Chapter 7

EVOLUTIONARY RATES AND TRENDS

If natural selection is acting constantly, "daily and hourly scrutinising," to use Darwin's phrase, why do many species accumulate comparatively little evolutionary change over geologic time?

Why do some kinds of species live for greater spans of geologic time than others? For example, why do species of snails whose larvae feed on plankton often endure longer than species with nonfeeding larvae?

Why do many higher taxa exhibit striking evolutionary trends over time? For example, why are many groups of mammals larger in body size today than they were at their time of origin tens of millions of years ago?

These and many other fundamental questions in paleontology are informed by the study of evolutionary rates and trends. Put another way, we would like to know where evolution is headed, how fast it is getting there, and why. In this chapter, we focus on methods used to study rates and trends, illustrating them with case studies that provide some preliminary answers. The questions remain open for the most part, but the tools discussed here will be essential to students of paleontology who hope to address them.

7.1 MORPHOLOGICAL RATES

By the **morphological rate** of evolution we mean the rate of change of one or more anatomical traits, typically represented by quantitative measures. We commonly distinguish morphological rates and trends as **phyletic** versus **phylogenetic** (Figure 7.1). Phyletic change, also known as **anagenetic** change, occurs within a single species-level lineage. Phylogenetic change pertains to the more inclusive clade: Without reference to the evolutionary relationships within the clade, how rapidly and in what direction is the average form changing? Phyletic or anagenetic change also stands in contrast with **cladogenesis,** the splitting of lineages [SEE SECTION 3.3]. Phyletic evolution and cladogenesis are the two elements that give rise to phylogenetic patterns [SEE SECTIONS 7.3 AND 7.4].

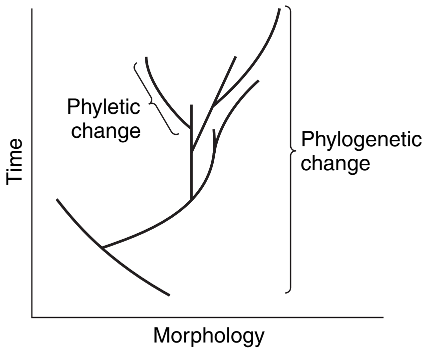

FIGURE 7.1 Phyletic versus phylogenetic change. Each line represents a single species-level lineage within a larger clade.

Nature and Measurement of Morphological Rates

In a mathematical sense, the rate of change of a trait is equal to the slope of the curve that tracks the trait as a function of time; in other words, it is the first derivative of the curve with respect to time (Figure 7.2a). Such a rate is comparable to the speed we estimate by glancing for a moment at an automobile's speedometer. Paleontological

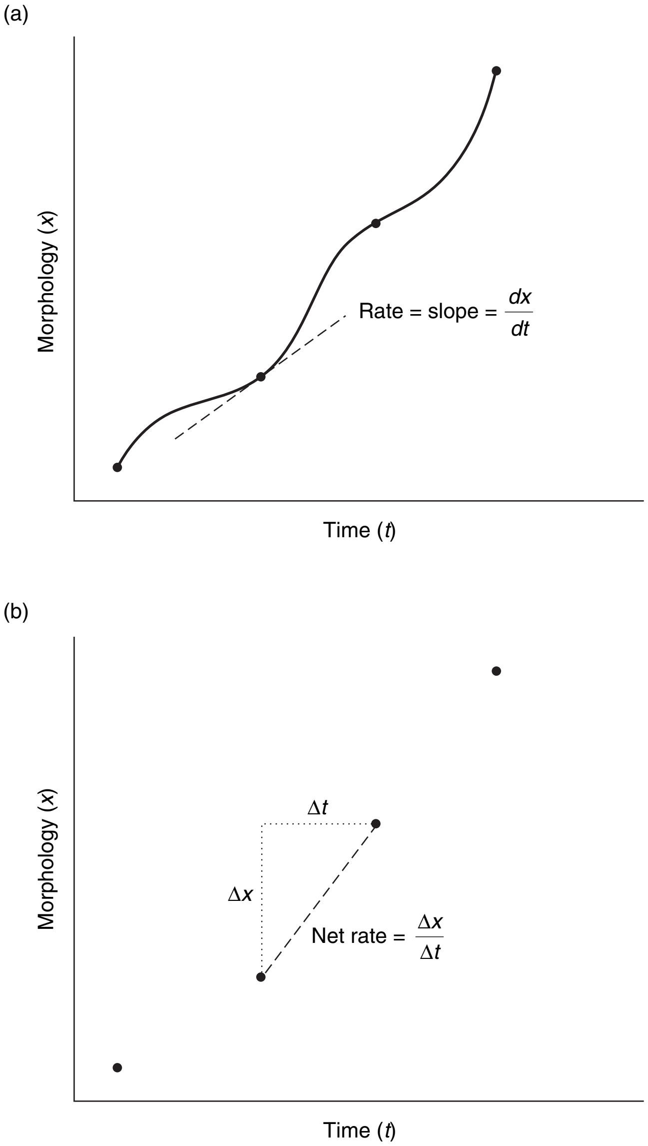

FIGURE 7.2 Calculation of evolutionary rates. (a) If change could be sampled continuously, the rate would be the slope of the curve at any point, in other words, the first derivative of the trait with respect to time, $\frac{dx}{dt}$. (b) In reality, the rate must be computed from the net change (Δx) over some elapsed time (Δt).

sampling is discontinuous in time, however. This reflects both gaps in the record and the discrete nature of sampling units, from beds up through stratigraphic zones and stages. Thus, it is generally not possible to observe evolutionary change at an instant in time. Instead, for a trait x, we observe a net change, Δx, over some interval of elapsed time, Δt (Figure 7.2b). Measuring rates of evolution, therefore, is not like checking a speedometer. Rather, it is akin to estimating an automobile's speed from the time and distance between a few mileposts, knowing nothing about acceleration, coffee breaks, the details of the route, or time spent driving slowly through construction zones.

Given the net change and elapsed time, how we estimate the rate of change depends on how evolution is assumed to proceed between the sampled points. Consider two possible models of the evolution of a trait such as body size. In the first, we assume that the **absolute rate** of evolution in some lineage is constant—for example, body mass at g grams per million years. In this model, the lineage will evolve in Δt million years from size x_1 to size x_2, such that $x_2 = x_1 + g\Delta t$ (Figure 7.3a). The pattern of change will be linear over time. Assuming this model, we would estimate the rate from observed data as $g = (x_2 - x_1)/\Delta t$, or $g = \Delta x/\Delta t$.

In the second model, we assume that the **relative rate** or **proportional rate** of evolution is constant at a value r, such as 10 percent per million years. The process is a multiplicative one, in which the evolutionary increments in the trait are larger when the trait is larger. This leads to exponential change in which the lineage evolves from size x_1 to size x_2, where $x_2 = x_1 \times e^{r\Delta t}$ and e is the base of natural logarithms (Figure 7.3b). Under this model, we would estimate the rate of evolution as $r = \ln(x_2/x_1)/\Delta t$, where ln denotes the natural logarithm. (Unless otherwise noted, logarithms referred to herein are natural logarithms.)

To emphasize proportional rather than absolute differences, traits are measured on a logarithmic scale [SEE SECTIONS 2.3 AND 8.3]. On this scale, an increase in size of 50 percent in a million years would represent the same rate of evolution whether the lineage were evolving from 10 to 15 g or from 100 to 150 kg. Because $\ln(x_2/x_1)$ is equal to $\ln(x_2) - \ln(x_1)$, the rate r can also be expressed as $[\ln(x_2) - \ln(x_1)]/\Delta t$. If we compare this with the estimate of the absolute rate of change, $g = (x_2 - x_1)/\Delta t$, we see that measuring a proportional rate of change is the same as measuring the absolute rate if the trait values have first been transformed to logarithms. In other words, if the trait is measured on a logarithmic scale, a constant proportional rate yields linear change between sampled points (Figure 7.3c). For many biological problems, it makes sense to think of logarithms as a natural scale of measure rather than as a transformation of arithmetic measures.

The validity of the two models of change depicted in Figure 7.3 could not be tested if, as in that figure, the evolving trait were observed at only two points in time. To evaluate the assumed model of evolution, it is necessary to turn to sequences in which the trait is observed in many successive time intervals. For example, Figure 7.4a shows

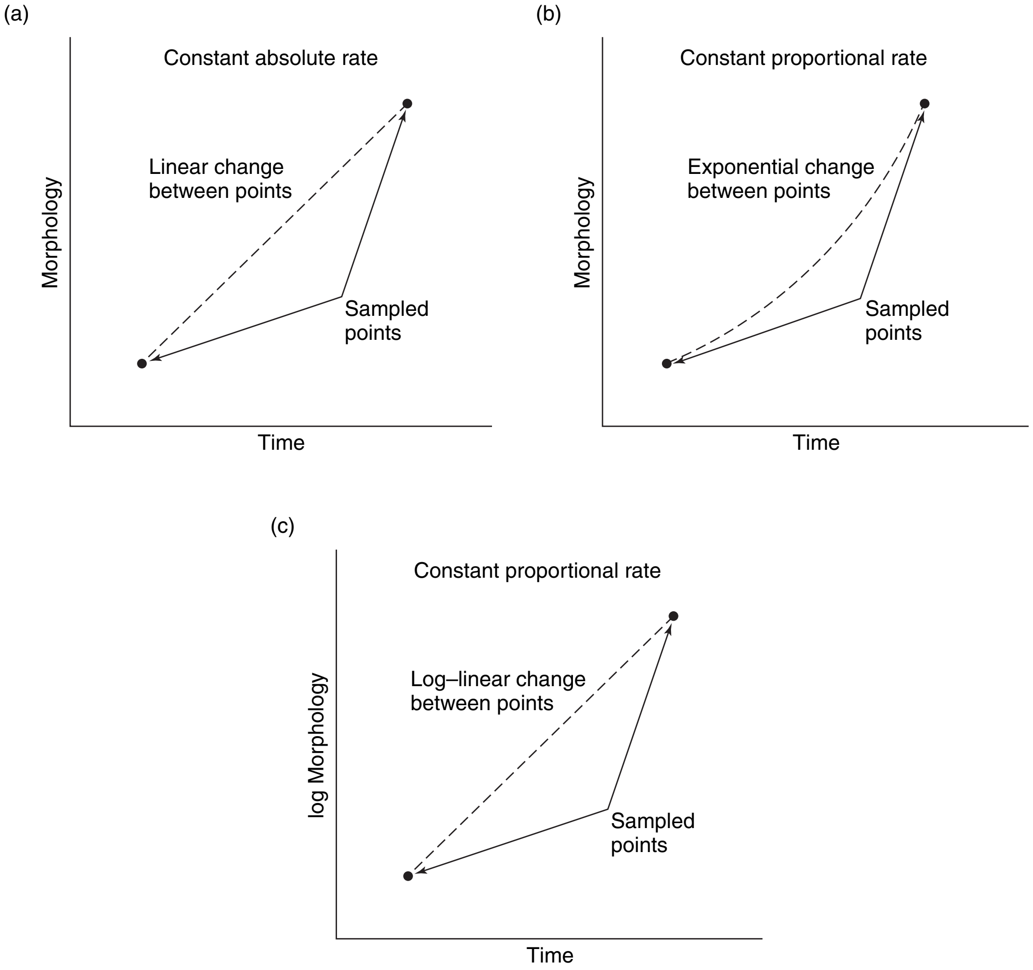

FIGURE 7.3 Change at (a) constant absolute rate versus (b and c) constant proportional rate. Change at a constant proportional rate is linear if the trait is measured on a logarithmic scale (c). The dashed line in each graph shows the assumed pattern of change between sampled points.

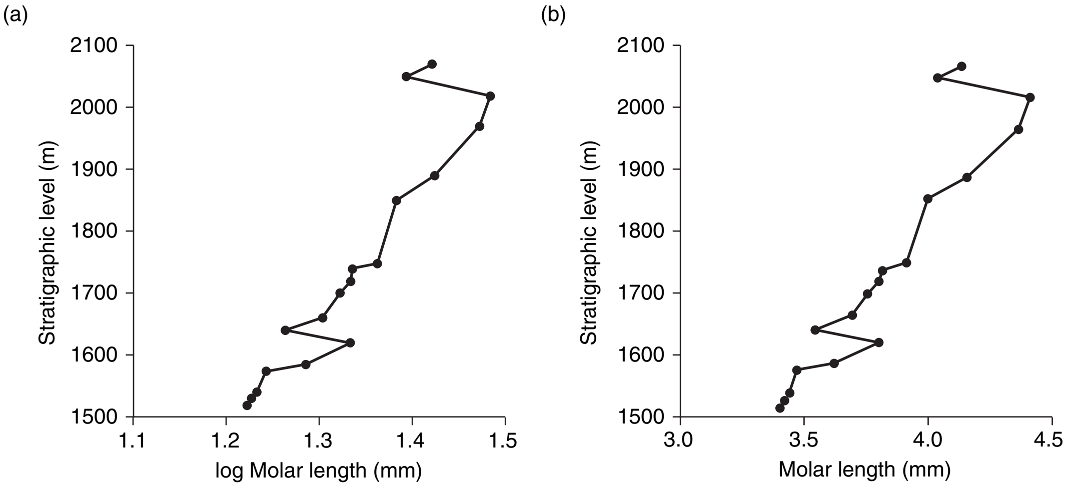

FIGURE 7.4 Evolution of size, based on the length of the upper right first molar, in a succession of chronospecies of the Eocene primate *Cantius* from Wyoming. Stratigraphic position is in meters above the base of the section. The elapsed time is about 1.5 m.y. The points show sample means. Part (a) depicts the logarithm of molar length, and part (b) depicts molar length on a linear scale. Because the net change is small, there is little difference between the patterns on logarithmic versus linear scales. *(Data from Clyde & Gingerich, 1994)*

an evolutionary sequence of molar tooth size in the Eocene primate *Cantius* over a span of about 1.5 million years. The sequence consists of a succession of five chronospecies [SEE SECTION 3.3] that make up a single evolutionary lineage. Molar length is measured on a logarithmic scale, and a line could reasonably be fit through the sequence of points. This would seem to justify the model of constant proportional change as opposed to the alternative of constant absolute change. In this instance, however, we cannot say with confidence which model is better supported. This is because the accumulated change is relatively small, with the result that the graph would not look very different if molar size were measured on an arithmetic scale, as in Figure 7.4b.

This example is rather typical. When the proportional rate of change is small and the elapsed time is relatively short, the multiplicative nature of proportional change is not very striking. The difference between arithmetic and logarithmic measures generally becomes important when we study evolution on longer timescales, however, and when we wish to compare the evolution of organisms that vary greatly in size.

The biologist J. B. S. Haldane (1949) suggested a standarized unit of measure for proportional rates of change, the *darwin* (denoted d), where one d is equal to one natural logarithmic unit per million years (m.y.). For example, a doubling of size in 2 m.y. would correspond to a rate of $\ln(2)/2$, or $0.346d$. Figure 7.5 shows the variation in rates of size change within a group of related species of Eocene mammals, with a "darwinometer" to allow easy visual assessment of the rates. Even in this rather homogeneous group of species, evolutionary change varies substantially in rate and direction. Such variation is indeed one of the most general results that has come from the study of evolution in the fossil record.

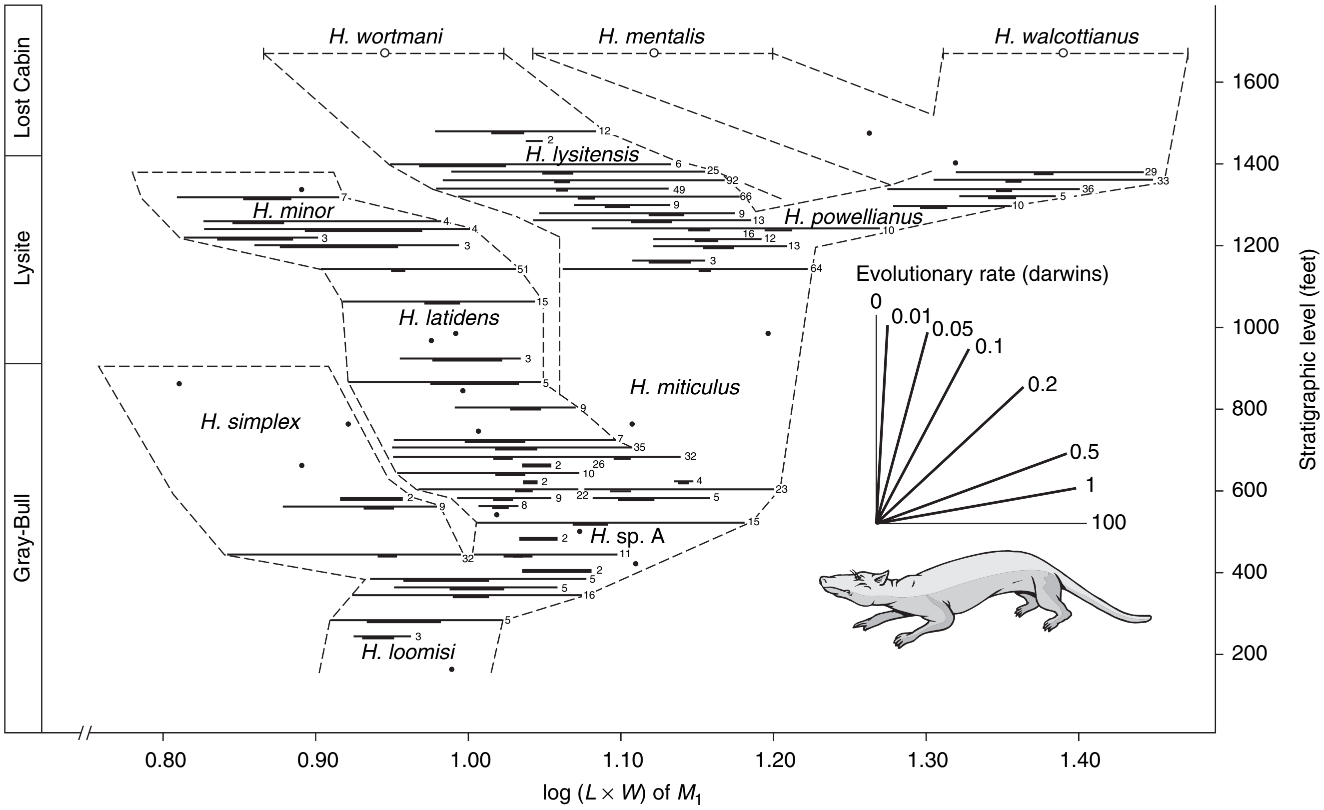

FIGURE 7.5 Evolutionary change in size of the lower right first molar in the mammal *Hyopsodus* from the Eocene of Wyoming, represented as the base-10 logarithm of the product of length and width (in millimeters). Stratigraphic position is shown as height in the section. The total elapsed time is about 5 m.y. For each sample, the light bar shows the range of values and the heavy bar the standard error of the mean. Number of specimens is given to the right of the light bar. Solid dots indicate single specimens. Open circles and dashed lines at the top are estimated means and ranges for species poorly sampled in this section but known from elsewhere. Net evolutionary rates can be assessed by comparing the slope of the line connecting two sample means with the reference slopes of the "darwinometer." *(From Gingerich, 1974)*

Two other considerations suggest an alternative measure of evolutionary rate. First, the raw material for evolution is heritable variation within populations [SEE SECTION 3.1]. The greater the variation, the greater is the potential for evolution. Think of two populations that undergo the same change in average size, Δx, via natural selection. If one of the populations has twice the variation of the other, then it requires only half the selection pressure to move its average by Δx. Second, the generation is a natural measure of time for evolving populations because new genetic variants and genetic combinations stem largely from gamete formation and reproduction. Paleontologist P. D. Gingerich (1993) has therefore proposed that rates be measured in terms of standard deviations per generation. Thus, the rate of evolution would be expressed as $(\Delta x/s)/(\Delta t/t_g)$, where s is the standard deviation [SEE SECTION 3.2] of the trait value within a fossil population, Δt is the elapsed time in years, and t_g is the generation time, also in years.

