

Chapter 8

GLOBAL DIVERSIFICATION AND EXTINCTION

The investigation of global diversity has flourished in paleontology during the past quarter century. In a sense, this can be viewed as the culmination of efforts spanning several centuries to catalogue the contents of the fossil record. But there is little doubt that diversity studies have also been spurred on by additional factors, including (1) the advent of computers, which permit the assembly and analysis of large databases; (2) a growing interest in the history of global diversity through geologic time, which relates to environmental change coupled with evolutionary patterns and processes highlighted throughout this book; and (3) present-day concerns about the ongoing crisis in diversity (or, as it is commonly known, **biodiversity**), for which the fossil record provides historical perspective at timescales far exceeding the human life span.

In this chapter, we consider the major features of global diversification and extinction, including large-scale transitions in taxonomic composition; time intervals characterized by significantly elevated extinction rates (**mass extinctions**); regional variations in global diversity trends; and the analysis of morphological diversity as a complement to the more traditional reliance on taxonomic diversity.

8.1 THE NATURE OF BIOLOGICAL DIVERSITY

The term **diversity** has taken on a variety of meanings in biological and paleontological research. For example, ecologists often characterize the diversity of a given set of taxa with metrics that account jointly for the number of

unique taxa in a sample (**taxonomic richness**) and the abundances of each taxon. Recently, paleontologists have also formalized the concept of **morphological diversity**, which provides an alternative to the strict assessment of taxonomic composition as a measure of macroevolutionary dynamics and trends [SEE SECTION 8.10].

With respect to global diversity, the main focus has been on the calibration and explanation of trends through time in global taxonomic richness. As we will see, these efforts throughout the Phanerozoic Eon, the interval of earth history characterized by an abundant record of multicellular organisms, are complemented by consideration of diversity trends at local and regional scales and how these combine to produce the patterns that we observe at the global level. But much of the motivation for local and regional studies came from the recognition of a set of intriguing patterns first observed at the global level. Thus, the initial focus in this chapter is on the tools that permit global-scale analyses, including the development of global taxonomic databases and the use of these data to construct global diversity curves. We have already considered, in Chapter 7, methods for measuring origination and extinction; these measurements will also be important to our discussions in this chapter.

8.2 GLOBAL TAXONOMIC DATABASES

Before constructing a graph that depicts the global history of diversity through successive intervals of geologic time, fossil taxa must first be catalogued in a database that

lists, for each taxon, the interval of its first and last known global appearances. Although there are various methods for actually tabulating a diversity curve (see below), the basic objective is to determine from these data the number of taxa that were extant from interval to interval.

Substantial efforts therefore have focused on the development of databases that accurately capture information on fossil occurrences collected worldwide. This has been aided for more than a century by the development of encyclopedic compilations of known fossil occurrences over broad regions, or, in the case of publications like the *Treatise on Invertebrate Paleontology*, the entire world. Historically, the development of regional or global diversity curves has followed closely on the assembly of these compilations. Among the earliest examples was John Phillips's pair of graphs (Figure 8.1), produced in 1860, for fossil marine biotas of Great Britain, based on John Morris's publication *A Catalogue of British Fossils* (1854). Despite the geographic limitation of the data that Phillips depicted, the clear implication was that he was capturing patterns of broader global significance, and, indeed, the major features of

these graphs are shared by global compilations produced more than a century later.

The best-known databases used to compile Phanerozoic global marine diversity curves in recent times were developed by Jack Sepkoski, at the family and genus levels. Other efforts have been equally ambitious, resulting in diversity curves that are quite similar to those derived from Sepkoski's databases. A portion of Sepkoski's genus-level compendium is shown in Figure 8.2, which illustrates two important features of the database. First, the degree of stratigraphic resolution in first and last known global appearances is highly variable, but, in general, Sepkoski sought to resolve these appearances to fine-scale subdivisions of the geologic timescale, such as subepochs. Second, while Sepkoski initiated his data compilations by extracting information from the *Treatise on Invertebrate Paleontology*, his efforts moved far beyond the *Treatise*. The collection of new data from the fossil record and the refinement of taxonomic designations is an ever-evolving process for even well-known taxa, and any single volume of the *Treatise* inevitably becomes outdated shortly after, or even during, its publication. Thus, Sepkoski

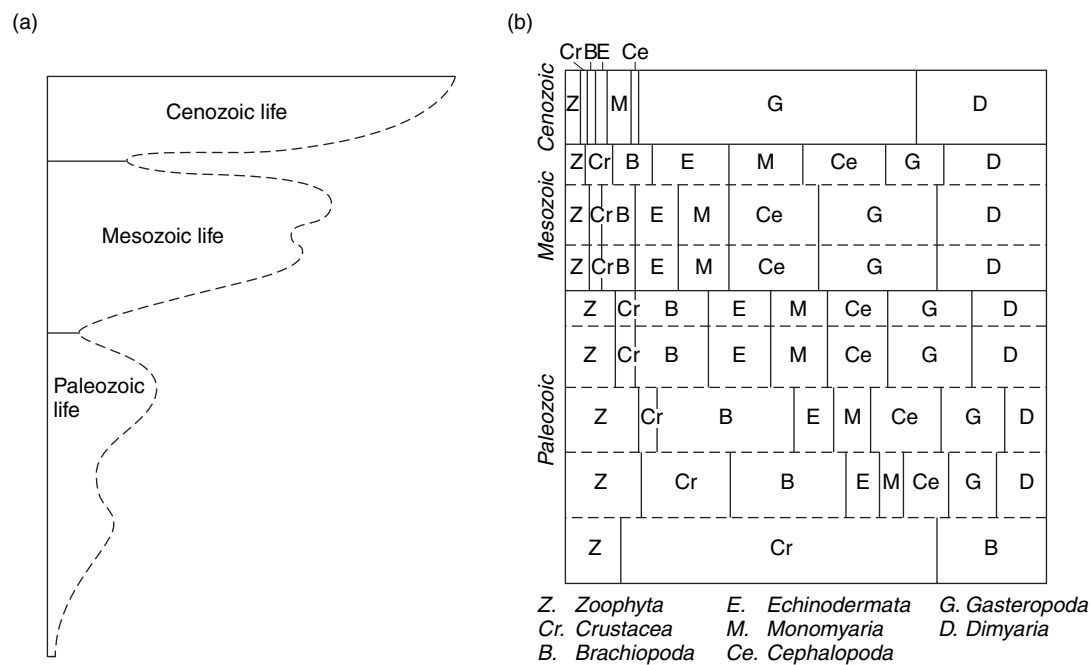


FIGURE 8.1 Phillips's (1860) depiction of the history of Phanerozoic marine diversity, based on the occurrences of marine fossils in Great Britain. (a) An illustration of changes through time in the number of species. (b) A summary of changes through time in the relative contributions of major taxa to the overall composition of the marine biota. Although some of the names are outdated (e.g., "Crustacea" refers primarily to trilobites and "Dimyaria" are bivalve molluscs), the transitions that Phillips depicted closely approximate those illustrated more than a century later by other researchers. (From Phillips, 1860)

<i>Rugosowerbyella</i>	O (Ashg-l) - O (Ashg-u)
<i>Rurambonites</i>	O (Cara-u)?- O (Ashg-u)
<i>Rutrumella</i>	O (Llvi)
<i>Sampo</i>	O (Cara-u) - O (Ashg-u)
<i>Sanjuanella</i>	O
<i>Schedophyla</i>	O (Aren-l) - O (Llvi)?
<i>Sentolunia</i>	O (Ashg-l)
<i>Sericoidea</i>	O (Llde-u) - O (Ashg-u)
<i>Shlyginia</i>	O (m)
<i>Sowerbyella</i>	O (Llvi-u)?- S (Ldov-l)
<i>Sowerbyites</i>	O (Llde-u) - O (Cara-u)
<i>Spanodonta</i>	O (Trem-u) - O (m)?
<i>Strophomena</i>	O (Llvi-l) - S (Ldov-l)
<i>Syndielasma</i>	O (Llvi-l)
<i>Taffia</i>	O (Aren-l) - O (Llvi)
<i>Taphrodonta</i>	O (Llvi-u)
<i>Teratelasma</i>	O (Cara-l)
<i>Tetraodontella</i>	O (Llvi-l)?- O (Cara-m)
<i>Tetraphalerella</i>	O (Llde) - O (Ashg-m)

FIGURE 8.2 A small portion of Sepkoski's (2002) genus-level global compendium, depicting the global stratigraphic ranges of several strophomenide brachiopods that were extant during the Ordovician Period, abbreviated in the compendium by the letter O. Intervals of first and last known global appearances are indicated, except when the genus is confined to a single interval, in which case only a single designation is provided (e.g., *Rutrumella*). Note that the stratigraphic resolution is variable. Designations in parentheses are abbreviated names for series or stages of the geologic timescale, some of which have changed in updated versions of the timescale. In many cases, finer subdivisions of these intervals are designated as lower (-l), middle (-m) and upper (-u).

relied on the primary literature to continually expand and refine his compendia.

This last point serves as a general reminder that, in the study of fossil biodiversity, the data are never complete because new discoveries and analyses that affect the data are almost continuously forthcoming in the literature. Nevertheless, as discussed in Chapter 1, there is substantial evidence that, for broad perspectives on Phanerozoic global diversity trends, databases like Sepkoski's compendia have matured sufficiently to capture accurately the main biotic transitions preserved in the fossil record [SEE SECTION 1.5].

8.3 CONSTRUCTION OF GLOBAL DIVERSITY CURVES

Methods for constructing global diversity curves are conceptually straightforward, but variations have been proposed over the past several years, as described and illustrated in Box 8.1. The objective is to characterize the number of taxa extant in consecutive stratigraphic in-

tervals and then to depict these values on an x - y plot. As explained in Box 8.1, there are many ways to count the number of taxa, all of which rest on the convention that each taxon *ranges through* the entire stratigraphic interval between its first and last appearances, as depicted in the database.

A potential problem with Phanerozoic-scale diversity curves is the possibility that values are inflated toward the present day, a pattern termed **Pull of the Recent**. Two separate aspects to this phenomenon concern us here. The first, as discussed in Chapter 1, is the increase, particularly in the Cenozoic, in the amount of sedimentary rock and hence the number of fossils available for sampling. The second is a direct consequence of the range-through assumption and the likelihood that the Recent (i.e., the present day) is far better sampled than even well-preserved parts of the fossil record (Figure 8.4). As the Recent is approached, it is probably not uncommon for taxa that occur in just one stratigraphic interval in the fossil record (stratigraphic singletons), or that are limited to a narrow stratigraphic window, to have a Recent representative. Whenever this is the case, the taxa in question are credited to the entire interval between the Recent and their first, and perhaps only, appearance in the fossil record. This inflates diversity above the level that would be achieved if no data from the Recent were available. This is of little or no consequence, say, for Paleozoic taxa, because they are unlikely to have Recent representatives. But it may happen frequently with late Mesozoic and, especially, Cenozoic taxa.

The actual inflation induced by the Pull of the Recent is difficult to quantify. One way of assessing this problem would be to develop a database that includes information not only on the global first appearance of a taxon that ranges to the Recent, but also on known occurrences that fall after the first appearance. With these data, it could be determined for a given extant taxon whether there remains a significant gap between its *last* known fossil appearance and the Recent.

In a pioneering analysis of bivalve molluscs that adopted this approach, David Jablonski and colleagues (2003) studied 958 fossil genera and subgenera that are still extant today. Of these, 906 (95 percent) have fossil representatives in Pliocene and/or Pleistocene strata, suggesting that, at least for this important Cenozoic group, the Pull of the Recent is minimal. Questions remain concerning the possibility that the Pliocene and Pleistocene records are, in themselves, so unusually outstanding that they produce a "Pull of the Plio-Pleistocene."

Box 8.1

CONSTRUCTION OF DIVERSITY CURVES

This box illustrates the construction of global diversity curves using methods discussed in the main text. The data for these curves, presented in Table 8.1, consists of 40 hypothetical genera whose first and last appearances fall within the epochs of the Cenozoic; 21 of the taxa are extant (i.e., their “last appearance” is in the Recent). These data are used to construct a set of values, presented in Table 8.2, that provide the basis for the curves depicted in Figure 8.3.

An important assumption in the construction of all diversity curves, known aptly as the **range-through** assumption, is that a taxon remains extant for the entire interval between its first and last known occurrences in the fossil record. Importantly, if a taxon that is represented in the fossil record is also extant today,

it is therefore assumed that the taxon ranged through the entire interval from its first appearance in the fossil record through the present day, even if its first appearance is its only known fossil occurrence (i.e., it is a fossil singleton).

To calculate diversity by the methods illustrated here, we must first determine the number of originations ($N. orig_t$) and the number of extinctions ($N. ext_t$) in each interval. For example, in perusing Table 8.1, we can see that there were nine first appearances and one last appearance in the Paleocene. Therefore, in Table 8.2, $N. orig_t$ for the Paleocene is 9, and $N. ext_t$ is 1. Once these values have been determined for all intervals, diversity can be calculated for the standard and boundary-crosser methods (Figures 8.3a and 8.3b)

TABLE 8.1

Global Stratigraphic Ranges for a Set of Hypothetical Genera

Genus	First Appearance	Last Appearance	Genus	First Appearance	Last Appearance
a	Paleocene	Recent	u	Pliocene	Recent
b	Miocene	Miocene	v	Oligocene	Pleistocene
c	Paleocene	Eocene	w	Eocene	Eocene
d	Eocene	Eocene	x	Pleistocene	Recent
e	Oligocene	Recent	y	Paleocene	Paleocene
f	Pleistocene	Recent	z	Miocene	Pliocene
g	Oligocene	Miocene	aa	Paleocene	Miocene
h	Paleocene	Eocene	bb	Eocene	Recent
i	Pliocene	Recent	cc	Pliocene	Recent
j	Eocene	Eocene	dd	Pleistocene	Pleistocene
k	Oligocene	Pleistocene	ee	Pleistocene	Recent
l	Pleistocene	Recent	ff	Paleocene	Eocene
m	Pleistocene	Pleistocene	gg	Miocene	Recent
n	Pliocene	Recent	hh	Oligocene	Recent
o	Miocene	Recent	ii	Paleocene	Eocene
p	Paleocene	Oligocene	jj	Pleistocene	Recent
q	Eocene	Recent	kk	Pliocene	Recent
r	Miocene	Recent	ll	Miocene	Recent
s	Paleocene	Eocene	mm	Pleistocene	Recent
t	Pleistocene	Recent	nn	Pleistocene	Pleistocene

TABLE 8.2
 Values and Equations Used to Calculate Diversity Curves
 for the Hypothetical Data from Table 8.1

Interval	Ma	N. orig _t	N. ext _t	N _{st}	d _t with All Data Included	N. orig _t without Singletons	N. ext _t without Singletons	d _t without Singletons	N. orig _t with Recent Occurrences Ignored	N. ext _t with Recent Occurrences Ignored	d _t with Recent Occurrences Ignored	Boundaries (for Boundary-Crosser Method)
Paleocene	60	9	1	1	9	8	0	8	9	2	9	Paleocene/Eocene
Eocene	45	5	8	3	13	2	5	10	5	10	12	Eocene/Oligocene
Oligocene	28	5	1	0	10	5	1	10	5	3	7	Oligocene/Miocene
Miocene	14	6	3	1	15	5	2	14	6	7	10	Miocene/Pliocene
Pliocene	4	5	1	0	17	5	1	17	5	6	8	Pliocene/Pleistocene
Pleistocene	1	10	5	3	26	7	2	23	10	12	12	Pleistocene/Recent

Key: d_t = diversity in interval t
 d_{t-1} = diversity in interval $t - 1$
 $d_{t/t+1}$ = diversity at boundary between intervals t and $t + 1$
 N. orig_t = number of originations in interval t
 N. ext_t = number of extinctions in interval t
 N. ext_{t-1} = number of extinctions in interval $t - 1$
 N_{st} = number of singletons in interval t

Standard Method for Calculating Diversity:
 $d_t = d_{t-1} + \text{N. orig}_t - \text{N. ext}_{t-1}$
 Example: When all data are included,
 $d_{\text{Oligocene}} = d_{\text{Eocene}} + \text{N. orig}_{\text{Oligocene}} - \text{N. ext}_{\text{Eocene}}$;
 thus, $d_{\text{Oligocene}} = 13 + 5 - 8 = 10$

Boundary-Crosser Method for Calculating Diversity:
 $d_{t/t+1} = d_t - \text{N. ext}_t$
 Example:
 $d_{\text{Oligocene}/\text{Miocene}} = d_{\text{Oligocene}} - \text{N. ext}_{\text{Oligocene}}$;
 thus, $d_{\text{Oligocene}/\text{Miocene}} = 10 - 1 = 9$

continued on next page

Box 8.1 (continued)

using the equations presented in the table. In addition, the table presents values based on variations of the standard method that exclude singletons (Figure 8.3c) and Recent occurrences (Figure 8.3d). The elimination of Recent occurrences, advocated by some researchers, automatically relegates to singleton status all genera that range to the Recent. In practice, a decision to ignore these occurrences should be coupled with an attempt

to discover the last known fossil occurrences of these taxa to avoid artificial inflation of the number of singletons (see text for further discussion).

