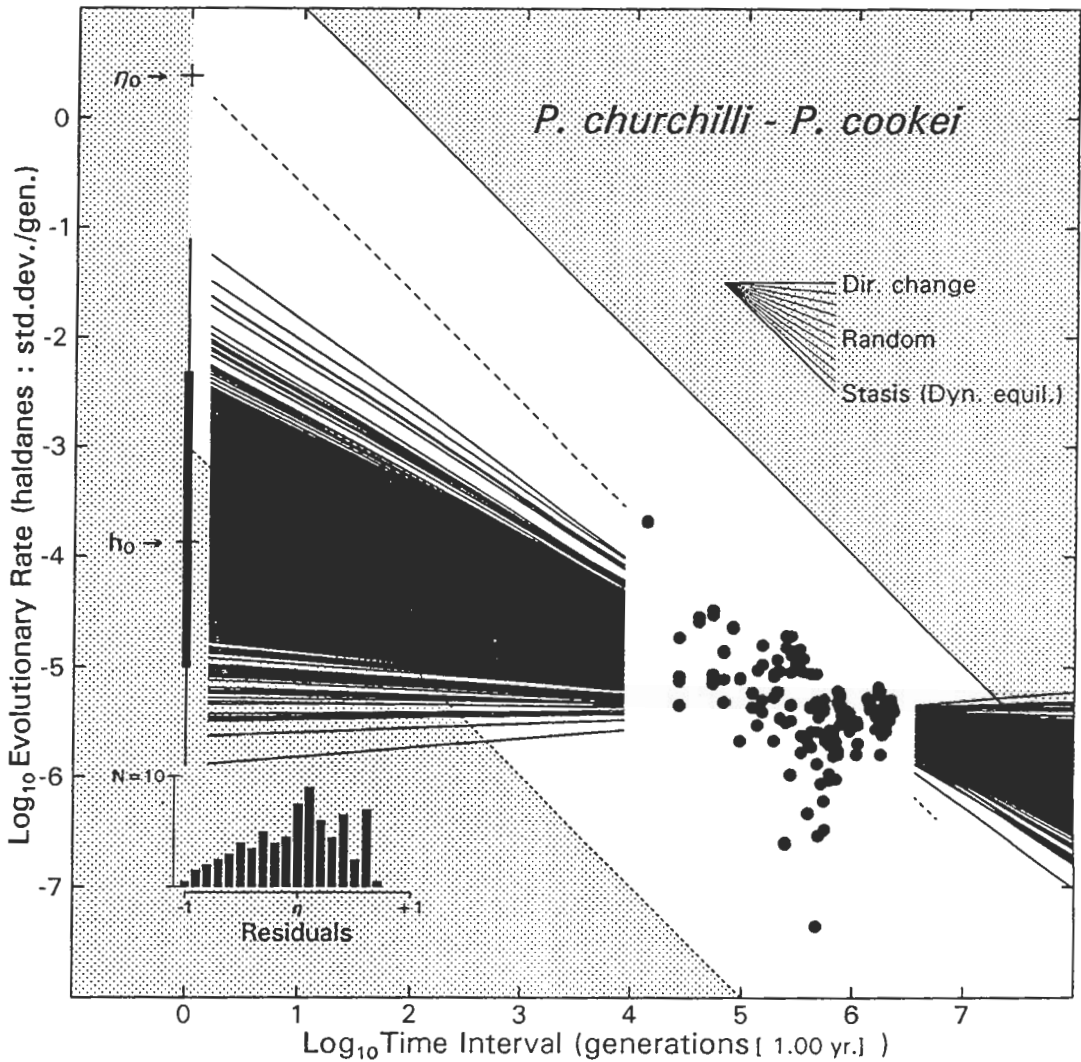
after *P. simonsi* is *P. gingerichi* with an incompletely known lower dental formula from levels 1080 and 1090 m. This is succeeded by *P. cookei* with lower dental formula 1.0.2.3, from levels 1180 through 1425 m.