Rates of evolution on the order of 0.1 standard deviation per generation are typical of modern populations. In practice, generation time is approximated in a number of ways for living organisms, such as the average time span between the birth of an organism and the production of its offspring. For extinct species, generation time is unknown, although it is often possible to approximate it using close living relatives.

We have discussed some assumptions of the three principal ways of measuring morphological rates: as change in arithmetic measures over time, as change in logarithmic measures over time, and as change in standard deviations per generation. There is an additional, tacit assumption underlying all of these measures. By their very nature, they compare net change to elapsed time (Figure 7.2). This approach is ideal only if the rate and direction of change are persistent over the time represented by the net change. Consider a hypothetical evolutionary sequence of body mass: 10 g, 15 g, 10 g, 15 g, 20 g. This sequence shows reversals in the direction of evolution. Thus, the net doubling of size from start to finish does not give a good idea of how rapidly evolutionary change can occur on shorter timescales.

Temporal Scaling of Morphological Rates

We just saw with a hypothetical example that reversals in the direction of evolution may lead to lower net rates as evolutionary change is studied over longer spans of time. There are abundant empirical data confirming that longer time spans do in fact yield lower net rates on average. Figure 7.6a depicts several hundred net rates measured on timescales ranging from days to millions of years. Evidently, the longer the time span over which rates are measured, the lower is the net rate of change on average. This should not be the case if rate and direction are constant. If the rate and interval data of Figure 7.6a are plotted on logarithmic axes, a linear relationship results, with a slope near -1 (Figure 7.6b). These figures depict rates in darwins, but other rate measures yield a similar relationship between net rate and interval length.

The highest rates that have been measured—on the order of 1000 darwins—are for artificial selection experiments in the laboratory and rapid changes in modern populations. These are so large that, if sustained, they could in principle change something the size of a mouse into something the size of an elephant in much less than one million years. Yet sustained changes at such high rates are not in fact observed; net change does not increase in direct proportion to the amount of elapsed time.

Figure 7.6 also shows that very low rates are generally not recorded over short intervals of time. This is because the amount of change produced would be so small as to be essentially undetectable.

There are two principal reasons for the inverse relationship between net rates and the length of time over which they are measured. The first is biological. As already discussed, longer intervals of time tend to incorporate frequent reversals of direction (Figure 7.4). The second is a mathematical necessity. Rate measures have Δt in the denominator; that is to say, they are proportional to $1/(\Delta t)$. Thus, unless the elapsed change increases in proportion to Δt, a plot such as Figure 7.6 will tend to have the form of Δt versus $1/(\Delta t)$, which contributes to an inverse correlation. The relative importance of these two factors has not yet been determined; to do so would represent a most significant advance for paleontology.

The dependence of net rates on the length of time over which they are measured implies that meaningful comparisons—such as whether some species evolve more rapidly than others, or whether different morphological traits evolve at different rates—must be based on rates measured over the same amount of elapsed time. If we compare the rate for a fossil species over a million years with that for a living species from one year to the next, we will almost certainly find a lower rate for the fossil species, simply because the net rate is calculated

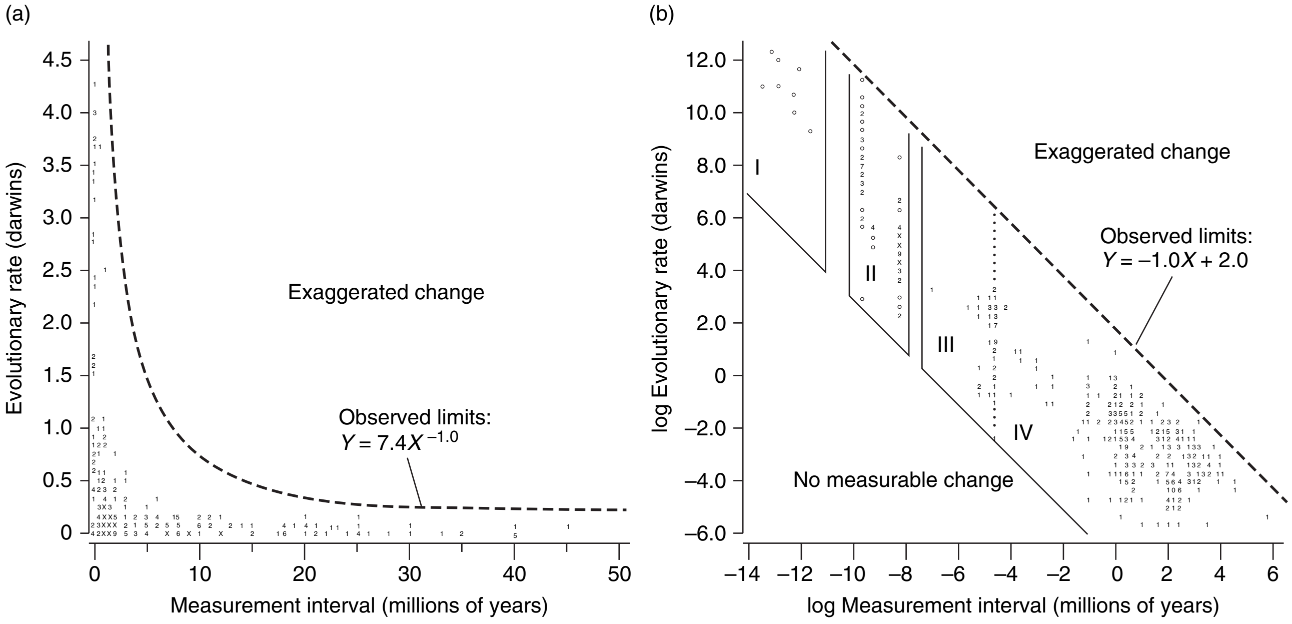

FIGURE 7.6 The relationship between evolutionary rate in darwins and the interval of time over which the change is measured. The graphs summarize over 500 calculated rates. Digits indicate the number of observations falling at that location on the graph; *X* denotes 10 or more observations. (a) The middle part of the whole distribution shown on linear axes. (b) The entire distribution shown on logarithmic axes. The field marked I shows rates for laboratory selection experiments; II is for colonization events in historical time; III is for evolutionary change following the Pleistocene glaciation; and IV is for paleontological observations. *(From Gingerich, 1983)*

over a longer time span. Of course, if we compare coeval lineages from the same sedimentary beds, or different traits within the same lineage, the problem of temporal scaling disappears.

7.2 TAXONOMIC RATES

By **taxonomic rates** of evolution, we mean the rates at which new lineages originate and existing lineages become extinct. Consistent with our use of the term *speciation* in Chapter 2, origination refers to the splitting of lineages and extinction to their termination. We will generally speak of taxonomic rates for species, but they can also be studied for more inclusive taxa.

The rate of extinction, typically symbolized *q,* is generally thought of on a **per-capita** basis, meaning that the number of extinctions is scaled to the number of lineages at risk and to the amount of time they are at risk. A useful way to express this rate is as the number of extinction events per lineage-million-years (Lmy). This quantity is analogous to person-hours; five species that each live for 2 m.y. collectively span 10 Lmy, as does a single species that lives for 10 m.y.

Figure 7.7 illustrates this concept with a set of hypothetical lineages over a span of 10 m.y. The solid vertical lines show their durations within this interval, and the broken line indicates a partial duration outside the interval. The sum of Lmy for this interval is 43, and there are 14 extinctions within the interval. The rate of extinction is therefore 14/43, or 0.33 per Lmy. The rate of origination, denoted *p*, is defined in an analogous way as the number of origination events per Lmy. In this example, there are 13 originations, so the origination rate is 13/43, or 0.30 per Lmy.

It is also evident from Figure 7.7 that the mean duration, that is, the sum of durations divided by the number of lineages, is equal to 43/14, or 3.1 m.y. Clearly, this is simply the inverse of the extinction rate. In general, for a group of lineages that are all extinct, the mean duration is equal to $1/q$, and the extinction rate can therefore be estimated as the inverse of the tabulated mean duration.

Species durations of paleontologically important groups are typically on the order of 1 to 10 m.y., but these may vary from less than 100,000 years up to 20 m.y. or more. The typical species extinction rate—the inverse of mean duration—therefore generally varies

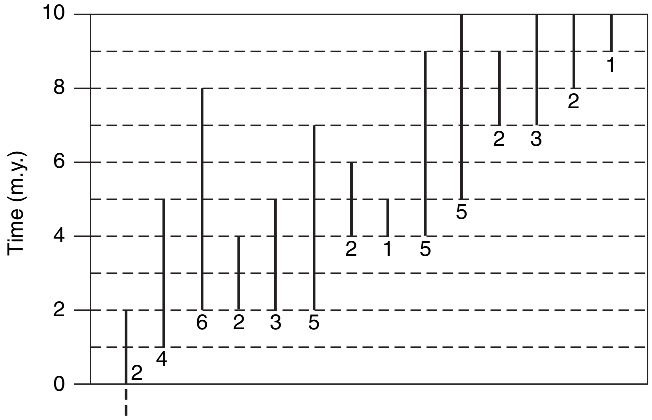

FIGURE 7.7 Hypothetical species through a 10-m.y. interval of time. The duration within the interval is shown near the base of each lineage. The number of lineage-million-years (Lmy) in this interval is the sum of durations, in this case, 43 Lmy. The dotted line at the base of the leftmost lineage indicates that it existed prior to this interval of time; this part of the duration is not counted in the tabulation. There are 13 originations and 14 extinctions in this interval. Thus, the origination and extinction rates would be 13/43 and 14/43, or 0.30 per Lmy and 0.33 per Lmy.

from about 0.1 per Lmy to 1.0 per Lmy. Genus durations typically vary from about 5 to 50 m.y., but there are long-lived genera that span well over 100 m.y.

If the per-capita extinction rate is the same for all species within a group and is also constant over time, then a constant *proportion* of the standing crop of species, rather than a particular absolute number of them, will become extinct in every unit increment of time. The proportion of species that survive *at least* to a duration of T will be equal to e^{-qT}. This fundamental relationship of **exponential survivorship** is depicted schematically in Figure 7.8a, which shows the duration on the x axis and the expected proportion of species with at least the given duration on the y axis. If the y axis is scaled logarithmically (Figure 7.8b), then a straight-line relationship results, and the magnitude of the slope of this line is equal to the extinction rate. This is analogous to the process of radioactive decay: If the amount of remaining parent material is plotted semilogarithmically against time, a linear relationship results, and its slope gives the decay constant.

Because distributions of durations tend to be skewed, with many short-lived taxa and a few that are long-lived, it is good practice to tabulate the median duration in addition to the mean [SEE SECTION 3.2]. Exponential survivorship implies that the median duration, or **half-life,** is equal to $\ln(0.5)/q$. Thus, another way of estimating the extinction rate is as $\ln(0.5)/T_{1/2}$, where $T_{1/2}$ is the tabulated median duration. This approach to rate estimation and most of the methods that we present below are underlain by the model of exponential survivorship.

Long-Term Characteristic Rates for a Biologic Group

Methods for estimating taxonomic rates of evolution all depend to some extent on **taxonomic survivorship analysis,** the statistical study of the durations of taxa. Many approaches to survivorship analysis have been developed. We present just a few simple and general methods as examples.

In contrast to the view in Figure 7.7, we often know only the broad intervals of first and last appearance of each

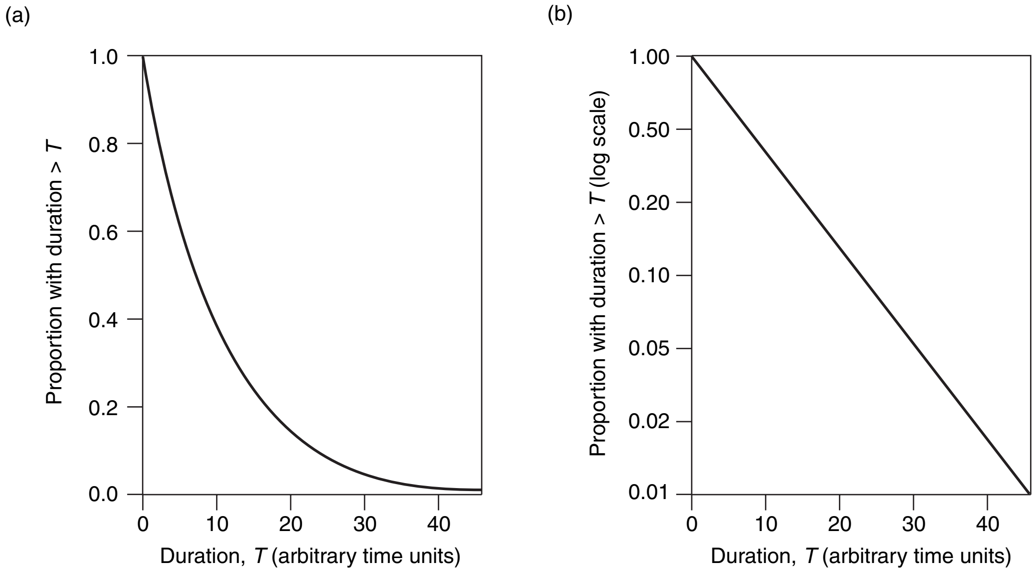

FIGURE 7.8 Exponential survivorship. The proportion of species with duration at least equal to T declines exponentially with T. This gives a hollow curve in (a) linear coordinates, or a straight-line relationship when proportion of species is expressed (b) logarithmically. The magnitude of the slope of the line in part (b) is the extinction rate.

lineage, not precisely when during each interval these events took place. This allows us to specify only a range within which the actual duration falls. Fortunately, several survivorship methods take advantage of the fact that minimum duration can often be specified accurately.

Dynamic Survivorship Analysis As we have already seen, the probability that a species will live at least to a duration T is equal to e^{-qT} (Figure 7.8). This reflects what is known as the cumulative probability distribution: the proportion of species with a duration of T *or longer.*

To use this relationship to estimate rates, we first tabulate species durations and construct from them the observed frequency distribution in the form of a **survivorship table.** Table 7.1 depicts survivorship data for species of North American Cenozoic mammals. This represents an unusual example, because the durations are specified to the nearest million years; temporal resolution is typically coarser than this. The data are depicted in two ways: as the number of species with a given duration and as the cumulative number with at least that duration. We express the frequencies on a logarithmic scale, then fit a line to the cumulative distribution (Figure 7.9a). Here the slope is −0.458; that is, the extinction rate is 0.458 per Lmy. The corresponding mean duration is 2.18 m.y. Such a figure would generally be reported in rough terms as 2.2 m.y. or even simply 2 m.y.

Since the expected proportion of species with duration T or longer is equal to e^{-qT}, the expected proportion with duration between T_1 and T_2 is equal to $e^{qT_1} - e^{qT_2}$. This is referred to as the *differential proportion*, *raw proportion*, or simply the *proportion* to distinguish it from the cumulative proportion. An important property of exponential survivorship is that both the differential and cumulative proportions are expected to yield log–linear relationships with slope equal to the extinction rate. Fitting a line to the raw proportions in Table 7.1 yields a slope of −0.476, which is not very different from the value of −0.458 for the cumulative proportions.

Figure 7.10 shows another example of dynamic survivorship analysis, here for Paleozoic crinoid genera. The genera are divided into two groups: subclass Camerata, all of which possess fine extensions of the arms called *pinnules*; and nonpinnulate members of the remaining Paleozoic subclasses. This division was chosen to reflect an important functional difference. Crinoids are filter-feeders [SEE SECTION 5.2]; pinnulate crinoids, because they form finer filtration fans, depend on higher current speed to feed effectively. Nonpinnulate crinoids, on the other hand, can feed in either fast or slow currents. In effect,

TABLE 7.1

Survivorship Table for North American Cenozoic Mammal Species

Duration (m.y.)	Number	Proportion	Cumulative Number	Cumulative Proportion
0–1	1718	0.584	2941	1.000
1–2	429	0.146	1223	0.416
2–3	331	0.113	794	0.270
3–4	200	0.068	463	0.157
4–5	91	0.031	263	0.089
5–6	64	0.022	172	0.058
6–7	38	0.013	108	0.037
7–8	31	0.011	70	0.024
8–9	14	0.0048	39	0.013
9–10	6	0.0020	25	0.0085
10–11	7	0.0024	19	0.0065
11–12	2	0.0007	12	0.0041
12–13	5	0.0017	10	0.0034
13–14	3	0.0010	5	0.0017
14–15	1	0.0003	2	0.0007
16–17	1	0.0003	1	0.0003

SOURCE: Alroy (1994b)

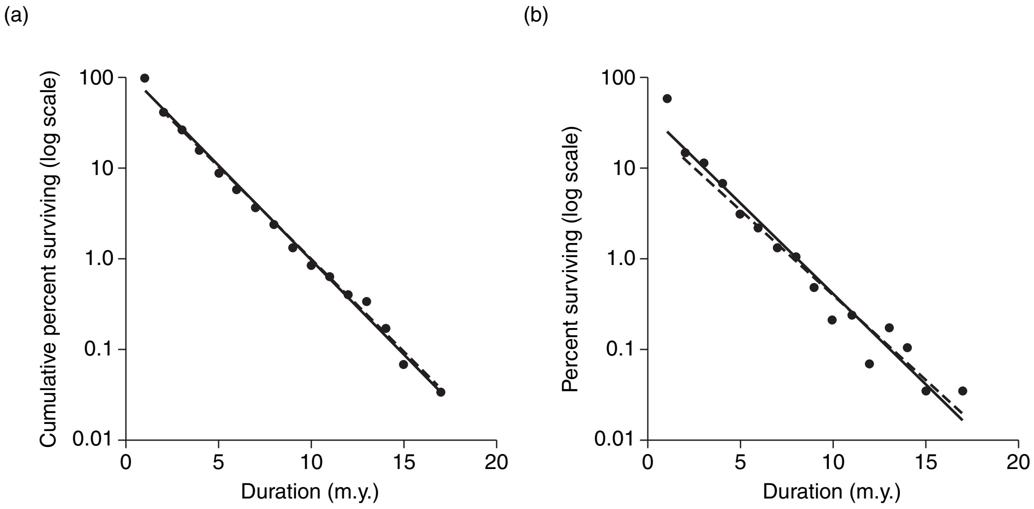

FIGURE 7.9 Dynamic survivorship analysis of Cenozoic mammal species from North America. Data are proportions from Table 7.1, converted to percentages. (a) Points show the percent of species with duration at least as long as the given value. (b) The percent with duration equal to the given value. The solid lines are fitted to the survivorship data; their slopes give estimates of the extinction rate. The dashed lines are fitted to all points except the left-most; these are explained in Box 7.2. *(Data from Alroy, 1994b)*

then, the pinnulate crinoids are ecologically more specialized. The survivorship curves show that nonpinnulate crinoid genera have an average duration nearly twice that of camerates—a difference that has been interpreted to reflect the degree of ecological specialization. The camerates, with stricter environmental requirements than nonpinnulates, may be more susceptible to extinction due to the loss of their preferred habitats.