It should also be noted that many of the values described here and depicted in Table 8.2 are also relevant to our discussion of evolutionary rates in Chapter 7, albeit with a slightly different terminology (see Box 7.2 for a comparison of these terms).

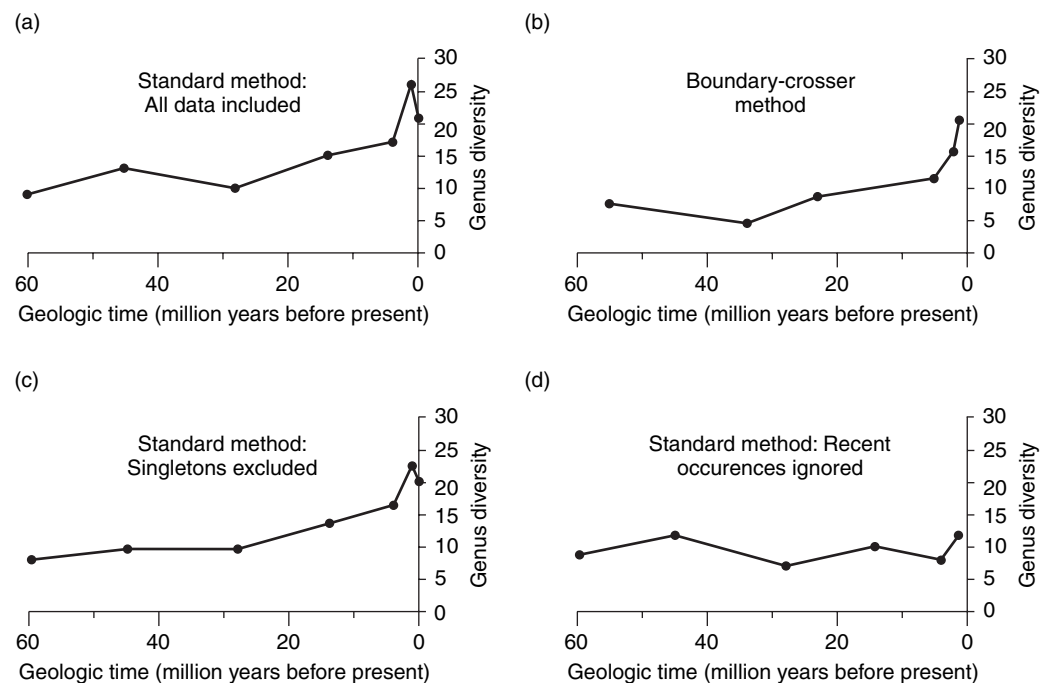


FIGURE 8.3 Four depictions of taxonomic diversity through the Cenozoic Era, based on four alternative treatments of the hypothetical data presented in Table 8.1. (a) “Standard” method, with all data included. (b) Boundary-crosser method. (c) Standard method with singletons excluded. (d) Standard method with Recent occurrences excluded.

This possibility has yet to be evaluated, and it also remains to be determined whether the pattern documented by Jablonski and colleagues will hold up for other taxa. Nevertheless, this analysis illustrates a promising, if time-consuming, procedure for addressing what has been a persistent question in paleontology.

The Pull of the Recent is but one feature that might cause a global diversity trend to depart from the true biological signal. Even in intervals far removed from the Recent, variations from interval to interval in the avail-

ability of fossil samples, the intensity of sampling, and interval duration could all cause further distortion. Sepkoski reasoned that one way to help overcome these problems would be to exclude singletons from consideration. In Sepkoski’s view, variations in the number of singletons from interval to interval relate directly to variations in sampling. If a particular interval has significantly more singletons than the intervals that surround it, this could be taken to indicate that the size of the sample for that interval is inflated in some way. Thus, in

	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Recent
A	F		L				X
B	F	L					X
C		F	L				X
D		F		L			X
E			F		L		X
F				F	L		X
G					F	L	X
H						F	X
Standing diversity	2	4	4	3	3	2	Recent excluded
	2	4	5	6	7	8	Recent included

FIGURE 8.4 A schematic illustration of the Pull of the Recent. The first (F) and last (L) known fossil occurrences are illustrated for eight hypothetical taxa that are all known to be extant. Using the “standard” method for calculating diversity (illustrated in Box 8.1), the inclusion of Recent occurrences significantly inflates standing diversity, beginning in the Oligocene, relative to what it would have been without the inclusion of Recent occurrences.

producing his genus-level depiction of Phanerozoic diversity (Figure 8.5b), Sepkoski did not include singletons. This procedure, which dampens interval-to-interval variations in diversity (see Box 8.1), has been adopted by several other authors, reflecting a growing consensus that this helps to mitigate variations in sampling intensity.

A diversity curve can be built at any taxonomic level. Family- and genus-level depictions of Phanerozoic diversity are illustrated in Figure 8.5 and are broadly similar to

one another, but they differ in two respects that relate to the hierarchical nature of taxonomic classification. First, and not surprisingly, there were substantially more genera than families during most Phanerozoic intervals. Second, the genus-level curve is more volatile than the family-level depiction, punctuated by increases and decreases that are more exaggerated. This is because a net change in family diversity during a given time interval will necessarily be accompanied by a change in genus diversity that is at least

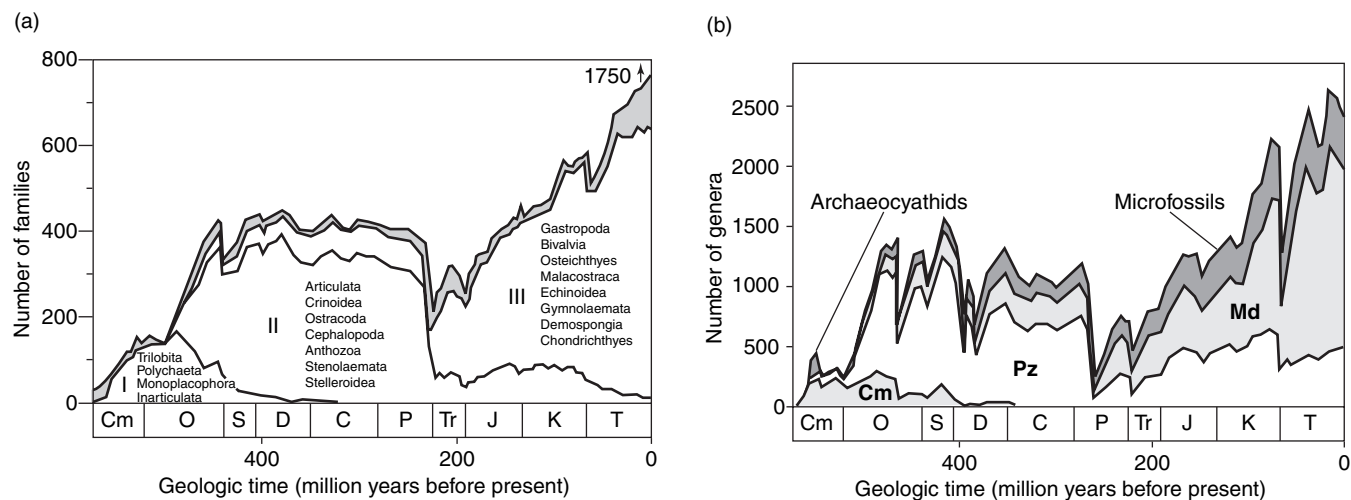


FIGURE 8.5 Sepkoski’s depictions of the Phanerozoic history of global marine diversity. In this and subsequent figures that depict multiple groups, the curves are “stacked,” meaning that they are cumulative. (a) Family diversity: The gray portion is for taxa classified by Sepkoski as poorly preserved. Subsets of the graph designated with roman numerals I through III delineate Sepkoski’s three evolutionary faunas (see text and Figure 8.8). (b) Genus diversity: The evolutionary faunas are designated with abbreviations: Cm for Cambrian, Pz for Paleozoic, and Md for Modern. The dark gray portion depicts archaeocyathid diversity in the Cambrian, and microfossils thereafter. (a: Sepkoski, 1981; b: Sepkoski, 1997)

as large: Every family contains at least one genus, and, given that many families contain more than one genus (sometimes many more), the accompanying change at the genus level will likely be more pronounced.

In contrast, a net change in genus diversity *need not* be accompanied by a change at the family level. In the most extreme cases, an increase in genus diversity could take place entirely within families that are already extant, and a decrease in genus diversity could take place without the extinction of any families to which the genera belong. Major intervals of extinction are marked by significant declines at both the genus and family levels, but the declines are inevitably more pronounced, on a percentage basis, at the genus level.

To further dampen the effects of variations in sampling and interval length (see Box 7.3), Richard Bambach and other researchers have advocated the use of only **boundary-crossing** taxa in Phanerozoic diversity compilations (Figure 8.6), in contrast to the “standard method” (Box 8.1) used by Sepkoski and many other workers. Bambach tabulated standing diversity at boundaries between intervals by determining the total number of genera extant in the older interval and then subtracting from that value the number of genera whose ranges ended in the older bin. If done sequentially for a set of boundaries, this conveys for each interval the change in the number of genera entering it and leaving

it (see Section 7.2 and Box 8.1 for an illustration of this method in comparison to others). Undoubtedly, the methods used to reconstruct the history of Phanerozoic global diversity will continue to evolve as researchers seek to extract meaningful biological signals from the raw material of the fossil record.

The main focus in this chapter thus far has been on the development of graphs depicting Phanerozoic diversity for marine animals and protists. Corresponding compilations and graphs have also been developed for terrestrial animals and for plants. Examples that illustrate Phanerozoic patterns among marine and terrestrial vertebrates and among terrestrial plants are illustrated in Figure 8.7. In these depictions, and in those of marine diversity that we looked at earlier, there are major transitions in taxonomic composition throughout the Phanerozoic, as well as significant increases in total diversity in the approach to the Recent. While the Pull of the Recent and other sampling issues might inflate the appearance of the Mesozoic–Cenozoic increase, there is little doubt that the underlying taxonomic transitions took place at the approximate times indicated by these graphs. A major challenge confronting paleontologists has been to explain these transitions, and to determine whether macroevolutionary themes common to all realms and taxa are responsible for them. We turn to these issues in the next section.

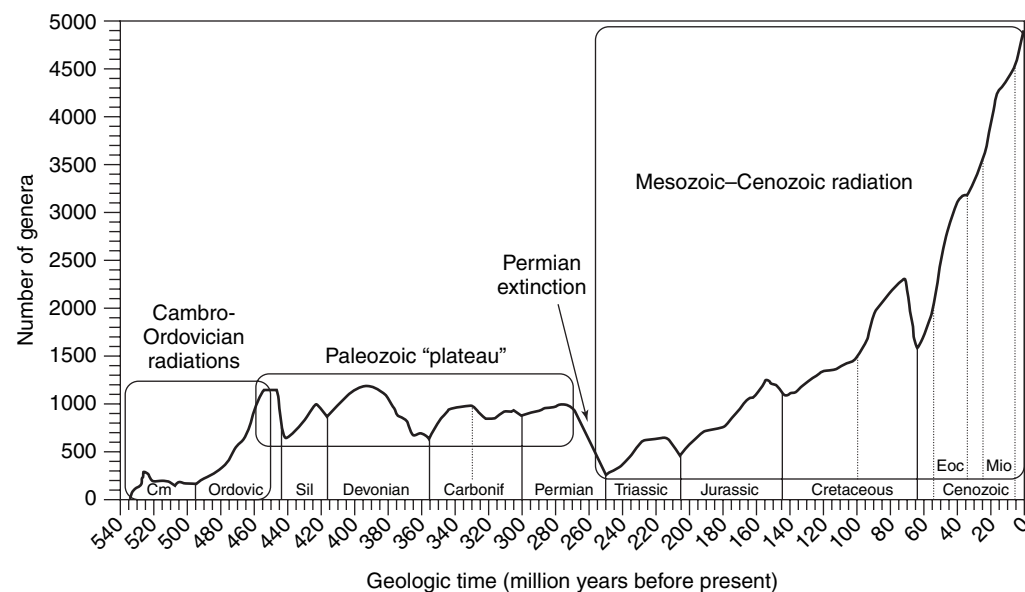


FIGURE 8.6 Bambach's depiction of the Phanerozoic history of global marine genus diversity, using only boundary-crossing genera. (Bambach, 1999)

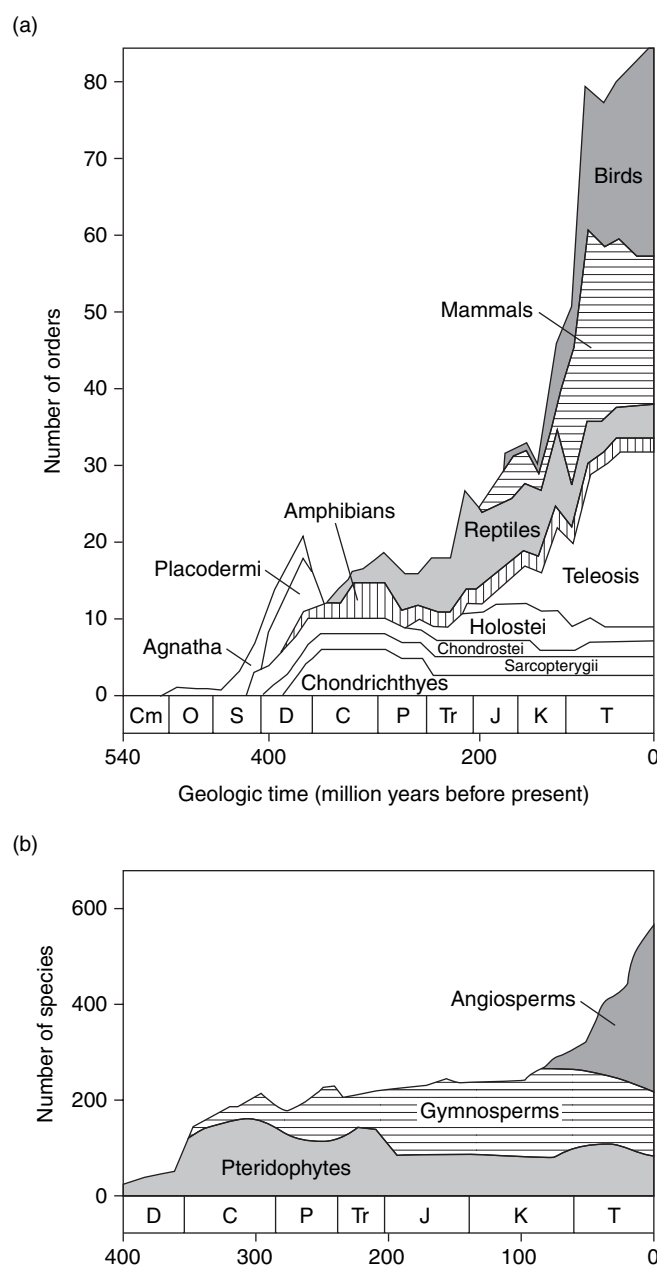


FIGURE 8.7 Other examples of Phanerozoic global diversity curves. (a) Vertebrate orders. (b) Terrestrial plant species. (a: Padian & Clemens, 1985; b: Niklas, 1997)

