

Macroevolution

Pattern and Process

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W. H. FREEMAN AND COMPANY

San Francisco

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Compositor: Bi-Comp, Inc.
Printer and Binder: The Maple-Vail Book
 Manufacturing Group

Cover drawing based on a photograph by Geoffrey Kinns.
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Library of Congress Cataloging in Publication Data

Stanley, Steven M.
 Macroevolution, pattern and process.

Bibliography: p.
 Includes index.

1. Evolution. 2. Paleontology. I. Title.
 QH1366.2.S68 575 79-15464
 ISBN 0-7167-1092-7

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Printed in the United States of America

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Rates of Speciation and Extinction

By treating adaptive radiation as a pattern of exponential increase, we can estimate rates of speciation and extinction for many taxa. This procedure is valuable because major evolutionary changes tend to be associated with adaptive radiation. When we compare different taxa, we find that rate of large-scale evolution tends to be correlated with rate of speciation (fraction of species added per unit time), which is a primary determinant of the total number of species formed during a given interval. Rate of speciation varies enormously among taxa. Thus, a typical radiating clade of mammals, when compared to a similar clade in the Bivalvia, speciates at a much higher fractional rate, produces many more total species per unit time, and undergoes much more rapid large-scale morphologic change. On the other hand, within a particular radiation of any taxon, the most rapid large-scale evolution usually does not occur late in radiation (when a large total number of species are being added per unit time) but early, because at the outset a higher percentage of speciation events are markedly divergent.

It is also instructive to consider the macroevolutionary fate of nonradiating clades. The punctuational view of evolution offers the prediction that most clades that persist for long intervals at low diversity will exhibit little evolution because there will be few opportunities for quantum speciation. The paleontologic record bears out this prediction. Virtually all extant members of such clades are primitive forms designated as "living fossils."

INTRODUCTION

If speciation is the locus of accelerated evolution and therefore accounts for most large-scale change, it is important to seek ways to assess the rates at which species multiply. The punctuational view implies that rate of macroevolution within and among higher taxa should vary with rate of speciation, but focusing on this inference should not cause us to ignore another variable: degree of divergence per speciation event. Speciation can produce increments of divergence that are almost imperceptibly small, as in the formation of sibling species, but can also contribute sizable morphologic steps. In this chapter, techniques will be presented for estimating rates of speciation and extinction. These techniques will be applied to particular problems that relate to the importance of quantum speciation, the nature of which will be considered in the following chapter. An important conclusion of the present chapter will be that production of a descendant species is a rare event in the lifetime of an average chronospecies, yet only a small fraction of such events can represent quantum speciation. The inference will be that a major evolutionary transition is typically accomplished by a small number of punctuational steps of great magnitude.

ADAPTIVE RADIATION
AS EXPONENTIAL INCREASE

Among the most important contributions of Simpson (1944, 1953) has been his focus upon adaptive radiation as the site of most large-scale morphologic transitions. Accordingly, in order to examine the origin of higher taxa, we will now direct our attention to speciation within adaptive radiation. How rapidly do species multiply in radiation, is our question: How many successive steps along any single phylogenetic pathway are available for possible punctuational transition? Another of Simpson's major points has been that radiation generally follows (1) the emptying of ecospace by extinction, (2) the achievement of an adaptive breakthrough (origin of an evolutionary innovation), or (3) both of these occurrences. A fourth opportunity for radiation, the formation of a new habitat, can be viewed as being equivalent to (1).

Sometimes an adaptive breakthrough is so novel as to permit the invasion of ecospace never before extensively occupied. In the marine realm, the evolution of infaunal modes of life (life within the substratum) represents an example. The basic obstacle to be overcome here is the difficulty of living in a buried position while maintaining communication with the overlying water mass for respiration and, often, feeding. Early in the Paleozoic, most skeletonized marine invertebrates were epifaunal (surface-dwelling). Late in the Paleozoic and continuing into the Mesozoic, there occurred trends toward the origin and refinement of

burrowing modes of life within groups of gastropod and bivalve mollusks and echinoids (Stanley, 1968; 1977). Presumably, comparable trends within soft-bodied taxa were initiated earlier, near the start of the Cambrian (Valentine, 1973; Stanley, 1976). In all cases, adaptive innovations are evident. For bivalves and gastropods, the key development was the evolution of siphons by mantle fusion; for echinoids, it was the origin of upward-directed petaloid tube feet; and for soft-bodied, worm-like taxa it seems to have been the evolution late in the Precambrian of a hydrostatic skeleton in the form of the coelom.

Perhaps the most famous example of radiation triggered by extinction is the rapid divergence of early Cenozoic mammals into ecospace vacated by the disappearance of the dinosaurs (Figure 4-5). Obviously, adaptive innovations played a role in the success of particular taxa that participated in the mammalian radiation.

A more recent and restricted radiation, but a dramatic one nonetheless, was the diversification of hydrobioid snails in the Mekong River, analyzed in an exemplary study by Davis (1979). The Mekong River system came into being in the Middle or Late Miocene, with the uplift of the Himalayas, as plate tectonic movements forced what is now peninsular India against the central landmass of Asia. Davis reconstructed an odyssey wherein hydrobioid snails of the southern hemisphere were rafted northward, with the fragmentation of Gondwanaland, as passengers on the small triangular landmass that became part of India. Their arrival automatically coincided with the Himalayan uplift and the formation of the Mekong drainage system approximately 12 My ago. The ensuing monophyletic radiation gave rise to at least 93 extant species of triculine snails in the Mekong River. The rate of radiation is uncertain, but the present level of diversity may have been approached very quickly. Davis attributed the success of the triculines to a lack of competitors in the newly formed river system and also to an adaptively plastic reproductive system that has allowed the triculines to occupy a wide variety of habitats. (Having evolved in southeast Asia, this subfamily of hydrobioids now ranges from India to the Philippines, with its highest diversity in the Mekong River.) Thus, Davis invoked both the presence of free ecospace and the origin of a key adaptation to explain the diversification of triculines. He noted, however, that in radiations of this type (those of newly formed lake or river systems) whether hydrobioid or cerithiacean snails dominate seems to be a matter of which group happens to arrive first.

The cichlid fishes of large African lakes and other bodies of water represent particularly striking examples of more recent radiations triggered by adaptive flexibility. As Liem (1973) has elegantly shown, the key development in cichlid evolution was the origin of a unique pharyngeal jaw that processes food and has thereby permitted the anterior mouth parts to evolve specializations for food gathering. When cichlids invade poorly inhabited bodies of water, they tend to radiate in the manner described for Lakes Victoria and Malawi (page 45; Figure 3-4). Among the feeding specialists that have evolved within Lake Victoria during the past 500,000 to 750,000 years are insectivores, mollusk crushers,

crustacean eaters, phytoplankton collectors, croppers of macroscopic algae, and predators upon other fishes. Some of the latter feed upon the embryos and yolk sacs of other cichlids, and one even sustains itself by scraping scales from other fishes! This radiation seems to have been nearly monophyletic (Greenwood, 1974).

Speciation is a multiplicative process, and adaptive radiation, whatever its cause, is fundamentally a phenomenon of geometric or exponential increase. Therefore, the appropriate measure for rate of addition of species is not the absolute number, but the percentage, added per unit time (the fractional rate of increase). A general analogy with populations of individuals is readily apparent. Here the net fractional rate of increase equals per capita birthrate minus per capita death rate. The equivalent for adaptive radiation is speciation rate minus extinction rate. Thus we can borrow from demography the standard exponential equation for population growth:

$$(5.1) \quad \frac{dN}{dt} = RN,$$

where N is number of species, t is time, and R is fractional increase per unit time.

Integrating,

$$(5.2) \quad N = N_0 e^{Rt},$$

where N_0 is the original number of species (unity for monophyly) and e is a constant, the base of natural logarithms.

Clearly, no radiation will follow exponential increase precisely or even approximate it for a long period of time. Presumably, a sigmoid curve is followed (Figure 5-1, A), like the one that typifies population growth in a confined habitat. If, however, we restrict our analysis to taxa in the early stages of adaptive radiation, increase will be approximately exponential. Suppose, therefore, that we consider an extant Cenozoic taxon well represented in the fossil record and currently in the midst of adaptive radiation. The immediate goal will be to calculate R , the net rate of increase. Knowing the approximate geologic time of origin of the taxon, we have a good estimate of t . We also have N , number of living species, to a good approximation. If we assume monophyly, N_0 will equal one. It is important to appreciate that both N and N_0 enter into the calculation of R logarithmically, allowing considerable room for uncertainty in the value of each. In other words, it is no problem that number of living species is often only approximately known, and the assumption of monophyly can be relaxed somewhat without major effect. It will be shown below, and in more detail in Chapter 10, that the characteristic value of R differs systematically among higher taxa, yet is remarkably consistent within a higher taxon (for example, among families of the Mammalia or Bivalvia, as will be shown below).

Equation 5.2 is equivalent to the equation describing radioactive decay,

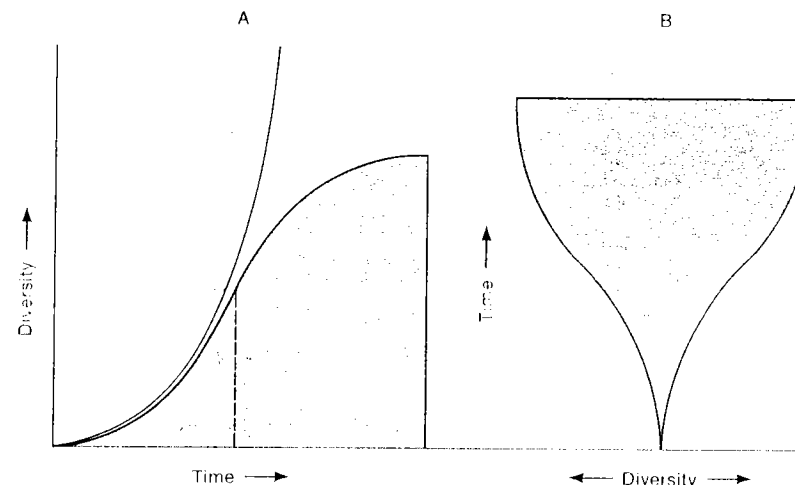


FIGURE 5-1

Graphic portrayal of unbridled and damped exponential diversification. A: Convex upward curve illustrates purely exponential increase. Sigmoid curve bounding the shaded area represents damped exponential increase, in which the fractional rate of increase declines as diversity increases. In the early stage of radiation (for example, the stage represented by the portion of the graph between the origin and dashed lines), there is little separation between the two curves. B: Shaded portion of A rotated 90° and replotted symmetrically about a vertical axis to form a balloon diagram of the sort commonly used to depict taxonomic diversity through time.

except that in the latter the exponent is negative. Just as radioactive decay is characterized by a half-life, exponential increase entails a doubling time (t_2), which can be calculated by setting $N/N_0 = 2$ in equation 5.2:

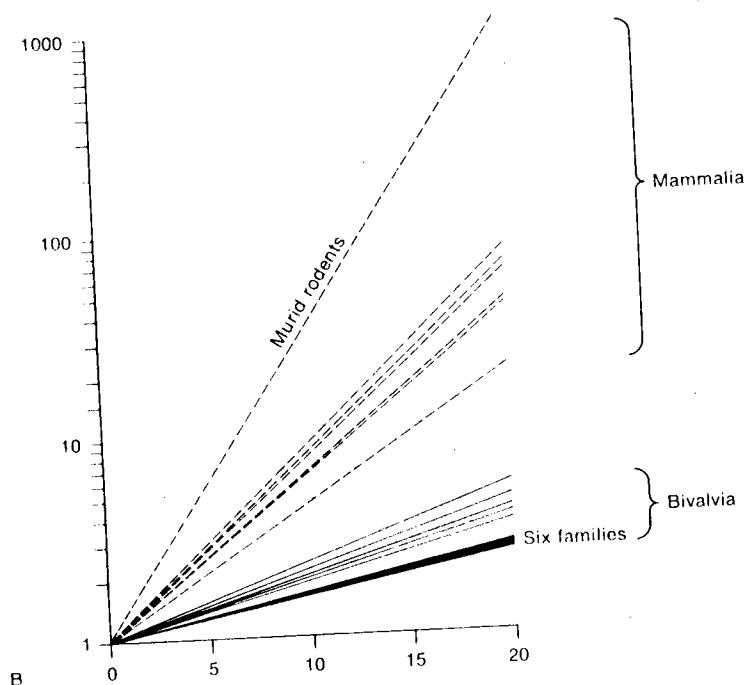
$$(5.3) \quad t_2 = \ln 2/R$$

Since first making use of the preceding exponential techniques to compare rates of radiation of different taxa (Stanley, 1975a; 1977), I have learned that Yule (1924), a mathematician who developed an interest in evolution, employed similar ones long ago and took them in directions not followed here. The same general methods can be applied to the study of higher taxa (Sepkoski, 1978).