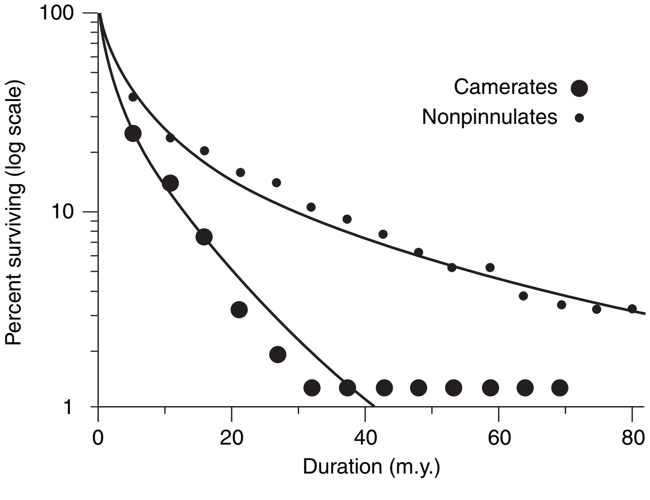

FIGURE 7.10 Dynamic survivorship analysis of Paleozoic crinoid genera. There are 245 genera of camerates and 324 genera of nonpinnulate crinoids. The points give percent of genera with duration at least as long as the time indicated, and curves are fitted to these points. Curves are nonlinear, indicating that the probability of genus extinction is not constant through the lifetime of a genus. *(From Baumiller, 1993)*

The curves in Figure 7.10 exhibit a feature often seen in the survivorship of genera and other taxa above the species level. These survivorship curves are apparently not log–linear. They become shallower with increasing duration, which means that the probability of extinction per unit time interval decreases as a genus becomes older. In other words, the longer a genus lives, the greater its chance of surviving yet another increment of time (Box 7.1). This pattern of age-dependent survivorship largely reflects the fact that older genera tend on average to contain more species and therefore to be less susceptible to extinction.

The method of dynamic survivorship analysis assumes that the full distribution of durations can be sampled. One of the main violations of this assumption occurs when the taxonomic group is young. A group that originated 10 m.y. ago, for example, can only have species with durations between 0 and 10 m.y. Also, as we discuss in Chapter 8, certain intervals of geologic time are marked by unusually high rates of extinction. Mass extinction events, as well as the periods of rapid origination that follow them, can keep the duration distribution from reaching a stable point.

Cohort Survivorship Analysis We just saw that dynamic survivorship ideally requires a distribution of taxonomic ages that is not changing over geologic time: For the sake of analysis, all taxa with a given duration are classed together regardless of when they lived. If the age distribution changed over time, this could present problems for the dynamic method. We can avoid these

Box 7.1

GENUS SURVIVORSHIP

Genus-level survivorship curves such as those of Figures 7.10 and 7.12 are typically nonlinear even on a semilogarithmic graph. The expected form of this nonlinearity can be determined with some simple mathematical modeling (see Raup, 1985). Assume that each genus originates with a single species at time $t = 0$, and assume that the species-level extinction rate (q) and the rate of origination of new species within the genus (p) are both constant. This last rate ignores those speciation events that give rise to new genera. Let $P_{s,T}$ be the probability that a genus survives *at least* until time $t = T$. Then

$$P_{s,T}\begin{cases} \dfrac{1}{1 + pT} & \text{if } p = q \\[2ex] \dfrac{(p - q)e^{(p-q)T}}{pe^{(p-q)T} - q} & \text{if } p \neq q \end{cases}$$

In practice, genus survivorship curves such as those of Figures 7.10 and 7.12 are produced with specialized curve-fitting techniques that yield the best-fit values of p and q (see Foote, 1988). Thus, by assuming a model of evolution—namely, that genera are monophyletic or paraphyletic and that species rates are constant—we are able to infer species-level rates even though the observed data are resolved only to the genus level.

problems by not combining taxa that lived at different times; this is the rationale behind **cohort survivorship analysis.** A cohort is a group of species or other taxa, all of which originated during a given time interval. A cohort is followed forward over geologic time, and the number of taxa still remaining is monitored as a function of elapsed time. Under the model of exponential survivorship, the expected proportion of taxa still extant at a time T after the origin of the cohort is equal to e^{-qT}. Therefore, the slope of a straight-line fit to a cohort curve on a semilog graph gives an estimate of the extinction rate. A different form of survivorship curve is expected for taxa above the species level (Box 7.1).

Table 7.2 presents just the first five lines of a cohort survivorship table for Cenozoic mammals; the data here are from the same source as Table 7.1. For example, of the

TABLE 7.2

Partial Cohort Survivorship Table for North American Cenozoic Mammal Species

Interval of Cohort Origin	Cohort Size	Number Extinct during Interval										Number Surviving at End of Interval									
		65	**64**	**63**	**62**	**61**	**60**	**59**	**58**	**57**	**56**	**65**	**64**	**63**	**62**	**61**	**60**	**59**	**58**	**57**	**56**
65	54	24	26	4								30	4	0							
64	31		19	11	1								12	1	0						
63	41			19	3	4	11	2	2					22	19	15	4	2	0		
62	49				20	13	7	7	1	1					29	16	9	2	1	0	
61	71					38	12	6	13	1	1					33	21	15	2	1	0

SOURCE: Alroy (1994b)

NOTE: Interval 65 spans from 65 to 64 million years ago, and so on.

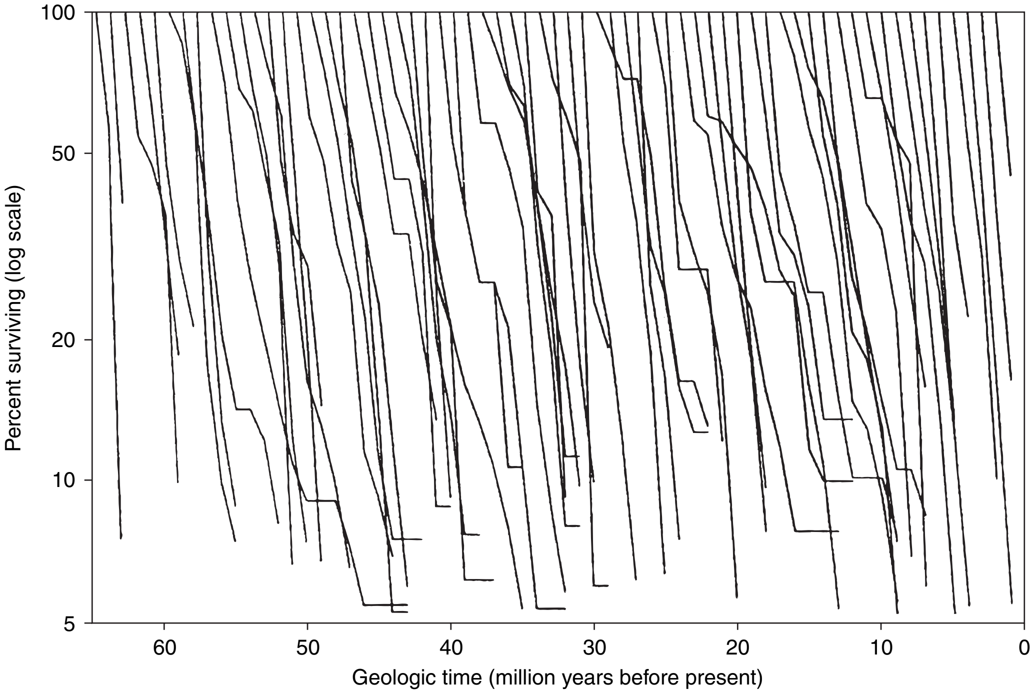

FIGURE 7.11 Cohort survivorship curves for the species of Cenozoic mammals analyzed in Figure 7.9. Each cohort consists of the species first appearing within a 1-m.y. increment of time. The proportion of species in each cohort that still survive is tracked forward through time. If this proportion is plotted on a log scale, the slopes of the cohort curves give the extinction rate. Curves are arbitrarily truncated at 5 percent survival, but many continue further than this. *(Data from Alroy, 1994b)*

41 species that first appear between 62 and 63 m.y. ago, 19 became extinct before 62 m.y. ago, 3 became extinct between 61 and 62 m.y. ago, 4 became extinct between 60 and 61 m.y. ago, and so on. In terms of cumulative survivorship, 22 species (54 percent) endured at least 1 m.y., 19 (46 percent) endured at least 2 m.y., 15 (37 percent) endured at least 3 m.y., and so on. Figure 7.11 shows the cohort survivorship curves corresponding to the cumulative data. If lines are fitted to these curves, they yield slopes ranging from -0.2 to -1.3, with a median of -0.5. This agrees well with the extinction rate of 0.46 to 0.48 per Lmy obtained earlier with the dynamic method (Figure 7.9).

Examples of genus-level cohort curves are shown in Figure 7.12. As with the dynamic curves of Figure 7.10, most of the curves become shallower as time goes on. Using the approach outlined in Box 7.1, it is possible to estimate species-level origination and extinction rates from the survivorship of genera. The speciation rate was about 0.40 per Lmy and the species extinction rate about 0.46 in trilobite genera that originated in the Cambrian; these rates were about 0.13 and 0.15 for genera that originated in the Ordovician. Based on the survivorship of genera, it is inferred that Ordovician species were about three times as long lived as Cambrian species.

Figure 7.12 shows another feature that is readily detected with cohort analysis. The sudden downturn of many cohort curves indicates a profound extinction event in the latest Ordovician [SEE SECTION 8.6], marked by the arrow. A temporal pattern such as this could not have been seen if all durations had been combined into a single distribution for dynamic survivorship analysis.

Lyellian Proportions Charles Lyell, in his classic *Principles of Geology* (1833), tabulated the number of molluscan species known from various epochs of the Cenozoic and how many of these are still extant today. Of the species sampled at some census point in the past, the proportion still extant today is the **Lyellian proportion** (commonly expressed as a percentage). Exponential survivorship implies that the expected Lyellian proportion at an age T before the Recent, L_T, is equal to e^{-qT}. Thus, the average extinction rate over the span of time is estimated as $q = -\ln(L_T)/T$.

The dynamic and cohort methods consider the entire frequency distribution of durations. Any one of the points in the distribution may be inaccurate because of sampling error, but these errors are averaged out by estimating a single rate for the whole distribution. By contrast, each Lyellian proportion is a single observation, rather than an entire distribution, and it may therefore yield an extinction rate that is not representative. For this reason, a number of Lyellian proportions will typically be computed. These may represent, for example, geographically distinct faunas of a given age or a series of faunas of different ages.

Figure 7.13 shows Lyellian proportions and ages for a number of Cenozoic molluscan faunas from Japan and California. The proportions for selected faunas are shown in Table 7.3, divided into bivalves and gastropods from the same fauna. There is some variation in the extinction rates calculated from these proportions, but it is clear that gastropods on average have had higher extinction rates than bivalves over the past 20 m.y. This is also evident from the fact that bivalves generally lie above gastropods in the plot of Lyellian proportions versus time (Figure 7.13). One postulated explanation for this difference is that bivalve species have broader geographic ranges and are therefore less susceptible to extinction by environmental perturbations (Stanley et al., 1980).

Incompleteness of the Fossil Record Our treatment of survivorship analysis has implicitly assumed that the stratigraphic range of a taxon is a good proxy for its true duration. In reality, ranges are truncated by incomplete sampling [SEE SECTIONS 1.3 AND 6.1]. This makes, extinction rates appear artificially high, and the effect is stronger as sampling becomes less complete. Lyellian proportions circumvent this problem by using the present day, where sampling is nearly complete, as the second census point for taxa known to be present at an earlier time. Another approach to the problem is given in Box 7.2.

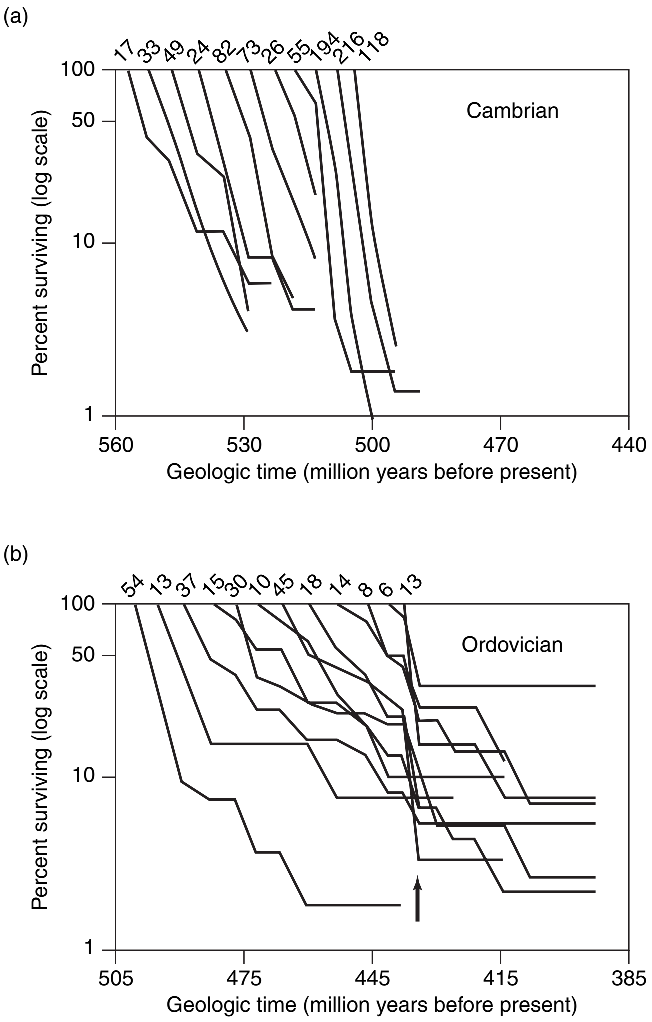

FIGURE 7.12 Cohort survivorship curves for trilobite genera, divided into those first appearing during the Cambrian and those first appearing during the Ordovician. Cambrian curves are steeper, indicating shorter genus durations. The arrow in the bottom figure marks the mass extinction at the end of the Ordovician. *(From Foote, 1988)*

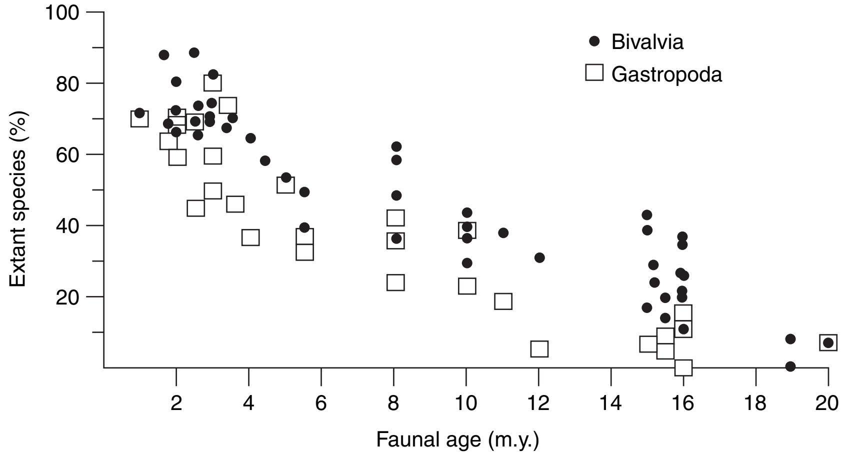

FIGURE 7.13 Lyellian percentages for Neogene molluscan faunas from California and Japan, separated into bivalves and gastropods. Each point shows the percent of species in the given fauna that are still extant today. Corresponding extinction rates for selected pairs of points are given in Table 7.3. *(From Stanley et al., 1980)*

TABLE 7.3

Lyellian Proportions for Species within Selected Neogene Molluscan Faunas

	Lyellian Proportion		**Extinction Rate (per Lmy)**	
Age of Fauna (m.y.)	**Bivalves**	**Gastropods**	**Bivalves**	**Gastropods**
2	0.67	0.60	0.20	0.26
4	0.65	0.35	0.11	0.26
8	0.38	0.42	0.12	0.11
10	0.46	0.25	0.08	0.14
12	0.30	0.05	0.10	0.25
16	0.38	0.15	0.06	0.12
20	0.08	0.08	0.13	0.13

SOURCE: Stanley et al. (1980)

Box 7.2

ESTIMATING TAXONOMIC RATES WITH INCOMPLETE SAMPLING

Figure 7.14 shows an ideal frequency distribution of stratigraphic ranges corresponding to the same simple model of sampling presented in Chapter 1 (Box 1.3, Figure 1.19). Extinction rate is assumed constant—in other words, survivorship is exponential. The probability of sampling a lineage in any given time interval is assumed to be less than 100 percent and to be constant throughout the history of the group in question. The frequency distribution of Figure 7.14 closely resembles the exponential case we have been considering all along—corresponding to 100 percent sampling—but there is one important difference. Here the distribution is log–linear, except that there is an excess of taxa with a stratigraphic range of one interval of time.

The proportion of such **singleton** taxa is a measure of the incompleteness of sampling; groups with less complete records will tend to have a higher proportion of singletons [SEE SECTION 1.3]. According to our simple model, if the singletons are disregarded, the remainder of the distribution is log–linear, and its slope gives the extinction rate. Therefore, we should ideally be able to fit a line to a distribution of stratigraphic ranges—*disregarding singletons*—to obtain an estimate of extinction rate that is not biased by incomplete sampling.

Dynamic survivorship data for mammal species were presented in Table 7.1 and Figure 7.9. The dashed lines in that figure are fitted to the survivorship data, omitting single-interval species. The lines through the raw and cumulative proportions yield extinction rates of 0.434 and 0.437 per Lmy. These are lower than the rates obtained earlier—namely, 0.458 and 0.476 per Lmy. This difference is in the direction we would expect; apparent rates are higher if the effect of incomplete sampling is not taken into account. In this case, however, paleontological completeness is comparatively high, thus the bias in average duration is small.