8.4 PHANEROZOIC TRANSITIONS IN TAXONOMIC COMPOSITION

The Marine Realm

Building on the pioneering efforts of Karl Flessa and John Imbrie (1973), Jack Sepkoski (1981) presented a quantitative description of transitions among marine taxa through the Phanerozoic. Sepkoski coined the term **evolutionary fauna** to describe broad sets of taxa that

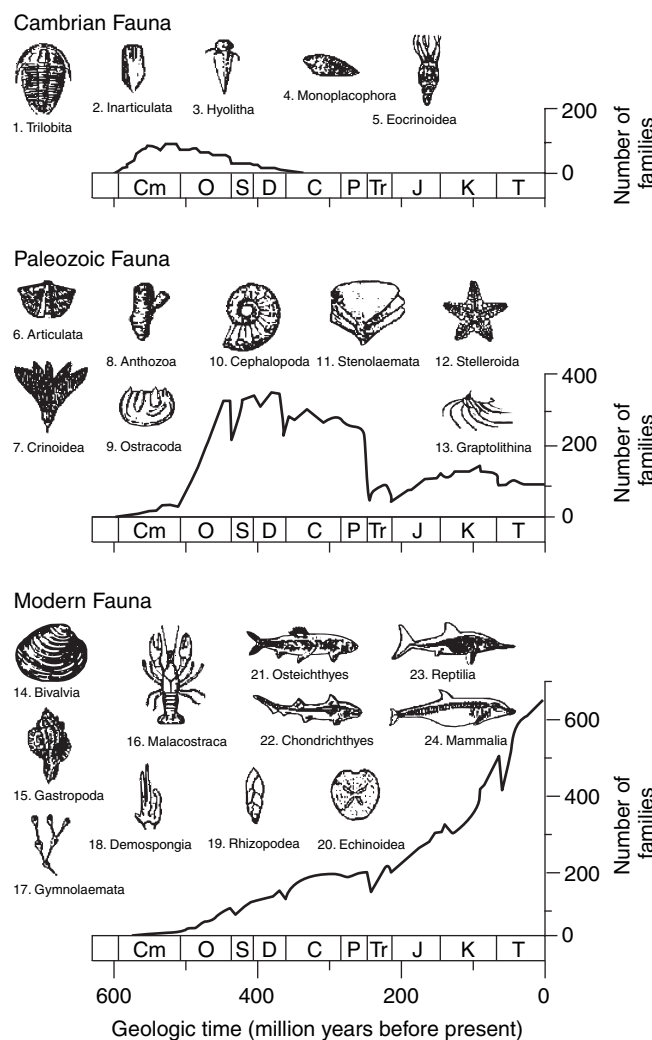


FIGURE 8.8 Sepkoski's (1984) depictions of the major taxa in each of his three Phanerozoic marine evolutionary faunas. (Sepkoski, 1984)

were globally dominant through extended geologic intervals. He recognized three Phanerozoic evolutionary faunas (Figures 8.5 and 8.8). The **Cambrian Fauna** dominated marine settings throughout the Cambrian following the initial burst of diversification at the start of the Phanerozoic known as the **Cambrian Explosion** [SEE SECTION 10.2]. The **Paleozoic Fauna** diversified significantly during the **Ordovician Radiation**, when global diversity attained unprecedented levels that were maintained through much of the remaining Paleozoic. The **Modern Fauna** exhibited limited diversity throughout the Paleozoic Era but diversified appreciably in the post-Paleozoic to become the dominant biota of the Mesozoic and Cenozoic Eras.

Sepkoski argued that the three evolutionary faunas were more than just coincidental collections of taxa. He viewed them as functional units that interacted with one another, *causing* the major global biotic transitions observed through the Phanerozoic. This perspective has been challenged by many paleontologists, in part because it is now understood that evolutionary faunas were neither as internally cohesive nor as distinct from one

another in space and time as Sepkoski once envisioned [SEE SECTION 9.4]. Nevertheless, it is important to consider Sepkoski's quantitative perspective of transitions among evolutionary faunas because of its central role in developing a large-scale, synthetic outlook in the investigation of biodiversity.

Sepkoski's goal was to develop a mathematical description of the major features of Phanerozoic marine

Box 8.2

DEVELOPMENT OF THE COUPLED LOGISTIC MODEL

The use of the coupled logistic model by Sepkoski and others to simulate Phanerozoic diversity patterns can be explained in three steps. We begin by first considering the simple case of a diversity trajectory exhibited during an exponential diversification. To simulate an exponential diversification, we can use the following equation:

$$d_t = d_{t-1} + rd_{t-1}$$

where d_t represents diversity (the number of taxa) in interval t , d_{t-1} represents diversity in interval $t - 1$, and r denotes a constant rate of increase (sometimes referred to as the *intrinsic* rate of increase). In simulations of Phanerozoic diversification, Sepkoski set the value of a simulated time unit to 1 million years.

An example of the application of this equation is presented in Figure 8.9. Here, the starting diversity at time interval 0 is set to unity, and the intrinsic rate of increase, r , is set to 2. For example, we can calculate the diversity at time 1:

$$\begin{aligned} d_1 &= d_0 + rd_0 \\ d_1 &= 1 + (2 \times 1) \\ d_1 &= 3 \end{aligned}$$

In Figure 8.9, the results of the simulation are plotted for time units 1 through 7, both linearly and semilogarithmically. The semilog plot illustrates an important attribute of an exponential diversification, indicated here by the straight line—a constant per-taxon rate of diversification. By this we mean that the rate of diversification exhibited by a single taxon remains unchanged throughout the simulation. In

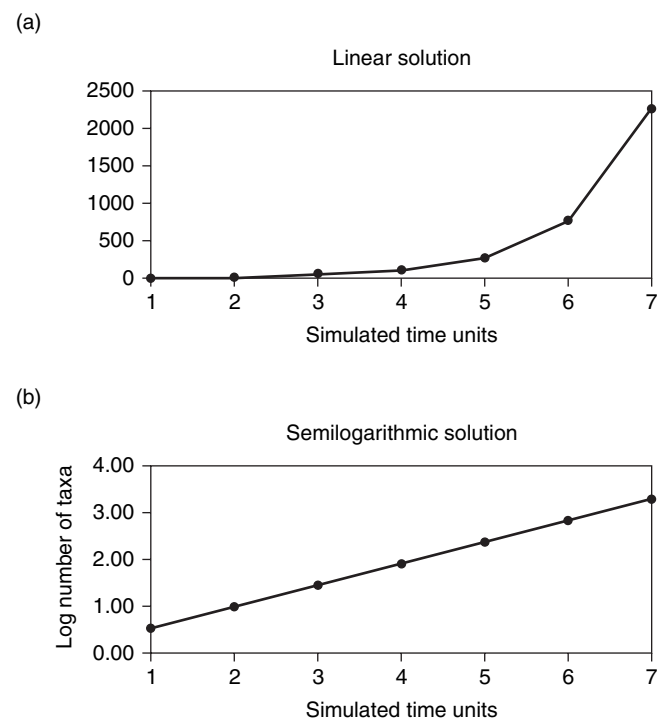


FIGURE 8.9 Trajectory of an exponential diversification for the example discussed in Box 8.2. (a) Linear (y) axis for diversity. (b) Logarithmic (y) axis for diversity. Note that when diversity is plotted logarithmically, the trajectory is a straight line.

this example, diversity always triples from one time unit to the next. For instance, as we move from time unit 6 to time unit 7, each of the 729 taxa extant in time unit 6 triples on average in number, thereby resulting in 2187 taxa in time unit 7.

Next, we consider simple logistic diversification (Sepkoski, 1978). The equation for a simple logistic diversification can be developed by first altering

diversification at the family level. At the heart of the model that he developed for this purpose is the **logistic equation**, which produces a sigmoidal (i.e., s-shaped) curve, describing an initial, nearly exponential growth in species richness, followed by a continuous decline in the rate of growth until an *equilibrium* level is approached (see Box 8.2 for a detailed explanation of the logistic model). Building on earlier research by R. H. MacArthur and

E. O. Wilson (1967) on the colonization of newly emergent islands, Sepkoski extended the concept of equilibrium to global marine diversity by reasoning that the earth's oceans collectively constitute a finite space with limited resources in which marine diversity cannot continue to increase indefinitely.

Sepkoski first suggested that a *simple* logistic equation (see Box 8.2) adequately describes the Phanerozoic

slightly the structure of our equation for exponential diversification:

$$d_t = d_{t-1} + (k_s - k_e)d_{t-1}$$

where k_s represents the rate of taxonomic origination, and k_e the rate of taxonomic extinction. This is in recognition of the fact that diversification (characterized earlier as the constant r) is the product of a balance between the origination and extinction of taxa: $r = k_s - k_e$. If $k_s - k_e > 0$, then diversity will increase; if $k_s - k_e < 0$, then diversity will decrease.

The premise of the simple logistic equation is that rates of origination and extinction are both affected by the number of taxa already present, because there is only a finite amount of space available for the subsistence of taxa. Thus, the rate of origination is thought to decrease, and the rate of extinction is thought to increase, as diversity increases. In their simplest forms, the relationships between evolutionary rates and diversity can be modeled as linear functions:

$$k_s = k_{s,0} - ad \quad \text{and} \quad k_e = k_{e,0} + bd$$

where $k_{s,0}$ and $k_{e,0}$ are the initial rates of origination and extinction at the start of the simulation, and a and b are constants that describe the slope (rate) of the decrease in the origination rate and the increase in the extinction rate as functions of increasing diversity. The right-hand sides of these equations can be substituted directly for k_s and k_e in our earlier equation:

$$d_t = d_{t-1} + [(k_{s,0} - ad_{t-1}) - (k_{e,0} + bd_{t-1})]d_{t-1}$$

This equation describes simple logistic diversification. While it may appear a bit intimidating, it is actually fairly straightforward. The primary difference from

the equation for exponential diversification is that instead of remaining fixed for the entire simulation, the rates of origination and extinction converge as diversity increases. Because of this convergence, the rate of diversification, which is nearly exponential at the start of the simulation, will begin to decrease until we reach equilibrium diversity—that is, the point at which the rate of origination is equal to the rate of extinction. From then on, diversity will remain unchanged.

An example of a curve generated with the simple logistic equation is illustrated in Figure 8.10a. This solution was produced using the parameters provided in the figure and by setting diversity at time 0 (d_0) to 4. Note that the curve is sigmoidal, reflecting the decrease in the total rate of diversification associated with the approach to equilibrium diversity. All simple logistic curves are sigmoidal in shape. However, several aspects of this curve vary from solution to solution, including the rate at which diversity increases initially, the rate at which diversification begins to decline as equilibrium is approached, and the actual value of the equilibrium. These attributes of the curve are contingent on the parameter values, like those used to generate Figure 8.10a. In general, a greater initial rate of diversification will be associated with a greater difference in the initial rates of origination ($k_{s,0}$) and extinction ($k_{e,0}$). The rate at which diversification decays as equilibrium is approached will be greater in cases where slopes are greater in the decay of the origination rate a and the increase in the extinction rate b .

Finally, we consider coupled logistic diversification (Sepkoski, 1979, 1984), which entails the simultaneous diversification of two or more groups. The premise of the model is that the rates of origination and extinction

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Box 8.2 (continued)

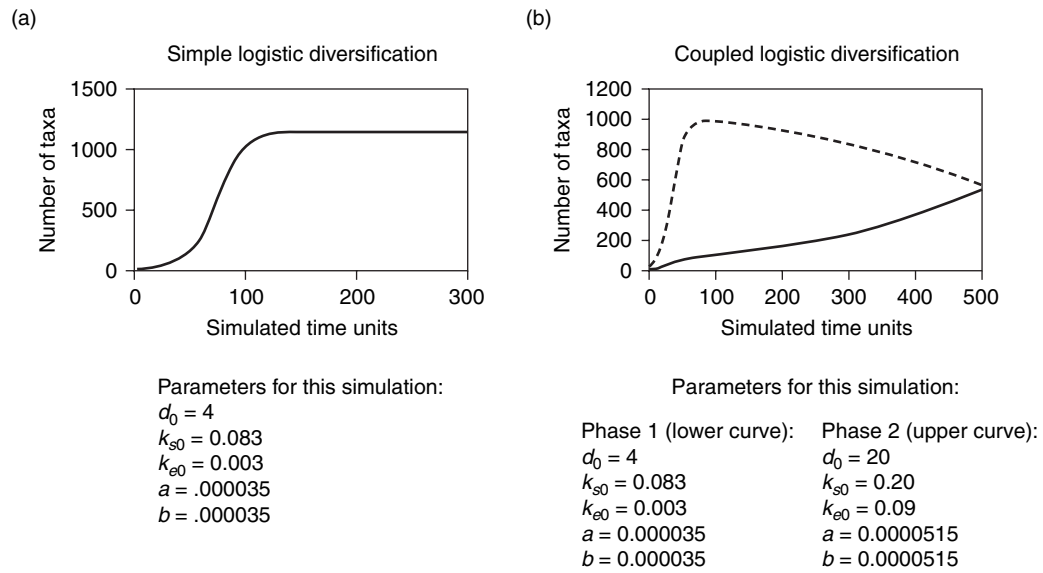


FIGURE 8.10 Trajectories for logistic diversification for the simple and coupled models. (a) Curve for a simple logistic model, based on parameters designated beneath the graph. (b) Curves for a two-phase (i.e., two-curve), coupled logistic model, based on parameters for each phase designated beneath the graph. Note that the parameters for the lower curve are identical to those used for the lone curve in the simple logistic solution.

for a given group are affected not only by the number of constituent taxa already present for the group, but also by the number of constituent taxa belonging to other groups diversifying at the same time. Thus, this model is viewed as interactive, or “coupled,” because the diversification of one group affects that of the others.

In a coupled logistic model, each modeled group is referred to as a phase; the diversification of a phase is governed by parameters defined in the coupled logistic equation:

$$d_{x,t} = d_{x,t-1} + [(k_{s0} - aDTOT_{t-1}) - (k_{e0} + bDTOT_{t-1})]d_{x,t-1}$$

where $d_{x,t}$ represents the diversity of phase x in interval t , $d_{x,t-1}$ represents the diversity of phase x in interval $t - 1$, and $DTOT_{t-1}$ is the total diversity of all phases in interval $t - 1$. All other parameters are identical to those of the simple logistic equation, but the actual values for the four constants— k_{s0} , k_{e0} , a , and b —usually vary among the phases.

history of marine diversity at the taxonomic level of orders (Figure 8.11). The diversity of orders increased dramatically through the Cambro-Ordovician, but then leveled off and maintained a fairly steady state thereafter. However, as we have already seen (Figure 8.5), this is a clear departure from the pattern of Phanerozoic diversification observed at the family and genus levels, both of which exhibit significant increases through the post-Paleozoic. This difference reflects the observation that the plurality of taxa at the order level and higher originated during the late Precambrian through Paleozoic,

whereas an increasing number of families, genera, and species continued to originate through the whole of the Phanerozoic.

To accommodate the post-Paleozoic family-level increase, Sepkoski developed a series of three *coupled* logistic equations (see Box 8.2), which corresponded to the three Phanerozoic evolutionary faunas. The central premise of coupling is that the level of diversity achieved at any point in time by any one of the components depends not only on its standing diversity, but also on the summed diversity of all three components. Using the

Comparison with the equation for simple logistic growth indicates only two differences between the simple and coupled equations: (1) the inclusion in the coupled version of $DTOT_{t-1}$ in place of d_{t-1} in the terms describing the decline in the rate of origination and the increase in the rate of extinction; and (2) the possibility that the rate of extinction can exceed the rate of origination as the simulation proceeds. This causes the diversification of a phase to be impeded by that of the other phases, in accord with the premise of the coupled model. Just as importantly, as illustrated by the following example, it opens up the possibility that a phase will experience a decline in total diversity in the event that the extinction rate does indeed exceed the origination rate.