Figure 5-2 displays estimates of t , N , and R for currently radiating families of Mammalia and of Bivalvia. What is particularly notable is that calculated values of R are relatively consistent within each class and do not overlap between the two classes. The highest value for mammals (0.35 My^{-1}) represents the Muridae

	$t_1(\text{My})$	$N(\text{Species})$	$R(\text{My}^{-1})$	$\bar{R}(\text{My}^{-1})$
Bivalvia				
Mesodesmatidae	47	40	0.078	
Cardiliidae	31	5	0.052	
Tellinidae	122	350	0.048	
Semelidae	47	60	0.087	
Veneridae	122	500	0.051	
Petricolidae	47	30	0.072	0.061
Myidae	61	20	0.049	
Teredinidae	61	66	0.069	
Lyonsiidae	47	20	0.064	
Mactridae	110	150	0.046	
Donacidae	76	50	0.051	
Mammalia				
Bovidae	31	115	0.15	
Cervidae	19	53	0.21	
Hystriidae	14	20	0.21	
Muridae	19	844	0.35	0.22
Cercopithecidae	19	60	0.22	
Cebidae	19	37	0.19	
Cricetidae	35	714	0.19	

A



B

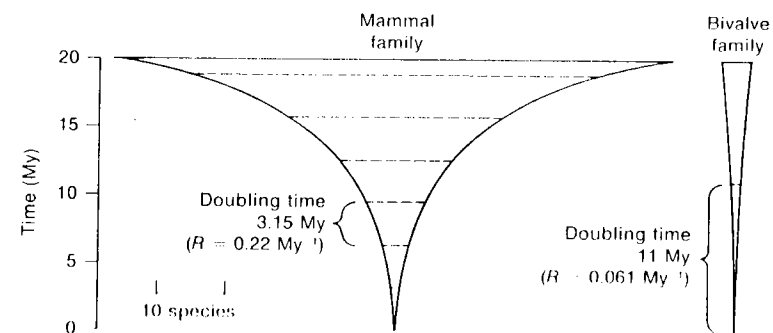


FIGURE 5-3

Patterns of diversification (plotted with an arithmetic scale) for an average mammal family and an average bivalve family during an initial interval of radiation lasting 20 My. The patterns are idealized in that it is assumed that radiation is perfectly exponential.

(Old World rats and mice), which possibly have radiated at an even higher rate than this because many sibling species may remain unrecognized; the lowest value (0.15 My^{-1}) represents the Bovidae (cattle, antelopes, etc.), which have been in existence for a rather long time and may have slowed from their initial rate. Clearly, exponential increase is very much more rapid in families of mammals, as illustrated in Figure 5-3, which depicts net rate of increase in an average family of each class. Doubling time (t_2) is approximately 11 My for the Bivalvia, compared to only 3 My for the Mammalia. The disparity between net rates of radiation in the two classes will be interpreted in Chapter 10.

It was my initial inclination to exclude very young families of bivalves from this kind of evaluation because most contain so few species as to seem aberrant in some way. Examples depicted in Figure 5-2 are the Cardiliidae, Petricolidae, and Lyonsiidae. As it turns out, these families are radiating as rapidly as somewhat older families. This finding serves to illustrate how, because we are accustomed to thinking in arithmetic terms, exponential increase can be misleading.

FIGURE 5-2

Rates of diversification of rapidly radiating extant families of bivalve mollusks and mammals. A: Values of R and data used for their calculation. Mean values (\bar{R}) for each class are shown at right. B: Logarithmic plots of paths that monophyletic exponential radiation would follow for intervals of 20 My at net rates calculated in A. (Data for bivalves from Stanley and Newman, 1979. Data for mammals from Romer, 1966, and Walker, 1975.)

The many groups of marine invertebrates that are characterized by very low rates of increase will, if they survive, automatically persist at very low diversities for long intervals of geologic time. Thus, the nature of exponential increase explains the characteristic pinched tail at the base of balloon diagrams depicting the stratigraphic distribution of well-studied taxa that have undergone an initial adaptive radiation (Figure 5-1, B and 5-3).

EXTINCTION AND SPECIATION

We have thus far considered only net rate of increase in number of species. This number (R) equals speciation rate (S) minus rate of termination of lineages (E). (A familiar analog here is the fate of money in a savings account, where net rate of increase equals interest rate minus rate of withdrawal.) Thus, if we can obtain an estimate of E , we can estimate speciation rate as

$$(5.4) \quad S = R + E$$

There is no way of estimating values of E as accurately as we can estimate values of R . It is, however, possible to employ a method that yields approximate values of E . For mammals and bivalves, these values differ greatly, and in the same direction as values of R for the two classes. These estimates show quite conclusively that rate of speciation in adaptive radiation has been much higher for mammals. (In fact, simple inspection of Figure 5-3 will suggest that the situation could hardly be otherwise.) We will be following rather circuitous pathways in the estimation of rate of termination of lineages, and the procedure may seem tedious, but the results will prove to be quite valuable.

It should be noted that rate of termination of lineages (E) is only one component of total rate of extinction, the other component being rate of extinction by phyletic transition. Total rate of extinction will be labeled E' . We will proceed to estimate values of E' and then convert them to values of E . [Note: This usage of the symbols is the reverse of that employed elsewhere (Stanley, 1977).]

First, we will simplify things in order to make an approximation. Let us assume that all lineages of a hypothetical taxon lasted the same length of time, whatever the relative proportions of extinction by termination and extinction by phyletic transition happen to have been. Then, if the lineages are distributed evenly through time, we can easily calculate overall rate of extinction (E') as the reciprocal of this uniform duration. As shown in Figure 5-4, for example, if lineages all last 5 My, then one in five will go extinct every million years, or E will equal 0.2 My^{-1} .

Even if lineages vary in longevity, each one can be viewed as having contributed its own extinction rate to the total. Thus, if one lineage survived for 5 My,

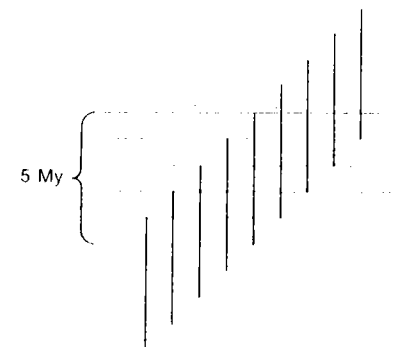


FIGURE 5-4
Species lasting 5 My, spread evenly through time (vertical bars). During every million-year interval, five species exist and one goes extinct. Therefore, the rate of extinction is 0.2 My^{-1} . (From D. M. Raup and S. M. Stanley, *Principles of Paleontology*, 2nd ed., W. H. Freeman and Company, San Francisco. Copyright © 1978.)

it can be viewed as having gone $\frac{1}{5}$ extinct every million years, or its contribution to the mean extinction rate (E) will be 0.2 My^{-1} . The individual extinction rates of all lineages must be averaged to give E . This average provides another explanation for E being 0.2 My^{-1} if all species last 5 My.

The lineages for which individual extinction rates are averaged to give mean extinction rate must be the set of lineages existing at an *instant* in time, because rate of extinction is a measure of instantaneous change. If instead we tally longevities of species that existed during an *interval* of time, we will obtain a different distribution of longevities. As shown in Figure 5-5, a slice of time, which provides the appropriate data for our calculation, preferentially encounters long-ranging members of the set of species that existed during an interval. In fact, as the figure illustrates, the sampling bias for the slice of time is directly proportional to species longevity. This means that to convert a histogram of lineage durations for an interval of time into a histogram representing an instant in time, it is necessary to multiply the size of each duration class by the duration represented (or by a number proportional to this duration).

Figures 5-6, A and 5-7, A display empirical "time interval" histograms of species longevities for two taxonomic groups that have extraordinarily good fossil records: European mammals that existed during the interval from the Eburonian Stage through the Mindel Stage of the Pleistocene and planktonic

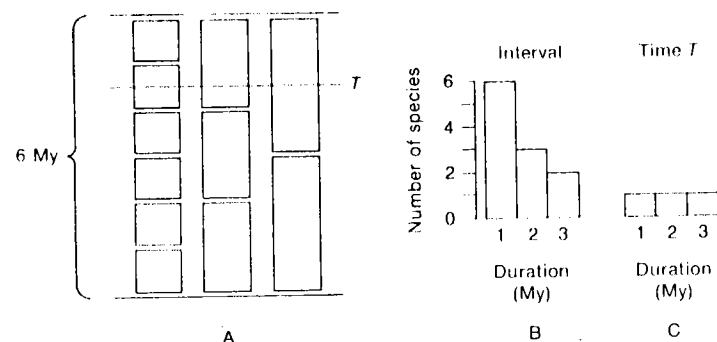


FIGURE 5-5

Conversion of a distribution of species longevitys that represents an interval of time to a distribution that represents an instant in time. During the 6 My interval of time depicted in A, a total of 11 species existed, with ranges represented by vertical bars. B: Histogram of species longevitys for the interval. C: Histogram of longevitys of species existing at an instant in time (T); as shown in A, at time T or any other time, only one species of each duration class is in existence. Time plane T encounters a larger percentage of long-ranging species than short-ranging species. In fact, the fraction (or probability of encounter) for each duration class is directly proportional to the duration. Therefore, the histogram for time T can be derived from that for the interval by altering the fraction of species in each duration class in proportion to the duration that the class represents.

Foraminifera that existed throughout the world during the interval extending from the Late Miocene to the present. The high quality of the record of Pleistocene mammals has already been discussed (page 74). Planktonic forams also have a superb record because they rain down upon the floor of the deep sea, where sedimentary sequences are relatively complete. Some uncertainty is introduced to the data for mammals by the inclusion of species that originated at unknown times long before the start of the interval sampled. In addition, the histograms for both taxa include many species that are alive today. If full durations for these species were known, the histograms would be shifted to the right, or toward longer mean duration. These factors contribute to the lack of uniformity of the distributions, and of course it must be borne in mind that the plotted durations underestimate *lineage* durations because they represent *species*, some of which were "terminated" by pseudoextinction. This problem will be dealt with below.

The two empirical histograms, which represent intervals of time, have been converted to instantaneous distributions by adjusting the fraction of species in each duration class in proportion to the duration of the class, as illustrated in

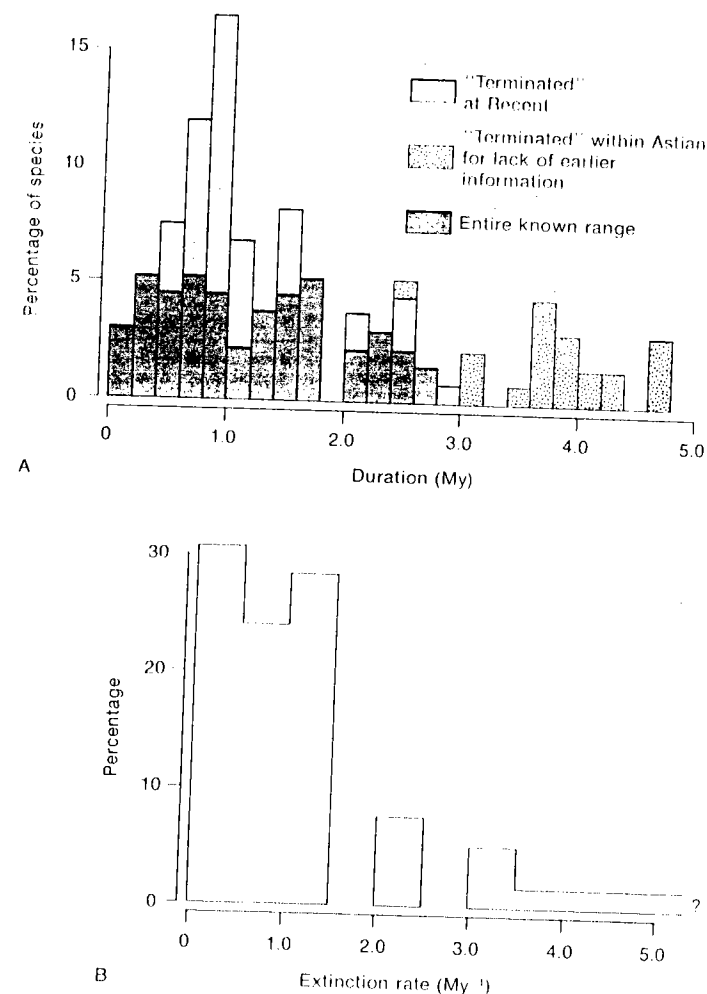


FIGURE 5-6

Durations and rates of extinction of mammal species in the Plio-Pleistocene of Europe. A: Histogram of durations. Data plotted are for all species considered to have existed during the interval extending from the base of the Eburonian Stage to the top of the Mindel Stage (Kurtén, 1968). For many species, only partial ranges can be plotted. B: Corresponding histogram of rates of extinction for an instant in time. To obtain this histogram, A has been converted to a histogram of durations for an instant in time by the technique shown in Figure 5-5. Next, the latter has been converted to the histogram depicting rates of extinction (B) by the technique shown in Figure 4-8. If data for full species ranges were available and if pseudoextinction could be excluded, the distribution of rates would be shifted to the left.