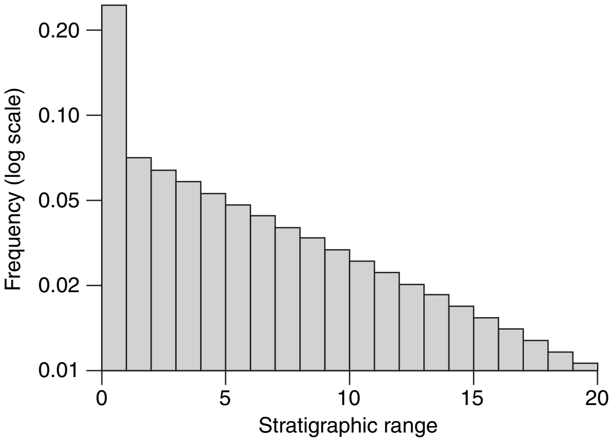

FIGURE 7.14 Distribution of stratigraphic ranges of species, assuming incomplete but uniform sampling. If single-interval species are disregarded, the rest of the distribution is log–linear with slope equal to the extinction rate. *(After Foote & Raup, 1996)*

Long-Term Rates of Origination How far forward a species endures from some specified time, such as its origin or any other census point, depends on the rate of extinction. Similarly, how far backward in time a species extends depends on the rate of origination. Therefore, the principle behind cohort survivorship analysis can also be applied in reverse. The taxa that became extinct in a given interval of time are followed backward to determine what proportion of them had already originated by a given time. Under the assumption of constant origination rate, these "reverse survivorship" curves are log–linear with a slope equal to the origination rate.

We have focused in this section on long-term rates of extinction that characterize different groups of organisms. We have largely bypassed the measurement of orig-

Box 7.3

TAXONOMIC RATE MEASURES WITHIN A TIME INTERVAL

All approaches begin with tabulations of taxa within an interval of time. Figure 7.15 shows a hypothetical time interval, with a number of taxa that are extant during all or part of the interval. These taxa fall into four categories: (1) those that make their first appearance sometime before the time interval and their last appearance during the interval; (2) those that make their first appearance during the interval and their last appearance afterwards; (3) those that make both their first and last appearance during the interval; and (4) those that make their first appearance before the interval and their last appearance afterwards.

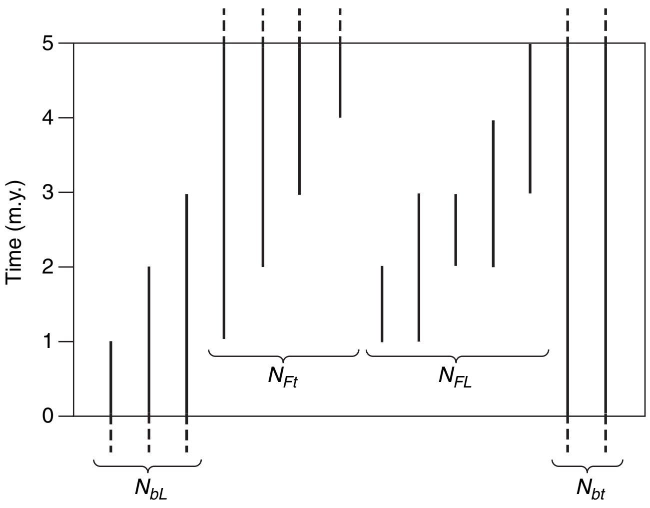

FIGURE 7.15 Stratigraphic ranges of hypothetical species relative to a time interval of interest. Dashed lines indicate ranges that extend beyond this interval. Species fall into four categories, depending on whether they cross the bottom (*b*) or top (*t*) interval boundary, and whether they have a first (*F*) or last (*L*) appearance within the interval.

Using the subscripts *b* and *t* to refer to taxa that cross the bottom and top boundaries of the time interval, and using *F* and *L* to refer to first and last appearance, we can denote the numbers of taxa in the four categories as N_{bL}, N_{Ft}, N_{FL}, and N_{bt}. The number of taxa making a first appearance in the interval is equal to $N_F = N_{Ft} + N_{FL}$ and the number making a last appearance is equal to $N_L = N_{bL} + N_{FL}$. The number alive at the beginning of the interval is equal to $N_b = N_{bL} + N_{bt}$, and the number alive at the end of the interval is equal to $N_t = N_{Ft} + N_{bt}$. Finally, the total diversity for an interval, including taxa sampled from the interval as well as those whose presence is inferred only because they are known both before and after the interval, is equal to $N_{\text{tot}} = N_{bL} + N_{Ft} + N_{FL} + N_{bt}$.

As discussed in Chapter 6, times of first and last appearance do not generally coincide with times of true origination and extinction, but let us consider how we would treat the data at hand with the assumption that first and last appearances represent a reasonable proxy for originations and extinctions.

The intensity of extinction could be measured simply by N_L, the number of last appearances (Table 7.4). This is problematic when we compare extinction intensity among different intervals of geologic time; we may well expect the number of extinctions to be greater when standing diversity is higher, simply because there are more taxa at risk. The simple number of extinctions is therefore seldom used, and it is much more common to measure the proportional extinction, P_E, defined as the number of extinctions divided by the total number of taxa in the time ination rates because, on long timescales, rates of origination and extinction within a group are nearly equal to one another. Any group that is entirely extinct has had, by definition, equal origination and extinction rates on average. Moreover, the diversification process, like compound interest, yields multiplicative growth [SEE SECTION 8.4]. Thus, groups with many species have generally attained high diversity via a small excess of origination over extinction compounded over a long period of time.

Interval Rates

In contrast to average rates over the entire history of a taxonomic group, origination and extinction rates within a single interval of time often differ profoundly. Box 7.3 discusses the estimation of rates for a discrete time interval such as a stratigraphic stage.

TABLE 7.4

Taxonomic Counts and Taxonomic Rate Measures (refer to Figure 7.15)

Quantity	**Symbol**	**Equivalence**
Taxa at beginning of interval	N_b	$N_{bL} + N_{bt}$
Taxa at end of interval	N_t	$N_{Ft} + N_{bt}$
Total diversity in interval	N_{tot}	$N_{bL} + N_{Ft} + N_{FL} + N_{bt}$
Number of first appearances	N_F	$N_{Ft} + N_{FL}$
Number of last appearances	N_L	$N_{bL} + N_{FL}$
Proportional origination	P_O	N_F/N_{tot}
Proportional extinction	P_E	N_L/N_{tot}
Proportional origination per m.y.	$P_{Om.y.}$	$P_O/\Delta t$
Proportional extinction per m.y.	$P_{Em.y.}$	$P_E/\Delta t$
Per-capita origination rate per Lmy	p	$-\ln(N_{bt}/N_t)/\Delta t$
Per-capita extinction rate per Lmy	q	$-\ln(N_{bt}/N_b)/\Delta t$

interval, N_L/N_{tot}. This is commonly expressed as percent extinction, $100 \times N_L/N_{\text{tot}}$. In the hypothetical case of Figure 7.15, the number of extinctions is 8, and the percent extinction is $100 \times 8/14$, or 57 percent. The corresponding numbers for origination are 9 and 64 percent.

Proportional extinction has the advantage of explicitly accounting for the number of taxa at risk. However, if extinction occurs fairly continuously throughout a time interval, then we expect more extinctions and a higher proportional extinction in longer time intervals, even if the extinction rate is constant. This expectation leads to the measurement of extinction as proportional extinction per million years, $N_L/N_{\text{tot}}/\Delta t$. This measure is also known as the *per-taxon rate of extinction,* which in Figure 7.15 is equal to 57 percent/5 m.y., or 11.4 percent/1 m.y. The corresponding origination rate is 12.9 percent/1 m.y.

Although percent extinction and the per-taxon rate are widely used, they have some undesirable properties that stem from the way they account for diversity. Because not all taxa present during a time interval exist throughout the entire interval, the total diversity of an interval of time overestimates the number at risk at any given time. This problem has been addressed by our last rate measure, which takes a census of taxa at precise moments in time—namely, the beginning and end of the interval—and which is based explicitly on the model of exponential survivorship.

continued on next page

Box 7.3 (continued)

Consider the lineages that are alive at the start of the interval; there are N_b of these. They are at risk of extinction during the interval, and the higher the extinction rate, the smaller the number of lineages that will survive to the end of the interval. The proportion of lineages that survive through the entire interval will be equal to $e^{-q\Delta t}$. Note that this proportion is equal to N_{bt}/N_b. Thus, under our ideal model of survivorship, $N_{bt}/N_b = e^{-q\Delta t}$. We can rearrange this equation to solve for the **per-capita extinction rate** as $q = -\ln(N_{bt}/N_b)/\Delta t$. This is just like estimating an extinction rate with the Lyellian method. Here the ratio N_{bt}/N_b, which is the proportion of taxa found at a census point that are still extant at a later census point, is analogous to the Lyellian proportion.

To estimate origination rate, we use the reverse survivorship of lineages alive at the end of the interval. The proportion of them that were already extant at the start of the interval is equal to N_{bt}/N_t, which, under our ideal model, is equal to $e^{-p\Delta t}$. Thus, we solve for the **per-capita origination rate** as $p = -\ln(N_{bt}/N_t)/\Delta t$.

In Figure 7.15, N_{bt}/N_b is equal to $2/5$, or 0.4. Therefore, the per-capita extinction rate is equal to $-\ln(0.4)/(5 \text{ m.y.})$, or 0.18 per Lmy. The origination rate is equal to $-\ln(2/6)/(5 \text{ m.y.})$, or 0.22 per Lmy.

Most measures of taxonomic rate rest on the idea that the number of first and last appearances should increase with interval length and that interval length must therefore be accounted for. If there is substantial uncertainty in estimates of numerical ages, however, then normalizing by a poorly known interval length may introduce more problems than it solves. For this reason, rates will often be expressed on a per-interval rather than per-m.y. basis, and workers will attempt to compare intervals of time that are roughly equal in duration. Moreover, normalizing by interval length tacitly assumes that the originations and extinctions are spread throughout the interval. The extent to which turnover is continuous, as opposed to being clustered at a small number of time horizons such as the boundaries between time intervals, is still an unsettled question.

Determinants of Taxonomic Rates

In the example of crinoid survivorship, taxa that are inferred to be ecologically specialized, and therefore more susceptible to environmental fluctuations, are shorter-lived. This illustrates one of the factors that is thought to be important in producing differences in taxonomic rates among groups of organisms.

Another factor that influences taxonomic rates is geographic range. Species with narrow geographic ranges will tend to be more vulnerable to environmental perturbations. This effect was invoked to explain the difference in survivorship between bivalves and gastropods (Figure 7.13). One factor that contributes to geographic range is dispersal ability. Species that do not disperse far during some stage of ontogeny will tend to have narrow geographic ranges. In such species, rare dispersal events may be more likely to produce new, geographically isolated populations. Poor dispersers may therefore also tend to have higher rates of speciation. We will see an example of this effect later in this chapter. In general, factors that lead to fragmented geographic range and population structure are likely to contribute both to speciation and to extinction. This may be one reason that groups with higher rates of origination also have higher rates of extinction.

Despite these successes in understanding variation in rates, there is still much to learn, particularly why different groups of organisms have characteristically different rates. Why, for example, do cephalopod molluscs have such high rates of taxonomic evolution relative to bivalves and gastropods, or trilobites relative to crustaceans? The answers may well lie in ecological differences such as specialization, dispersal, and population structure, but this is still not known with certainty in the majority of cases.

7.3 RELATIONSHIPS BETWEEN MORPHOLOGICAL AND TAXONOMIC EVOLUTION

One of the outstanding features of morphological evolution is that it can vary greatly in rate and direction. The search for regular patterns in this variation has been an

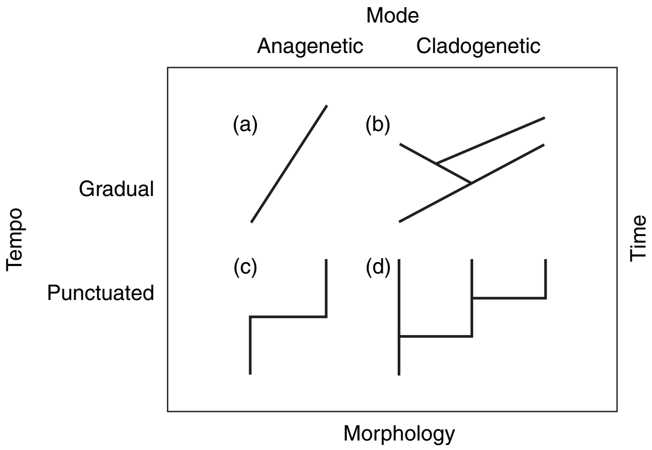

FIGURE 7.16 Hypothetical combinations of evolutionary tempo and mode. Morphology is depicted on the *x* axis and time on the *y* axis. These figures portray idealized patterns continuously with respect to time; in practice, these would be sampled discontinuously. *(Courtesy of David Jablonski)*

important endeavor in paleontology: Is change steady and continuous on average, with little variation in rate? Or is it highly abrupt, with long intervals of little or no change punctuated by brief intervals of substantial change? These two alternatives of evolutionary tempo represent extreme end-members. It is also useful to contrast two alternative evolutionary modes: anagenetic change, which involves evolution within lineages, and cladogenetic change, which involves the splitting of lineages.

Focusing on these end-members, there are four conceivable combinations of tempo and mode (Figure 7.16). Evolution can be smooth and gradual within a lineage, with no cladogenesis (Figure 7.16a); this has been referred to as **phyletic gradualism.** This same pattern of evolution within lineages can be superimposed on a cladogenetic pattern (Figure 7.16b). Highly abrupt change in the absence of cladogenesis has been termed **punctuated anagenesis** (Figure 7.16c), while the pattern of stasis interrupted by short-lived intervals of abrupt change that coincide with cladogenesis is referred to as **punctuated equilibrium** (Figure 7.16d).

Macroevolution and the Importance of Tempo and Mode in Paleontology

Almost since the start of paleontology as a science, pronounced stasis within lineages and abrupt morphological change have been observed repeatedly in the fossil record. These patterns have generally been attributed to imperfections in the geological record. In fact, Charles Darwin (1859, pp. 280–293) argued that the temporal span of a species in the fossil record is generally a small fraction of its true duration, and that there are extensive gaps in the recorded history of species. Darwin's arguments together imply a model for the generation of stasis and punctuation as artifacts of the stratigraphic record (Figure 7.17). Little change would accrue during the preserved parts of a species' duration, and much change would accrue in the intervening gaps, only to be observed at the discontinuities between sedimentary beds.

In the century after Darwin published *On the Origin of Species*, the idea of punctuated change was often advocated. The idea did not take hold, however, because the idea that punctuations are artifacts held sway, and because the proposed mechanisms for punctuation were considered inadequate. Stasis was often observed in the fossil record, even for hundreds of thousands to millions of years—essentially the full duration of a typical species. However, because natural selection had been recognized as a major factor in evolution, it came to be expected that substantial change within species would generally

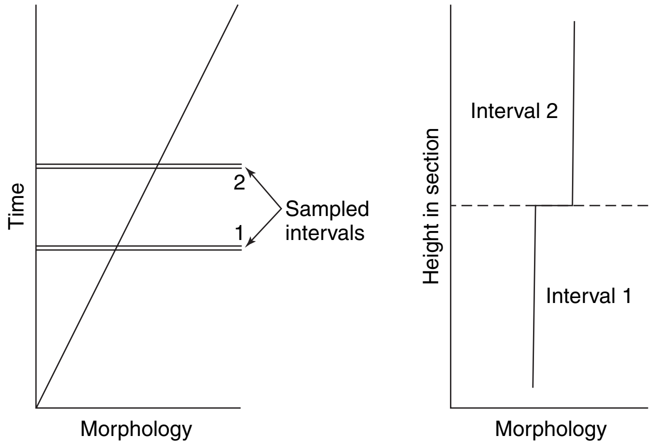

FIGURE 7.17 A model to explain stasis and abrupt change as artifacts of discontinuous sedimentary accumulation. The left side of this figure depicts the true evolutionary pattern; the right side depicts that pattern as seen in the stratigraphic record. The lineage evolves gradually over a long span of time, but only two short segments, indicated by the arrows, are actually sampled. These will be superimposed in a stratigraphic section, as on the right. The amount of change during the sampled intervals is the same on the left and the right. The change is so slight, however, that the lineage appears to be in approximate stasis during the sampled intervals. Change that accumulates during the span of time between the two sampled intervals appears as a punctuation.

be found if fossil lineages were followed in detail. The observation of stasis was therefore seen as something of a disappointment, even an embarrassment.

In the late 1960s and early 1970s, a number of paleontologists began to suspect that the fossil record supports the punctuated equilibrium model (Eldredge & Gould, 1972). This view was based on a few lines of reasoning. First, stasis had been seen over spans of time long enough to rule out the explanation of Figure 7.17. Second, some of the classic cases of gradual evolution did not stand up to closer scrutiny. Third and most important, it was reasoned that punctuated change associated with cladogenesis is exactly what one should expect if speciation were to be viewed through the lens of the fossil record. Speciation may be a slow process on ecological timescales, but even many thousands of years would seem like an instant when compared with species durations of millions of years. Provided that the morphological differences between species tend to evolve during the period of time when they are becoming reproductively isolated from one another [SEE SECTION 3.3], or shortly thereafter, speciation would be seen in the fossil record as a relatively abrupt change associated with branching. Later in this chapter we will return to the question of why morphological evolution may be associated with cladogenesis.

It is difficult to overstate the significance of the punctuated equilibrium hypothesis in the development of paleontology. This is partly because it forced a theoretical and empirical reevaluation of the combinations of evolutionary tempo and mode that best characterize the history of life. Moreover, it stimulated thought on the mechanisms of long-term evolutionary change and of the relationship between long-term change and short-term evolution within species. Evolutionary biologists and paleontologists have long distinguished between **microevolution** (change within populations and species) and **macroevolution** (change at or above the species level). Macroevolution includes, among other things, phylogenetic rates and trends (Figure 7.1) and changes in the relative diversity of different clades over geologic time. Paleontology has always been essential for the documentation of macroevolutionary *patterns*. The discussion that followed the proposal of punctuated equilibrium focused on *mechanisms* that entail paleontological research and cannot be fully understood solely from the study of evolution within living populations.

In the section on trends, for example, we discuss the possibility that large-scale evolutionary patterns may be attributable to differences in speciation and extinction rates, whereby some branches of the evolutionary tree accumulate diversity more rapidly than others. Such patterns have been collectively referred to as **species sorting** (Gould, 2002). This is a descriptive term that refers to the differential net production of species. **Species selection** (Stanley, 1975) is a more interpretative term intended to draw a parallel with natural selection among organisms, as outlined in Table 7.5. Just as natural selection describes a cause-and-effect relationship between organismal properties and their reproductive success, species selection describes a cause-and-effect relationship between properties of species and their tendency to

TABLE 7.5

Parallels between Natural Selection and Species Selection

Feature	Organism Level	Species Level
What is the individual?	Organism	Species
What is a collection of individuals?	Population, species	Clade
Production of individuals	Birth	Speciation
Elimination of individuals	Death	Extinction
Biased direction of production	Mutation pressure (some mutations occur more often than others)	Directed speciation (daughter species differ from parent species in nonrandom ways)
Differential replication	Natural selection	Species selection
Higher production	Higher fecundity	Higher speciation rate
Lower elimination	Preferential survival	Lower extinction rate

SOURCE: Based on Gould (2002)

produce daughter species or to become extinct. It is therefore important to consider what is meant by a species-level property. The issue is more complex than suggested by the following discussion; certain sources listed at the end of this chapter (Stanley, 1979; Jablonski, 2000; and Gould, 2002) should be consulted for a more thorough treatment.