Examples of two simultaneously diversifying curves generated with coupled logistic equations are presented in Figure 8.10b. The parameters for Phase 1 are identical to those used in the example of simple logistic diversification. Note, however, that the trajectory of Phase 1 is rather different from that in the simple logistic example. The diversification of Phase 1 is impeded early in the simulation, and its subsequent growth is much slower than in the simple case. This is a consequence of its numerical interaction with Phase 2, which initially diversifies much more rapidly than Phase 1 and thus adds significantly to the DTOT term. The added diversity included in the DTOT term accelerates the rate of decline in Phase 1's origination rate and the rate of increase in its extinction rate, relative to the simple model.

Despite the initial lag in Phase 1, its diversification slowly accelerates, quite literally at the expense of Phase 2. Ultimately, it would have overtaken Phase 2 had the simulation been continued beyond 500 time units. Why? It is a direct consequence of the relative values of the parameters for the two phases. Comparison of the initial origination and extinction rates for the two phases shows that the initial rate of diversification ($k_s - k_e$) is greater for Phase 2 than for Phase 1 (0.11 versus 0.08). Thus, early in the simulation, Phase 2 diversifies at a rate that far exceeds that of Phase 1. However, the rate of decay in origination and growth in extinction (a and b) for Phase 1 is also less than that for Phase 2 (0.000035 versus 0.0000515). Thus, as the summed diversity (DTOT) of both phases grows, the cost to Phase 2 is greater than that to Phase 1: It experiences a more rapid decline in origination and a more rapid growth in extinction, moving beyond the point where extinction exceeds origination, causing a steady decline in the diversity of Phase 2 (Miller & Sepkoski, 1988).

In folktale parlance, Phase 1 is the "tortoise" and Phase 2 the "hare." Much the same relationship exists among the three phases of Sepkoski's (1984) coupled logistic model that describes the Phanerozoic diversity trajectories of his three evolutionary faunas: the modeled Cambrian Fauna has a greater initial rate of diversification, but a greater rate of decay in diversification than the modeled Paleozoic Fauna. The modeled Modern Fauna, in turn, initially diversifies at an even slower rate than the modeled Paleozoic Fauna, but the rate of decay in its diversification rate is less than that of the modeled Paleozoic Fauna.

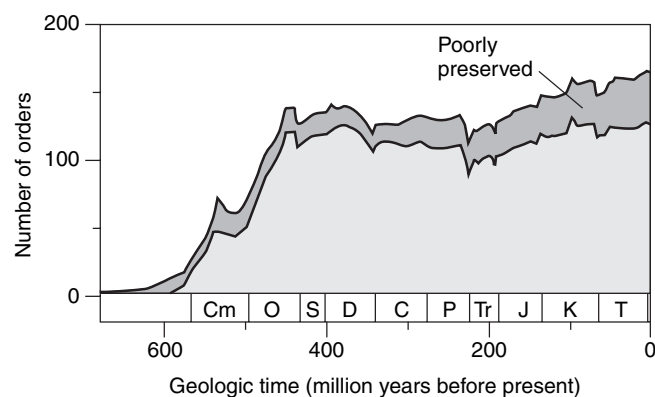


FIGURE 8.11 Sepkoski's depiction of Phanerozoic marine diversity at the order level. The darker portion is for orders that Sepkoski described as poorly preserved. (Sepkoski, 1978)

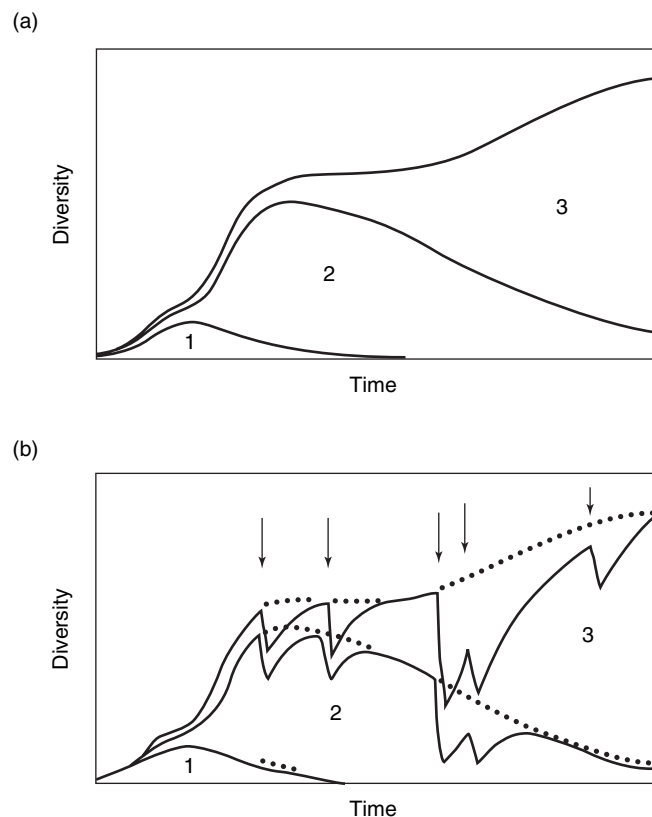


FIGURE 8.12 Sepkoski's simulation of the Phanerozoic history of global marine family diversity, based on the three-phase coupled logistic model. (a) Without mass extinctions. (b) With the "big five" Phanerozoic mass extinctions included in the simulation, as indicated by the arrows. Dotted curves show the trajectory without mass extinctions [i.e., the trajectory in part (a)] for comparison; solid curves show the trajectory with mass extinctions. (Sepkoski, 1984)

coupled approach, Sepkoski produced a simulated family-level trajectory (Figure 8.12) that closely approximated the actual pattern, particularly when major extinction events [SEE SECTION 8.6] were imposed in the simulation (compare Figure 8.12b with Figure 8.5a). The details of the simulated diversity trajectories in Figure 8.12 depend on whether mass extinctions are imposed, but note that the ultimate fates of the three phases are the same whether or not there are mass extinctions.

The ability of the model to depict diversity trajectories for the three faunas rests on the assumption that the Paleozoic Fauna could attain a higher level of equilibrium diversity than the Cambrian Fauna, and that the Modern Fauna could achieve a higher level than the Paleozoic Fauna. This was accomplished by selecting model parameters for each of the three curves that cor-

responded to observed, relative characteristics of the Cambrian, Paleozoic, and Modern Faunas: an average decline from one fauna to the next in initial diversification rates, a similar decline in average origination and extinction rates, and an increase in equilibrium diversity (see Box 8.2).

Although the volume of the earth's oceans has varied through the Phanerozoic, there is little reason to think that there has been a significant net increase in their total volume or in the area of sea floor available for colonization. Thus, the increase in equilibrium diversity for successive faunas, if real, could not have resulted from a simple increase in the amount of space available for colonization. Instead, an increase in ecological space, or the variety of ways that organisms make a living, may have been responsible for the differences among evolutionary faunas. We will return to this topic in Chapter 9.

While the success of the model in describing the observed pattern of marine biotic transitions opens up the possibility that biological interactions among members of the three evolutionary faunas caused the transitions (e.g., through competition for resources or for space), the close match certainly *does not demonstrate* that this was the case. To strengthen the argument of a key role for interactions as agents of long-term change, it is important to document both the precise nature of the interactions and the likelihood that these interactions persisted for extended intervals of geologic time. It is virtually impossible to do this at the broad level of evolutionary faunas, but we might do better if we restrict our analyses to small sets of taxa for which the nature of interactions can be understood.

With this in mind, Sepkoski and colleagues developed a coupled logistic model that described the global transition from cyclostome to cheilostome bryozoans through the Cretaceous Period and the Cenozoic Era (Figures 8.13a and 8.13b). In this case, not only did the model successfully describe the global diversity trajectories of the two groups, but there is also evidence from the fossil record that cheilostomes overgrew cyclostomes in a significant majority of observed cases (Figure 8.13c), opening up the possibility that over the long term, cheilostomes might have outcompeted cyclostomes.

As we suggested earlier, the coupled logistic model has not been accepted universally by paleontologists, and several alternative scenarios have been proposed in recent years. These range from the suggestion that the entire Phanerozoic trajectory of marine diversity is best described as an exponential diversification (Box 8.2; Benton,

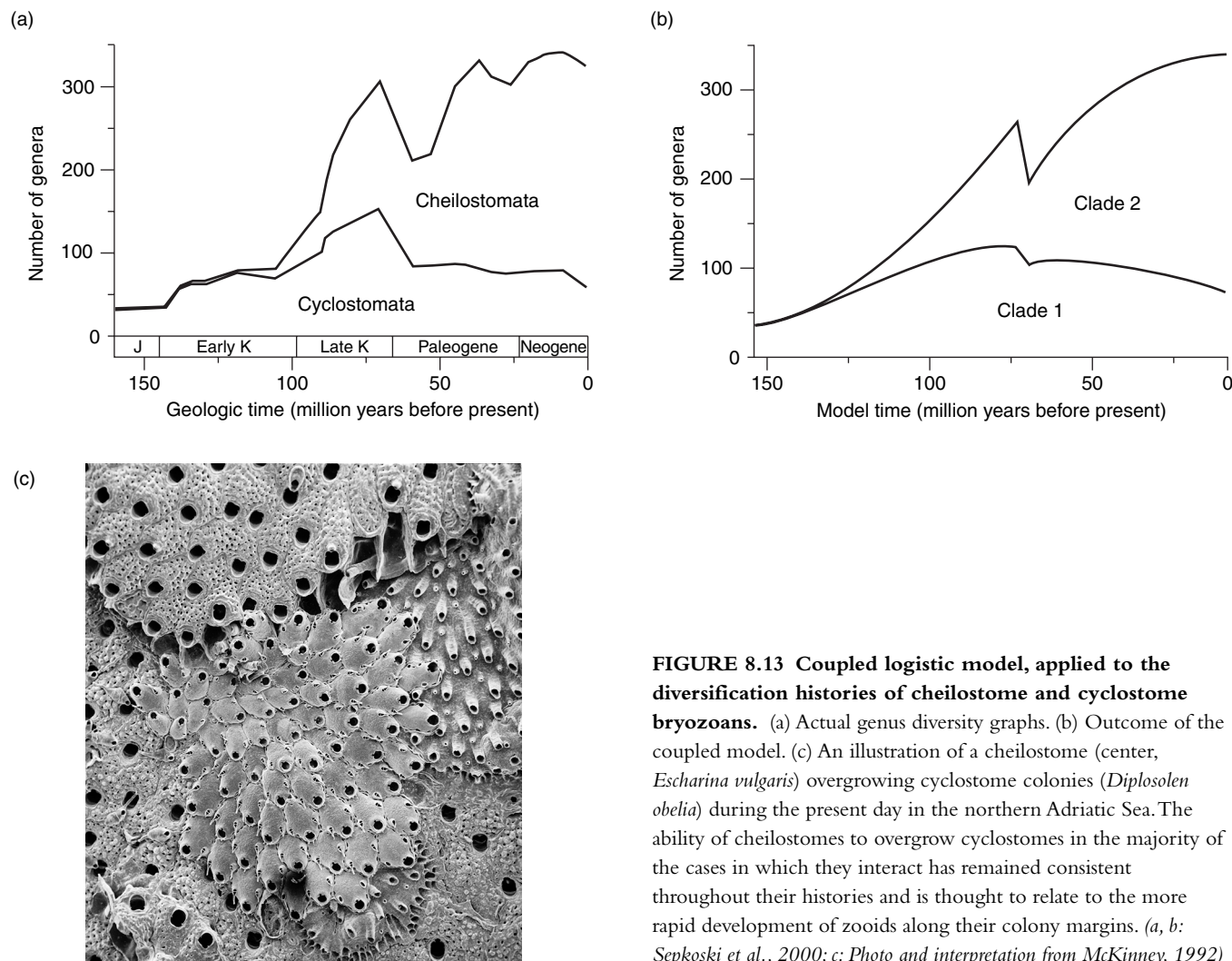


FIGURE 8.13 Coupled logistic model, applied to the diversification histories of cheilostome and cyclostome bryozoans. (a) Actual genus diversity graphs. (b) Outcome of the coupled model. (c) An illustration of a cheilostome (center, *Escharina vulgaris*) overgrowing cyclostome colonies (*Diplosolen obelia*) during the present day in the northern Adriatic Sea. The ability of cheilostomes to overgrow cyclostomes in the majority of the cases in which they interact has remained consistent throughout their histories and is thought to relate to the more rapid development of zooids along their colony margins. (a, b: Sepkoski et al., 2000; c: Photo and interpretation from McKinney, 1992)

1995), punctuated and sometimes impeded by major extinction events (Stanley, 1999), to the hypothesis that it is best represented as a sequence of simple logistic (Box 8.2) diversification intervals, demarcated and reset by major extinctions (Courtyllot & Gaudemer, 1996).

In addition, it has been demonstrated that the turnover rates of taxa in the Modern Fauna increased significantly in the Mesozoic and Cenozoic, which is not accounted for in Sepkoski's set-up of the coupled logistic model (Alroy, 2004). However, even though in the end it may be demonstrated that Sepkoski's coupled model is not appropriate as an explanation of Phanerozoic marine diversification, the model endures as the intellectual starting point for virtually all alternative views. It also continues to provide students of paleontology with a unique opportunity to understand how biodiversity trends can be assessed numerically.

The Terrestrial Realm

Figure 8.7 exhibits a series of transitions among vertebrates and plants that can be likened to the transitions among Sepkoski's evolutionary faunas. However, the sequential pattern of decreasing turnover rates from one fauna to the next that characterizes the marine realm, and which underlies Sepkoski's coupled logistic model for marine biotas, is not clearly exhibited by the major biotas of the terrestrial realm. For example, whereas all major plant groups may have experienced an initial burst of speciation followed by a rapid decline in speciation rates, there is no evidence that the "evolutionary floras" illustrated in Figure 8.7b exhibited successively lower turnover rates.

In fact, there are indications that, if anything, the opposite was the case, as demonstrated by James Valentine

and colleagues (1991). While not ruling out the possibility that a coupled logistic or some alternative model could be developed to describe transitions among terrestrial plants, its numerical dynamics would obviously be different from those for marine animals. Whether these differences would reflect anything meaningful about differences in the evolutionary dynamics of marine and terrestrial systems remains to be seen, as paleontologists have only recently begun to attempt these kinds of comparisons.

8.5 PHANEROZOIC DECLINE IN ORIGINATION AND EXTINCTION RATES

Given the observation that marine diversity increased during the Phanerozoic, it follows that overall, the number of originations must have exceeded the number of extinctions, particularly during intervals marked by major increases in diversity (see Box 8.2). Likewise, during intervals of declining diversity, the number of extinctions exceeded the number of originations. But what of longer-term patterns of origination and extinction? Even if there was a long-term increase in diversity, this does not necessarily mean that origination rates must have increased in parallel with diversity. An increase in diversity could also have been caused by a long-term decline in extinction rates. In fact, origination rates might have even declined through the Phanerozoic, so long as extinction rates declined at a greater rate.

An initial representation of average extinction rates for marine families was presented by David Raup and Jack Sepkoski in 1982 (Figure 8.14). Although the main intent of the analysis was to provide a statistical basis for delineating mass extinctions (see the next section), another important aspect of extinction was also documented: a significant, long-term decline in extinction rates through the Phanerozoic. This decline has also been documented at the genus level, and a similar Phanerozoic long-term decline has been shown for origination rates (Figure 8.15) as well. There was a temporary rebound in origination rates at the beginning of the Mesozoic Era in the aftermath of the most extensive extinction event in the history of life [SEE SECTION 8.6], but origination rates then began to decline anew.