Each of these taxa has the dental variability characteristic of living mammalian species (Gingerich 1974). Some taxa like contemporary *P. dubius* and *P. cookei* are so different in size that they cannot possibly belong to the same mammalian species. Other contemporary taxa like *P. fodinatus* and *P. simonsi* are more similar but together exceed the range expected for a single species. Successive taxa in lineages do not show clearly defined discrete differences, but do differ recognizably in the shape of upper incisors, the relative frequency of premolars in the lower dental formula, and the degree of crenulation on upper and lower molars (Gingerich 1976). When compared through time (up-section stratigraphically), successive fossil assemblages form time series interpreted as successive samples of evolutionary lineages. McKenna *et al.* (1977) criticized this approach to study of *Plesiadapis*, and caricatured it as "connect-the-dots art." Art or science, time series for rate analysis cannot be constructed any other way. Time and temporal ordering are independent variables in evolution that cannot be recovered from dependent morphological consequences of the evolutionary process without assuming the very rates we wish to determine. If we knew all of the simple or complex relationships of morphology to time in advance, there would be no reason to study rates (and little reason to study fossils).

TEST OF CHARACTER DISPLACEMENT

It is clearly desirable to extend character displacement, following Grant (1972), from the static description of geographic patterns of variation at an arbitrary instant in time to include a *sequence of patterns diverging through time* (displacement in a dynamic sense) permitting interpretation of the *process* by which displacement appeared. Evolutionary processes can be studied in terms of per-generation step or base rates and inferred directionality. When morphological characteristics change in one species lineage due to natural selection caused by competition from an ecologically similar species present in the same place and environment, we expect divergent directional change in both lineages. Thus any claim of character displacement in the fossil record requires (1) a pattern of character divergence through time, with positive rates predominating in one lineage and negative rates in the other for each diverging characteristic; (2) theoretical step rates of the processes in both lineages falling in the usual range for such base rates; and (3) temporal scaling slopes of observed rates in each lineage indicating a directional component of change: divergence must be significantly different from random and must be directional rather than static to be considered displacement.

All three parts of this test of character displacement require investigation of the interdependence of rates of change in evolutionary time series, studied on as wide a range of time scales as possible, with the rates scaled against the time intervals over which they were calculated. Figure 1 shows that part (1) of a test of character



<i>P. churchilli - P. cookei</i>		M/I length and width			Clarks Fork Basin	
Total rates	156	MAX. LIKELIHOOD (M.Abs.Dev.: 0.260)				
NONZERO RATES	155		Minimum	Median	Maximum	Fractal D
Min. log int.	4.130		(0.025)	(0.500)	(0.975)	1.257
Max. log int.	6.373	SLOPE		-0.257		Interpret.
MEDIAN LOG INT.	5.738	CI*	-0.064	-0.268	-0.526	R
Min. log rate	-7.361	T. INTERCEPT		0.385		Theoretical η_0
Max. log rate	-3.680	CI*	0.277	0.384	0.474	2.4283
MEDIAN LOG RATE	-5.374	C. INTERCEPT		-3.874		Calculated h_0
POSITIVE rates	113	CI*	-5.005	-3.814	-2.314	0.0001
Med. log int.	5.886	TEST POINT (Log int. = 5.738)				
Med. log rate	-5.380	CI*	-5.395	-5.350	-5.293	
NEGATIVE rates	42	PI*	-6.373	-5.352	-4.827	
Med. log int.	5.519	*Confidence and prediction intervals, bootstrapped with			{ N=155 B=1000	
Med. log rate	-5.360					

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displacement is satisfied: there are two lineages derived from *Plesiadapis churchilli* that diverge through time. Part (1) can also be satisfied by noting that negative rates predominate in the *P. churchilli* to *P. dubius* species lineage (Table 1), while positive rates predominate in the *P. churchilli* to *P. cookei* species lineage.

Part (2) of a test of character displacement indicates whether the observed distribution of evolutionary rates, taken as a whole, has the expected location relative to empirical upper and lower bounds (solid and dotted lines enclosing the diagonal white space in Fig. 2). This location can be simplified by considering the height of the distribution within the diagonal white space or, equivalently, the theoretical base intercept η_0 expected if the lineage were a lineage in stasis. Comparison of η_0 values calculated here with the histogram of η_0 values for 29 other case studies shows that *Plesiadapis* theoretical base rates fall within the expected range.