If one kind of species is relatively resistant to extinction simply because individual organisms are very well adapted to their environment, then this is usually seen as organism-level selection; it can lead to species sorting, but it is not species selection. On the other hand, if the difference in taxonomic rates between two kinds of species results from a difference in a trait that logically cannot be expressed by individual organisms but only by species, this is generally seen as species selection. An example, which is discussed below, concerns higher speciation rates in gastropods with poorly dispersed as opposed to widely dispersed larvae. Although the dispersal of larvae is an organism-level trait, poor dispersal leads to species with narrower geographic distributions and a more subdivided population structure. Geographic range and population structure are properties of species rather than individuals. Thus, if differences in these properties contribute to differences in speciation rate, this is an example of species selection. Earlier in this chapter, we saw that differences in geographic range and population structure are likely to contribute to differences in extinction rate as well.

Punctuated equilibrium is not necessary for macroevolutionary patterns to be caused by species sorting; trends within clades that consist of gradually evolving lineages can be caused by the differential diversification of various branches within the clade. But if punctuated equilibrium predominates, then phylogenetic trends are quite likely to arise from species sorting rather than evolutionary trends within species. Because the punctuated equilibrium hypothesis is of such great importance to the subject of macroevolution, we must first discuss some of the problems involved in testing this hypothesis.

Testing for Punctuated Equilibrium

A case study that tests the hypothesis of punctuated equilibrium should ideally satisfy several criteria (Jackson & Cheetham, 1999):

1. *A relatively continuous morphological record.* Of course, the record is always incomplete to some extent, but the strata should not contain major gaps that would lead to the spurious appearance of punctuations. The pattern of stasis is less sensitive to this problem, provided that the strata span a large part of the species' durations.
2. *Sufficient stratigraphic resolution.* The shorter the intervals of time in which morphological change is concentrated, the finer the stratigraphic resolution must be to record this change. It may not be necessary, however, to capture these intermediate steps in order to have some confidence that change was rapid. If the stratigraphic record is fairly complete and if stasis greatly predominates, then these facts together suggest that change, when it occurred, must have taken place over a short period of time. If change were more protracted, then more intermediate stages should be found.
3. *Well-resolved estimate of phylogeny.* Under the punctuated equilibrium hypothesis, punctuations correspond to lineage branching. An understanding of genealogy is especially important to determine whether both ancestor and descendant coexist after the observed morphological change, in order to have confidence that the change was cladogenetic rather than anagenetic.
4. *Adequate geographic control.* It is insufficient to study evolution in a single stratigraphic section, because what appears in one section as a punctuated morphological change may represent an immigration event of a species that had been diverging slowly elsewhere. For this reason, it is important to study the fossil record broadly. The possibility of prolonged evolution outside the area of study can never be ruled out conclusively, but this possibility becomes ever less likely as the study area increases.
5. *Assessment of ecophenotypic variation.* A sudden environmental change could cause punctuations in morphology that are not evolutionary and that do not represent transitions between parent and daughter species. It is therefore important to rule out ecophenotypic change [SEE SECTION 3.3] as a plausible explanation for observed punctuations.

In addition to these basic criteria, there are other features that could help to test for punctuated equilibrium in particular cases. For example, if some lineages are undergoing continuous, gradual change in the same stratigraphic sections and at the same levels at which others exhibit punctuated change, it is implausible that the punctuations are artifacts of gaps in the record. This is because such gaps would produce jumps in the gradually evolving lineages as well (Fortey, 1985b).

A Case Study: Neogene Caribbean Bryozoans

An exemplary study of the genus *Metrarabdotos* by paleontologist Alan Cheetham (1986) illustrates the steps needed to test for punctuated equilibrium. One noteworthy aspect of this work is that the punctuated pattern was found despite a number of operational protocols that bias against detecting it. The evidence for punctuated equilibrium is therefore especially compelling.

Morphology and Phylogeny Morphological species were defined on the basis of a number of measured traits, using multivariate methods described in Chapter 3, and their phylogenetic relationships were inferred using the method of **stratophenetics.** This method, which can be useful when stratigraphic sampling is dense and fairly continuous, begins by forming an array of samples arranged by stratigraphic intervals. From one interval to the next, samples that are most similar morphologically are linked together. This is shown schematically in Figure 7.18. Like all phylogenetic methods, stratophenetics has both strengths and weaknesses. For purposes of this discussion, what is important is that stratophenetics tends to bias against the punctuated pattern. This is because it minimizes the change between ancestor and descendant and thus also minimizes the implied evolutionary rate associated with the transition.

The reconstructed evolutionary tree of *Metrarabdotos* is shown in Figure 7.19, in which the *x* axis represents a multivariate measure of morphological dissimilarity [SEE SECTION 3.2]. Clearly, there is a multiplication of species and a persistence of pairs of related species following morphological changes. Thus, unless the new species have migrated in from elsewhere, the mode of evolution must be cladogenetic. Visually, the pattern of evolution in Figure 7.19 suggests that the punctuated equilibrium model holds. A statistical test, described in Box 7.4, supports this inference.

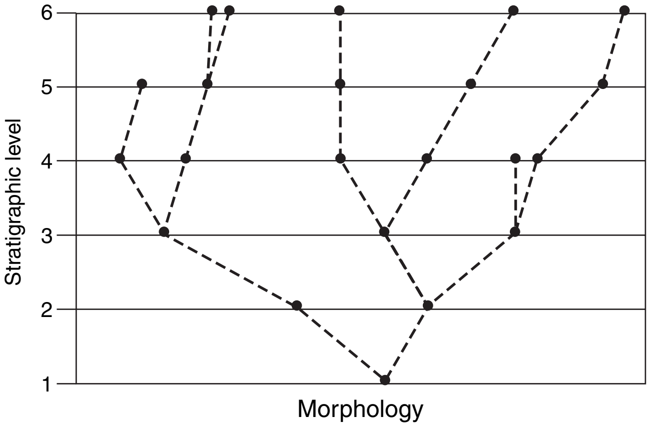

FIGURE 7.18 Stratophenetic reconstruction of phylogeny illustrated with hypothetical data. Each point represents a population mean. At each stratigraphic level, populations are connected with the most similar populations in adjoining levels.

Completeness and Resolution The study focuses on the more densely sampled part of the record—after about 10 m.y. ago (Figure 7.19). The temporal spacing between samples varies from about 20,000 years to about 1 m.y., with an average of about 160,000 years.

In Chapter 1, we discussed methods for estimating the proportion of species that have left a fossil record. There are analogous approaches for estimating the proportion of elapsed time that is represented by preserved sedimentary beds. In this case, such methods have been used to determine that the record is greater than 60 percent complete at the level of temporal resolution of the samples. What this means is that, of all the 160,000-year time intervals that elapsed during the time span covered by this study, more than 60 percent of them are represented by some preserved sediment. Sampling is uneven over time, however. In many cases, the sampling levels are closely spaced, so that it is possible to rule out protracted divergence between ancestor and descendant over many hundreds of thousands of years. In other cases, sampling is sparser, and the duration of the ancestor–descendant transition is difficult to infer directly—for example, the transition from *M. lacrymosum* to *M. unguiculatum*. The statistical test described in Box 7.4 takes this fact into consideration.

Geographic Control Although the majority of data for this study are from the Dominican Republic (D.R.), samples were collected broadly from within the Caribbean region, including Haiti, Jamaica, Trinidad, and the Gulf and Atlantic coasts of the United States. A few long-lived species are found throughout the Caribbean, but most are restricted to the D.R. There is no indication that the derived species evolved over a long period of time outside the D.R. and migrated in, and studies of the fossil record outside the Caribbean region do not reveal species that appear to be closely related to those found in the Caribbean.

Geographic sampling always leads to an asymmetrical test. It is possible to demonstrate that what appears to be

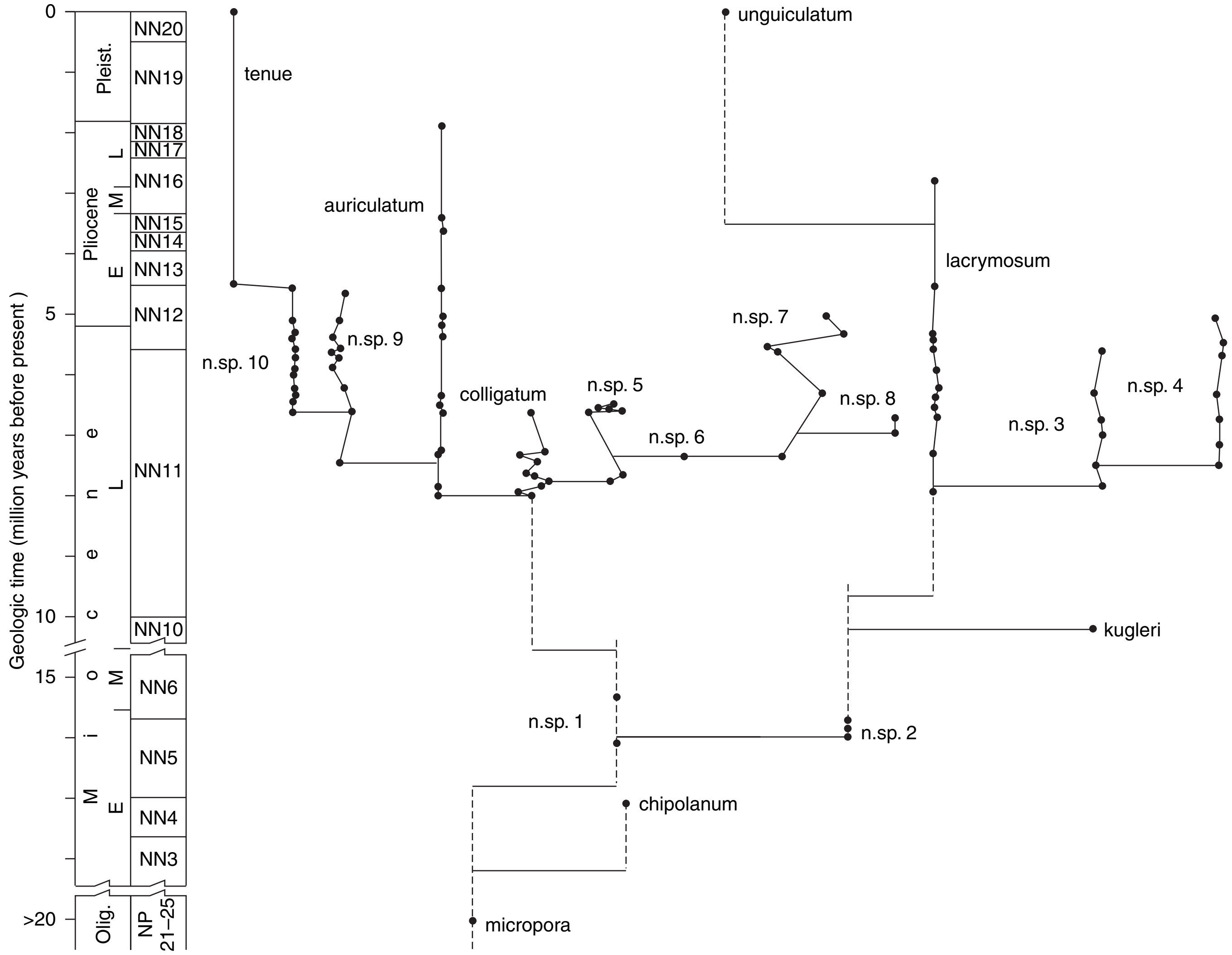

FIGURE 7.19 Stratophenetic tree of species of the Neogene bryozoan *Metrarabdotos* from the Caribbean region. The *x* axis summarizes multivariate information on morphology in such a way that the morphological distances between closely related species are represented with little distortion. Each point shows the average of a sample. Intervals on the timescale marked NP and NN are biostratigraphic zones based on microfossils [SEE SECTION 6.1]. *(From Cheetham, 1986b.)*

a punctuation in fact represents a migration event, but it is never possible to rule this out conclusively. Just how extensively one must sample remains a point of contention. Nevertheless, in this case, the breadth of geographic sampling leaves us with considerable confidence, if not complete certainty, that the rapid morphological changes observed in samples from the D.R. represent evolutionary rather than migrational events.

Ecophenotypic Variation Two lines of evidence suggest that the observed morphological punctuations are genetic rather than ecophenotypic. First, if these changes were induced by an environmental shift, we should expect to see many or most species changing in form simultaneously in response to the shift. This is not the case (Figure 7.19). In general, we see many lineages in stasis while others are changing. In particular, ancestors remain in stasis while their descendants change rapidly. Second, there is a strong correlation between morphological and genetic variation, with little ecophenotypy, in cheilostome bryozoans related to those studied here [SEE SECTION 3.3].

In general, morphologically defined species are thought to be genetically distinct. Cryptic species may be

Box 7.4

OPERATIONAL TEST FOR PUNCTUATED EQUILIBRIUM

An upper limit on the duration of a speciation event is defined by assuming that the event extends from the first appearance of the ancestor to the first appearance of the descendant (Figure 7.20). By assuming that the ancestor and descendant originated at the same time, the implied rate of evolution between ancestor and descendant is minimized. This protocol therefore biases against the punctuated pattern.

For each ancestral species, the mean rate of within-species evolution is calculated from the long-term net change over the entire duration of the species, as shown in Figure 7.20. Next, the rate of change between each pair of successive samples within a species is tabulated to determine the variance in within-species rate. The ancestor–descendant rate is then compared to the average within-species rate, scaled to the variance in within-species rate.

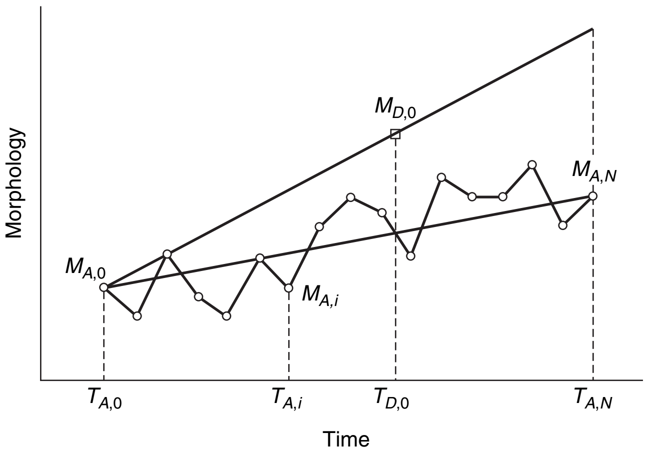

FIGURE 7.20 Calculation of within-species and between-species rates of evolution. Time and morphology are in arbitrary units. Times $T_{A,i}$ (from $T_{A,0}$ to $T_{A,N}$) are all the times at which the ancestor is sampled, its first appearance being at $T_{A,0}$. The first appearance of the descendant is at time $T_{D,0}$. Circles represent the ancestor; the one square is the descendant at its time of first appearance in the fossil record. The average within-species change in the ancestor is the slope of the line from point $(T_{A,0}, M_{A,0})$ to point $(T_{A,N}, M_{A,N})$, in other words, $(M_{A,N} - M_{A,0})/(T_{A,N} - T_{A,0})$. The variance in within-species rate is based on the slopes of all lines between adjacent points. The between-species change is the slope of the line from point $(T_{A,0}, M_{A,0})$ to point $(T_{D,0}, M_{D,0})$, or $(M_{D,0} - M_{A,0})/(T_{D,0} - T_{A,0})$. This assumes that the descendant has been evolving gradually since the first appearance of the ancestor and therefore yields a minimum estimate of the rate of between-species change. *(From Cheetham, 1986b)*

common, however; the absence of morphological distinction need not imply the lack of genetic difference between populations [SEE SECTION 3.3]. For the assessment of punctuated equilibrium, cryptic species are generally thought not to present a problem. This is because the punctuated equilibrium hypothesis states that change, *when it occurs*, tends to be associated with cladogenesis. Cladogenesis without morphological change is compatible with punctuated equilibrium, but significant morphological change without cladogenesis is not.

Considering how much is involved in the *Metrarabdotos* study, it is not surprising that there have been few entirely conclusive demonstrations of either the presence or absence of punctuated equilibrium. Stasis is easier to document, and it has been very widely observed in the fossil record. Although the overall predominance of punctuated equilibrium remains largely unknown, the case of *Metrarabdotos* is not unique. Next, we briefly consider some of the mechanisms that may contribute to punctuated equilibrium when it occurs.

Mechanisms of Stasis

Several plausible explanations for stasis have been proposed by paleontologists and biologists. All are likely to play a role, but their relative importance still has not been determined.

According to the mechanism of **habitat tracking,** populations do not remain in stasis in a single locality. Rather, as environmental conditions change over time, This statistical comparison starts with the assumption that the between-species rate is drawn from the same distribution as the within-species rates. This assumption, or null hypothesis, must be explicitly rejected before the alternative of punctuated equilibrium can be accepted. Gradualism is therefore treated as the preferred hypothesis, and the test biases against the punctuated model.

The result of this analysis is that the rates of change between ancestors and descendants are overwhelmingly too large to be part of the same statistical distribution that characterizes rates of change within species (Table 7.6). The gradualistic hypothesis is rejected in favor of the alternative of punctuated equilibrium.

TABLE 7.6

Evolutionary Rates for Ancestor–Descendant Pairs of Species in the Bryozoan *Metrarabdotos*

Ancestor	**Descendant**	**Within-Species Rate**	**Between-Species Rate**
M. auriculatum	*M.* n. sp. 9	0.002	30.20
M. n. sp. 9	*M.* n. sp. 10	0.083	9.34
M. n. sp. 10	*M. tenue*	−0.031	5.38
M. colligatum	*M.* n. sp. 5	0.169	50.37
M. n. sp. 5	*M.* n. sp. 6	−0.158	27.96
M. n. sp. 7	*M.* n. sp. 8	1.065	51.74
M. lacrymosum	*M.* n. sp. 3	0.014	118.9
M. n. sp. 3	*M.* n. sp. 4	−0.009	69.13
M. lacrymosum	*M. unguiculatum*	−0.021	7.56

SOURCE: Cheetham (1986)

NOTE: Calculation of rates is explained in Figure 7.20. Rates are expressed in terms of synthetic morphological units (Figure 7.19) per m.y.

the geographic distributions of populations and species shift to track local conditions to which they are adapted. Habitat tracking underlies the facies dependence of species [SEE SECTION 6.4]. Detailed evidence comes from the late Cenozoic fossil record, where temporal resolution is fine enough to document changes in distribution that take place in as little as 1000 years. Figure 7.21 shows an example for a number of insect species. Although this process clearly occurs, there are cases of stasis within a single geographic area, and therefore other mechanisms are needed. One that is commonly invoked is **stabilizing selection.** Observations on many living species have shown that, in stable environments, there tends to be a preferred, modal phenotype that is better adapted than others. If environments were stable over long periods of time, this modal form would be maintained. Although there is no reason to doubt the operation of stabilizing selection in principle, it is difficult in the fossil record to identify the particular selective forces that favor certain phenotypes over others. More important, many cases have been documented in which species are in stasis despite major changes in climate and other aspects of environment. Additional mechanisms are therefore required.