A long-term decline in origination rates can also be recognized in several groups of animals and plants in terrestrial settings (Figure 8.16). Therefore, any explanation

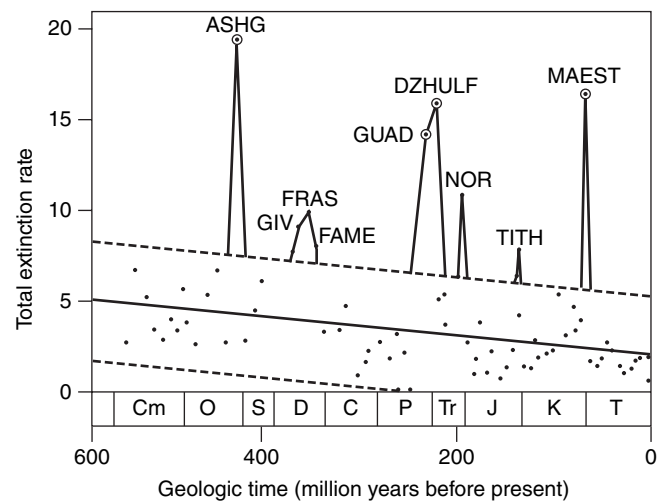


FIGURE 8.14 Raup and Sepkoski's depiction of extinction rates of marine families, as the number of extinctions per million years, stage by stage through the Phanerozoic. The solid line is a linear regression fit to the data, and the dotted lines define a 95 percent statistical confidence interval around the regression. Abbreviations for stage names are provided in cases where extinction rates for the stage fall outside the upper 95 percent confidence band (i.e., they are judged to be statistically significant by the standards of this analysis). The circled points (e.g., the Ashgill interval of the Ordovician) fall outside the upper 99 percent confidence band (i.e., they are highly significant). Note the long-term decline in extinction rates. (Modified from Raup & Sepkoski, 1982)

for a decline in origination or extinction rates should transcend the fundamental biological differences among individual higher taxa or the places where they live. Some researchers have proposed that the rate decline indicates a general change through time in the nature of interactions among taxa. For example, as we will see in Chapter 9, the history of life may have been marked by profound “arms races” in marine and terrestrial settings between predator and prey lineages. One potential outcome of these arms races over the long term could have been an increased resistance to extinction, but this does not explain why origination rates also declined.

In marine settings, the decline in origination and extinction rates appears to reflect the overall biotic transition, discussed earlier, from taxa exhibiting high turnover rates (members of the Cambrian and Paleozoic Faunas) to others exhibiting lower turnover rates (members of the Modern Fauna). This, of course, raises the question: Why is it that different higher taxa exhibit turnover rates

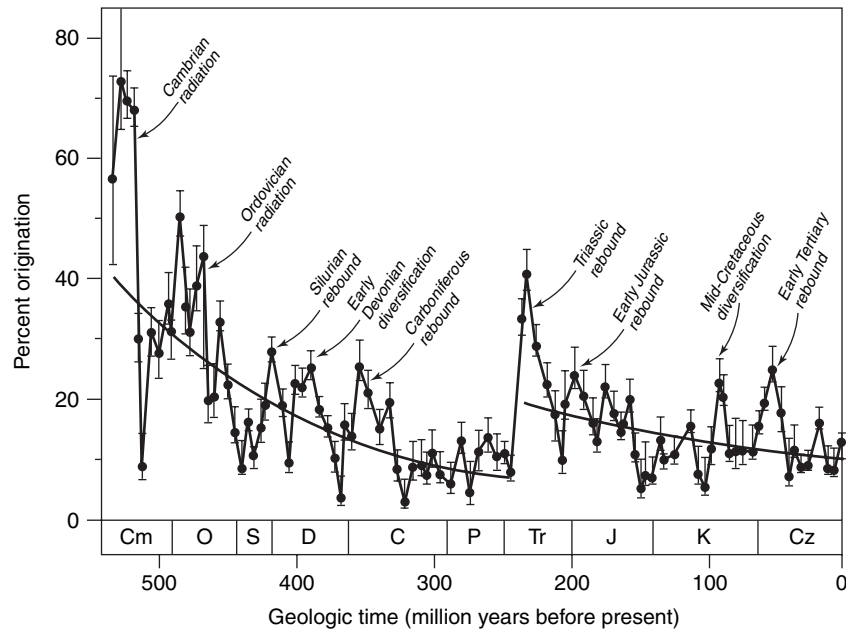


FIGURE 8.15 Sepkoski's depiction of declining genus origination rates through the Phanerozoic. Origination was measured in this case as the percentage of genera extant in a given substage that had their first appearance in that substage. Percent origination is simply 100 times proportional origination (see Table 7.4). Note the temporary rebound in rates following the Late Permian mass extinction. (Sepkoski, 1998)

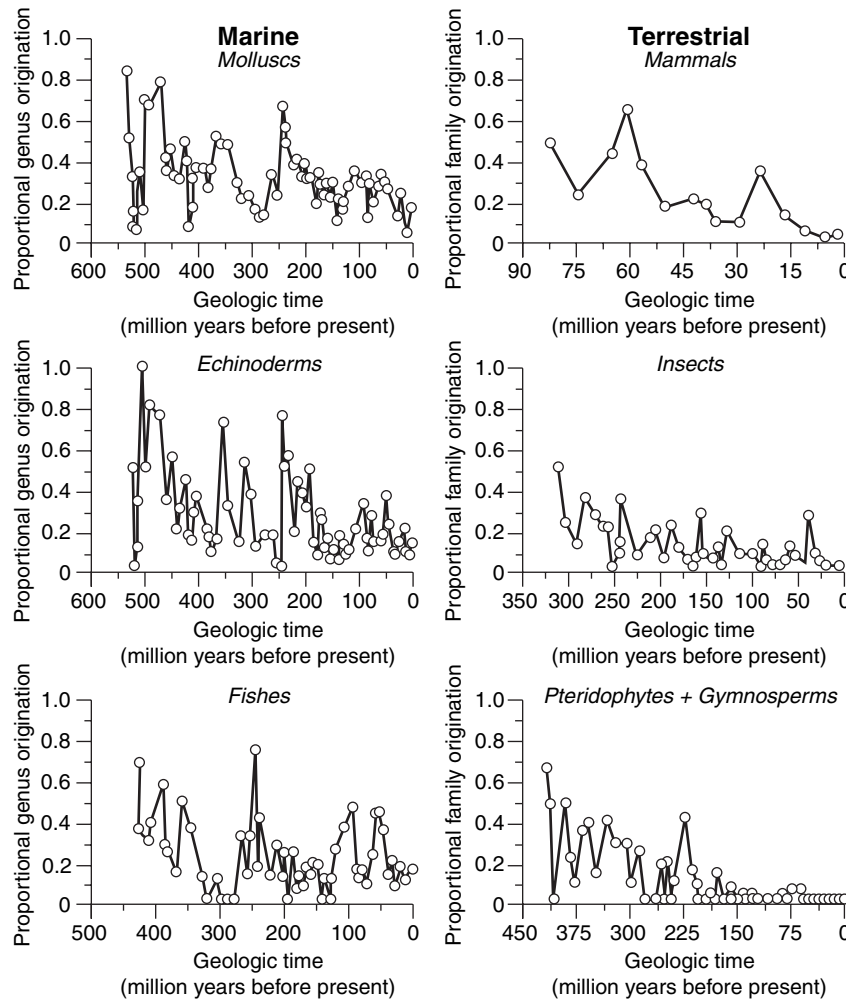


FIGURE 8.16 Eble's depiction of declining genus origination rates in several marine and terrestrial groups during the Phanerozoic. These are measured as proportional origination (see Table 7.4). (Eble, 1999)

that can be so strikingly different from one another but that can nevertheless be maintained fairly consistently among their constituent families, genera, and lineages? (See Chapter 7 for additional discussion.) This remains one of the unsolved mysteries of evolution, and it is certainly worthy of intensive paleontological research in the future.

8.6 MASS EXTINCTIONS

The Diagnosis of Mass Extinctions

In the past quarter century, perhaps no subject has received more attention from paleontologists than **mass extinctions**. This interest and excitement was spurred on by a finding reported by Nobel prize-winning physicist Luis Alvarez and his son Walter, a geochemist. The upshot of the discovery, which we will discuss later, was that a major, global extinction event at the end of the Cretaceous Period may have been caused by the impact of a large asteroid or comet. The scientific debate that was triggered by the Alvarez investigation helped paleontologists recognize that catastrophic events, whatever their causes, have probably affected life profoundly. More broadly, it has motivated paleontologists and other geologists to investigate the complex relationships between physical and biological processes on earth throughout the history of life.

A mass extinction can be defined as *an unusually large extinction of the earth's biota that takes place in a relatively short interval of geologic time*. While this definition is easy to understand, it inevitably motivates one to ask *how large* an extinction and *how short* a time interval. Indeed, considerable effort has been aimed at providing an unambiguous definition of a mass extinction that would enable someone to label an interval of apparently elevated extinction definitively as a mass extinction.

Perhaps the most straightforward means of diagnosing a mass extinction is to assess the percentage of taxa that became extinct (or, more precisely, exhibited their last global appearances), interval by interval, throughout the Phanerozoic, and then determine whether there were intervals during which these percentages were elevated substantially. Although this might not seem like a very precise method, paleontologists have nevertheless been able to designate five intervals in which percentages stood well above the levels exhibited at most other times; these constitute the “big five” mass extinctions of the

Phanerozoic. By far, the largest of these occurred during the Late Permian [SEE SECTION 10.3], when upwards of 40 percent of families and 60 percent of genera became extinct. Other major extinctions, with extinction percentages on the order of 20 percent of families and 50 percent of genera, took place at or near the ends of the Ordovician, Devonian, Triassic, and Cretaceous periods.

In an analysis discussed in Section 8.5 in relation to the long-term decline in origination and extinction rates, Raup and Sepkoski also suggested a statistical definition for a mass extinction, based on an assessment of the number of extinctions per million years for the 76 Phanerozoic stages included in their analysis. A mass extinction was defined as any interval during which the extinction rate exceeded the statistical confidence interval for a regression line that was fitted to the data (Figure 8.14). By this standard, of the big five, only the Late Devonian extinction did not stand significantly above “background” levels. However, as Raup and Sepkoski pointed out, the Late Devonian appears to be unique relative to the other extinctions in that extinction rates were elevated for three successive stages.

This was not the only statistical definition of a mass extinction that Raup and Sepkoski offered. In a series of subsequent analyses on the extinction record from the Late Permian to the Recent, they defined a mass extinction as any interval during which the percentage of families or genera becoming extinct during a given interval stood significantly above the percentages for the intervals that immediately surrounded it (Figure 8.17). On this basis, several additional mass extinctions were delineated, particularly at the genus level, beyond the two post-Paleozoic members of the big five. Interestingly, nearly all of these were episodes that paleontologists had recognized previously as significant extinctions based on their experiences with regional patterns of faunal change.

Causes of Mass Extinctions

In 1980, the Alvarez team published a paper in which they reported elevated levels of the element iridium (Ir) across the Cretaceous–Tertiary (K/T) boundary at a locality in Italy (Figure 8.18a). Because Ir is rare at the earth's surface but is more common in meteorites, the team suggested that the source of the Ir was a large comet or asteroid that impacted the earth at the end of the Cretaceous Period. Moreover, based on the amount of Ir found at the K/T boundary, the team estimated that the impacting body had a diameter of about 10 km. The team

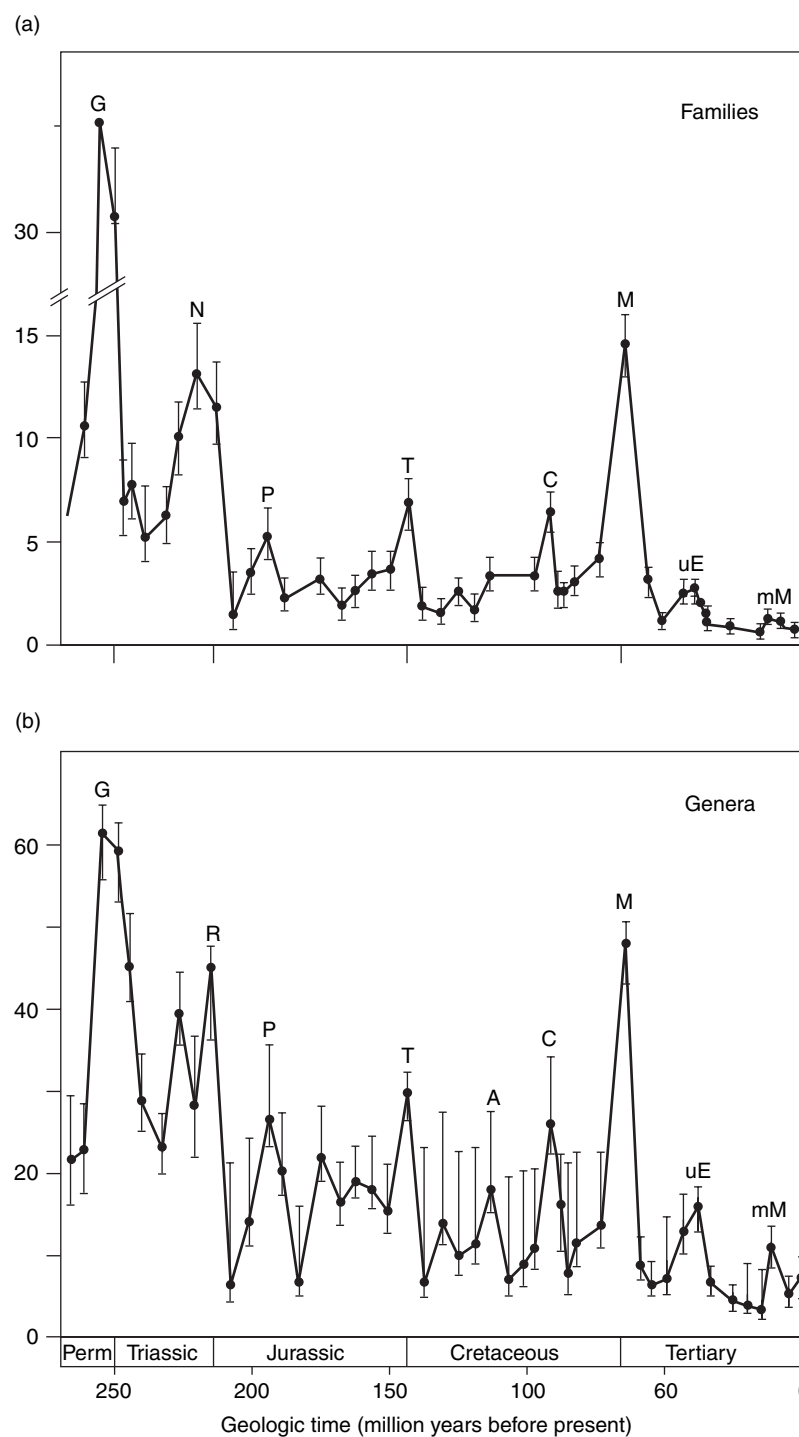


FIGURE 8.17 Raup and Sepkoski's delineation of mass extinctions in the Late Permian and after. (a) Families. (b) Genera.

Error bars give 1 standard error on either side of the observed percentage extinction. Mass extinctions (labeled with lettered abbreviations for the stages in which they occurred) were defined as intervals ("peaks") during which extinction percentages stood significantly above those in immediately surrounding intervals. (From Raup & Sepkoski, 1986)

proposed a mechanism linking the impact to the K/T mass extinction that involved a collapse of the food chain globally, caused by a severe reduction in the amount of sunlight reaching the earth's surface. Among the ramifications of this and related mechanisms is that the mass extinction took place rapidly, an issue that has been debated and analyzed in detail by paleontologists.