Finally, part (3) is the most important part of a test of character displacement because it indicates whether an observed divergence of lineages is directional, reflecting competitive displacement. Directional change is distinguished from random change and from stasis by analysis of temporal scaling of rates on different time scales. Temporal scaling involves calculation of the slope of a line fit to a log rate – log interval or LRI graph (see Fig. 2 and Gingerich 1993a, for details). A single line fit to an LRI distribution of evolutionary rates is, by itself, not very useful because it gives no information about variability to be expected in independent samples drawn from the same distribution of rates. Figure 2 shows a best fit line with slope -0.257 and calculated intercept h_0 , with a 95% confidence interval for the slope ranging from -0.064 to -0.526 , as determined by bootstrapping (details in Gingerich 1993a). This confidence interval narrowly excludes a slope of 0.0 expected for a lineage changing directionally, and excludes by a wide margin a slope of -1.0 expected for a lineage in stasis. A slope of -0.5 expected for a lineage changing randomly lies within the observed confidence interval, meaning that the observed distribution of evolutionary rates is best interpreted as resulting from random change on the scale of time studied here. Neither of the divergent lineages studied here (**b** and **c** in Table 1) pass this part of the test of character displacement because neither lineage can be distinguished from random change, while both can be distinguished from directional change (and from stasis).

Figure 2.— Log rate versus log interval [LRI] distribution for 155 non-zero rates of change in *Plesiadapis churchilli* through *P. cookei* species lineage (**c**) shown in figure 1. Rates of change are calculated in phenotypic standard deviations per generation (haldanes) for all possible intervals ranging from $10^{4.130} = 13,500$ to $10^{6.373} = 2,360,000$ generations. A total of 113 rates are positive and 42 rates are negative, reflecting the overall increase in size in this lineage. Temporal scaling slope of LRI distribution is -0.257 , indicating that the fractal dimension of the original time series is 1.257 . Bootstrapped 95% confidence interval for this slope ranges from -0.064 to -0.526 , which just excludes purely directional change (slope of -0.0), just includes purely random change (slope of -0.5), and excludes stasis (slope of -1.0) by a wide margin. Null expectation of random change cannot be rejected on this evidence, and interpretation is thus random (R; meaning multifactorial). Theoretical base rate η_0 is $10^{-.385} = 2.4283$ haldanes, which falls within the available sample of comparable intrinsic rates (**c** in Fig. 3). The calculated base rate h_0 , based on the location of the sample of rates and its temporal scaling slope, is $10^{-3.874} = 0.0001$ haldanes: the observed change can be explained by directional and random change at the very low rate of 0.0001 phenotypic standard deviations per generation on a scale of one generation (that is, a generation-by-generation time scale).

Non-zero rates	Mean abs. dev.	Median log ₁₀ intercept	Median log ₁₀ rate	Pos. rates	Neg. rates	Calculated LRI slope and interpretation (95% confidence interval)	Theoretical		Calculated	
							log ₁₀ base rate (95% confidence interval)	log ₁₀ base rate (95% confidence interval)	R(D)	R
(a) <i>Pronothodectes jepi</i> — <i>Ples. churchilli</i> (Polecat Bench levels 60 - 550 m)										
20	0.159	5.703	-5.296	17	3	0.304 (+0.900 ↔ -0.949)	0.365 (+0.136 ↔ +0.715)		-7.059 (-10.633 ↔ +0.293)	
(b) <i>Plesiadapis churchilli</i> — <i>Ples. dubius</i> (Polecat Bench levels 550 - 1400 m)										
90	0.225	5.800	-5.693	16	74	-0.391 (-0.001 ↔ -0.670)	0.133 (-0.018 ↔ +0.233)		-3.378 (-5.728 ↔ -1.782)	
(c) <i>Plesiadapis churchilli</i> — <i>Ples. cookei</i> (Polecat Bench levels 550 - 1425 m)										
155	0.260	5.738	-5.374	113	42	-0.257 (-0.064 ↔ -0.526)	0.385 (0.277 ↔ 0.474)		-3.874 (-5.005 ↔ -2.314)	

Table 1.— Rates of size change in the three late Paleocene *Plesiadapis* species lineages illustrated in figure 1, analyzed as shown in figure 2. Change is interpreted as random, R, or random with a directional component, R(D), because randomness cannot be rejected in any of the three studies (random with a directional component means stasis can be rejected but directional change cannot be). Theoretical base rates reported here are compared to those in previous evolutionary case studies in figure 3.