A number of potential causes of stasis recognize abundant evolutionary change within species but postulate that, for various reasons, this change does not accumulate to yield substantial net evolution in the long run. First, if relevant environmental conditions fluctuate around a stable long-term average, and the species

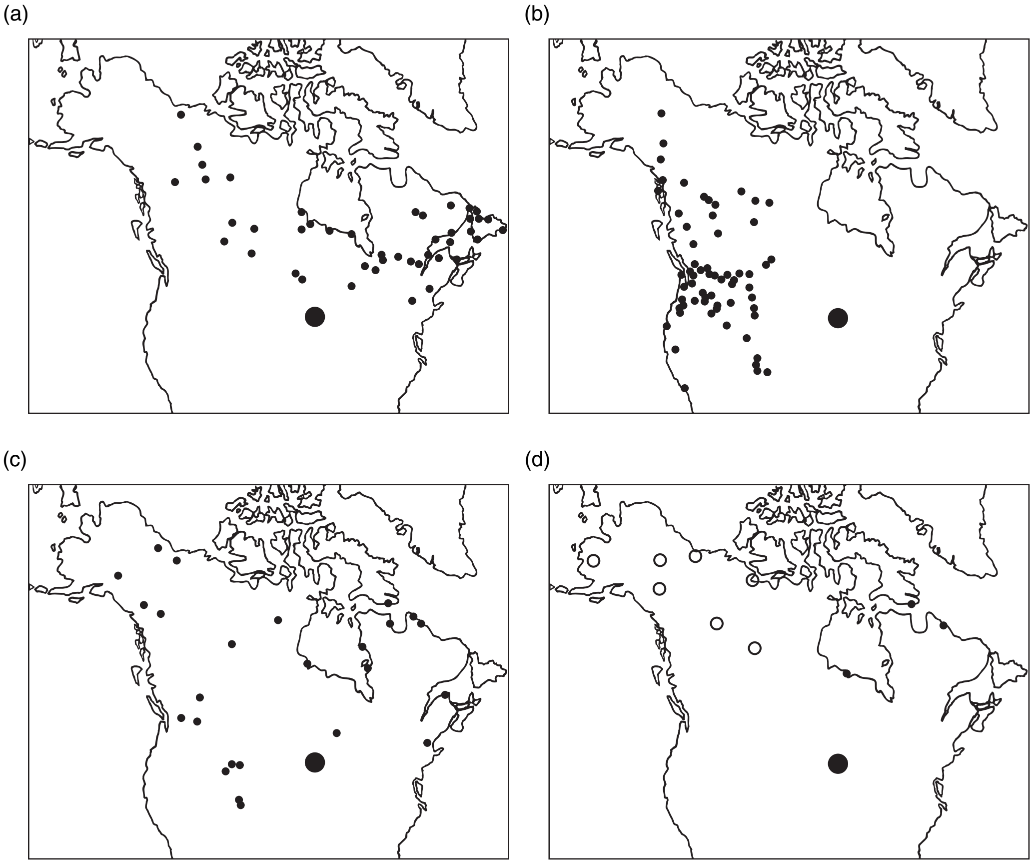

FIGURE 7.21 Shifting distributions of insect species in northern North America. Present-day occurrences of five species are given. Parts (a), (b), and (c) each show a single species (small filled circles); part (d) shows two species (small filled circles and open circles). The large filled circle in each part shows the same sample from lake sediments at a locality in Minnesota, about 12,000 years old. All five species are found together in that sample. Today, however, only one of the distributions includes this locality, and none of the species is found anywhere today with any of the others.

evolves in response to these short-term environmental changes, the species may show little net evolutionary change. In a similar vein, abrupt environmental changes caused by variation in climate and other factors may alter which traits are favored by natural selection, effectively erasing any accumulated evolutionary change.

The subdivision of species into geographic populations provides another way for stasis to occur despite substantial evolution within species. Gene flow between geographically subdivided populations may contribute to stasis by hindering the accumulation of change in any one local population. Environmental fluctuations, by fostering geographic range shifts and therefore greater gene flow, would enhance the stability of species.

Finally, there is a class of related mechanisms that can be grouped together as developmental constraint [SEE SECTION 5.1]. Constraints are thought to bring about stasis when a species expresses extremely limited phenotypic variation, due to either a paucity of genetic variation or a tendency for developmental processes to produce a limited array of phenotypes. Although the explanation of constraint makes sense in principle and can be documented in living species, it is for most practical purposes untestable in fossil populations.

Mechanisms of Punctuated Change

There are two components to abrupt change in the punctuated equilibrium model: It takes place over a time span that is short relative to the duration of a species, and it is associated with cladogenesis. Conventional biological views posit that the process of speciation is generally fast enough that it would appear to be instantaneous in the fossil record. The essential question, therefore, is why morphological change should be concentrated in events of cladogenesis. Rather than review the long and complex history of this question, we will present a cogent explanation offered by evolutionary biologist Douglas Futuyma (1987). This explanation agrees with what is known of evolution within populations and the population structure of species, and it is also closely tied to one of the mechanisms for stasis described previously.

A species consists of numerous geographic populations, with varying amounts of gene flow between them [SEE SECTION 3.1]. Because these populations are in different places, they may be adapted to local conditions. Therefore, evolutionary change may be possible anywhere and at any time in the history of a species. However, local populations do not generally become distinct; they either suffer extinction or maintain gene flow with other populations. Any change that accumulates within local populations will therefore tend to be short-lived. Only in those rare cases in which local populations do persist and attain reproductive isolation will the evolutionary change that accumulated through local adaptation be maintained. Thus, there may be abundant evolutionary change within the history of a species, but that change will be permanent only if it occurs in a population that founds a new species. Therefore, the net evolutionary change seen in the fossil record will be associated with cladogenesis.

It is important to keep in mind that much of the importance of stasis and punctuated change is independent of what causes these phenomena. The very pattern of punctuated equilibrium shapes our understanding of trends and other aspects of macroevolutionary change.

7.4 EVOLUTIONARY TRENDS

The punctuated equilibrium hypothesis has led to a reevaluation of the mechanisms of macroevolution. Nonetheless, many paleontologists had long been aware that large-scale trends in the history of life may be caused by mechanisms other than the tendency for individual species to evolve in the same direction. Appreciation for the complexity of macroevolutionary patterns is captured well in the following passages from George Gaylord Simpson's *The Major Features of Evolution* (1953), on the subject of horse phylogeny (Figure 7.22) and trends in body size, limb and foot form, and skeletal and dental anatomy:

> Even in some of the most recent works . . . this phylogeny is [incorrectly] presented as a single line of gradual transformation of *Hyracotherium* into *Equus* [the only living genus in the family]. It has been well known to the better informed for more than two generations that the phylogeny includes considerable branching, and for the last ten or fifteen years it has been increasingly evident that the really striking and characteristic part of the pattern is precisely its repeated and intricately radiating splitting. Its botanical analogue would be more like a bush than like a tree, and even if the tree figure of speech were used, *Equus* would not correctly represent the tip of the trunk but one of the last bundles of twigs on a side branch from a main branch sharply divergent from the trunk. (p. 260)

> The Equidae had no trends that: (1) continued throughout the history of the family in any line, (2) affected all lines at any one time, (3) occurred in all lines at some time in their history, or (4) were even approximately constant in direction and rate in any line for periods longer than on the order of 15 to 20 million years at most (usually much less). . . . The whole picture is more complex, but also more instructive, than the orthogenetic progression that is still being taught to students as the history of the Equidae. It is a picture of a great group of real animals living their history in nature, not of robots on a one-way road to a predestined end. (p. 264)

Like the history of horses (Figure 7.22), the broader history of life is replete with evolutionary change. In some cases, evolution is persistent in direction, toward larger size or more efficient food capture, for example. We single out these cases as **evolutionary trends.** An understanding of a specific trend often starts with a statistical consideration of just how persistent it is.

Tests for Persistent Directionality

A number of statistical tests for persistence have been developed, and here we present just two of the simplest ones.

To understand the rationale behind these tests, consider a highly simplified model of evolutionary change known as a **random walk.** According to this model, a trait value has a certain probability of increasing or decreasing at every time step, and which way it goes is a matter of chance, independent of previous changes.

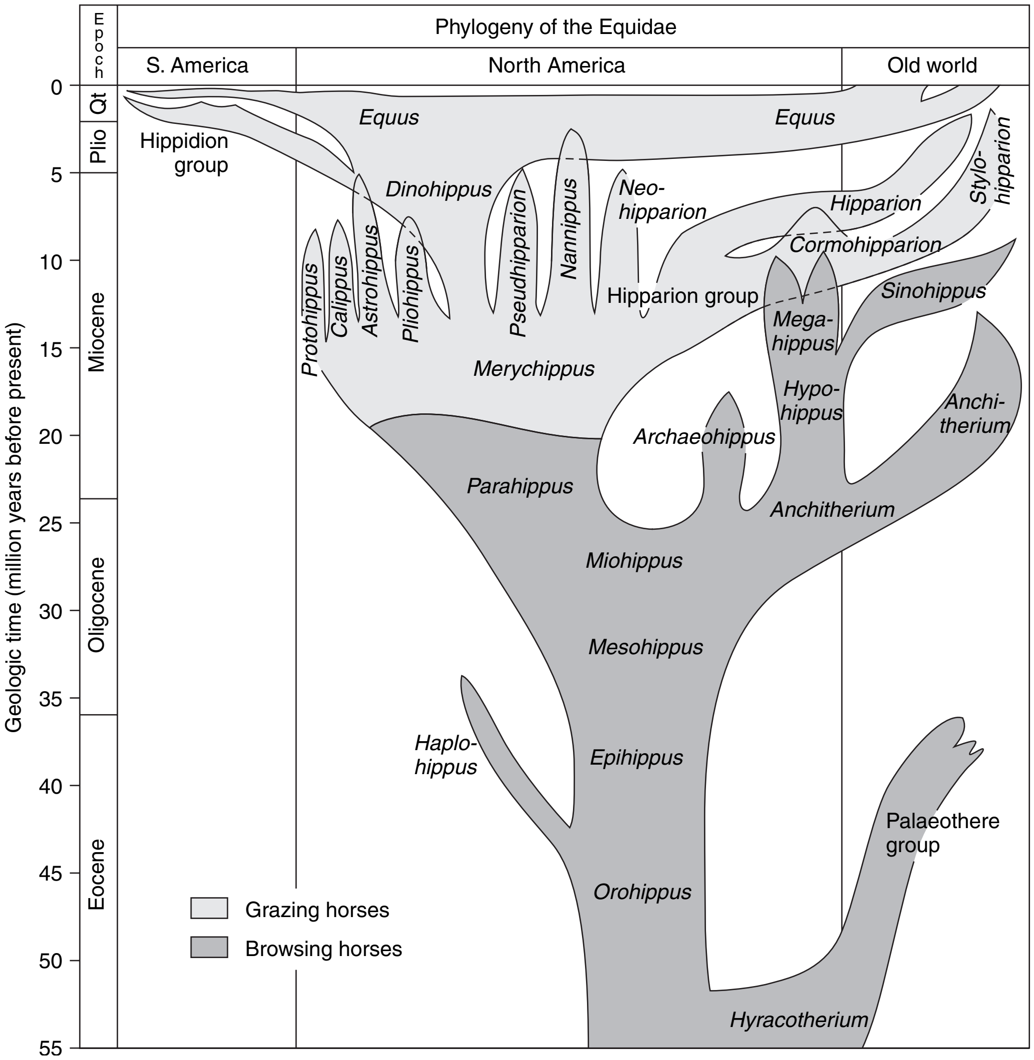

FIGURE 7.22 Inferred evolutionary tree of horses. *(From MacFadden, 1985)*

Random walks with a probability of increase substantially less than or greater than one-half would tend to produce trends downward or upward. In a **symmetric random walk,** the probability of increase is exactly one-half, so there is no inherent directionality.

Figure 7.23 shows a few examples of evolutionary patterns simulated by a computer programmed to generate symmetric random walks. In the first case, the random walk appears to have a tendency to stay near its starting point ("stasis"). In the second, it is relatively stable, then shifts over a brief interval of time ("punctuation"), then continues to be stable at a new point. In the third, the overall appearance is that there is a strong directionality. This exercise reveals that sequences that appear to have a striking pattern may potentially be produced by a process with no inherent directionality or stability. Thus, the impression created by the pattern should not by itself be taken as strong evidence for prevailing evolutionary tendencies.

Figure 7.23, especially the third panel, also illustrates why it is generally inappropriate to interpret correlation coefficients [SEE SECTION 3.2] in which one of the variables is time. Temporal series of data generally consist of successive values that are not independent of one another, each one being the previous value plus some increment. The standard statistical analysis of correlation coefficients, in contrast, assumes independent data points.

One test for directionality considers the mean size of evolutionary steps between successive time horizons. If there is a tendency for evolutionary change to proceed in a particular direction, then the mean evolutionary step

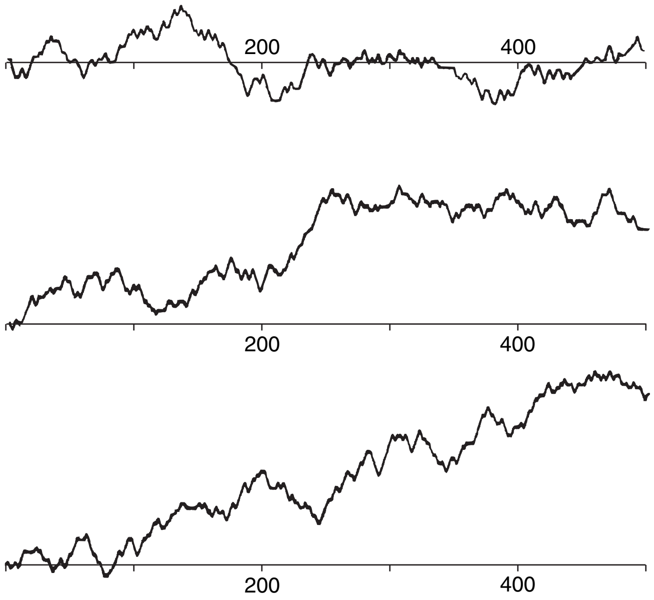

FIGURE 7.23 Examples of computer-generated, symmetric random walks of 500 steps. In each example, time is on the *x* axis and morphology is on the *y* axis. At each time step, morphology has an equal chance of moving up or down one step, independent of prior history. Striking patterns may emerge even though the process has no inherent directionality or stability. *(From Raup, 1977)*

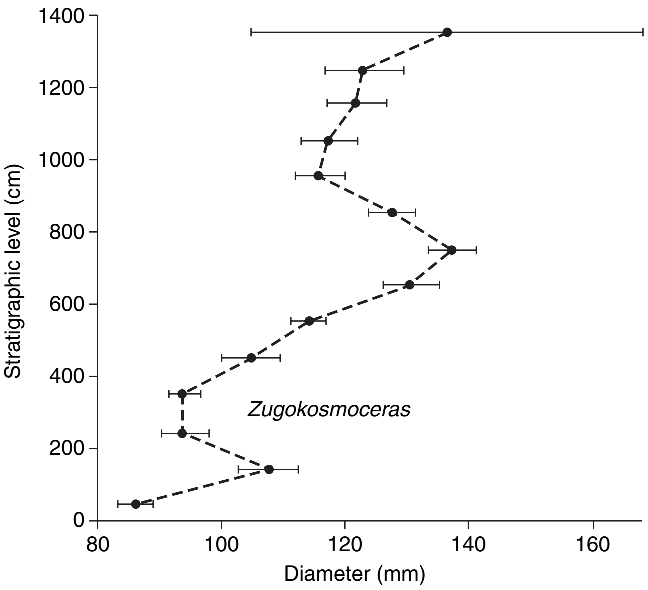

FIGURE 7.24 Shell diameter in the Jurassic ammonite *Zugokosmoceras* through 14 m of section. Each point shows the mean ±2 standard errors of the mean, for a 100-cm interval. *(From Raup & Crick, 1981)*

should differ appreciably from zero. For example, consider shell diameter in the Jurassic ammonite *Zugokosmoceras*. Figure 7.24 shows a summary of this lineage through 14 meters of section. There is an overall increase in size, but there are several reversals as well; thus, it is not clear just how strong the tendency is toward size increase. Each point in Figure 7.24 depicts the mean of all specimens within a 100-cm interval. In fact, the section was sampled much more finely than this, with nearly 300 distinct, *Zugokosmoceras*-bearing horizons.

Figure 7.25 gives the frequency distribution of changes in shell diameter between adjacent horizons at the finer level of temporal resolution. There is a slight preference for positive steps, but there are many reversals, and the mean step size is not substantially different from zero. Thus, there does not appear to be a strong directionality.

A second test for directionality ignores the magnitudes of change and simply tabulates the number of positive and negative changes. This test determines the probability that a symmetric random walk would yield at least as many changes in the same direction as were actually observed in the data (Box 7.5). In the sequence of molar sizes in Figure 7.4, there are 17 steps, of which 15 are increases. The probability of obtaining 15 or more steps in the same direction, if the probabilities of increase and decrease are truly equal, is only 0.0023. We therefore reject the random-walk model in favor of the hypothesis of persistent change.

The tests for a persistent tendency within a single evolutionary sequence require that we observe multiple

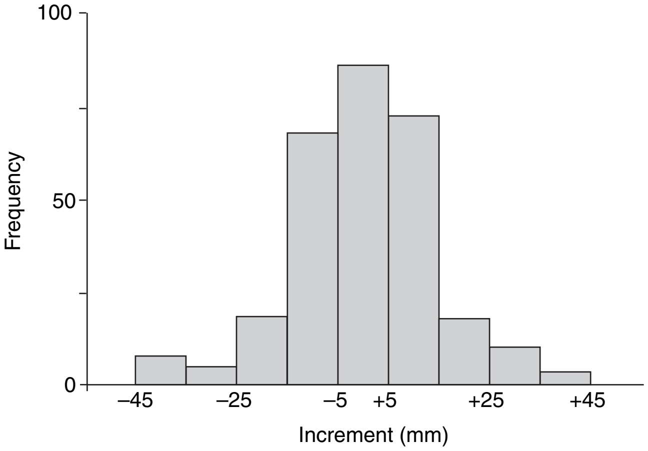

FIGURE 7.25 Frequency distribution of evolutionary steps in shell size between adjacent, *Zugokosmoceras*-bearing horizons in the same section depicted in Figure 7.24. The mean is near zero, suggesting that there is not a strong directionality. *(From Raup & Crick, 1981)*

Box 7.5

TESTING FOR DIRECTIONALITY OF EVOLUTIONARY SEQUENCES

Here we give details on statistical assessment of the number of changes in a given direction and make some general points about testing for trends.