Subsequent findings at the K/T boundary have firmly supported the hypothesis of a major impact at the end of the Cretaceous, including elevated iridium levels worldwide, microspherules (impact droplets; Figure 8.18b), and quartz marked by shock features (Figure 8.18c). Sedimentary deposits consisting of coarse, angular fragments, likely produced by impact-related

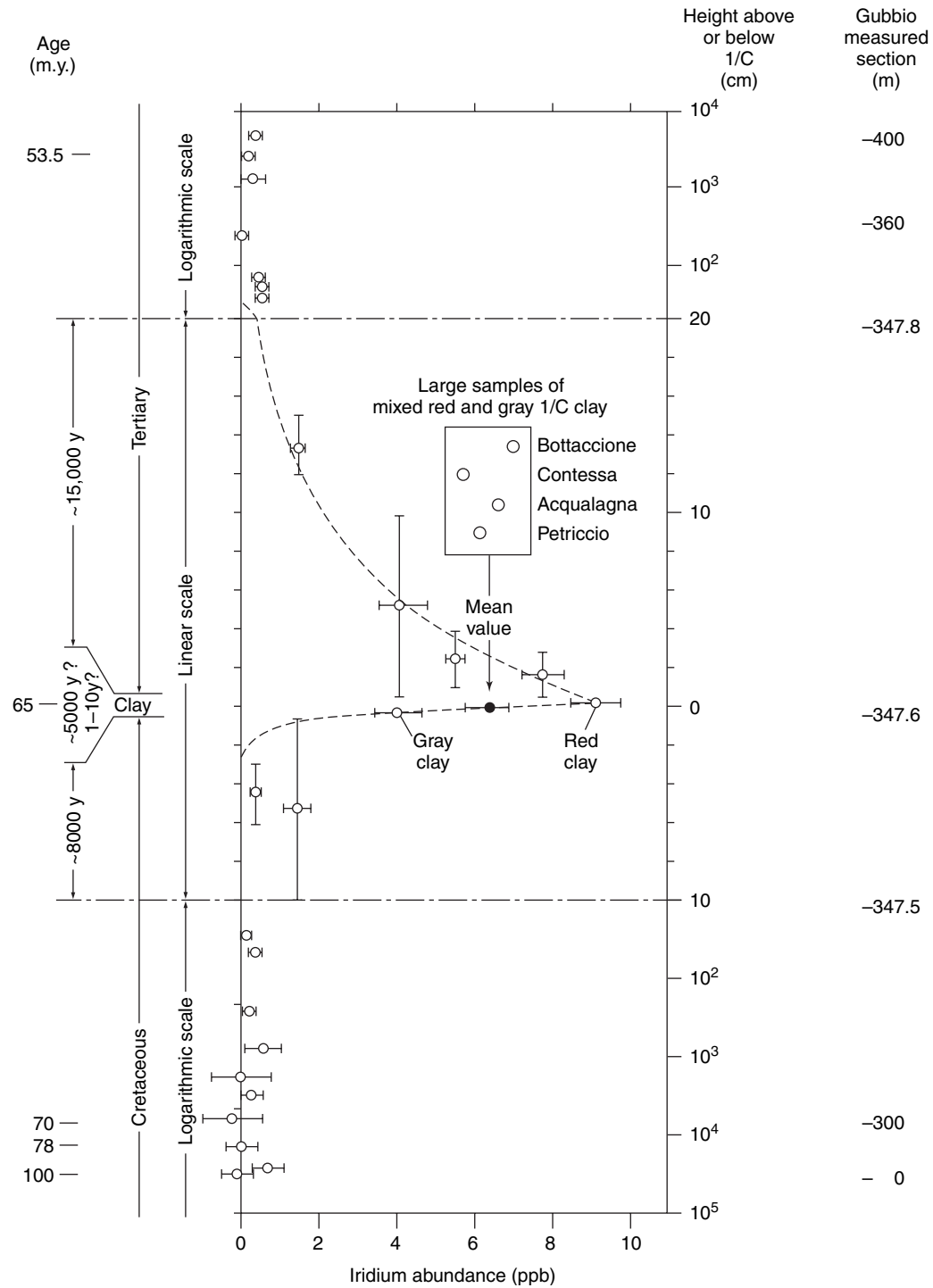


FIGURE 8.18
Evidence for the impact of a large meteorite at the K/T boundary.
 (a) Dramatic increase in the abundance of the element iridium at the K/T boundary near Gubbio, Italy. Iridium is rare at the earth's surface but is more common in meteorites.
 (a: From Alvarez et al., 1980)

tsunamis, have been found at Late Cretaceous localities near the present-day coast of the Gulf of Mexico. And deep sea cores extracted from the K/T boundary in the western Atlantic Ocean reveal evidence of massive submarine flows that were likely induced by the impact. But the real “smoking gun” in this case was the discovery of the likely site of impact, off the coast of the Yucatan

Peninsula of Mexico. There, geophysical soundings of the sea floor revealed a concentric-ringed structure with a diameter of approximately 200 km (Figure 8.19). Detailed sampling of the site has recovered melt rocks that return a radiometric date of 65 million years and have compositional similarities to microspherules collected at the K/T boundary in Haiti. This similarity implies that

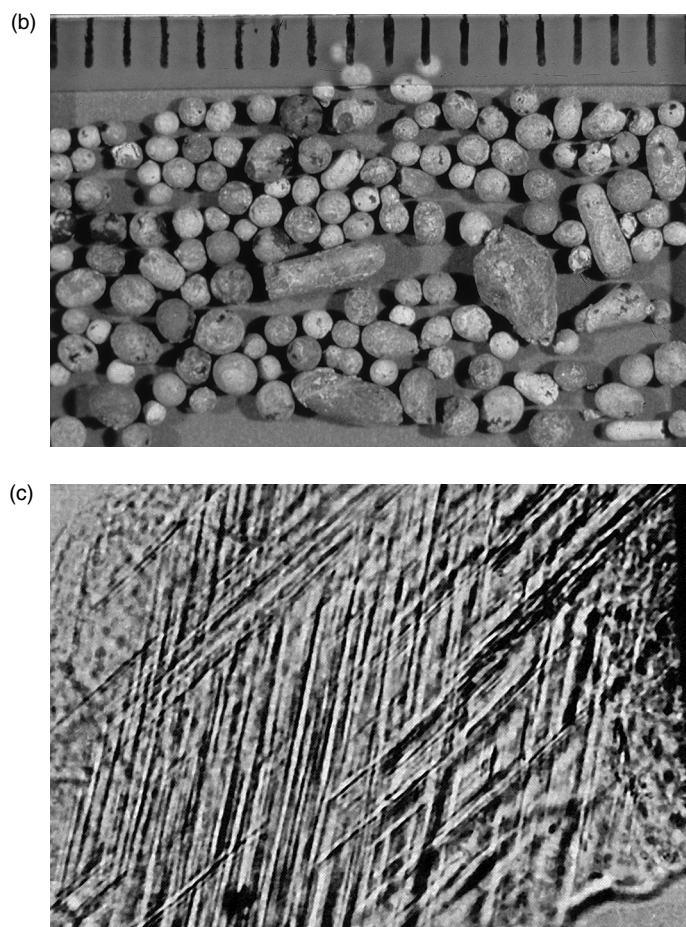


FIGURE 8.18 (cont.) (b) Glassy microspherules and other glassy objects from the K/T boundary in northeastern Mexico (2 to 3 mm in diameter) that formed from molten droplets produced during the impact. (c) Photomicrograph of shocked quartz from a K/T boundary section in southern Colorado (field of view is approximately 0.2 mm); parallel striations imparted on quartz grains by the cataclysmic explosion are associated with the impact. (b: Courtesy of David A. Kring, Lunar and Planetary Laboratory; c: From Kerr, 1987)

the bedrock from the putative crater region was the source of the Haitian microspherules. Thus, while the hypothesis of a K/T impact was initially quite controversial, the evidence is now considered overwhelming that such an impact actually took place.

Given the geophysical, geochemical, and sedimentological underpinnings of much of the evidence, paleontologists have played only marginal roles in gathering data to test the hypothesis that an impact took place at the end of the Cretaceous. However, paleontologists have worked to assess the possible link between an impact and the extinction itself. Initially, many paleontologists resisted suggestions of such a linkage, in part because

of indications that species became extinct gradually, rather than catastrophically, prior to the K/T boundary, or even that some nonavian dinosaurs survived into the Tertiary. These views have changed dramatically over the past two decades, motivated by reconsideration of the pattern that we should expect to see at a boundary if extinction were rapid rather than gradual.

Owing to issues of preservation and sampling, the last appearances of taxa in the fossil record are likely to predate their actual extinctions [SEE SECTION 6.1]. In other words, many taxa will disappear from the fossil record below the horizon in which they actually became extinct. Because the interval of disappearance will likely differ from taxon to taxon—contingent, in part, on variations in the abundance or rarity of taxa [SEE SECTION 6.5]—this should cause any major extinction event to appear more gradual than it actually was. Philip Signor and Jere Lipps (1982) were the first paleontologists to fully articulate this view, which predicts that the nature of preservation will cause an abrupt extinction to appear gradual (the so-called **Signor-Lipps effect**).

Some researchers have begun to quantify the likelihood of this kind of local and regional artificial-range truncation at the K/T boundary and in association with

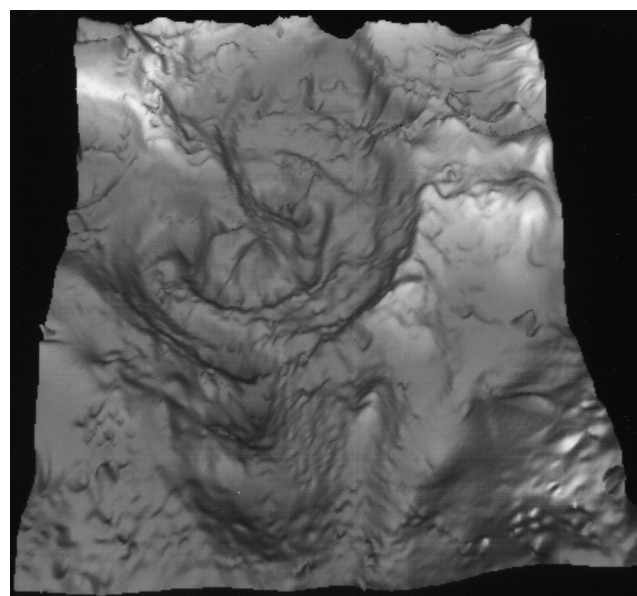


FIGURE 8.19 Gravity anomaly map of the feature off the coast of the Yucatan Peninsula that is thought to be the site of a large impact at the end of the Cretaceous. (From http://solarsystem.nasa.gov/multimedia/display.cfm?IM_ID=791)

other mass extinctions, but it is still too soon to make definitive statements about the relative abruptness of any of these events on a global scale. Certainly, knowledge of whether a given mass extinction was abrupt or gradual would be helpful in determining what caused it. Whereas the K/T impact scenario appears to call for a fairly abrupt extinction, several “earthbound” mechanisms (e.g., sea-level changes or global cooling) might have been tied to extinctions that were more gradual, perhaps taking place over millions of years.

We will discuss this issue further in Chapter 10, when we consider the Late Permian extinction in more detail. In the same way that the K/T extinction has provided a focal point for consideration of possible links between impacts and extinctions, the Late Permian event has been a focus for the investigation of earthbound extinction mechanisms [SEE SECTION 10.3]. In the wake of the research presented by the Alvarez team, geoscientists began to look for evidence of major impacts in association with several extinction horizons. To date, these efforts have met with only limited success, and in cases such as the Late Permian, for which evidence of an impact is still being pursued actively, the quality and interpretation of the primary data have been controversial.

However, the possibility of a broad linkage between mass extinctions and impacts was given impetus during the mid-1980s, when David Raup and Jack Sepkoski statistically analyzed the Phanerozoic extinction record from Late Permian, using harmonic analysis (see Box 2.2) and other methods. Raup and Sepkoski suggested that post-Paleozoic peaks in extinction (Figure 8.17) have been spaced roughly at 26-million-year intervals (e.g., Raup & Sepkoski, 1984, 1986). This diagnosis immediately fueled a burst of research and speculation among scientists about its possible causes and ramifications. Following, as it did, on the initial research suggesting a K/T impact, it was not surprising that researchers began to propose possible astronomical mechanisms that would dramatically increase the probability of large bodies hitting the earth during narrow time intervals every 26 million years.

The most notorious of these proposed mechanisms was the *Nemesis theory*, named for a hypothetical, unseen solar companion. The orbit of this solar companion would take it near the Oort Cloud of comets once during its 26-million-year orbit around the sun, disturbing the orbits of some comets sufficiently to cause them to move into the inner solar system, thereby increasing the

probability that at least one comet would strike the earth (Davis et al., 1984).

Although it is purely hypothetical, the Nemesis theory predicts, with some precision, the characteristics of the unseen companion. Armed with this information, researchers began to search star catalogues in the hopes of finding an object with the appropriate characteristics. To date, no such object has been found. Beyond that, the actual diagnosis of periodicity has been challenged on statistical grounds and because of possible problems with absolute dates of some of the extinction events.

Regardless of whether extinction periodicity is a reality, the entire exercise has raised the consciousness of paleontologists regarding the likelihood that large-body impacts have affected the history of life on earth. In this vein, Raup (1991, 1992) developed a numerical curve depicting the average waiting time between impacts of various sizes and showed that it was rather similar to a curve depicting the average expected waiting time between extinctions of varying magnitudes. While this certainly does not demonstrate that large-body impacts have been responsible for most extinctions during the Phanerozoic, it does remind us that impacts, particularly of objects that span up to a few kilometers in diameter, have been very common throughout earth history. Their role in mediating the history of life should therefore be explored further.

Selectivity of Mass Extinctions

Various extinction mechanisms would be expected to preferentially affect taxa living in particular environments or climatic regimes, or exhibiting certain life habits. Therefore, knowing whether mass extinctions were selective would help researchers determine what caused them. For example, episodes of global cooling might be particularly severe among tropical taxa because it would not be possible for these taxa to migrate to warmer climates during a cooling episode. By contrast, a large-body impact above a certain size threshold, such as that implicated in the K/T event, would likely have a global reach, with no real expectation of a latitudinal gradient in extinction rates. In the case of an impact, however, researchers have suggested that an associated reduction in sunlight penetration for an extended period of time would cause a collapse in primary productivity, with an associated extinction of primary producers and taxa dependent on them as sources of food.

In much the same way that extinction rates can be measured for the earth as a whole, rates can also be measured and compared among different areas of the world by amassing and analyzing databases separately for the fossils preserved within each area. In the case of the K/T extinction, David Raup and David Jablonski (1993) evaluated previous suggestions that the extinction was concentrated in the tropics by dividing the world into bins, each with a dimension of 10 degrees latitude by 10 degrees longitude, and then analyzing variations in the extinction rates of bivalve genera among the bins (Figure 8.20).

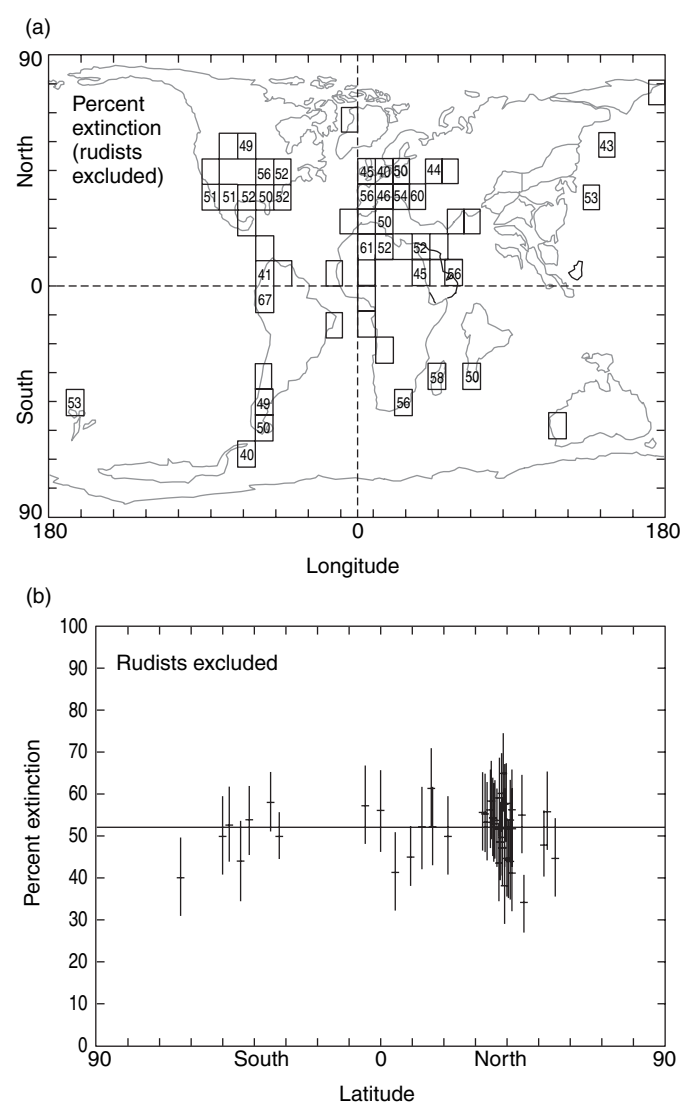


FIGURE 8.20 Assessment of geographic patterns in bivalve extinction (excluding rudists) during the K/T extinction.