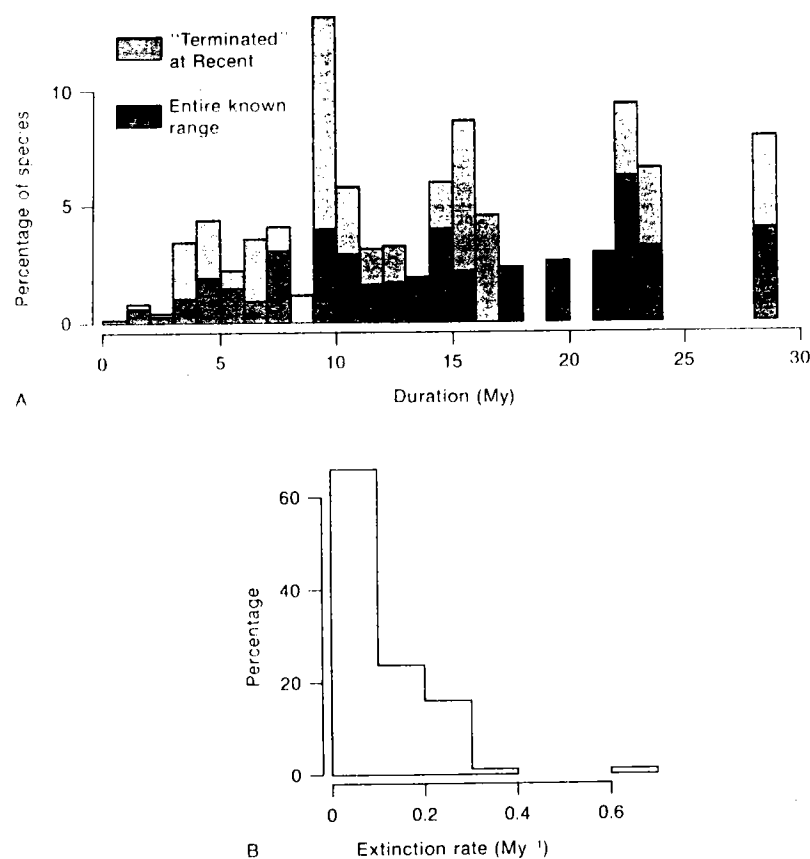


FIGURE 5-7. Durations and rates of extinction of planktonic foraminifera species of the late Cenozoic. A: Histogram of durations. Data plotted are for all species considered to have existed during the interval of time extending from the Late Miocene to the Recent (Blow, 1969). B: Corresponding histogram of rates of extinction for an instant in time, derived from A in the same way that Figure 5-6,B was obtained from Figure 5-6,A; this histogram, like Figure 5-6,B, would be shifted to the left if full species ranges were available and if pseudoextinction could be excluded from the tabulation.

Figure 5-5. Mean extinction rates have then been calculated for mammals and planktonic Foraminifera by averaging the individual extinction rates of species (the reciprocals of species durations) for the set of species represented in the instantaneous distributions. The sets of individual extinction rates are displayed as Figure 5-6,B and Figure 5-7,B. The estimate of E' for planktonic forams is about 0.1 My^{-1} and for mammals, about ten times as high. Because the reciprocal of a duration, rather than the duration itself, is averaged, seemingly large errors in estimated longevity have a weak effect on the mean when lying toward the left-hand portion of the histogram, where all individual extinction rates are very low. There is such an enormous disparity between mean species durations and mean extinction rates for the two groups considered that the empirical data, though imperfect, are quite adequate for comparative purposes. For both groups, rate of termination of lineages is overestimated because of the inclusion of incomplete ranges of species and ranges terminated by pseudoextinction, but obviously a difference in the impact of these biases cannot account for the enormous difference in calculated rates of extinction.

It is no accident that mammals and planktonic forams were chosen here, because data of comparable quality to those plotted in Figures 5-6 and 5-7 are lacking for nearly all other taxa. Fortunately, there is another simple procedure that enables us to obtain a rough estimate of E' for a taxon with a reasonably good Cenozoic fossil record. This method employs the simple fact that as we look backward through the Cenozoic history of a taxon, we will find a decreasing percentage of still living species. I will refer to the plot depicting this decrease as a Lyellian Curve, after Charles Lyell (1830), who noted that percentages of extant species in fossil faunas decrease with the geologic antiquity of Cenozoic deposits.

Given past confusion, it is important to clarify the nature of a Lyellian Curve. Each point on such a curve represents faunas of a given age and indicates for these ancient faunas the percentage of species that are alive today. The curve does *not* depict percentages of living species that extend backward to various points in geologic time. A curve of the latter type would be much less accurate because of the incompleteness of the record.

A Lyellian Curve for mammals is shown in Figure 5-8,A. The beginning of the Würm serves as an endpoint here, in place of the Recent, because of the disruption that would otherwise be introduced as a result of the Würm and post-Würm mass extinction of mammals (page 75). At some point on such a curve, 50 percent of the species in an average fossil fauna will be extant. Doubling the age of this fauna will yield the approximate interval of time required for complete faunal turnover. This, then, is a rough estimate of mean species duration (Figure 5-9). The use of a single slice of time (that represented by the 50 percent point) is appropriate here because we wish to estimate rate of extinction, for which we require a sample of the lineages coexisting at an instant in time. Our estimate would be quite accurate if all species were of equal duration. In fact, like most distributions in nature, the histogram representing species dura-

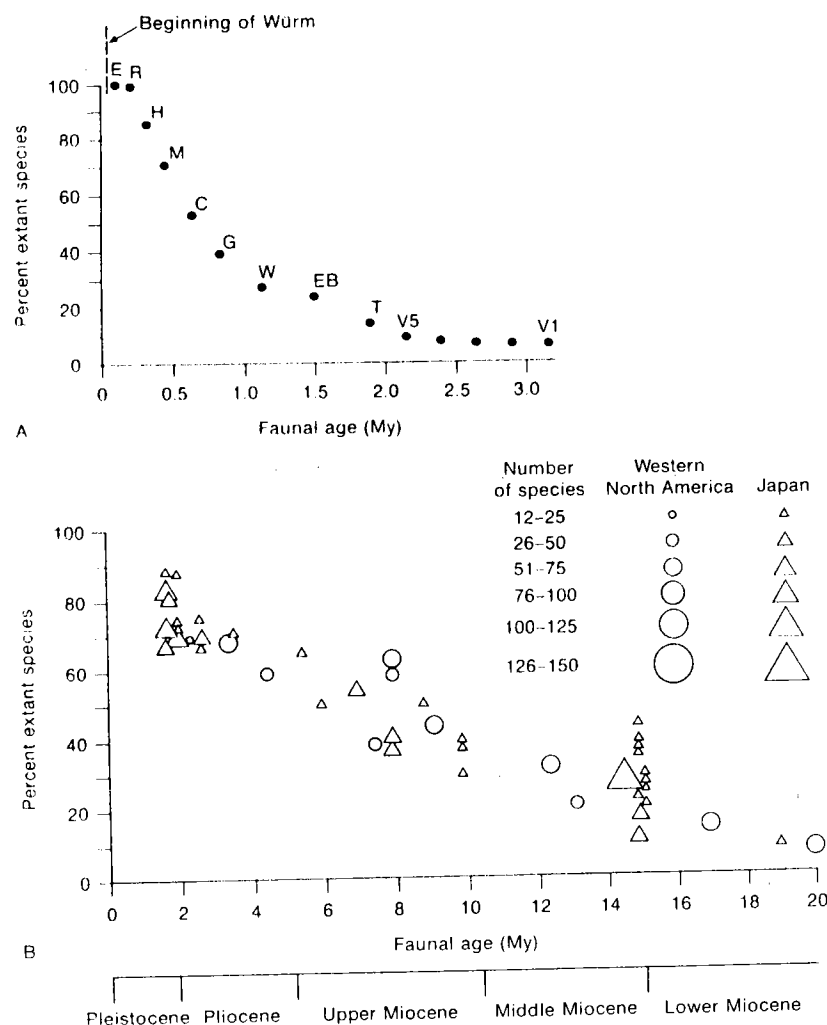


FIGURE 5-8
Lyellian Curves. A: Plot for Plio-Pleistocene mammals of Europe. This plot is terminated at the beginning of the Würm stage 40,000 years ago. Each point represents, for faunas of a given stage, the percentage of species that survived to the beginning of the Würm. Abbreviations used are the same as in Figure 4-7, A. (Data from Kurtén, 1968.) B: Similar plot for temperate and subtropical Bivalvia of the Pacific. This curve is terminated at the Recent. (From Stanley *et al.*, 1979.)

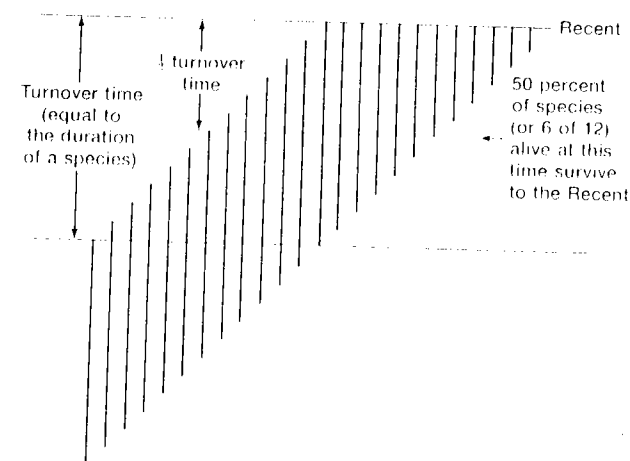


FIGURE 5-9
Diagram showing how, if all species are of equal duration and are evenly distributed through time, faunal turnover time will equal an average species duration, or twice the age of faunas in which 50 percent of all species survive to the Recent. (From D. M. Raup and S. M. Stanley, *Principles of Paleontology*, 2nd ed., W. H. Freeman and Company, San Francisco. Copyright © 1978.)

tions is presumably skewed to the right, meaning that more than half of the species will have ranges shorter than the mean. It should be evident that this condition will cause us to underestimate mean duration slightly when we use the 50 percent point, which relates to the median, in estimating one-half of the mean species duration. It will be shown below, however, that the error introduced here is relatively unimportant.

We can test the method described in the previous paragraph by comparing its results to the direct estimate of mean duration of 1.6 My obtained from the data plotted in Figure 5-6. The latter is manifestly an underestimate, because some species last longer than their recognized records indicate and because some ranges abut backward against the starting point of the interval considered or forward against the Recent time plane. The estimate (also a slight underestimate) obtained by doubling the age of the 50 percent point of a Lyellian Curve for mammals (Figure 5-8, A) is 1.4 My, which is in close agreement. Numbers of species of Late Cenozoic planktonic forams are too low to permit mean species duration to be meaningfully estimated from the 50 percent point of a Lyellian Curve. The general agreement of the two techniques, as applied to mammalian

data, however, supports the notion that the indirect "50 percent point" method should provide a reasonably accurate estimate.

If we take mean duration of a mammal species to be 1.4 My, as estimated by the indirect method, total extinction rate (E') will be the reciprocal, or 0.71 My^{-1} . It might be assumed that the calculated value for E' is erroneously high because, as noted, the value for mean species duration obtained from the Lyellian Curve is an underestimate. Operating in the opposite direction, however, will be the error introduced by the use of mean species duration to calculate E' . This can be appreciated by referring back to Figure 4-8,B. Here rate of phyletic evolution is equivalent to rate of pseudoextinction. Recall that this plot is obtained from the plot for durations (Figure 4-7,B) by altering the horizontal scale of the survivorship curve in a nonlinear fashion. The result is that the true rate of pseudoextinction (1.1 My^{-1}) is considerably higher than the rate ($<1 \text{ My}^{-1}$) that would have been estimated from Figure 4-7,B as the reciprocal of mean chronospecies longevity ($>1 \text{ My}$). In a similar way, the "individual rate" of extinction of a species of average longevity based on data from a Lyellian Curve must represent an underestimate of true rate of extinction. Perhaps the degree of underestimation here approximately offsets the error in the other direction that results from the use of the 50 percent point of the curve. At least there must be a partial cancellation of errors.