THEORETICAL BASE RATES

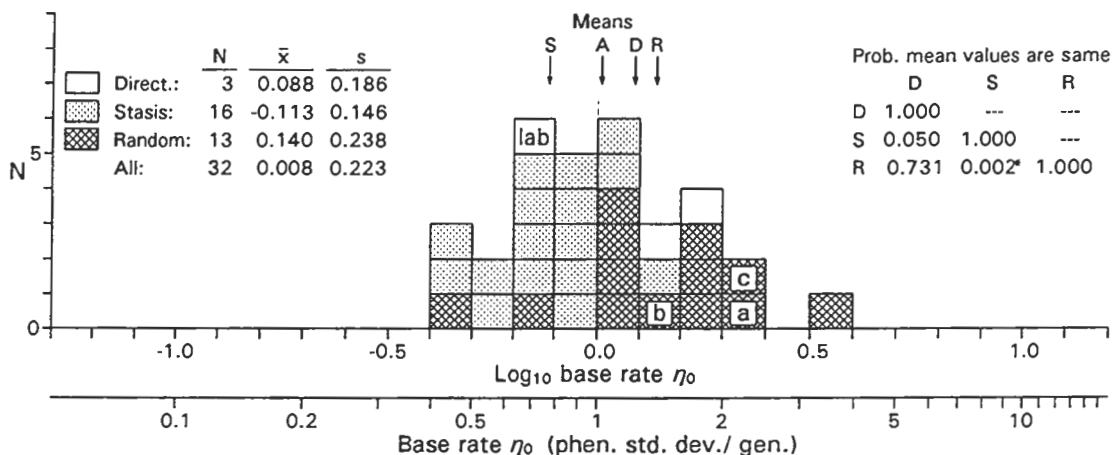


Figure 3.— Histogram of theoretical base rates, η_0 , in one laboratory selection study (labelled “lab”) reported in Gingerich (1993a), and 31 empirical case studies of the fossil record reported in Gingerich (1993a), Gingerich (1993b), Gingerich & Gunnell (1995), and this study. Three species lineages studied here are labelled “a”, “b”, and “c” as listed in table 1. Note that all theoretical base rates studied to date form a single distribution with considerable overlap in rates between case studies interpreted as reflecting directional change, stasis, and random change. Theoretical base rates associated with random change appear to be significantly greater than those associated with stasis.

DIGRESSION ON FRACTAL DIMENSION

A scaling slope similar to that used here is commonly employed to study the regularity (or irregularity) of lines in other contexts, expressed in terms of a fractional or *fractal* dimension (e.g., the fractal dimension, or relative length and irregularity, of the west coast of Britain; Mandelbrot 1967). The limiting fractional dimension of a simple regular time series exhibiting directional change is 1.0, approaching a perfectly linear trend. The limiting fractional dimension of a perfectly irregular time series in stasis is 2.0, meaning that the time series appears to fill a two-dimensional area, however narrow, as it progresses. Random time series lie between these two limits, with fractional dimensions indistinguishable from 1.5. In general, in evolutionary studies, fractal dimension $D = 1 + |S|$, where $|S|$ is the absolute value of the LRI slope. Fractal dimension conveys the same information as an LRI slope does, but the latter is in some ways easier to comprehend because it is a more direct description of the empirical scaling of rates. LRI slopes are used for interpretation here, but it helps to know that in general an LRI slope, appropriately transformed, expresses the fractal dimension of a time series under study.