(a) Extinction rates (expressed as percentages) in 10-by-10-degree grids for which sufficient data were available. (b) Extinction rates depicted with respect to latitude. In either grouping, there is no discernible geographic selectivity in extinction rates. (From Raup & Jablonski, 1993)

When rudists, an extinct group of reef-building bivalves limited to the tropics, were excluded from the analysis, there was no evidence of latitudinal selectivity in extinction rates. In addition, Raup and Jablonski found no evidence of K/T extinction selectivity among bivalves with respect to body size, position along an onshore-to-offshore bathymetric gradient, or life position above or below the sediment-water interface. They did find that the extinction rate among deposit-feeders was significantly less than that among suspension-feeders, but there were indications that this was a taxonomic rather than an ecologic effect: Certain taxonomic groups of deposit-feeders exhibited extinction rates that were significantly higher than others and that were comparable to rates exhibited by suspension-feeders. Raup and Jablonski also found that genera with broader geographic distributions exhibited significantly lower extinction rates than did more localized genera, indicating that a wide geographic range provided something of a buffer against extinction, at least at the genus level.

Peter Sheehan and colleagues (1996; Sheehan, 2001) described a two-phase pattern of extinction among brachiopods during the Late Ordovician mass extinction that bears similarity to, as well as striking differences from, the K/T event. During the Late Ordovician, there was a major southern hemisphere glaciation and associated drop in sea level that partially drained epicontinental seas, the broad, shallow bodies of water that covered large portions of several continents at that time. This caused the extinction of significant percentages of the genera restricted to the areas that were drained. By contrast, genera that were geographically widespread preferentially survived the event, a pattern that was comparable to that observed among bivalves during the K/T event.

However, in the wake of the initial Ordovician event, a broadly distributed biota (the so-called Hirnantia Fauna) became established worldwide in association with the global climatic cooling. Major elements of this biota, in turn, became extinct during a distinct, second phase of extinction as the glaciation waned, sea level rose, and the climate warmed. In this case, therefore, broad geographic range did not provide an extinction buffer, and extinction was apparently triggered by the global climatic shift back to warm water conditions.

One of the most intriguing instances of selective extinction known to paleontologists has now been documented for the Late Pleistocene extinction, during which large mammals were particularly hard hit. This extinction is unique in the geologic record because it may represent

the first instance in which *Homo sapiens* was implicated directly as a significant agent of extinction. Because of its particular relevance to the question of extinction in the present day, we provide a detailed overview of the Late Pleistocene extinction in Chapter 10.

The Evolutionary Significance of Mass Extinctions

While the study of selectivity is informative with respect to extinction mechanisms, there is another important reason to investigate selectivity. Mass extinctions have arguably played major roles in causing biotic transitions throughout the Phanerozoic, by abruptly causing the extinctions of some taxa while leaving others relatively unscathed. In fact, Stephen Jay Gould (1985) and others have suggested that mass extinctions were capable of undoing accumulated evolutionary change that took place during the intervals between them. By contrast, as we noted earlier [SEE SECTION 8.4], in constructing his three-phase coupled logistic model (Figure 8.12), Jack Sepkoski suggested that global biotic transitions among evolutionary faunas were caused by interactions among taxa, and that mass extinctions did not significantly alter diversification patterns among the main groups of higher taxa in the three evolutionary faunas.

There is a middle ground between these two end-member views that may best explain the evolutionary role of mass extinctions—that these events and smaller-scale, regional extinctions resulted in biotic transitions primarily because they remove *incumbent* taxa (*the taxa that are already present*), thereby freeing up **ecospace** for the diversification of other taxa. In contemplating this possibility, it is helpful to consider the role of incumbency in electoral politics. It is well understood that in a political election, incumbent candidates enjoy significant advantages over their challengers, even in cases where a dispassionate observer might determine that the challenger would do a better, more effective job if elected. Thus, even a “competitively superior” challenger stands little chance of dislodging an incumbent, unless some unexpected event, such as a political scandal, intervenes to severely weaken the fortunes of the incumbent or, better yet, removes the incumbent from office shortly before the election!

Similarly, in the evolutionary arena, a well-entrenched incumbent taxon, particularly one that is abundant and widespread, is thought to enjoy a major advantage over a less entrenched taxon, even in cases where the less entrenched taxon appears to possess features that, if all else were equal, would provide it with a clear competitive

advantage over the incumbent. As an example, consider the case of evolutionary transitions among turtles. Michael Rosenzweig and Robert McCord (1991) investigated the replacement of turtles incapable of retracting their heads into their shells by turtles with flexible necks that permitted head retraction (Figure 8.21).

Rosenzweig and McCord argued that the advent of neck flexure constituted an important advance that was responsible for the radiation of taxa that possessed this feature. However, they also noted that the actual replacement took place at different times in different regions of the world, related in each case to a regional extinction event that first removed incumbent groups of turtles that could not flex their necks. For example, in the case of western North America, the percentage of neck-flexing turtles increased significantly in association with the K/T mass extinction, but replacements elsewhere took place at other times. That the same replacement occurred not just once, but several times in different regions, provides strong support for the argument that neck flexure constituted a competitive advantage, ultimately leading to the global demise of turtles that do not flex their necks.

The turtle example reminds us that there is much more to the investigation of extinction events than the quantitative assessment of extinction rates. In considering their possible roles as agents of evolutionary change, it is also important to ask whether mass extinctions differ

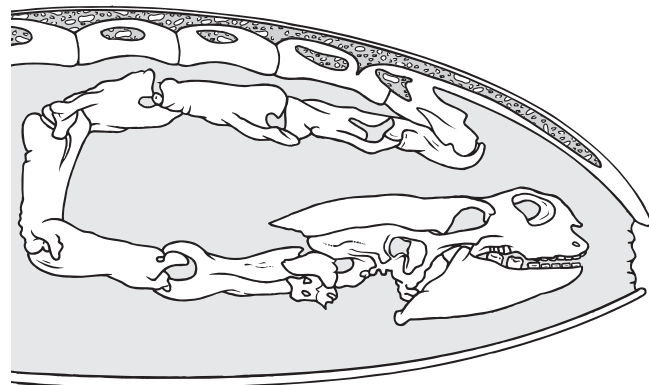


FIGURE 8.21 A sketch of the turtle *Trionyx*, illustrating the flexibility of the neck, which is a prerequisite for head retraction. Rosenzweig and McCord (1991) argued that straight-necked turtles (Amphichelydia) were replaced in several venues worldwide by turtles capable of head retraction (Pleurodira and Cryptodira), but the timing of replacement varied among different paleocontinents, contingent on events that first decimated incumbent, straight-necked species.

qualitatively from extinctions that take place at other times. For instance, we can ask whether a mass extinction eliminates advantages that some taxa enjoyed prior to its onset.

As an example, David Jablonski investigated gastropod extinction and survival before and during the K/T mass extinction. The early growth stages preserved in the gastropod shell permit a paleontologist to determine whether the larval stage of a species was planktotrophic or nonplanktotrophic [SEE SECTION 7.4] (Figure 8.22a). By examining the shells of numerous Cretaceous gastropods, Jablonski classified the species into these two groups. He also determined the geologic durations of each species and demonstrated that species with planktotrophic larvae tended to have longer durations than species with nonplanktotrophic larvae (Figure 8.22b).

Thus, in general, a planktotrophic larval stage was associated with a decreased likelihood of extinction because the absence of a planktotrophic stage reduces the opportunity for widespread dispersal, thereby increasing the likelihood that genetic discontinuities will develop among populations of a species—factors that enhance both speciation and extinction [SEE SECTION 7.4]. Inversely, the presence of a planktotrophic stage lessens the likelihood of isolation.

During the K/T extinction, however, there was no significant difference in extinction rates with respect to larval type (Figure 8.22b). Therefore, an important factor affecting extinction rates during background times did not operate during the mass extinction. This lack of a difference may reflect the global reach of the K/T event. Even widespread species were susceptible to

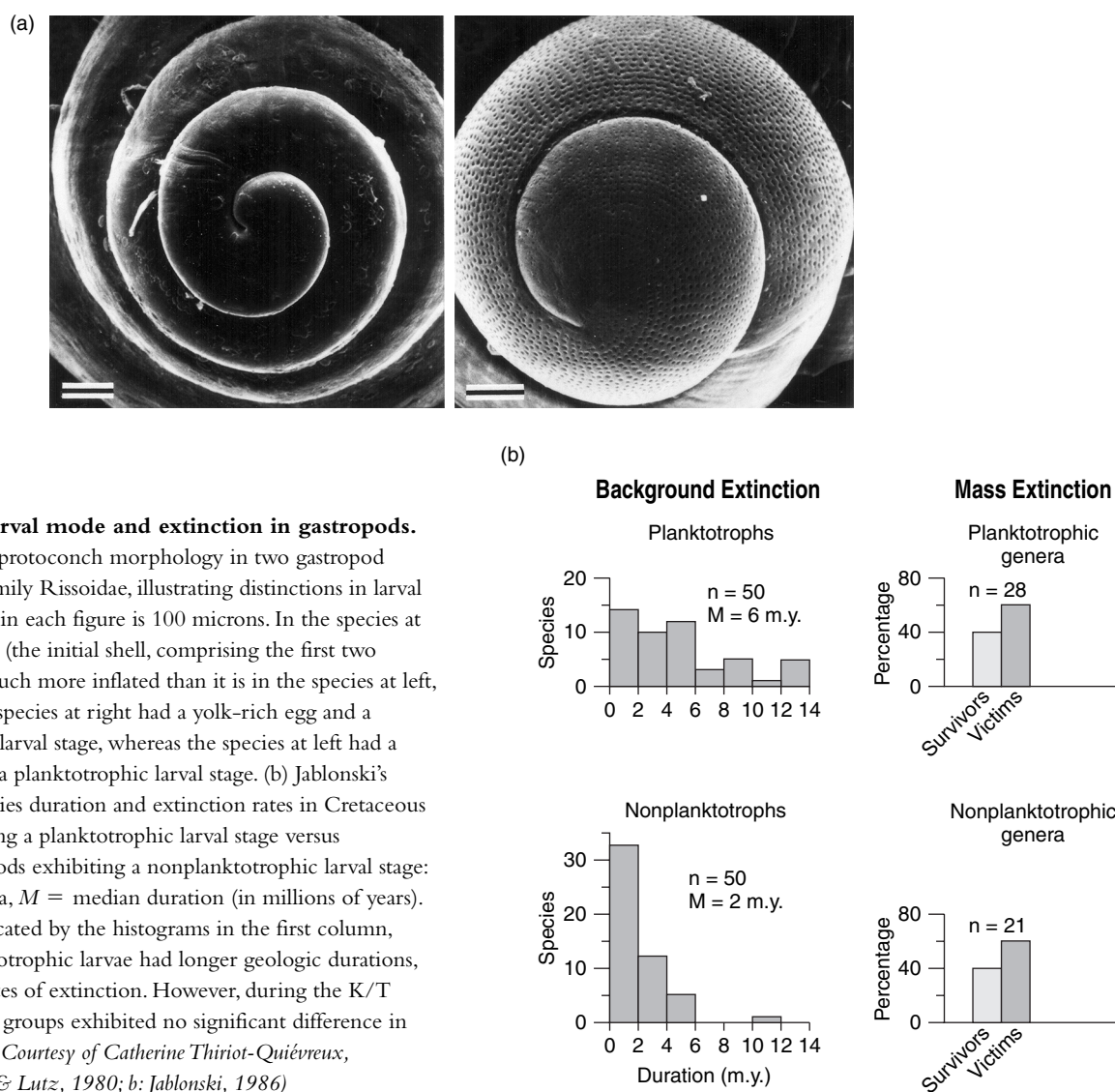


FIGURE 8.22 Larval mode and extinction in gastropods.

(a) Comparison of protoconch morphology in two gastropod species from the family Rissoidae, illustrating distinctions in larval stage. The scale bar in each figure is 100 microns. In the species at right, Protoconch I (the initial shell, comprising the first two whorls or less) is much more inflated than it is in the species at left, indicating that the species at right had a yolk-rich egg and a nonplanktotrophic larval stage, whereas the species at left had a yolk-poor egg and a planktotrophic larval stage. (b) Jablonski's comparison of species duration and extinction rates in Cretaceous gastropods exhibiting a planktotrophic larval stage versus Cretaceous gastropods exhibiting a nonplanktotrophic larval stage: n = number of taxa, M = median duration (in millions of years). On average, as indicated by the histograms in the first column, species with planktotrophic larvae had longer geologic durations, indicating lower rates of extinction. However, during the K/T extinction, the two groups exhibited no significant difference in extinction rates. (a: Courtesy of Catherine Thiriot-Quévrevreux, C.N.R.S./Jablonski & Lutz, 1980; b: Jablonski, 1986)

extinction at that time, an inference supported by Jablonski's additional findings that neither the species richness of a genus nor the geographic ranges of its constituent species affected its chances of surviving the K/T event.

8.7 THE NEXT GENERATION OF PALEONTOLOGICAL DATABASES

The question of regional versus global transitions, such as that highlighted in the Rosenzweig and McCord example, is one of many issues motivating the development of new paleontological databases that include data not available in earlier global compendia. Although older databases (e.g., Figure 8.2) permitted the construction of global diversity curves, it is not possible to determine from them whether diversification patterns during any interval varied regionally with respect to paleogeographic, paleoenvironmental, or tectonic settings. To address these possibilities, newer paleontological databases have moved beyond earlier efforts in two significant respects:

1. Instead of including information on just the first and last known appearances of fossil taxa, newer databases catalogue multiple occurrences of taxa, wherever they occur globally or within the regions to which the database may be limited.
2. When possible, a variety of additional information is collected for each catalogued occurrence. Typically, these data include geographic location, stratigraphic interval, characteristics of the enclosing sediments, and the inferred paleoenvironmental and tectonic settings.

Two examples of major database initiatives in paleobiology are illustrated in Figures 8.23 and 8.24. The objective of *The Paleobiology Database* (PBDB, found at <http://paleodb.org>; Figure 8.23) is to produce an exhaustive compilation of Phanerozoic marine and non-marine paleofauna and flora for the entire world. As suggested by its title, the scope of the *Neogene Marine Biota of Tropical America* database (NMITA, found at <http://porites.geology.uiowa.edu/>; Figure 8.24) is more limited, given its focus on research questions related to the marine evolutionary history of tropical America during the past 25 million years. Both projects endeavor to collect similar classes of subsidiary information. While the PBDB emphasizes the collection of existing taxonomic and geologic information from the literature,

however, NMITA has focused on the collection of new data directly from strata in the region of focus. As such, NMITA has significantly augmented the relatively scarce data available from the region previously.

8.8 DISSECTING DIVERSIFICATION AND RECOVERIES FROM MASS EXTINCTIONS

As the PBDB, NMITA, and similar large-scale databases continue to grow, they will inevitably include the information available in earlier compendia (Figure 8.2) on the first and last global appearances of taxa. However, the additional data that they contain on the geography, lithology, and environments of individual taxonomic occurrences permit researchers to assess in more detail the nature of diversification within and among regions during important transitions in the history of life. Several examples are illustrated in this section, and this is a persistent theme throughout the remainder of the book.

The Ordovician Radiation

As we have already seen, there was a major global diversification of marine organisms during the Cambrian and Ordovician periods. Although it was once commonplace to view the entire interval as a single "event," it is now understood that the biological nature of the Cambrian Explosion was rather different from the subsequent Ordovician Radiation. The Cambrian Explosion represented the initial, major diversification of multicellular animal life, during which most present-day animal phyla observed in the fossil record first evolved their characteristic anatomical features and began to diversify, although they may have originated much earlier. Because it has been a focus of intensive, multidisciplinary research, we provide an extended discussion of the Cambrian Explosion in Chapter 10.