For comparison with mammals, let us now return to the Bivalvia, for which we have excellent data for values of R in radiating families (Figure 5-2). The 50 percent point on a Lyellian Curve for temperate or subtropical bivalve faunas falls in the Late Miocene, representing a time about 7.5 My ago (Figure 5-8,B). Doubling this interval and taking the reciprocal of the result gives an estimate for E of 0.07 My^{-1} . This estimate is fully an order of magnitude lower than the one for mammals, reflecting much greater species longevity among bivalves. This disparity should dispel concern over the imperfect estimation of E' discussed above. At least in relative terms, the estimates are quite revealing. We can, then, combine the values of R calculated for these two classes (Figure 5-2), with estimates of E to obtain estimates of rates of speciation. First, a digression is necessary, to deal with the contribution of extinction by phyletic transition (pseudoextinction).

The preceding methods fail to take into account pseudoextinction. What is desired for estimation of S is not total rate of extinction (E'), but only rate of termination of lineages (E). The incidence of pseudoextinction is by no means negligible, as illustrated by the phylogeny of the Elephantinae (Figure 4-11), in which nearly half of the extinctions are thought to have been of this type (and some terminations may be the aberrant products of human activity). Other rather well-studied phylogenies, like that of the scallop *Argopecten* (Waller, 1969), reveal a similarly high incidence of pseudoextinction (Figure 2-2).

In the absence of precise information, we can obtain a maximum value of S by assuming that there is no pseudoextinction. We can then establish boundaries in the other direction by postulating various incidences of pseudoextinction, expressed as values of the ratio E/E' . This procedure is followed in Table 5-1,A, in

TABLE 5-1. Estimates for exponential variables in the Mammalia and Bivalvia, assuming various incidences of pseudoextinction (E/E'). A: Estimates of E and S . B: Estimates of N for radiations of 20 My and, for mammals, 10 My.

	A			B	
	E/E'	$E(\text{My}^{-1})$	$S(\text{My}^{-1})$	$N(20 \text{ My})$	$N(10 \text{ My})$
Mammalia					
$(R = 0.22 \text{ My}^{-1})$	1.00	0.71	0.93	345	38
$E' = 0.71 \text{ My}^{-1}$	0.80	0.57	0.79	293	32
	0.50	0.36	0.58	215	24
	0.30	0.21	0.43	159	18
Bivalvia					
$(R = 0.062 \text{ My}^{-1})$	1.00	0.090	0.15	8	
$E' = 0.09 \text{ My}^{-1}$	0.80	0.072	0.14	8	
	0.50	0.045	0.11	6	
	0.30	0.027	0.09	5	

which a ratio of unity represents a condition in which there is no pseudoextinction, and decreasing values of the ratio represent an increasing incidence of pseudoextinction (to a level of 70 percent). It is very important to recognize that the degree of flexibility represented here greatly exceeds uncertainties in the value of E' discussed above.

Thus, while I am making use of Lyellian Curves in only a crude manner, by employing only the 50 percent point, I see no way in which they can practically be used more precisely for the calculation of lineage durations and E . There is simply no way of factoring out pseudoextinction. Furthermore, as will now be shown, the estimates of E employed here are accurate enough to be of value.

An estimate of speciation rate (S) is obtained by adding various estimates of E to the mean value of R in Figure 5-2. Note that even if pseudoextinction constituted 70 percent of E in mammalian phylogeny and were nonexistent in bivalve phylogeny (an absurd contrast), estimated speciation rate would still be more than twice as high for mammals (0.21 My^{-1} versus 0.09 My^{-1}). Certainly, the actual disparity in values of S must be much greater, because it is unlikely that incidence of pseudoextinction is appreciably higher for mammals (compare Figures 2-2 and 4-11). If incidence of pseudoextinction is more or less the same in the two classes, the value of S for mammals is estimated to be about five times as high. The importance of the difference in rate of speciation can hardly be over-emphasized. Because S appears exponentially in the calculation of N , a five-fold increase in its value has an enormous effect. Recall that less than a three-fold difference in value of R produced the disparity in net diversification depicted in Figure 5-3. (Note that it has been tacitly assumed that the value of E in adaptive radiation, for which S is being calculated here, is approximately equal to its value in phylogeny in general, from which it has been estimated.)

Clearly, rate of extinction and rate of speciation in adaptive radiation are

much higher within the Mammalia than within the Bivalvia. While it happens that this contrast accompanies a similar disparity for values of R , it is important to recognize that, arithmetically, this need not be the case. A given value of R can result from high or low values of S and E . It will, nonetheless, be shown in Chapter 9 that the comparison between the Mammalia and Bivalvia is typical: Values of R , E , and S within taxa tend to be intercorrelated throughout the animal world.

RATE OF SPECIATION AND RATE OF LARGE-SCALE EVOLUTION

In asserting that speciation is the locus of most large-scale change, the punctuational model offers the prediction that taxa characterized by high rates of speciation will also be typified by high rates of large-scale evolution. Taxonomically, we would expect to find that families and orders of such taxa originated in brief intervals of time and, morphologically, we would predict that adaptive innovations should have appeared very rapidly. These predictions seem to be borne out by an abundance of fossil evidence, part of which will be discussed in this and subsequent chapters. It is interesting to compare rates of appearance of families in the phylogenies of the two classes whose rates of speciation have been contrasted: the Mammalia and the Bivalvia (Stanley, 1977). For Cenozoic mammals, peak diversity was attained early in the Oligocene, only about 30 My after the modern radiation began (Figure 5-10,A). Number of families has actually declined slightly since Oligocene time. Bivalves show a much slower build-up of family diversity: There is no evidence that a limit is being approached even after more than 400 My of radiation (Figure 5-10,B).

There is, of course, no reason to believe that a family of bivalves is in some way equivalent to a family of mammals. Judging from the adaptive traits of families in each group, however, it would appear that after only 30 My of radiation, the basic adaptive limits of the mammalian body plan had been approached. Subsequent diversification has been largely a matter of adaptive refinement. In contrast, origins of the basic modes of life of modern bivalves required long spans of geologic time. For example, an interval of more than 200 My was required for the evolution of epifaunal attachment by cementation and also for the evolution of habits that simply entailed an unattached existence on the substratum. The origin of deep-burrowing habits, except perhaps in the unusual Lucinacea, required about 150 My. The ability to burrow rapidly, by modern standards, and to secrete shell ornamentation that aids in burrowing took even longer to appear.

Body size is perhaps the simplest and most directly comparable morphologic feature that serves to contrast rates of diversification for bivalves and mammals.

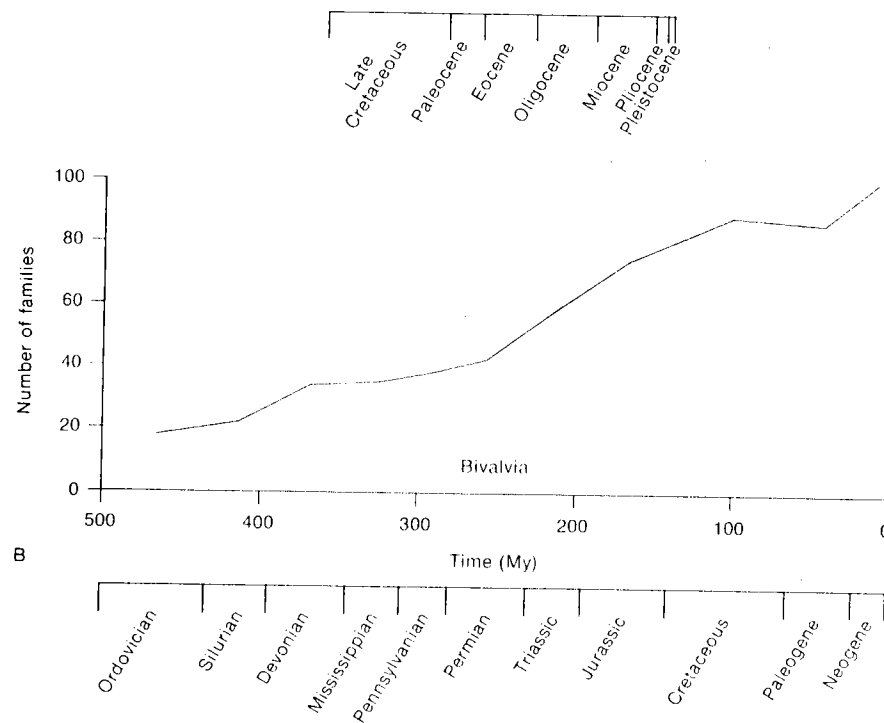
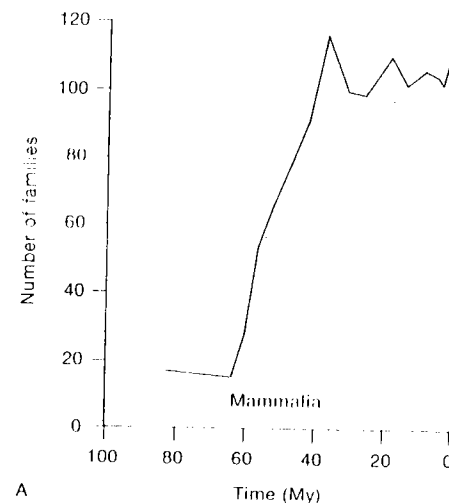


FIGURE 5-10
Diversity of families through time for the Mammalia (A) and Bivalvia (B). (Data for A from Lillegraven, 1972, and for B from Stanley, 1973c.)

Terrestrial mammals that were large by modern standards had evolved from small ancestors by the Late Paleocene and Early Eocene, after only about 10 to 15 My of mammalian radiation. By the Early Oligocene, only about 30 My after the radiation began, the largest land mammal of all time, *Indricotherium*, was in existence (Kurtén, 1971). The mammalian record is replete with examples of rapid phylogenetic size increase. In contrast, the first relatively large free-burrowing clam was *Megalomoidea*. This animal did not appear until after nearly 100 My of radiation. Even more strikingly gradual was the filling out of the modern spectrum of sizes in the epifaunal realm (the adaptive zone of bivalves that rest on the surface of the substratum). Not until the Jurassic and Cretaceous did the epifaunal inoceramids and rudists independently attain huge sizes (sizes comparable to those of modern tridacnids).

The many fundamental adaptations of the bivalves that were slow to originate cut across adaptive zones and taxonomic boundaries, and there is no evidence that general rate of speciation within the class was appreciably lower in the Paleozoic than at later times. Furthermore, comparable adaptive transitions within subtaxa arising in the Mesozoic and Cenozoic were equivalent, in rate, to those of the Paleozoic.

The mammals, then, have speciated at much higher rates than the bivalves and have accomplished major adaptive transitions much more rapidly. These conditions are compatible with the punctuational prediction that rate of large-scale evolution should correlate with rate of speciation. It might, however, be argued that the same correlation would be expected if phyletic evolution prevails in phylogeny. The point would be that number of rapidly evolving lineages, as a stochastically constant fraction, should increase with total number of lineages. A way of choosing between these possibilities is to hold phyletic evolution constant, in effect, by examining what happens when speciation is increased within the Bivalvia themselves. A natural experiment of this type has been provided by Late Cenozoic physiographic changes in the region now occupied by the Caspian Sea.