Suppose there are n evolutionary steps, of which m_i are increases and m_d are decreases. Under the symmetric random-walk model, which serves as the null hypothesis of the test, the probabilities of increase and decrease are each equal to 0.5. The probability of exactly m_i increases, if increases and decreases are in fact equally likely, is given by:

$$P(m_i, n) = \frac{n!}{m_i!(n - m_i)!} 0.5^n$$

where $n!$ ("n factorial") is the product $n \times (n-1) \times (n-2) \times \cdots \times 1$, and $0! = 1$ by convention. The derivation of this binomial equation can be found in any elementary textbook on probability and statistics. Referring to the example of molar tooth size in the mammal *Cantius* (Figure 7.4), the probability of obtaining exactly 15 increases out of 17 steps is equal to

$$P(15, 17) = \frac{17!}{15!(17 - 15)!} 0.5^{17}$$

which is approximately equal to 0.00103.

For a sequence of n steps, the number of increases can be anything from 0 to n, and the number of ways the steps can be arranged is enormous. Therefore, the exact probability of any particular sequence of steps is minuscule. In statistical analysis, we are generally not interested in such isolated probabilities; these have no special significance other than as part of a whole family of outcomes with something important in common. In this case, a given number of increases may seem higher than expected under the random-walk model; if so, then any number of increases greater than the observed value would also seem high. We are therefore interested in the sum of probabilities of all outcomes at least as extreme as the one observed. By "extreme" we mean deviating from the expectation of an equal number of increases and decreases.

We thus take the larger of m_i and m_d, which we denote simply m, and calculate the sum of a number of changes *greater than or equal to* the number observed:

$$P_{\geq m(n)} = \sum_{k=m}^{n} P(k, n)$$

If this is a small number, conventionally less than 0.05, we reject the null hypothesis in favor of the alternative that change in one direction is more likely than in the other. Again taking the mammal example, the probability of 15 or more increases out of 17 steps is equal to:

$$\begin{aligned} P_{\geq 15(17)} = & \frac{17!}{15!(17 - 15)!} 0.5^{17} \\ & + \frac{17!}{16!(17 - 16)!} 0.5^{17} \\ & + \frac{17!}{17!(17 - 17)!} 0.5^{17} \end{aligned}$$

steps. Sometimes we simply have before-and-after comparisons, but we have them for numerous lineages. In such a case, we can apply the same tests for persistence.

It has been proposed, for example, that there is a general tendency for body size to increase in evolution—a generalization sometimes referred to as *Cope's Rule*. Figure 7.26 shows estimated body size for species of fossil horses, a group which, as a whole, has increased in size over time. To determine whether there is such a tendency at the lineage level, we study ancestor–descendant comparisons. In Figure 7.27, the rate of evolution between inferred ancestors and descendants is shown, with increases and decreases indicated separately as solid and open circles. Of 24 observed changes in body size, 19 are increases. The probability of this many increases, if increases and decreases are equally likely, is only 0.0033. Thus, it is reasonable to reject the hypothesis of a symmetric random walk in favor of the alternative that increases in body size are more likely.

which is equal to 0.00103 + 0.00013 + 0.000008, or about 0.00116.

As with many statistical tests, it is important to determine whether the test should be one-sided or two-sided. If we had no prior reason to test for a preponderance of positive or negative steps, we would perform a two-sided test. Suppose, for example, that there were more positive than negative steps. We first set m equal to m_i and calculate $P_{\geq m(n)}$, which tells us the probability of at least m positive steps. However, a result at least this extreme in the opposite direction might also have occurred, and, since we had no prior reason to test for positive rather than negative deviations, the probability of both alternatives must be taken into consideration. What we wish to evaluate, therefore, is $2P_{\geq m(n)}$. Only if this is sufficiently small can we reject the null hypothesis.

We used a two-sided test to evaluate the sequence of steps in the case of mammal tooth size (Figure 7.4) and the mean step size in the case of ammonite shell size (Figure 7.24), because we were simply testing for change in a preferred direction, *either direction*. In the mammal case, for instance, the probability of 15 or more increases out of 17 steps is equal to 0.00116, as was just shown. Therefore, the probability of 15 or more changes in one direction is twice this number, or approximately 0.0023. This is a rather small probability, so we would reject the idea that there is no directionality in favor of the alternative that there is a preferred direction of change.

On the other hand, if we are testing a specific evolutionary hypothesis that predicts change in a particular direction, we perform a one-sided test. We tabulate the number of changes in this direction and calculate the probability of at least this many changes *in that direction*, regardless of whether the observed number is greater or less than expected under the null hypothesis. We used a one-sided test to check for an increase in the body size of horses (Figure 7.27) because there is a specific hypothesis that body size tends to increase in evolution. This hypothesis was supported by the test. If fewer than half of the observed changes had been increases, we would simply have considered the hypothesis of body-size increase not to be supported by the data.

There is an important asymmetry in these and other statistical tests. If we can reject the null hypothesis, we can be confident that there is some directionality in the evolutionary sequence. If we cannot reject it, however, that does not imply that the sequence was in fact the result of a symmetric random walk. It is possible that there is a preferred direction of change but that it has not been detected statistically because the tests lack sufficient power. This can happen if the observed sequence is too short or if within-species variance makes the estimation of successive average trait values too uncertain.

Mechanisms of Phylogenetic Trends

The average morphology of a clade can change directionally over time if many of the lineages in that clade are evolving directionally. That is, a phylogenetic trend could in principle be reducible to a series of phyletic trends. When evolutionary stasis overwhelmingly predominates, however, this possibility is logically ruled out. It is therefore important to consider some of the ways that evolutionary trends within a clade may result if lineages within the clade are in stasis (Figure 7.28). For the most part, these mechanisms are simply logical possibilities that have not yet been well documented, and determining the causes of trends in particular cases remains an important task for paleontology. The mechanisms we will discuss do not presuppose that punctuated equilibrium predominates; they can produce trends even if most evolutionary change is gradual. But because we are discussing clade-level trends, some cladogenesis is assumed.

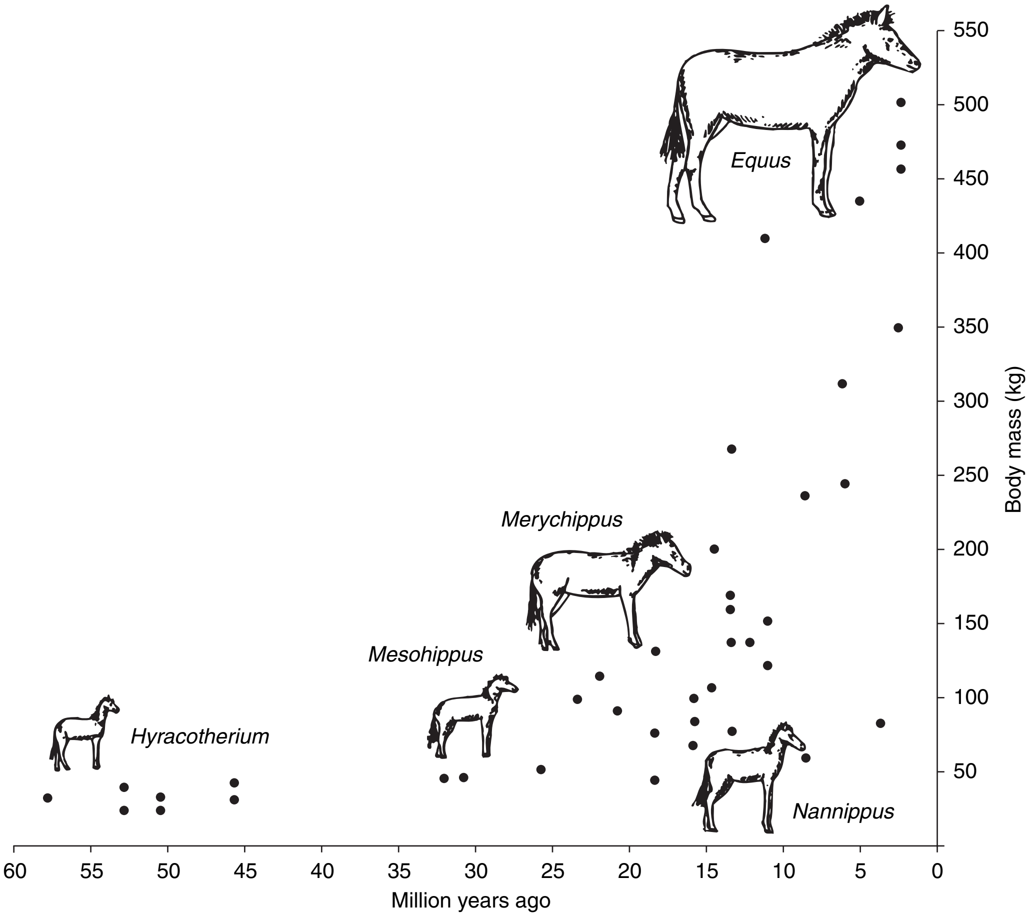

FIGURE 7.26 Estimated body mass in horse species over time. Body mass is estimated from skeletal measurements, using methods described in Section 3.2. Sketches show examples of genera. Compare with the evolutionary tree of Figure 7.22. *(From MacFadden, 1986)*

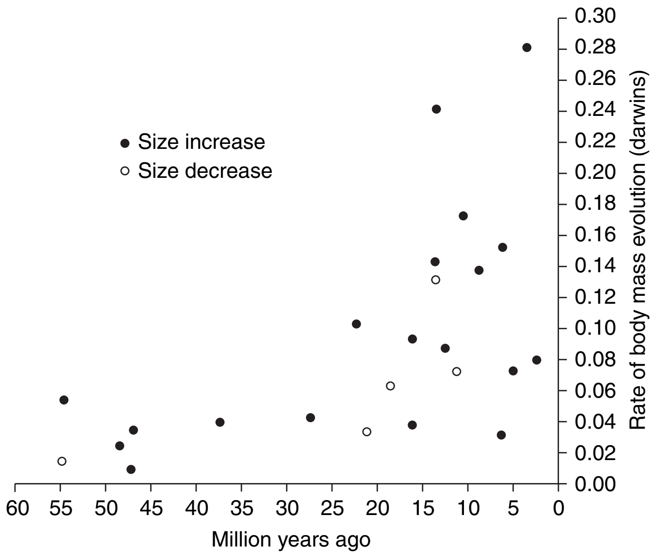

FIGURE 7.27 Evolutionary rates (in darwins) for ancestor–descendant pairs of horse species in Figure 7.26. Closed circles show increases in body mass, and open circles show decreases. There are many more increases than decreases, suggesting directionality in the evolution of body size. *(From MacFadden, 1986)*

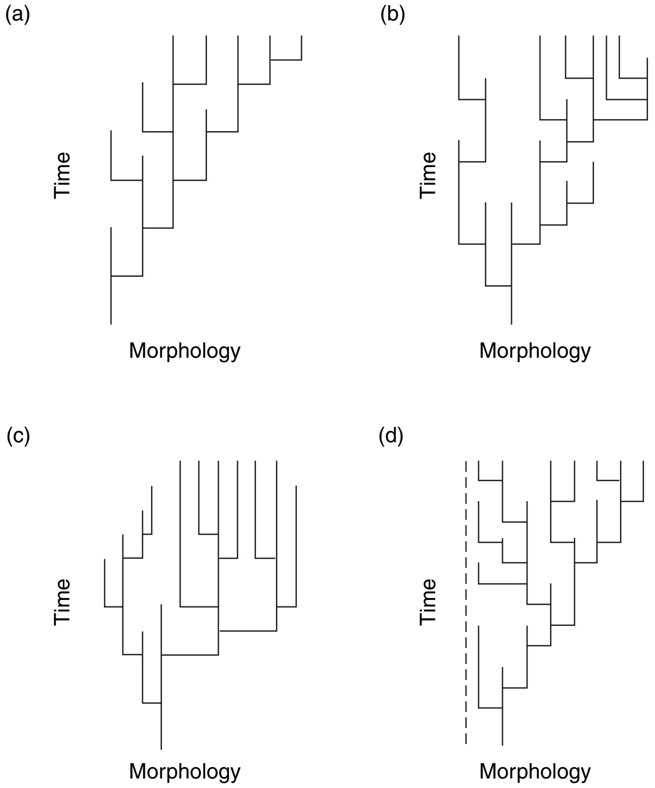

FIGURE 7.28 Hypothetical evolutionary trees showing different ways that phylogenetic trends can develop even if species are in stasis. These can also apply if species are evolving gradually. (a) *Directed speciation.* Cladogenesis produces daughter species that are preferentially to the right of their ancestors. (b) *Speciation-rate bias.* The rate of production of new species is higher on the right, leading to an accumulation of diversity and a trend in the average morphology of the clade. (c) *Extinction-rate bias.* The rate of extinction is lower on the right, also leading to an accumulation of diversity. (d) *Asymmetric increase in variance.* The clade originates near a lower limit, indicated by the dashed line. The maximum and mean morphology increase because there is more room for evolutionary change to the right of the starting point. *(a–c: After Gould, 1982; d: After Stanley, 1973)*

Directed Speciation This mechanism posits that change is concentrated at speciation events and that descendant species tend to shift in a preferred direction relative to their ancestors (Figure 7.28a).

A possible example concerns larval mode in certain gastropod taxa. The larvae of marine gastropods can be roughly divided into planktotrophic and nonplanktotrophic forms. Planktotrophs swim freely and feed on plankton. Some nonplanktotrophs do swim, but many are entirely benthic and all depend on yolk or other food supplied with the egg. The planktotrophic mode generally involves complex swimming and feeding organs that tend to be absent in nonplanktotrophs. Fortunately for paleontologists, observations on living species show that some characteristics of the larval shell, including size and number of whorls, allow planktotrophic and nonplanktotrophic species to be distinguished fairly accurately from preserved shell features (Figure 7.29) [SEE SECTION 8.6].

A number of gastropod families show an increase in the proportion of nonplanktotrophic species during the Early Tertiary (Figure 7.30)—in other words, a phylogenetic trend toward nonplanktotrophy. Planktotrophic mode is thought to be primitive within these families. Although the nonplanktotrophic larval mode was presumably selected for in those particular lineages in which it evolved, there is no compelling reason to believe that either mode is *generally* advantageous relative to the other.

The complex swimming and feeding organs used by planktotrophs tend to be lost in the transition to the nonplanktotrophic mode. Because complex organs, once lost, may be difficult to reevolve, it is generally thought that the transition from planktotrophic to nonplanktotrophic mode is more likely than the reversal. In fact, some phylogenetic analyses bear this out. Thus, there is

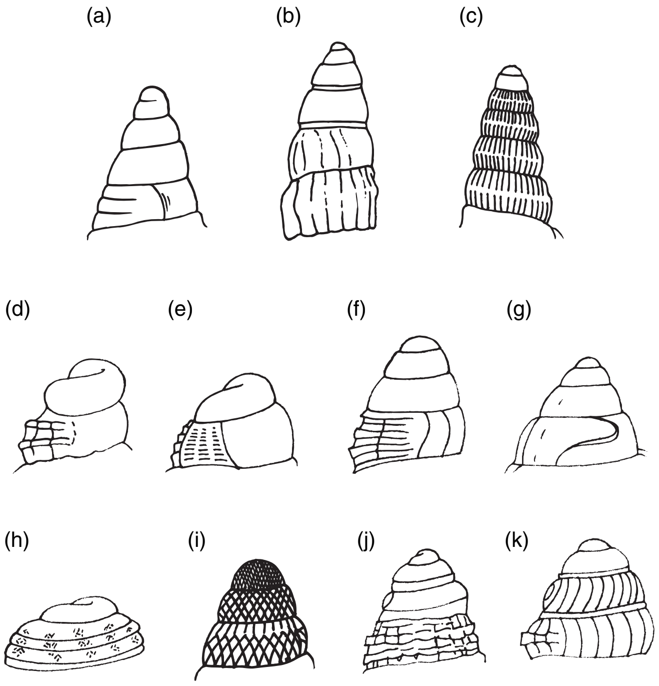

FIGURE 7.29 Larval shells of some gastropods. Parts (a) through (c), (f), (g), and (i) through (k) show planktotrophic shells. Parts (d), (e), and (h) show nonplanktotrophic shells. In contrast to nonplanktotrophic forms, planktotrophic larvae tend to have more whorls and a high, conical shape. *(From Shuto, 1974)*

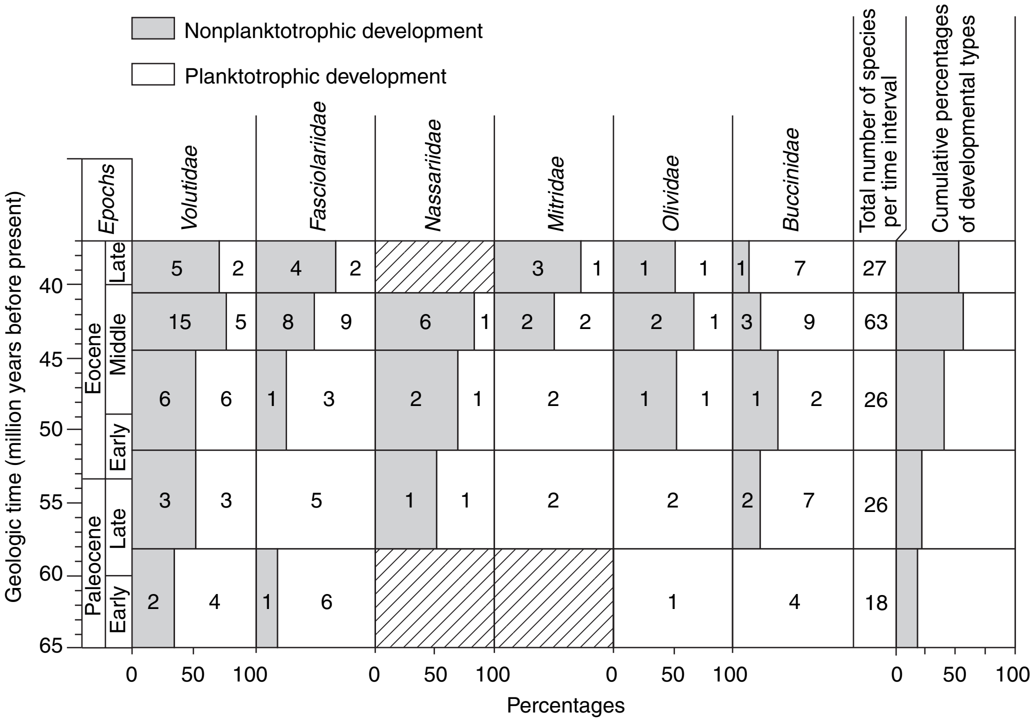

FIGURE 7.30 Number of planktotrophic and nonplanktotrophic species within several gastropod families during the Early Tertiary of the Gulf and Atlantic coasts of the United States. Numbers are counts of species for which larval mode could be assessed. Hatched boxes indicate cases in which species are known but there are no preserved protoconchs that would allow larval mode to be determined. The percentage of nonplanktotrophic species increases over time. *(From Hansen, 1982)*

a biased direction of change, and the phylogenetic trend toward increasing nonplanktotrophy appears to be influenced by directed speciation.