RATES OF PREMOLAR LOSS

Rates can be calculated for premolar loss in the lineage from *Plesiadapis rex*, with a lower dental formula of 1.0.3.3, to *P. dubius*, with a lower dental formula of 1.0.2.3. Calculation of rates of change for a discrete characteristic like presence or absence of a tooth requires variable samples for estimation of the standard deviation. For a sample of seven *Plesiadapis churchilli* with four specimens scored 1 because they have P_2 and three specimens scored 0 because they lack P_2 , the mean is 0.57 and the standard deviation is 0.535. For a sample of 40 *Plesiadapis fodinatus* with 16 specimens scored 1 because they have P_2 and 24 specimens scored 0 because they lack P_2 , the mean is 0.40 and the standard deviation is 0.496. Here premolar number is assumed to be a threshold characteristic determined by the location of an underlying normal distribution: the part of the underlying distribution lying below 0.5 generates no premolar (for a score of 0), while the part of the underlying distribution lying above 0.5 generates a premolar (for a score of 1). The progression of means from *P. rex* through *P. churchilli* and *P. fodinatus* to *P. dubius* is 1.00, 0.57, 0.40, and 0.00, and the weighted standard deviation here is 0.50. Calculation of rates yields a theoretical \log_{10} base rate $\eta_0 = -0.004$, which is very close to the mean for all $\log_{10} \eta_0$ shown in figure 3. Premolar reduction is, however, indeterminate as an evolutionary analysis because there is insufficient statistical power to constrain a confidence interval on the slope.

CHARACTER DIVERGENCE AND CHARACTER DISPLACEMENT

This study highlights the difference between character divergence, like that due to random change in *Plesiadapis*, and character displacement, which requires competitive interaction and directional as opposed to random divergence. There are two possible explanations for failure of character divergence in *Plesiadapis* to pass the test of character displacement. It is possible that the observed divergence is really an example of displacement, but both divergent lineages are too poorly sampled to reveal the underlying directional displacement. This idea can be tested by constructing a model assuming displacement, and sampling this at random with the observed density and spacing of samples to see whether failure to reject the null hypothesis of randomness can be explained by random sampling.

Alternatively, and more importantly, it is possible that the observed random divergence is due to random (or multifactorial) change taking place on too long a time scale at too great a separation of lineages for either to exert any simple directional selection on the other. The average theoretical intrinsic rate is $\eta_0 = 1$ standard deviation per generation (Fig. 3), which would require truncation of about 62% of a large population and selective retention of only 38% of the population in each generation (Falconer 1981, p. 174-175). This is strong selection, which, if maintained, could move two diverging lineages like those in figure 1 as far apart as *P. dubius* and *P. cookei* are observed to be (their means are separated by about 12 standard deviation units) in six or

so generations. A lower and more realistic selection intensity of 0.1 standard deviations per generation, corresponding to truncation of 4% and selective retention of 96% of a large population, could achieve 12-standard-deviation separation in 60 generations of selective displacement. Evolution can be very fast, and, as Fagerstrom (1978) anticipated, competitive interactions like those postulated during character displacement are not likely to be observable in the fossil record where time is rarely resolvable on the required scale.

CONCLUSIONS

Rates of evolution in *Plesiadapis* are similar to those in other laboratory and fossil lineages studied to date, but divergent lineages leading to *P. dubius* and *P. cookei* appear to be diverging randomly (multifactorially), not directionally, and hence this is not an example of character displacement in the fossil record. Character displacement is likely to move populations far enough apart to minimize competition within too few generations to make the process amenable to study in the fossil record.

ACKNOWLEDGMENTS

Donald Russell published the first quantitative study of European *Plesiadapis* in his 1964 thesis monograph on Paleocene mammals of Europe. It is a special pleasure to remember his generosity when I came to Paris in 1972 to study European *Plesiadapis* for comparison with North American species: he gave me advice, encouragement, his office, his library, his microscope, his collections, and his home in Paris while he went to the field for the summer. Much of what I know about variation in *Plesiadapis* and the diagnosis of closely related sympatric fossil species I learned that summer working on *Plesiadapis* from Cernay and Berru. This experience made study of North American species worthwhile, yielding the understanding of phylogeny and evolution summarized in figure 1, which has proven reassuringly robust in accommodating discoveries of the past twenty years.

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