During the Pliocene Epoch, the Caspian region was occupied by the Pontian Sea, a brackish body (or group of bodies) of water isolated from the Mediterranean. Here, in less than 3 My there arose numerous species of cockles of diverse morphologies (Figure 5-11). The exact number is not certain, but more than thirty endemic genera are recognized (Gillet, 1946; Zenkevitch, 1963; Ebersin, 1965). These are assigned to four subfamilies. Many of the genera are quite unusual in shape and ornamentation pattern when compared to typical cockles. Apparently all of the genera arose from one or a small number of species of *Cerastoderma*, the genus of the familiar living European cockle. The point is that speciation occurring at rates which were extraordinarily high for the Bivalvia was accompanied by unusually rapid rates of morphologic evolution. Meanwhile, in the ocean, *Cerastoderma* speciated at the slow rate that typifies marine bivalves. It contains three living species in England, for example, and one in the United States. This low rate of speciation was accompanied by very little evolu-

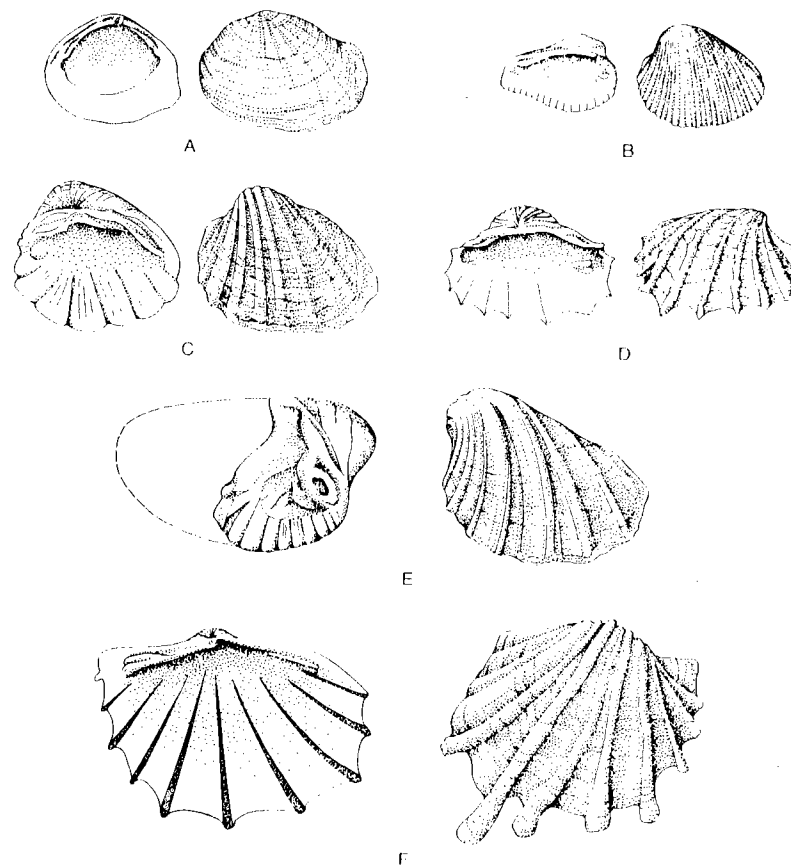


FIGURE 5-11
Some of the cockles of the family Limnocardidae that evolved in the Pontian Sea. A: *Phyllicardium planum*. B: *Pseudoprosodacna sturi*. C: *Limnocardium squamulosum*. D: *Limnocardium fittoni*. E: *Prosodacna baueri*. F: *Budnania semseyi*. (From Gillet, 1946.)

tionary change. Modern members of the genus look much like those of the Late Oligocene, when *Cerastoderma* first appeared. As noted for cichlids and other taxa that have speciated and evolved rapidly in large African lakes (page 45), we cannot rule out, as an alternative explanation, the phenomenal acceleration of phyletic evolution. Still, this alternative is utterly fanciful. We have neither documentation nor theoretical explanation for any such acceleration. What we

do have is direct evidence that speciation was occurring at an extraordinarily high rate. We have, in effect, tested the punctuational model and it has passed, which is to say that it remains intact, if not proven.

I previously suggested that the gradualistic model be put to a complementary test, called the test of generation time (Stanley, 1975a). If rate of speciation should correlate with rate of large-scale evolution in a punctuational scheme, then in a gradualistic scheme, rate of evolution should correlate with the equivalent parameter, birthrate. Net rate of population increase, a parameter generally equivalent to R of this chapter, is closely tied to birthrate, but also to generation time, which is a more widely measured variable. (Figure 7-8, (page 210), displays the inverse correlation.)

It is a self-evident tenet of population genetics that, all else being equal, rate of phyletic evolution should vary inversely with generation time. From this condition, we can predict that if the phyletic component of evolution dominates in the history of life, we should find among higher taxa an inverse correlation between generation time and large-scale evolution. It has, in fact, long been recognized that no general correlation of this type exists (Zeuner, 1931; Simpson, 1949). As we have already noted, marine invertebrates with generation times in the order of one or two years exhibit more sluggish large-scale evolution than mammals that mature after five or ten years. Unfortunately, a problem is now evident for the test of generation time. This is that generation time does not seem to be a major determinant of rate of phyletic evolution even within individual classes. In particular, recall that the most rapid phyletic evolution currently recognized in the Mammalia has occurred within the elephant family (Figure 4-11), whereas the most ancient living mammal species of Europe are animals of very small body size and short generation time (page 79). I would agree with Mayr (1970, p. 344), that the overriding factor here is population size. The stabilizing effects of spatial heterogeneity (pp. 48-51) would be expected to be less effective within small populations than within large ones.

The test of living fossils (Stanley, 1975a), which will now be described, represents a more fruitful avenue of departure from the exponential methodology introduced in the previous section. It should be stressed, at this point, that the analysis of the preceding chapter would seem to refute the gradualistic model. The arguments of the present chapter that relate to the controversy over gradualism are presented as corroboration.

LIVING FOSSILS REINTERPRETED

Rather than examining what happens when species multiply at exceptionally high rates, we can investigate the results of unusually sluggish speciation. A corollary of the punctuational model is that small clades persisting for long

intervals of geologic time should exhibit little net evolutionary change. (The most extreme case would be that of a clade consisting of a solitary lineage.) The gradualistic model offers no such prediction, for if phyletic evolution normally proceeds at a moderately rapid pace, lineages belonging to very small clades, like those belonging to large clades, should often exhibit considerable change during long intervals of geologic time.

These deductions permit us to formulate a test of the two models. Do small clades persisting for long periods display very little evolution or varying, and often substantial amounts? The fossil evidence here is quite clear: Such clades seem almost invariably to exhibit morphologic stagnation. They are what are commonly called **living fossils**. This label has been used in a variety of ways, but I would restrict its application to extant clades that fulfill the following qualifications: (1) They must have survived for relatively long intervals of geologic time at low numerical diversity, often as the sole survivors of previously diverse taxa. (2) They must today exhibit primitive morphologic characters, having undergone little evolutionary change since dwindling to low diversity at some time in the past. Thus, it is appropriate to label this test (passed by the punctuational model and failed by the gradualistic model) the test of living fossils (Stanley, 1975a).

The name of this test might seem to suggest circularity, in that if only living fossils were considered, then little evolution *could* be found. But this is not the procedure followed. Rather, the test is conducted by examining *all* clades of low diversity that can be traced by fossil evidence over long intervals. It would be tempting to include here small, extant groups that clearly are living fossils but that are not connected by known fossil evidence to similar, obviously ancestral forms recognized far back in the record. This would be unfair, however, because we would know in advance that all such forms (e.g., *Neopilina*, *Sphenodon*, *Tarsier*) have undergone very slow change, yet we would automatically be excluding from our compilation any small, extant clades that might have undergone considerable phyletic evolution without leaving a record to tie them to their otherwise unrecognizable ancestors. We must therefore restrict our analysis to small clades that have fossil records continuous enough to be traced backward for a substantial period of time, regardless of the rate of change recorded. As it turns out, all such clades that I have been able to identify have evolved very little. In other words, their Recent representatives are living fossils—a condition that stands in opposition to the gradualistic model. A compilation of examples appears in Table 5-2. (It should be noted that for a slowly evolving invertebrate group, 100 My is a long interval to survive with little change; for a rapidly evolving group like the Mammalia, 10 to 20 My is a long period.)

A detailed look at examples from Table 5-2 will more fully elucidate the test. The lungfishes represent a particularly well-studied group (Westoll, 1949; Simpson, 1953). They underwent rapid changes in morphology only when speciating rapidly in the mid-Paleozoic, soon after appearing (Figure 5-12). Then, in the late Paleozoic, rate of speciation decreased abruptly and so did rate

TABLE 5-2 Compilation of clades that contain few lineages but have persisted to the present from distant geologic intervals while leaving relatively continuous fossil records. The approximate time at which each clade began existence at low diversity is given in parentheses. Note that none of the clades exhibits appreciable evolutionary change; the extant representatives of each are living fossils. Few invertebrate clades are listed, in part because few that would otherwise qualify display persistent fossil records. Other invertebrate taxa, like the lingulid brachiopods, pleurotomariid gastropods, and pinnid bivalves, are excluded because they contain several species today and may have undergone a rather large total number of speciation events during long intervals of persistence with little evolutionary change.

Echinoneid sea urchins (Late Cretaceous—80 My)

There are only three living species assigned to the Echinoneidae, as now constituted. These are assigned to two genera, one of which is represented by a meager Cenozoic fossil record. Only one other genus, containing a single Upper Cretaceous species, is recognized (Mortensen, 1948). The family has undergone little structural evolution.

Horseshoe crabs (Early Triassic—230 My)

The superfamily Limulacea has a sparse Mesozoic and Cenozoic fossil record. An Atlantic and a Pacific subgroup exist today, the Pacific one bearing the greater resemblance to *Mesolimulus* of the Mesozoic. Daniel C. Fisher informs me that the group displays a larger degree of evolutionary change than has often been assumed.* Still, there are strong similarities among post-Paleozoic members of the Limulacea, considering the long interval during which the superfamily has persisted.

Bairdiid ostracods (Early Triassic—230 My)

The family Bairdiidae has survived since the Paleozoic with little multiplication of species and little morphologic change. *Bairdia*, the likely ancestral genus, exhibits an enormous stratigraphic range (Ordovician to Recent). The genera of the post-Paleozoic portion of the clade, numbering about four, are quite similar to *Bairdia* of the Late Paleozoic (Sylvester-Bradley, 1961).

Galatheid anomuran crabs (Middle Jurassic—170 My)

The family Galatheididae is represented by only two living genera. Its fossil record exhibits much lower taxonomic diversity than is found in other groups of crabs (Glaessner, 1969). During this long period, it has undergone little structural change, remaining as a morphologically primitive decapod.

Notostracan crustaceans (Late Carboniferous—305 My)

The very small clade represented by the order Notostraca exhibits almost no morphologic change whatever. One of the two living genera extends back to the Late Carboniferous and the other, to the Jurassic. No other fossil genus is known. Two Triassic forms are assigned to living species, making them the oldest living animal species on record (Longhurst, 1955).

Bowfin fishes (Albian—105 My)

The family Amiidae has never speciated to speak of and has not been transformed appreciably since first appearing in the record (Figure 5-13). Boreke (1974) has

TABLE 5-2, continued

documented an excellent Cenozoic fossil record, which never displays more than two contemporaneous species.

Sturgeons (Late Cretaceous—80 My)

Today only two living genera represent the family Acipenseridae. Most species of the family are assigned to the living genus *Acipenser*, which extends back to the Cretaceous with little morphologic change (Romer, 1966).

Garfishes (Late Cretaceous—80 My)

Lepisosteus, one of the two living genera of the family Lepisosteidae, contains only four living species and the other genus, *Altractosteus*, comprises three. The known fossil records of both genera extend back to the Upper Cretaceous, by way of fossil material scattered throughout several Cenozoic stages. The records exhibit little evolution (Wiley, 1976).

Sirens (Late Cretaceous—80 My)

The amphibian suborder Sirenoidea includes only three living species that are assigned to two genera, both of which extend back to the latter part of the Cretaceous without essential change (Estes, 1970).

Snapping turtles (Late Paleocene—57 My)

There are three living species of snapping turtles (family Chelydridae) belonging to two genera (Ernst and Barbour, 1972). There is little morphologic difference between the oldest known species of the late Paleocene and the living representatives (Estes, 1970).

Alligators (Early Oligocene—35 My)

The alligator clade (subfamily Alligatorinae) includes only two living species and apparently has at no time harbored a large number of species (Steel, 1973). It also exhibits little structural evolution.

New World porcupines (Early Oligocene—35 My)

Wood and Patterson (1959) found evidence for very few lineages of the Erethizontidae and very little morphologic change since the Early Oligocene. Of the four living genera, three are monophyletic. The fourth, *Coendou*, contains about 20 named species (Walker, 1975), but the morphologic diversity represented is low, and they may represent taxonomic oversplitting. In any event, *Coendou* is a young genus, leaving a long interval apparently spanned by few lineages.

Aardvarks (Early Miocene—20 My)

There is but a single living species belonging to the order Tubulidentata, and the fossil record reveals only a small number of lineages as far back as the base of the Miocene, where the earliest known representatives are found (Patterson, 1975). Only modest structural changes have occurred since this time. Patterson believes that the distinctive genus *Plesiorcterus* of Madagascar represents a clade separated from that of other known aardvarks since the Eocene.