Speciation-Rate Bias If species of a certain form have a higher rate of production of daughter species than do species of an alternative form, the number of the first kind will tend to increase over time, shifting the clade average as it does so (Figure 7.28b).

This mechanism may also play a role in the increase in nonplanktotrophy in gastropods. Given their lower dispersal abilities, we would expect nonplanktotrophs to be more likely to form isolated populations and thus to have a higher speciation rate. This difference in speciation rate can be demonstrated in a rather simple way. Figures 7.31a and 7.31b show the durations of planktotrophic and nonplanktotrophic species in the family Volutidae. Nonplanktotrophic species have about half the average duration of planktotrophic species, implying that the extinction rate of nonplanktotrophs is about twice as high.

The higher extinction rate of nonplanktotrophs may be a consequence of their smaller geographic ranges (Figures 7.31c and 7.31d), which would make them more susceptible to chance environmental fluctuations. Regardless of the reason why nonplanktotrophs are more extinction-prone, they increase in diversity at a higher rate despite their higher extinction rate. It is therefore a logical necessity that they also have a higher speciation rate. If the results for volutids are typical, this may help to account for the increasing phylogenetic trend in the proportion of nonplanktotrophic species.

There are two potential complications with this example. First, to explain a trend in terms of differences in speciation rate, we must tacitly assume that like species give rise to like: planktotrophs to planktotrophs and nonplanktotrophs to nonplanktotrophs. Although some switching between larval modes is known, as we saw earlier, a number of phylogenetic studies suggest that switching is limited. However, much more work is needed before we can generalize.

Second, the inference of higher speciation rate in nonplanktotrophs depends on the accurate estimation of extinction rates. Because nonplanktotrophic species have smaller geographic ranges, it is conceivable that they have a less complete fossil record than planktotrophs and therefore exhibit artificially short durations and an

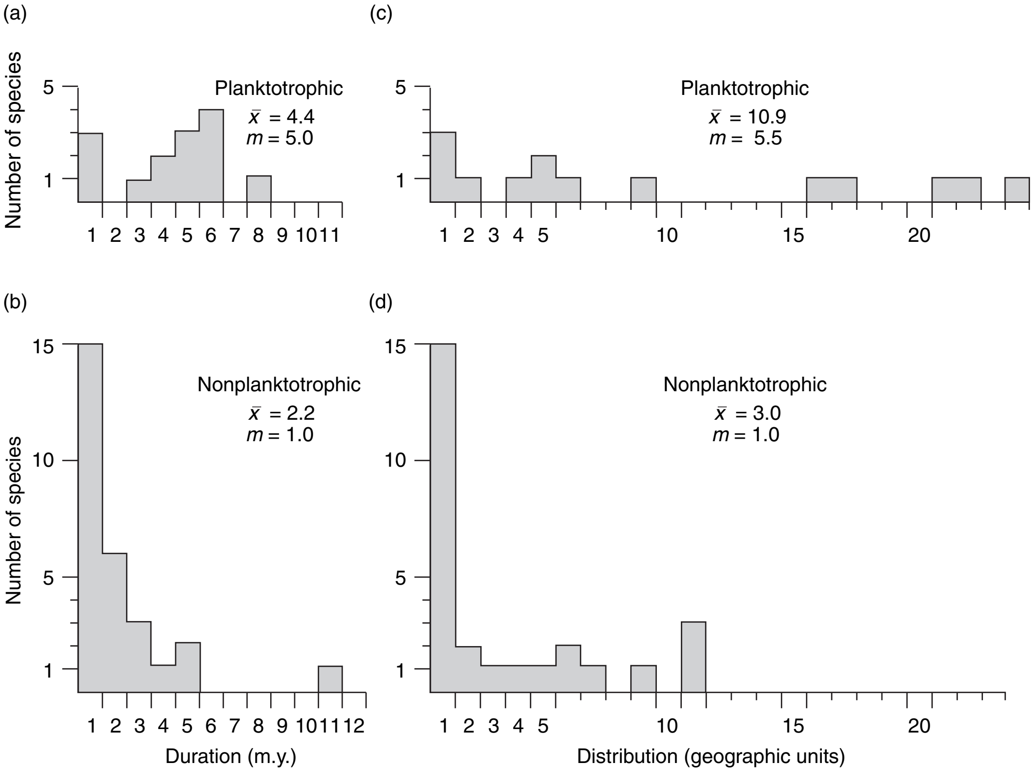

FIGURE 7.31 Duration and geographic range of planktotrophic and nonplanktotrophic species of the gastropod family Volutidae from the Early Tertiary of the United States. The outcrop belt of the Gulf and Atlantic coasts was divided into units roughly 75 km wide. Geographic range is measured as the number of these units spanned by the species. The mean and median longevity and geographic range are indicated by $\bar{x}$ and *m*. Nonplanktotrophic species have smaller geographic ranges and shorter durations on average. *(From Hansen, 1980)*

artificially high extinction rate relative to planktotrophs. This is a classic conundrum in paleontology: We observe a striking pattern—in this case, a correlation between geographic range and longevity—which can seemingly be explained as either a true biological effect or an artifact. Fortunately, we can resolve this problem.

Earlier we showed that the effects of incompleteness on extinction rates can be mitigated by disregarding species known from a single stratigraphic interval (see Box 7.2). If we omit the leftmost bars in the histograms of Figures 7.31a and 7.31b, we find that the planktotrophic species have a mean duration of 5.3 m.y., or an extinction rate of 0.19 per Lmy, while nonplanktotrophs have a mean duration of 3.5 m.y, or an extinction rate of 0.28 per Lmy. Median durations are similar. Thus, the higher extinction rate of nonplanktotrophs is not an artifact of a less complete fossil record. Moreover, the magnitude of the difference—roughly 50 percent higher extinction rate in nonplanktotrophs—is biologically significant. It is comparable, for instance, to differences between groups of crinoids, and between gastropods and bivalves, that were presented earlier in this chapter.

Extinction-Rate Bias We just saw that a phylogenetic trend can be produced by a speciation differential that increases the relative numbers of one form versus another. Likewise, a trend can also result from a difference in extinction rates (Figure 7.28c). A likely example of such a trend is seen in the planktonic Foraminiferida (Norris, 1991). Several times during the Late Cretaceous and Cenozoic, planktonic forams went through cycles of increasing and decreasing diversity. During the increasing phases in the Paleogene and Neogene, forms lacking a pronounced keel became predominant relative to keeled forms (Figure 7.32). As shown in Figure 7.33, the durations of unkeeled species are longer on average than those of keeled species. In other words, unkeeled forms have a substantially lower extinction rate. Although

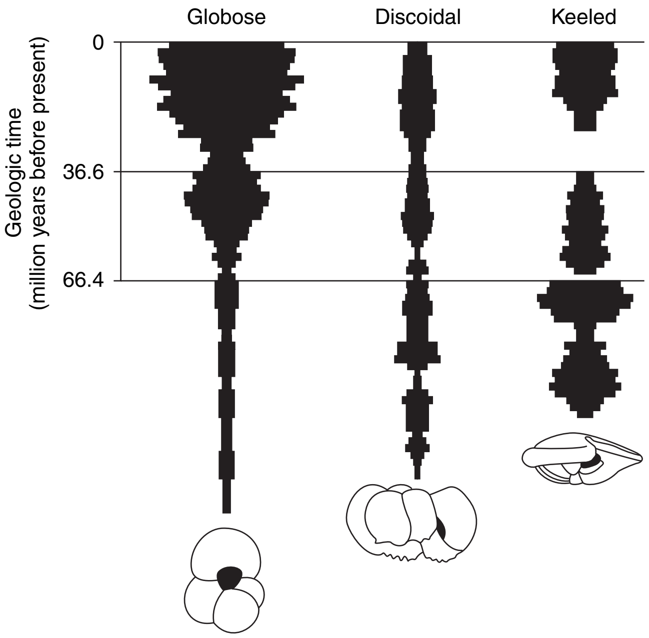

FIGURE 7.32 Species diversity of keeled and unkeeled (globose and discoidal) planktonic foraminifera during the Late Cretaceous and Cenozoic. The width of each bar is proportional to the number of species. The proportion of unkeeled forms increases over the course of the Cenozoic. *(From Norris, 1991)*

the reasons for this are still unclear, the lower extinction rate of unkeeled species evidently contributes to their preferential diversification.

Asymmetric Increase in Variance It is possible that trends within clades are explained not so much by what happens during the evolution of the clade but rather by the form possessed by its founding member—in other words, not by where the clade is headed but by where it began (Figure 7.28d). As an explanation for Cope's Rule, Steven Stanley (1973) noted that orders of mammals tend to originate at small body size and to reach larger sizes over time as the number of species increases (Figure 7.34). There is a minimum size that a mammal must attain in order to function properly—for example, a size below which it is impossible for a tiny mammal to garner sufficient food to support its high metabolism. Other biologic groups also face similar limits. Starting near the lower limit, there is more opportunity for a clade to increase in body size (or some other trait) than to decrease. Both the maximum and mean trait value of such a clade will tend to increase over time.

The reason for origination of mammal orders at small size may be that large body size often brings with it

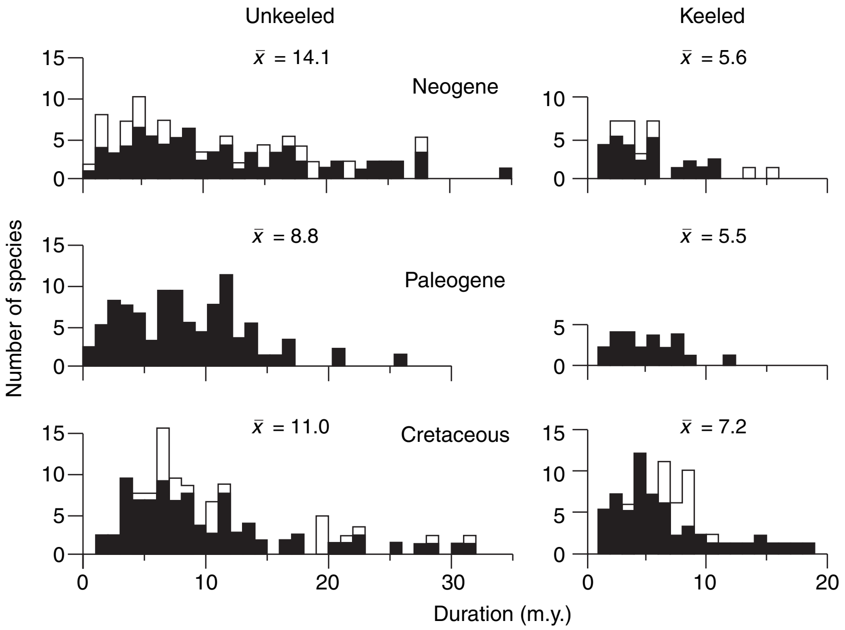

FIGURE 7.33 Species durations of keeled and unkeeled planktonic foraminifera. Open bars show durations that are truncated either by the end-Cretaceous extinction event or by the present day. Mean durations are indicated $\bar{x}$. Average duration of unkeeled forms is longer than that of keeled forms. *(From Norris, 1991)*

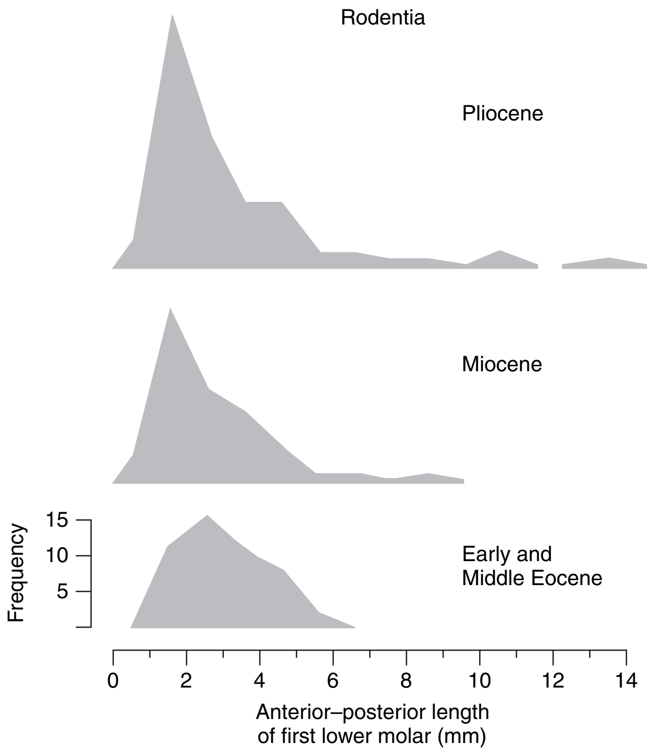

FIGURE 7.34 Body size (estimated by molar length) in Tertiary rodents. Each species is represented by the largest recorded size. Frequency distributions for species in different time intervals show that the mean and maximum size increase while the modal and minimum sizes stay roughly constant. *(From Stanley, 1973)*

many structural and ecological specializations. A transition to a major new way of life, which would characterize the origin of a new order, is generally thought to be unlikely in a very specialized lineage.

A number of important trends in the history of life may be at least partly attributable to the origin of major biologic groups near some lower limit. In addition to the increase in body size just mentioned, there is the case of structural complexity. Although complexity can be difficult to define, a number of reasonable operational measures have been developed, including number of cell types, number of kinds of organelles within cells and organs within organisms, amount of DNA, and differentiation among serial structures such as vertebrae. The first organisms of which we have a fossil record were single-celled and morphologically simple. Even though bacteria still dominate the earth's ecosystems today, the maximal complexity attained by organisms seems to have increased throughout earth history.

The fact that a clade may have originated near some structural limit does not necessarily mean that this is the *cause* of a phylogenetic trend. Returning to the horse example, this family originates at small body size and seems to spread out asymmetrically (Figure 7.26). Yet we have already seen that there is a strong tendency for body size to increase from ancestors to descendants (Figure 7.27). Thus, the origin at small size may contribute to the trend in horses, but it cannot be the sole explanation.

7.5 CONCLUDING REMARKS

This last point underscores the complexity that underlies evolutionary rates and trends. Out of convenience and necessity, we generally contrast alternative, simple models. But in actual cases, it is almost certain that a mixture of mechanisms was at work. A single lineage sometimes evolves directionally and sometimes is static. A taxonomic group whose average extinction rate we wish to estimate actually consists of some lineages that are highly susceptible to extinction and others that are nearly immortal. Several causes of trends may be acting simultaneously—for example, directed speciation and biased speciation rate in the case of larval mode in gastropods—and they may in principle act in opposition. The simplicity of models should not be seen as a flaw, however. Without them, we would have abundant data on morphology and stratigraphic occurrence, but we would be hobbled in our ability to interpret these data.

We have conspicuously ignored the role of adaptation in phylogenetic trends. Yet in our discussion of theoretical morphology in Chapter 5, we assumed that adaptation is a major cause of the relative numbers of species with different morphological features. In some cases, it is clear that phylogenetic trends are likely to be adaptive in nature—most confidently when they are underlain by phyletic trends in the same direction. In other cases, this is not so obvious. We might posit that superior adaptation leads to a decrease in extinction rate, and perhaps even to an increase in origination rate through the reduced extinction probability of isolated populations that have the potential to become new species [SEE SECTION 3.3]. One difficulty with this line of reasoning is that it implies a negative correlation between origination and extinction rate, when the two are in fact positively correlated in general. Moreover, many documented differences in origination and extinction rates appear to be underlain by differences in geographic range and other aspects of population structure, which are not organism-level adaptations.

In summary, it is likely that adaptation often plays a role in phylogenetic trends. Given the shortage of detailed case studies, however, we do not know just how strong its role is in general. The broader issue here is that of bridging the gap between the microevolutionary timescale, where adaptation may be most important, and the timescale of macroevolution.

We have taken a brief look at some of the fundamental ways in which paleontology has provided unique insights into evolution, especially on geologic timescales. Our examples illustrate the richness of data and approaches brought to bear on macroevolutionary questions: morphology, geologic duration, geographic range, and phylogeny, to name but a few. Our understanding of large-scale evolution has been significantly enhanced by considering mechanisms such as species selection that involve processes other than accumulated, generation-by-generation evolution within populations. Insights from the fossil record have helped both paleontologists and biologists to understand better the relationships between micro- and macroevolution. Macroevolution must, of course, be consistent with microevolution. But, practically speaking, it is often impossible to predict particular outcomes of macroevolution from microevolutionary observations alone.

Other reasons why this is so are discussed in the next chapter, when we consider the possible role of mass extinction episodes in eliminating accumulated evolutionary change within lineages, removing ecologically established taxa, and generally changing the rules of evolutionary success and failure that operate at other times.

SUPPLEMENTARY READING

Erwin, D. H., and Anstey, R. L. (eds.) (1995) *New Approaches to Speciation in the Fossil Record*. New York, Columbia University Press, 342 pp. [A series of papers illustrating a variety of ways that speciation can be studied in the fossil record, with particular emphasis on the question of punctuated equilibrium.]

Gould, S. J. (2002) *The Structure of Evolutionary Theory*. Cambridge, Mass., Harvard University Press, 1433 pp. [Comprehensive overview of punctuated equilibrium and related topics in macroevolution.]

Jablonski, D. (2000) Micro- and macroevolution: Scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology* **26** (Suppl. to No. 4):15–52. [Comprehensive overview of major themes in macroevolution, including species selection and determinants of taxonomic longevity.]

Levinton, J. (2001) *Genetics, Paleontology, and Macroevolution*, 2nd ed. New York, Cambridge University Press, 617 pp. [Treatment of macroevolution in the fossil record from the standpoint of biology.]

McNamara, K. J. (ed.) (1990) *Evolutionary Trends*. Tucson, Ariz., University of Arizona Press, 368 pp. [Series of papers on theoretical issues in the analysis of trends and case studies from the fossil record.]

McShea, D. W. (1994) Mechanisms of large-scale evolutionary trends. *Evolution* **48:**1747–1763. [Critical assessment of models for explaining phylogenetic trends.]

Raup, D. M. (1985) Mathematical models of cladogenesis. *Paleobiology* **11:**42–52. [A useful summary of models of orignation and extinction, with a detailed appendix giving equations for survivorship and other important properties of species and clades.]

Roopnarine, P. D. (2003) Analysis of rates of morphological evolution. *Annual Review of Ecology, Evolution and Systematics* **34:**605–632. [Overview of technical problems in the measurement and interpretation of rates of evolution.]

Simpson, G. G. (1953) *The Major Features of Evolution*. New York, Columbia University Press, 434 pp. [Landmark in the quantitative study of rates and trends.]

Stanley, S. M. (1979) *Macroevolution: Pattern and Process.* San Francisco, W. H. Freeman and Company, 332 pp. [Important treatment of the factors that give rise to macroevolutionary patterns.]

Van Valen, L. M. (1973) A new evolutionary law. *Evolutionary Theory* **1:**1–30. [Pioneering application of the exponential survivorship model to paleontological data.]