TABLE 5-2, continued

Sewellels, or mountain "beavers" (Middle Miocene—15 My)

The family Aplodontiidae contains only one living species and has existed at very low diversity since mid-Miocene times (Romer, 1966). When the group was speciating more rapidly early in the Miocene, it apparently gave rise to the Mylagaulidae, a highly specialized family of burrowers. The subsequent history of the Aplodontiidae accounts for little morphologic change.

Tapirs (Early Miocene—20 My)

The family Tapiridae contains only four living species (Walker, 1975). During the past 15 My, only two genera are known to have existed. Diversity was apparently also low in the Oligocene and Early Miocene, when there were a few additional genera, but "generic distinctions are slight" (Romer, 1966, p. 220). Very little change in form is apparent since the Oligocene.

Pangolins (Early Oligocene—35 My)

There are seven living species of the family Manidae, which has diversified quite slowly, the oldest recognized species being Early Oligocene (Emry, 1970). The living species are similar enough that some workers refer them to one genus. A total of seven extinct species are recognized, apparently documenting low diversity since the Early Oligocene. The overall degree of morphologic change has not been great.

* Daniel C. Fisher, University of Rochester, 1977.

of morphologic change. (In the absence of adequate fossil data at the species level, generic diversity is plotted in Figure 5-12 as an index of species diversity.) A better documented example is that of the bowfin fishes (Borreske, 1974). The small extant clade of bowfins can be traced back to the Late Cretaceous. Fossil data, which are available for every epoch of the Cenozoic, reveal the existence of no more than two species at any time (Figure 5-13A, B). During an interval of about 100 My, change of form was restricted largely to phyletic transformation and was also quite trivial (Figure 5-13.C).

Various hypotheses have been advanced to account for the highly problematical nature of living fossils in the context of gradualism, but generally with expressions of uncertainty (see review by Simpson, 1953, pp. 327–335). Darwin (1859, pp. 105–108), who introduced the phrase "living fossils," saw these forms as resulting from a combination of long survival of lineages and remarkably slow phyletic evolution, both of which he attributed primarily to an absence of ecological competition. Delamare-Deboutteville and Botosaneanu (1970), who reviewed numerous examples of living fossils, saw them as creatures that have "stopped participating in the great adventure of life," being confined by narrowness of adaptation. Simpson (1953, p. 331), on the other hand, considered them to be characterized by broad adaptation. In short, they have defied satisfactory explanation in the framework of gradualism. Why is this?

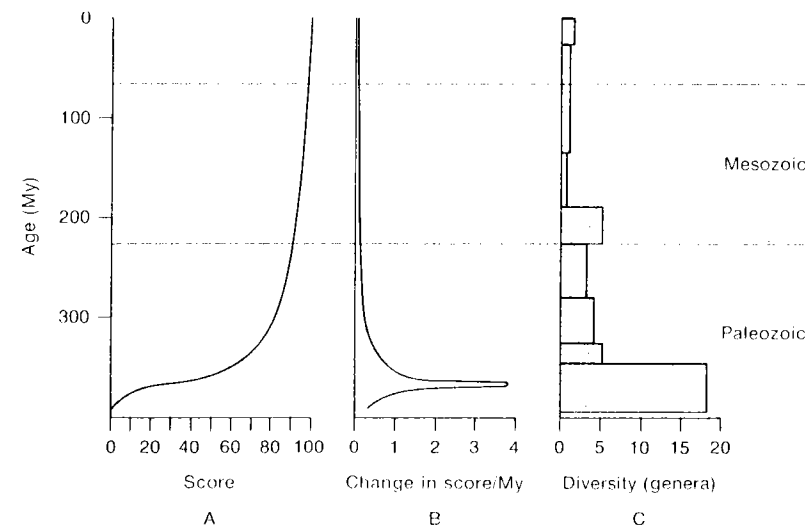


FIGURE 5-12

Rates of evolution in the lungfishes (Dipnoi). A and B: Plots showing changes in skeletal morphology since the group appeared, about 400 My ago. Scores are composite estimates of degree of advancement relative to the most primitive condition. (From Simpson, 1953, based on data from Westoll, 1949.) C: Diversity through time. Note that little morphologic change has occurred since the mid-Paleozoic, when rate of production of species and genera declined to a low level. (From Stanley, 1975a.)

The postulation of aberrantly sluggish rates of phyletic evolution to account for living fossils has persisted in part because of a general misconception about the distribution of rates of phyletic evolution within higher taxa. Many people have believed rapid evolution to be the norm. Simpson (1944; 1953), for example, plotted survivorship curves for extinct genera of carnivorous mammals and of bivalves, and with the tacit assumption that generic durations are inversely related to rates of phyletic evolution, he attempted to convert the data upon which these curves were based into histograms depicting evolutionary rates (Figure 5-14, A–D). Two difficulties must be pointed out here. First, the idea that generic durations are primarily the product of phyletic rates is strongly gradualistic. (Even many gradualists have assumed that most genera go extinct by termination of lineages.) In a punctuational framework, the distribution of generic longevities should be some complex function of (1) the distribution of numbers of lineages within genera and (2) the distribution of lineage durations within genera. Second, Simpson unfortunately assumed that, if rate of evolution

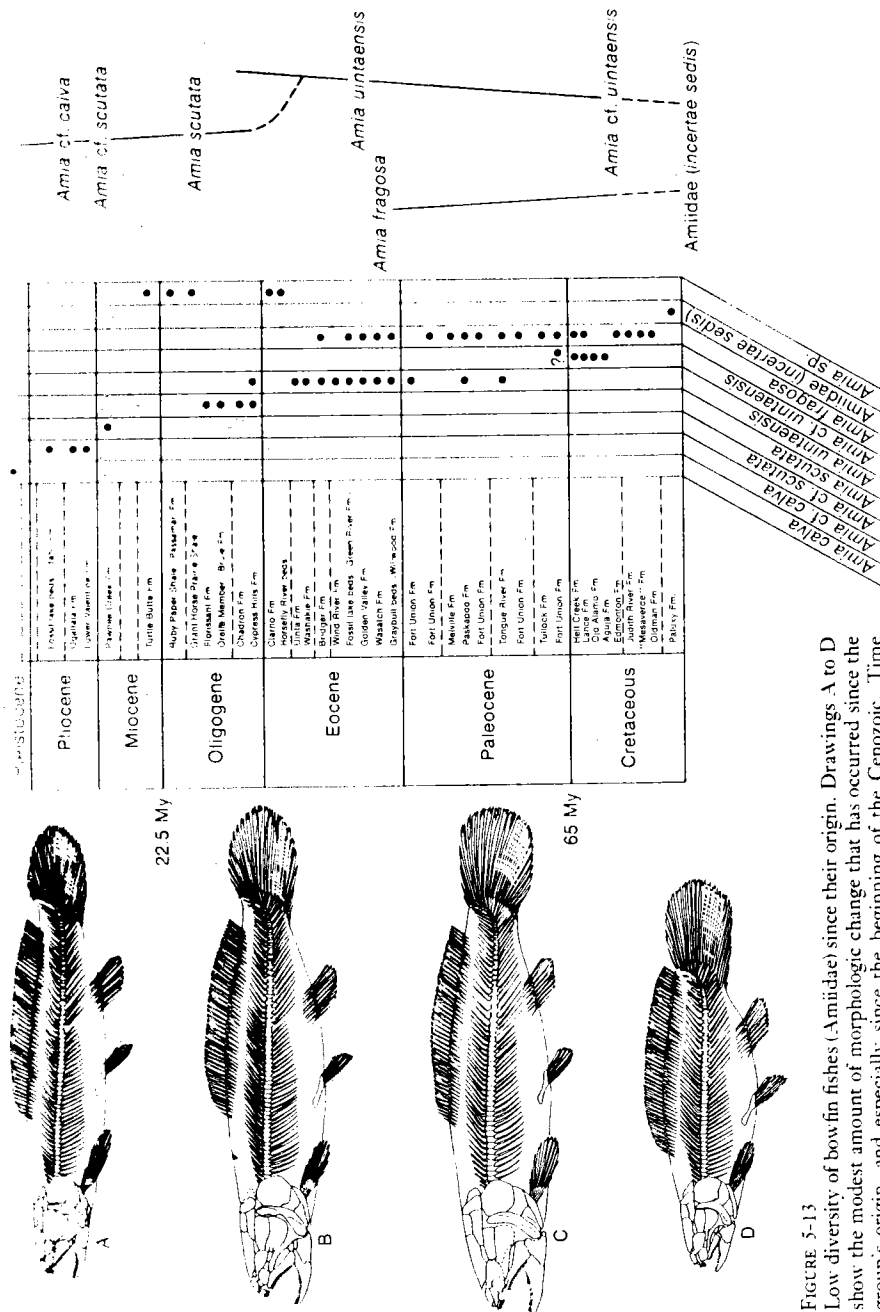


FIGURE 5-13
Low diversity of bowfin fishes (Amiidae) since their origin. Drawings A to D show the modest amount of morphologic change that has occurred since the group's origin, and especially since the beginning of the Cenozoic. Time scale nonlinear. (After Borenske, 1974.)

is the reciprocal of taxonomic longevity, the distribution of rates should be the mirror image of the distribution of longevity. This assumption produces a spurious, negatively skewed shape (Figure 5-14,C and D). As was shown in Chapter 4 (Figure 4-8), to plot a histogram for rates it is necessary not only to reverse the horizontal scale, but to distort it. The distributions derived in this manner from Figure 5-14,A and B are shown as Figures 5-14,E and F, which are positively skewed. These distributions have also been calculated to represent an instant in time (see Figure 5-5), whereas Simpson's histograms (Figures 5-14,C and D) represent an interval.

From Figures 5-14,C and D, Simpson inferred that only a very small fraction of taxa undergo very slow evolution. Given this gradualistic conclusion, living fossils seemed to represent entities that would be expected to exist as the predictably rare products of slow phyletic transformation. (The reason for phyletic stagnation remained a mystery.) Because even the proper histograms for genera primarily represent rate of termination rather than rate of phyletic transition, let us focus upon Figure 4-8, which represents only phyletic evolution. Here the mode lies adjacent to the ordinate. It is rapid, not slow, phyletic evolution that is rare. So low are phyletic rates, in general, that rates for living fossil taxa can easily fall in the vicinity of the mode. A clade that consists of a small number of lineages evolving at the average phyletic rate needs simply to *survive* in order to yield living fossils.

Simpson (1944) coined the term **bradytelic** to describe lineages that seemed to exhibit extraordinarily slow evolution in comparison to rates for related taxa. Based on the idea that rates of phyletic evolution are negatively skewed within classes (Figure 5-14,C and D), it seemed possible to single out as bradytelic the lineages forming the left-hand tail of an unusually strongly skewed distribution. Given the actual positively skewed shape of distributions, the concept of bradytelic loses its utility: The mode of the distribution lies where the bradytelic tail was thought to be.

To be more specific, from Figures 4-8, 4-11, and other data and inferences presented in Chapter 4, it seems reasonable to conclude that phyletic evolution will seldom accomplish a genus-level transition within a mammalian lineage spanning 5 My. Even in 20 My, rather little phyletic change is to be anticipated and, in fact, few mammalian lineages survive as long as this. Still, some lineages would be expected to span 20 My because the distribution of lineage durations is certainly positively skewed. The more youthful representatives of such long-ranging lineages, if alive today, would be predicted to be exactly what they are: living fossils.

It is important to recognize that the punctuational model predicts that some taxa should also persist with little change within clades that undergo extensive branching. This is to be expected, first, because some lineages within such clades will happen to be unusually long-lived and, second, because not all speciation produces marked divergence. In other words, the punctuational model does not predict the absence of primitive taxa from groups that are diverse today.

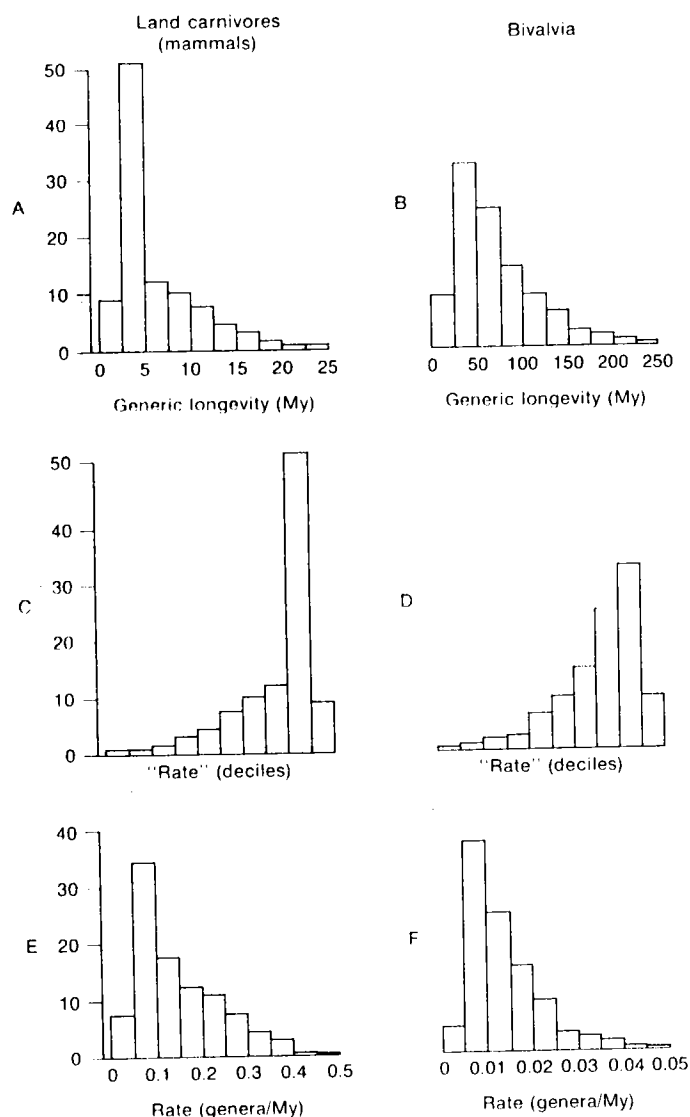


FIGURE 5-14
Inference of the distribution of rates of evolution—or, more properly, rates of extinction—from longevity of genera. A, B: Histograms, for an

Such taxa do, in fact, exist. One example is the moderately diverse nuculoid bivalves, which seem to have changed little since the early Paleozoic. Certain members of the Didelphidae (opossum family) may also represent examples (Simpson, 1953, p. 328). *Dicrorhinus*, the two-horned Malaysian rhino and one of the oldest living genera of mammals, with an antiquity of about 35 My, seems to be another. While surviving with little change, it has apparently given rise to other distinctive rhinos (Kurtén, 1971, p. 91).

It is also important to recognize that an example or two of substantial change within a small clade would not refute the conclusions reached above. As will be shown below, even a single speciation event can produce marked divergence. Although it is improbable that one or two such events will occur within a small clade, it is not impossible.

It might be claimed that in transferring the evaluation of living fossils to a punctuational framework, I am simply switching the problem from the previously alleged difficulty of accounting for unusually slow phyletic evolution to a problem of explaining failure to speciate. Why should a lineage or small clade almost cease to cast off descendants over a long span of geologic time? I find this question in no way perplexing. It will be argued in Chapter 7 that adverse conditions more readily stifle speciation than they cause the extinction of large, established species. Thus, it is not difficult to imagine that a species or small clade, faced with changing biotic conditions, as when more advanced competitors and predators evolve, might be adversely affected to the degree that it would speciate very little, but not to the degree that it would become extinct. While clades of living fossils are geologically long-lived, there is no evidence that the same is true of the individual lineages that form them. If component lineages are characteristically long-lived, however, the resulting co-occurrence of longevity and low rate of speciation might be explained in part by the fact that both traits characterize species that disperse readily (see Chapter 9). Of course, many living fossil forms are not widespread, but occupy geographic refugia. Here the explanation may be that while protection is afforded within such an area, there is little opportunity for speciation because of severely restricted opportunities for isolation and partitioning of the environment.

Finally, it should be noted that the persistence within cichlid faunas in and around the Great African lakes of species of apparently ancestral morphologies (pp. 45–47) represents a kind of microcosmic test of living fossils. Here, in considering the persistence of an ancestral form, we are perhaps evaluating a single

instant in time, of generic longevity for mammalian land carnivores and bivalve mollusks. (Data from Simpson, 1944; 1953.) C, D: Histograms purported to depict rates of phyletic evolution; these rates are the mirror images of those displayed in A and B. (From Simpson, 1944; 1953.) E, F: Correct histograms of rates of evolution (actually rates of extinction) for genera; these are derived from A and B by way of survivorship curves by the method illustrated in Figure 4-7. Like the distributions of durations (A and B), they are strongly skewed to the right.

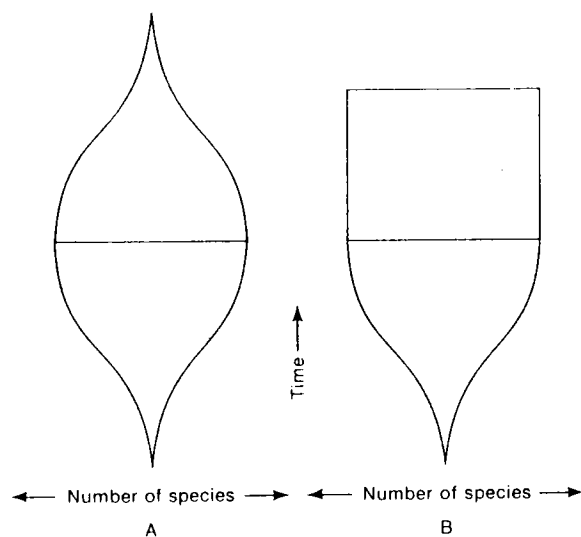


FIGURE 5-15

Relative numbers of speciation events occurring within a higher taxon during radiation, decline, and persistence without change in diversity. Balloon diagrams depict species diversity. It is assumed that species duration is brief with respect to the longevity of the higher taxon. If the distribution of longevity of lineages remains roughly constant, approximately the same number of speciation events will occur during the radiating phase of a symmetrical phylogeny (A) as during the declining phase. Many more will occur during a period of stasis at high diversity (B) than during the preceding radiating phase.

I am sure that I am not alone in previously having assumed that adaptive radiation accounts for most evolutionary transition partly because radiation is the site of rampant speciation. This is clearly not the case. The simple observations described above show that the total number of speciation events in radiation is not relatively large. Rather, the critical factor must be the high incidence of quantum speciation (large fraction of speciation events that are markedly divergent) at early stages of radiation. The reason that quantum speciation is distributed in this manner will be considered in the following chapter.

The parameter \bar{N} can be employed to evaluate more rigorously numbers of speciation steps within a radiating taxon. We will apply this method of estima-

tion to a typical family of Cenozoic mammals. This choice offers excellent opportunities for interpretation of results. Values of R are reasonably consistent among radiating families of mammals (Figure 5-2), so that the average value for R is accurately estimated as 0.22 My^{-1} . A chosen value of t , will yield a particular value of N . In the calculation of \bar{N} for a given initial interval of adaptive radiation (t), the only highly uncertain value will be that of E . The problem is that our estimate (page 108) is for total extinction (E'), and the degree to which the value of E is lower than this value will depend upon the incidence of pseudoextinction. As in the earlier estimation of S (Table 5-1), we can establish boundary conditions by employing maximum and minimum values for this incidence, as shown in Table 5-1, B for $t = 10$ million years. Clearly, there could not be so much pseudoextinction that as few as 10 total speciation events would have occurred, or so little that the number would exceed 40 (see, for example, Figure 4-11, where pseudoextinction represents slightly under 50 percent of total extinction). A liberal estimate would be that 25 speciation events would occur in a typical family of mammals during its initial 10 My of adaptive radiation.

From equation 5.2, it can be calculated that after 10 My of radiation, nine species will be extant. Another class of animals exhibiting a different value of R will, of course, attain a diversity of nine species after a different period of time. Let us ignore the time dimension, however, by focusing on mammals. In this way, we can direct our attention to the geometry of phylogeny, in order to examine numbers of speciation steps along single pathways. Figure 5-16 displays two hypothetical phylogenies representing the adaptive radiation of a family of mammals. For simplicity, each of these is constructed so as to be as nearly homogeneous and symmetrical as possible. In one, the number of speciation steps in each through-going pathway is 3. In the other, it is 13. These differing numbers of speciation steps and the differing durations of lineages in the two phylogenies reflect differing values of E , based on uncertainty about the incidence of pseudoextinction (Table 5-1). The two incidences of pseudoextinction illustrated (70 percent and 20 percent) are taken to bracket the typical value for mammals. Thus, Figure 5-16 indicates that, whatever the normal incidence of pseudoextinction may be, number of speciation steps along any pathway must be quite low.

In all the foregoing discussions, we have been considering homogeneous, symmetrical phylogenies. The only way in which phylogeny can deviate from such a pattern so as to yield a much larger number of steps is to follow a pattern resembling, to some degree, that shown in Figure 5-17. For the multistep pathway on the right of Figure 5-17 to form, a very unlikely set of conditions is required. It is necessary for every lineage of the sequence to have a high probability of speciation soon after forming, and then a low probability after producing one new lineage, even though the descendant lineage immediately has a high probability of speciating. If we make the reasonable assumption that probability of speciation for a full-fledged lineage is not heavily dependent on the age of the lineage, then it is very unlikely that a pattern like that of Figure 5-17 will

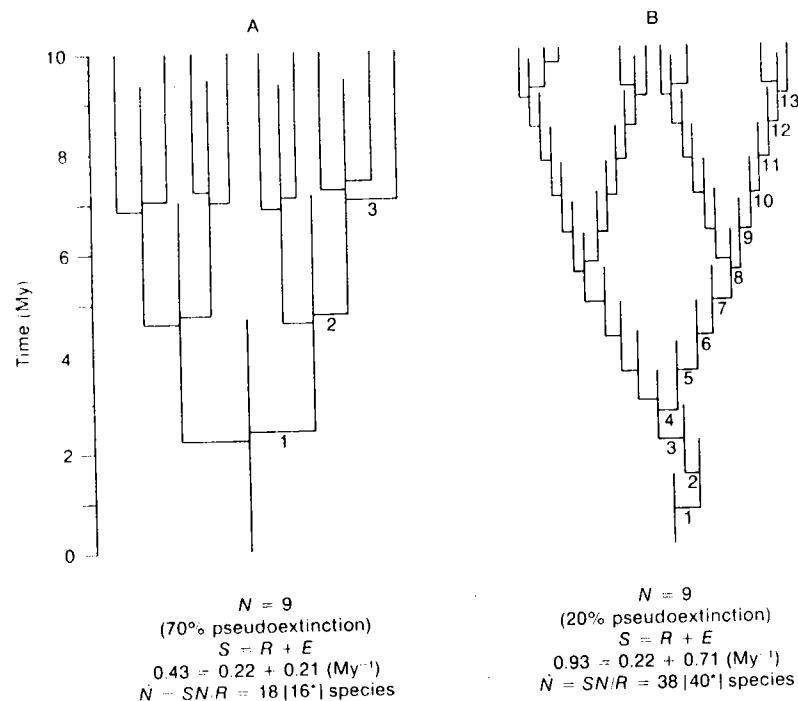


FIGURE 5-16

Nearly symmetrical and homogeneous hypothetical phylogenies depicting radiation at rates of speciation and extinction calculated for mammalian families. The two phylogenies display identical net values of R (both yield nine species in 10 My) but differ in rate of extinction according to boundary conditions established by varying the incidence of pseudoextinction (Table 5-1). Average number of speciation steps along a single pathway within actual mammalian families presumably lies somewhere between the numbers estimated here (3 and 13).

develop. Moreover, even the rather ridiculous phylogenetic pathway on the right of Figure 5-17 does not embrace a very large number of speciational steps.

The well-known phylogeny of the Elephantinae (Figure 4-11) represents a concrete example. By the time of its peak diversity, about 0.5 My ago, the subfamily had diversified from its origin, about 7 My ago, at a net rate of 0.33 My^{-1} . This value of R is relatively high even within the rapidly speciating Mammalia (Figure 5-2), yet no species can be shown to have more than four speciation events in its ancestry. Even if more than one speciation event is

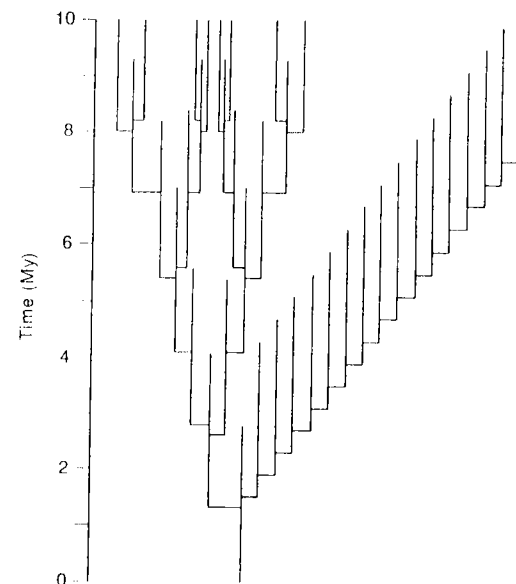


FIGURE 5-17

Hypothetical phylogeny in which a large number of speciation events form along one pathway. The pattern differs from Figure 5-16 in its asymmetry and a tendency in the right-hand segment for lineages to speciate only soon after they appear. Development of such a pattern is highly improbable.

allowed for the origin of the earliest known species, *Primelephas gomphotheroides*, no chain of lineages within the subfamily could include more than six or seven.

It seems clear that our estimated values for the parameters R , E , and S , with support from what is known of elephant phylogeny, impose severe constraints on the possible number of successional steps in mammalian radiation. We have used boundary values for E (Table 5-1) and a value of R derived from consistent empirical values (Figure 5-2). The results have great significance in part because it is in adaptive radiation that the most rapid sequences of speciation are to be found. Our conclusion, in effect, is that few speciational steps are available along a pathway in one radiating family for the origin of another family. The numerical constraint is further tightened by the observation that many speciation events are known to account for little divergence. These events are, in effect, wasted in terms of large-scale transformation.

The implication is that evolutionary transitions at the family level entail a small number of quantum speciation events. This conclusion extends to a higher taxonomic level the punctuational claim of the previous chapter that a typical genus forms by one or a small number of markedly divergent speciation steps. We must modify our view of the radiation of Pontian cockles (page 120) accordingly. Presumably here it was not simply number of speciation events but also a high degree of divergence per speciation event that led to the rapid formation of many new genera.

At the beginning of Chapter 4, it was observed that there may be a retrospective factor in the formal recognition of higher taxa (Figure 4-1). We may designate a clade as a discrete family only after it has diversified to a moderate degree. Nevertheless, the preceding paragraphs suggest that forms *deserving* status as families arise very quickly. The monophyletic nature of many transitions is indicated by the distinctive chromosomal patterns of many major taxa of plants and animals. These will be discussed in the following chapter.

Direct evidence is contributed by solitary lineages and clades of low diversity that represent discrete subfamilies and families of rather recent origin. Perhaps the most striking mammalian example is the giant panda, *Ailuropoda*, which will be discussed in the following chapter with reference to the origin of distinctive taxa by means of a small number of genetic changes. *Ailuropoda* evolved from a bear and certainly differs morphologically from living bears at what would normally be considered a family level. Only a desire to emphasize origin from bears rather than from raccoons led Davis (1964) to favor, mildly, status for *Ailuropoda* as a subfamily within the Ursidae. All recognized fossils of the family have been assigned to two species (including the living one) that belong to the extant genus (Pei, 1974; Wang, 1974). None are known from pre-Pleistocene deposits, although the fossil record in the region of the living representatives is admittedly not well known. Still, the absence of evidence of substantial diversification and antiquity, in combination with the simplicity of the genetic transformation underlying the bear-panda transition (page 158), leaves little doubt that very few speciation events were involved in the origin of the family or subfamily of the giant panda. In fact, it seems possible that a single event of quantum speciation accomplished the transition.

Another example, but one entailing only generic transition, is the origin of the white rhino, *Ceratotherium*, from the black rhino, *Diceros*. This event apparently occurred in Africa early in the Pliocene (Hooijer and Patterson, 1972; Hooijer, 1976). It had considerable adaptive significance because the white rhino is a grazer with high-crowned cheek teeth and a square lip, whereas the ancestral black rhino is a browser with low-crowned cheek teeth and a pointed lip (Figure 5-18). Only two species of white rhino are known. The living form, *C. simum*, extends back more than 3 My, and the apparently ancestral form, *C. praecox*, of the earlier Pliocene has a record spanning something like a million years and is intermediate between *Diceros* and *C. simum* in some morphologic characters. The transition from *C. praecox* to *C. simum* took place sometime between 3 and 4

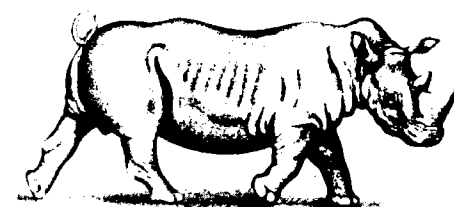


FIGURE 5-18
The African white rhino, *Ceratotherium simum* (above)
and the black rhino, *Diceros bicornis* (below). (From
Hutchinson, 1965.)

My ago, which is brief with respect to the longevity of the descendant species. Clearly, very few speciation events separate *Ceratotherium* from *Diceros*. The existing evidence points to just one.

It is interesting to consider whether the preceding calculations for families of mammals apply to the initial mammalian radiation of the Cenozoic, when many larger, ordinal transitions were occurring. The radiation of eutherian mammals that led ultimately to the ecologic replacement of the dinosaurs clearly began late in the Cretaceous, even though large body sizes did not develop immediately. This radiation continued into the Cenozoic without interruption at the close of the Cretaceous (Lillegraven, 1969). It is now apparent that the dominant groups of early Cenozoic mammals can be traced to a minimum of about three lineages existing early in the Maestrichtian, about 70 My ago (Figure 5-19). Let us then postulate a diversity of 1,000 species (about one-quarter of the number alive today) 15 My later, at the end of the Paleocene. Equation 5.2 yields a value of R for this radiation of 0.39 My^{-1} . Note that this is only about 75 percent higher

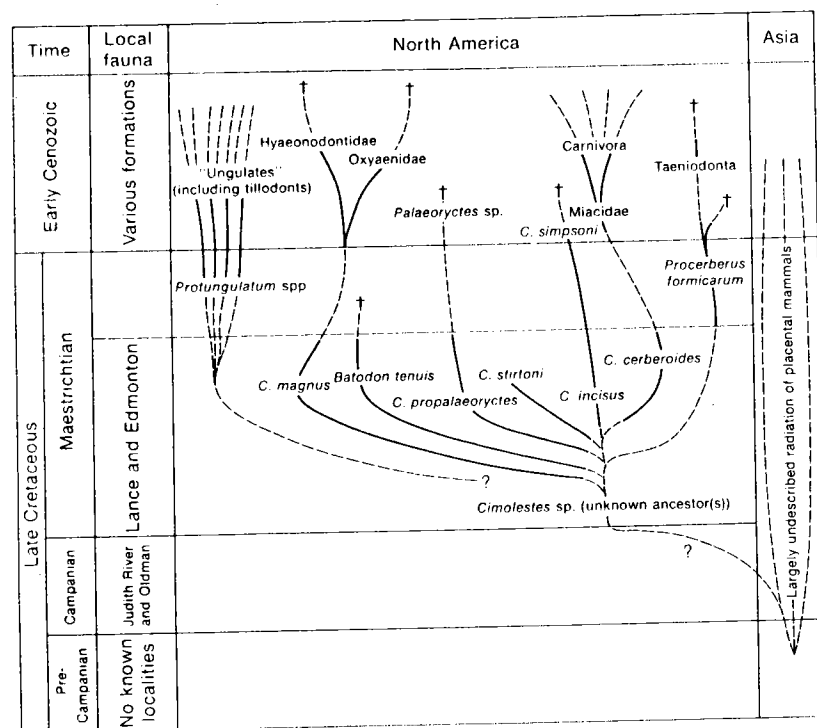


FIGURE 5-19 Interpretation of the early phylogeny of the placental mammals. The dominant modern groups may have shared a common ancestry in the Cretaceous. (From Lillegraven, 1969.)

than the average value for a family of mammals (0.22 My^{-1}), resembling the rate for the late Cenozoic murid rodents (Figure 5-2) and Elephantinae (Figure 4-11). In other words, speciation was perhaps not occurring at an exceptional rate by the standard of a modern subfamily or family, and there could not have been many speciation events in the ancestry of distinctive new orders.

Having calculated that phyletic evolution is generally too slow a process to contribute significantly to evolutionary transitions between higher taxa, we have now looked to speciation and found that few speciational steps are available in adaptive radiation for the piecemeal accomplishment of such transitions. This leaves us no recourse but to adopt a strongly punctuational view. In effect, these lines of evidence uphold the idea of Simpson (1944; 1953) that a higher taxon

typically arises rapidly through the occurrence of a sudden adaptive breakthrough. Ensuing diversification that takes place within the adaptive zone entered via the breakthrough is a matter of elaboration of the ancestral adaptive theme. Occasionally, a simple speciation event or a short succession of events produces such dramatic divergence that the resulting forms will be recognized as a new genus, subfamily, or family. Following some transitions of this type, including the origins of the giant panda and white rhino, adaptive radiation does not immediately ensue. In the latter examples, ecologic specialization or geographic confinement may have reduced opportunities for speciation. In other examples, such as the origin of the Elephantinae, the adaptive transition was followed by persistent radiation (Figure 4-11). In the elephants, the adaptive breakthrough seems to have been the evolution in the Pliocene of adaptations for processing high-fiber food. According to Maglio (1973, p. 87), "once established, the superbly adapted skull and dental complex underwent relatively minor (in a structural sense) alteration in response to selection pressures." Clearly, radiation of major new taxa from an existing taxon should be favored by the opportunity for rapid speciation within the potential ancestral group and by the tendency for speciation events to be markedly divergent. The nature of these optimal conditions will be speculated upon in the chapter that follows.

As a final point, I wish to dispel what might seem to be an inconsistency or paradox. In this section I have concluded that, in the inception and transformation of a clade, it is the incidence of quantum speciation that is most important, not the number of speciation events. This is true because the anatomy of a clade is inhomogeneous: Quantum speciation occurs with greatest relative frequency at the outset. On the other hand, early in the chapter, in the comparison of mammals and bivalve mollusks, I related rate of large-scale evolution to rate of speciation in adaptive radiation and, more specifically, to number of speciation events (N). In such a comparison, however, *totally different* clades are being compared. Early in radiation, when the incidence of quantum speciation is highest, many more speciation events typically occur in a radiation of the Mammalia than in a radiation of the Bivalvia. Thus, in the comparison of taxa characterized by different rates of speciation and extinction, rate of large-scale evolution *does* relate to number of speciation events.

SUMMARY

Adaptive radiation, the site of most evolutionary change, entails geometric, or exponential, increase in number of species. Just as per capita birthrate in a population equals net per capita rate of population growth plus per capita death rate, speciation rate in adaptive radiation (S) equals fractional rate of increase in diversity (R) plus extinction rate (E). The value of R can be estimated for a

presently radiating taxon from (1) the number of living species within the taxon and (2) the time interval for the radiation (both of which we commonly know, to a good approximation). Mean extinction rate for a higher taxon can be estimated as being the inverse of mean lineage duration. The latter can be estimated by doubling the geologic age of faunas comprising 50 percent extant species. This is imprecise, in part because some species go extinct by phyletic transition, but boundary conditions for the value of E can be established by specifying various percentages of pseudoeextinction. Rate of speciation (S) can be estimated as the sum of R and E . Values of these parameters are much higher in the Mammalia than in the Bivalvia. As would be expected, rates of large-scale evolution are also much higher in the Mammalia. Not surprisingly, exceptionally high rates of speciation of cardiid bivalves in the Pontian Sea yielded extraordinary rates of evolution.

Clades that have existed for long intervals of geologic time at low diversity (with little speciation) invariably exhibit little evolutionary change (are so-called living fossils). This correlation is highly improbable in the framework of the gradualistic model but is predicted by the punctuational model. Because modal rates of phyletic evolution are very slow (as demonstrated in Chapter 4), living fossils are simply the extant members of lineages that happened to have survived for relatively long intervals at normal rates of phyletic evolution. They are not the problematic products of extraordinary phyletic stagnation, as traditionally envisioned.

Calculated rates of speciation and extinction show that only short chains of speciation steps are available in adaptive radiation for the production of new families. This inference is supported by specific examples, such as the phylogeny of the elephants and the origin of the giant panda. No more speciation events are available in the radiating phase of clade development than in the declining phase, and the total rate of speciation in a clade of high, constant diversity is higher than the rate for the radiation leading to this high diversity. We must conclude that major adaptive transitions are typically accomplished by few quantum speciation events and that these tend to occur early in radiation. It can be estimated that fractional rates of speciation early in the Cenozoic diversification of the Mammalia, when many ordinal transitions were occurring, were not greatly higher than fractional rates within families that are radiating today. This estimation suggests that even ordinal transitions are accomplished by few speciation steps. Thus, it is only in the comparison of different kinds of clades (such as families of mammals versus families of bivalves) that rate of speciation explains differences in rates of evolution. Within a clade, it is the uneven distribution of quantum speciation that determines the location of rapid transformation.