From a taxonomic perspective, the Ordovician Radiation was most pronounced at the order level and below (Figures 8.5 and 8.11), and it was characterized by a major transition in marine settings from the Cambrian evolutionary fauna to the Paleozoic evolutionary fauna (Figures 8.5 and 8.8). Moreover, by the end of the Ordovician, standing diversity, measured at the genus and family levels, had increased three- to fourfold, relative to Cambrian levels. Because of these profound changes, coupled with the excellent preservation of Ordovician rocks


The Paleobiology Database


Home • View • Download • Analyze • About • Contributor's area

USNM 41352 CENSUS: Wasatchian, Wyoming
 (PBDB collection number 28135)

Basic information

Also known as: PW9549 CENSUS

Authorizer: P. Will

Enterer: P. Will

Modifier: P. Will

Research group: paleobotany

Created: 2003-01-24 13:24:50

Last modified: 2003-03-09 12:03:40

Released: 2003-01-24 13:24:50

Access level: the public

Geography

Country: United States

State/province: Wyoming

County: Sweetwater

Coordinates: 41° North, 108° West (View map)

Basis of coordinate: unpublished field data

Scale of geographic resolution: small collection

Time

***Period:** Tertiary

***Epoch:** Early/Lower Eocene

***Local age/stage:** Wasatchian

Key time interval: Wasatchian

* legacy (obsolete) database fields

Stratigraphy

Formation: Wasatch

Member: Ramsey Ranch

Scale of stratigraphic resolution: bed

Lithology

Primary lithology: carbonaceous lithified siltstone

Secondary lithology: carbonaceous lithified 'shale'

Fossils collected from primary lithology: Y

Environment: wet floodplain

Tectonic setting: intermontane basin

Taphonomy

Modes of preservation: adpression

Assemblage components: microfossils

Spatial orientation: random

Feeding/predation traces: external foliage feeding, arthropod mining, arthropod galling, piercingsucking

Temporal resolution: snapshot

Spatial resolution: parautochthonous

Collection methods and comments

Collection methods: field collection, bulk, mechanical

Collection size: 802

Collection size unit: specimens

Rock censused: 8000000 cm3 (volume)

Reason for describing collection: general faunal/floral analysis

Collection comments: Great Divide Basin, Sourdough flora. Only dicot leaves censused. See USNM 41352 corresponding non-census locality for presence-absence data for all species. Collected 8/1/95, 7/29/96, and July 1998. For voucher specimens, Smithsonian NMNH accession number OR420051. Occurrence of *Cephaloichnites strongi* (hispidine beetle damage on *Zingiberopsis*, see Will et al. 2000). Insect damage census site for Will and Labandeira 1999 and Will et al. 2001. Total collection size here includes earlier component (for Will 2000) without insect damage tally as well as insect damage tally (Will and Labandeira 1999, Will et. al. 2001). See online supplement of Will et al. 2001 for insect damage data for each specimen in the insect damage census.

Reference information

Primary reference: 7696 P. Will. 2000. Late Paleocene-early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. *Geological Society America Bulletin* 112(2):292-307 [P. Will, P. Will, P. Will]

Secondary references: 8331 P. Will and C. C. Labandeira. 1998. Response of plant-insect associations to Paleocene-Eocene warming. *Science* 284(5423):2153-2156

8332 P. Will, C. C. Labandeira, W. J. Kress, C. L. Starnes, D. M. Windsor, A. L. Allen, and K. R. Johnson. 2000. Timing the radiations of leaf beetles: Hesperes on gingers from latest Cretaceous to Recent. *Science* 289(5477):291-294

8332 P. Will, C. C. Labandeira, K. R. Johnson, P. D. Coley, and A. D. Culler. 2001. Insect herbivory, plant defense, and early Cenozoic climate change. *Proceedings of the National Academy of Sciences* 98(11):8221-8226

Taxonomic list for USNM 41352 CENSUS: Wasatchian, Wyoming
 (PBDB collection number 28135)

Class	Order	Family	Taxon	Abundance	Comments
Dicotyledonae	Magnoliales	Lauraceae	<i>Lauraceae</i> informal RR46	3 specimens	Lauraceae sp. 2 RR46
			aff. <i>Sciocarya</i> sp.	1 specimen	
			<i>Hesperis</i> cf. <i>oregonensis</i>	92 specimens	
			* <i>Dombyea novimundi</i> Hickey 1977	8 specimens	'Dombyea' novi-mundi
Dicotyledonae	Magnoliales	Magnoliaceae	cf. <i>Magnoliaceae</i> informal RR36	5 specimens	RR36
			<i>Syrgioides americana</i>	3 specimens	
Dicotyledonae	Fagales	Betulaceae	<i>Alnus</i> informal RR14	156 specimens	RR14
Dicotyledonae	Violales	Salicaceae	<i>Populus wyomingiana</i>	48 specimens	
			<i>Allophylus flexibilis</i>	39 specimens	
			<i>Cinnamomophyllum</i> sp.	19 specimens	RR19
Dicotyledonae	Gentianales	Apocynaceae	<i>Apocynaceae</i> informal RR17	400 specimens	RR17
Dicotyledonae			<i>Dicotyledonae</i> informal RR48	6 specimens	
Dicotyledonae			<i>Dicotyledonae</i> informal RR37	5 specimens	
			<i>Stillingia casca</i> Hickey 1977	1 specimen	
Dicotyledonae			<i>Dicotyledonae</i> informal RR31	6 specimens	
Dicotyledonae			<i>Dicotyledonae</i> informal RR88	3 specimens	
Dicotyledonae			<i>Dicotyledonae</i> informal RR63	2 specimens	
Dicotyledonae			<i>Dicotyledonae</i> informal RR35	2 specimens	
Dicotyledonae			<i>Dicotyledonae</i> informal RR65	1 specimen	
Dicotyledonae			<i>Dicotyledonae</i> informal RR66	1 specimen	
Dicotyledonae			<i>Dicotyledonae</i> informal RR94	1 specimen	

Analyze collection 28135's abundance data
Tabulate collection 28135's ecological data

FIGURE 8.23 An example of a collection contained in the Paleobiology Database (PBDB: <http://paleodb.org>). This is a paleobotanical collection from Lower Eocene strata of Wyoming. Any of the information contained in a collection can be searched and downloaded.


Neogene Marine Biota of Tropical America

Zooxanthellate Corals

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- Identification Tools
- Glossary of Morphologic Characters
- Taxa (Formal and Alphabetic Listings of Families and Genera)
- Specimens
- Localities
- Repositories
- References
- Link to:
 - Type Collection of Stony Corals at NMNH
 - Hexacorallians of the World

FIGURE 8.24 A portion of a Web page for the NMITA database (Neogene Biota of Tropical America: <http://porites.geology.uiowa.edu/>), illustrating a partial range of the data available for searching.

and fossils in several places around the world, the Ordovician has become a focal interval for the assessment of biotic patterns at local and regional levels in comparison to the global signal. In this research, paleontologists have sought answers to two important questions:

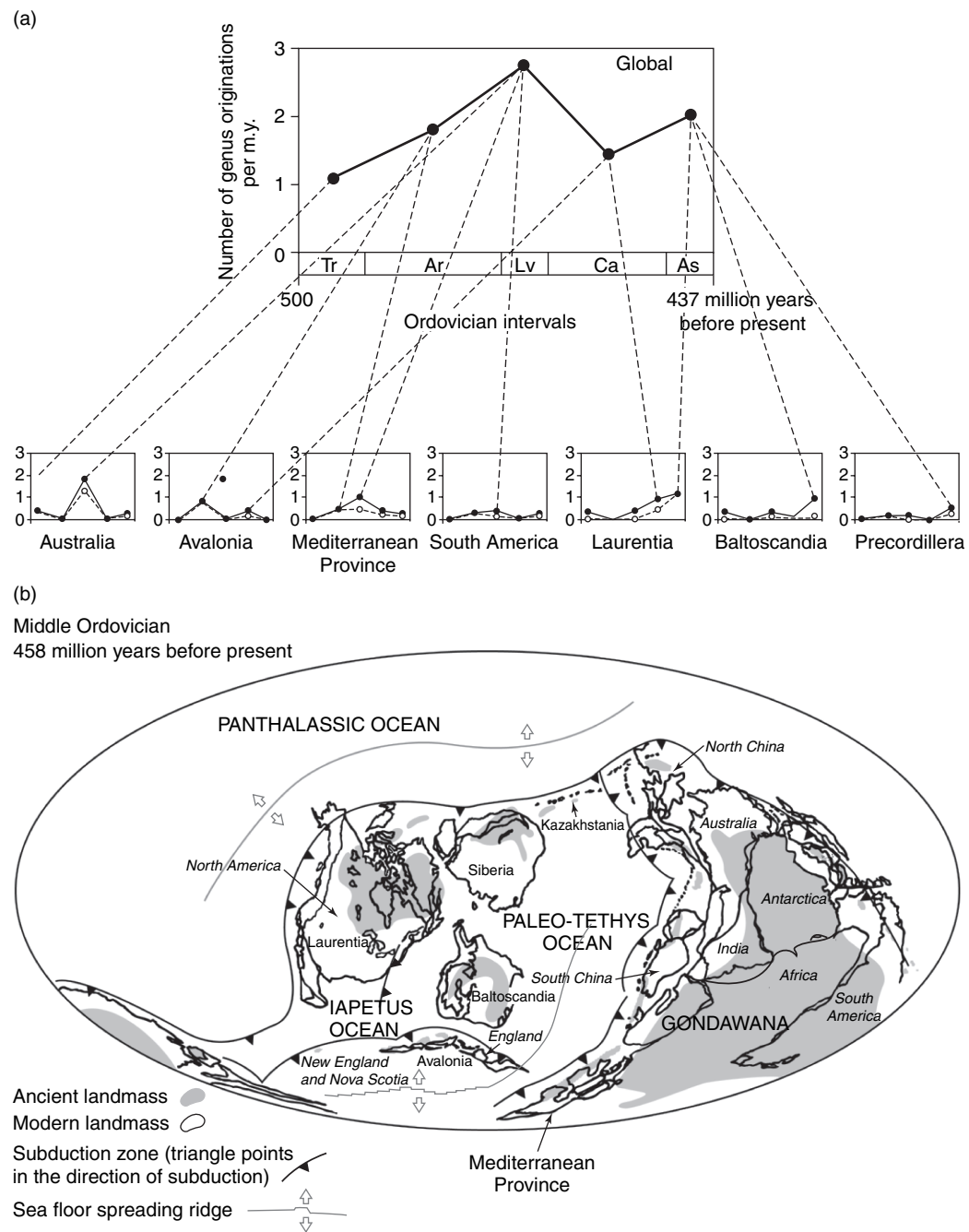
1. Did diversification patterns at regional levels simply mirror what we observe at the global level or, alternatively, were there significant differences between global and regional patterns, as well as from region to region?

2. If there were substantial differences in diversification patterns among regions, can we explain what caused these differences?

In a series of analyses, Arnie Miller compared the diversification of major higher taxa in different regions worldwide. The example in Figure 8.25, for bivalve molluscs, illustrates regional origination rates in comparison with the global signal. The methodology for determining regional evolutionary rates was the same as that used

FIGURE 8.25 Variations among Ordovician paleocontinents in bivalve origination rates throughout the Ordovician period.

(a) Graphs depicting origination rates for several Ordovician paleocontinents, in comparison to the aggregate, global pattern. The dashed lines connect portions of the global curve to “peaks” of origination in various paleocontinents that contribute most significantly to global origination during each Ordovician series. For example, significant bivalve diversification did not take place in Laurentia (much of present-day North America) until late in the period. In the graphs for each paleocontinent, the dashed curve is the number of true originations. The solid curve includes genera that originated elsewhere but were making their first appearances on the paleocontinent. (b) A paleogeographic reconstruction for the Middle Ordovician, illustrating the positions of paleocontinents, including those highlighted in Figure 8.25a. (a: From Miller, 2001; b: From a map available from the Web site of Christopher Scotese: www.scotese.com/newpage1.htm)



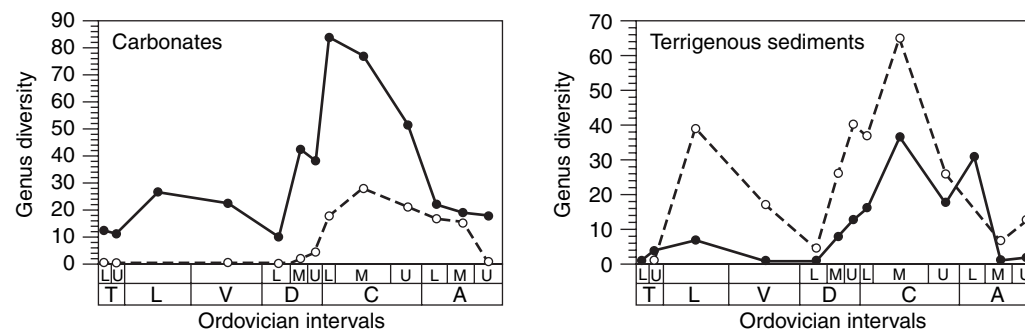


FIGURE 8.26 Diversity trajectories of bivalves (dashed lines) and gastropods (solid lines) in terrigenous and carbonate settings worldwide through the Ordovician. Note that bivalves were far more diverse in terrigenous sediments than in carbonates through most of the period. The opposite was the case for gastropods. (From Novack-Gottshall & Miller, 2003)

for global rate determination [SEE SECTION 7.2], except that the data on first and last appearances were confined to the regions in question. Based on this figure, it can be seen that bivalve diversification varied significantly throughout the Ordovician and that different regions contributed to global diversification at different times.

The regions contributing diversity early in the Ordovician were located mainly in high southern latitudes, whereas the low latitude setting of Laurentia (present-day North America) did not exhibit a bivalve diversification until later. Differences in the geological characteristics of these regions appear to have governed this pattern, as can be demonstrated by determining the lithologies in which bivalves occurred worldwide. Collectively, bivalves exhibited a significant preference throughout the Ordovician for substrates that were rich in terrigenous sediments eroded off of nearby landmasses (Figure 8.26). These substrates were readily available at high southern latitudes, such as in the Mediterranean Province, during the Early Ordovician but did not become widespread in Laurentian seas until the Middle and, especially, the Late Ordovician in association with the onset of a major episode of mountain building that provided a significant source of terrigenous sediments.

These regional variations raise a basic question: In general, were global Phanerozoic diversity trends (e.g., Figure 8.5) caused primarily by global-scale evolutionary processes, or did they represent the summation of environmentally mediated transitions operating mainly at regional scales? From the patterns that we just considered, one might get the impression that it is the latter. Nevertheless, we should bear in mind that, while these observations can explain why some higher taxa thrived when appropriate environmental conditions were available and,

conversely, why others did not, they probably do not explain why total diversity increased so dramatically at that time. Like the Cambrian Explosion [SEE SECTION 10.2], it appears that diversity increased throughout the entire world during the Ordovician Radiation, so it seems probable that the ultimate explanation for this increase was also global in scope.

Regional Marine Cenozoic Transitions in Tropical America

There is a particular urgency to understand the regional, evolutionary history of reef ecosystems throughout the Cenozoic Era, given their relevance to present-day concerns about the health of coral reefs in high-diversity tropical regions. The NMITA database, which we discussed earlier, is an outgrowth of these efforts. It has permitted paleontologists to understand the responses to environmental perturbations of fossil reef corals that are closely related to, and in some cases include, present-day species. After assembling these data, Nancy Budd (2000) examined the history of Early Eocene through Late Pleistocene Caribbean coral diversity in the light of region-wide environmental changes. The data for this analysis came from samples of 57 assemblages spanning the Eocene to Recent, depicting the presence of 294 coral species and 66 genera.

Compilations of stratigraphic ranges (Figure 8.27a illustrates genera) and representations of total diversity and evolutionary rates (Figures 8.27b and 8.27c) permitted the recognition of a series of diversity plateaus and peaks in the Middle to Late Eocene, Late Oligocene to Early Miocene, and Late Pliocene. Origination and extinction rates, particularly at the species level, appeared to be

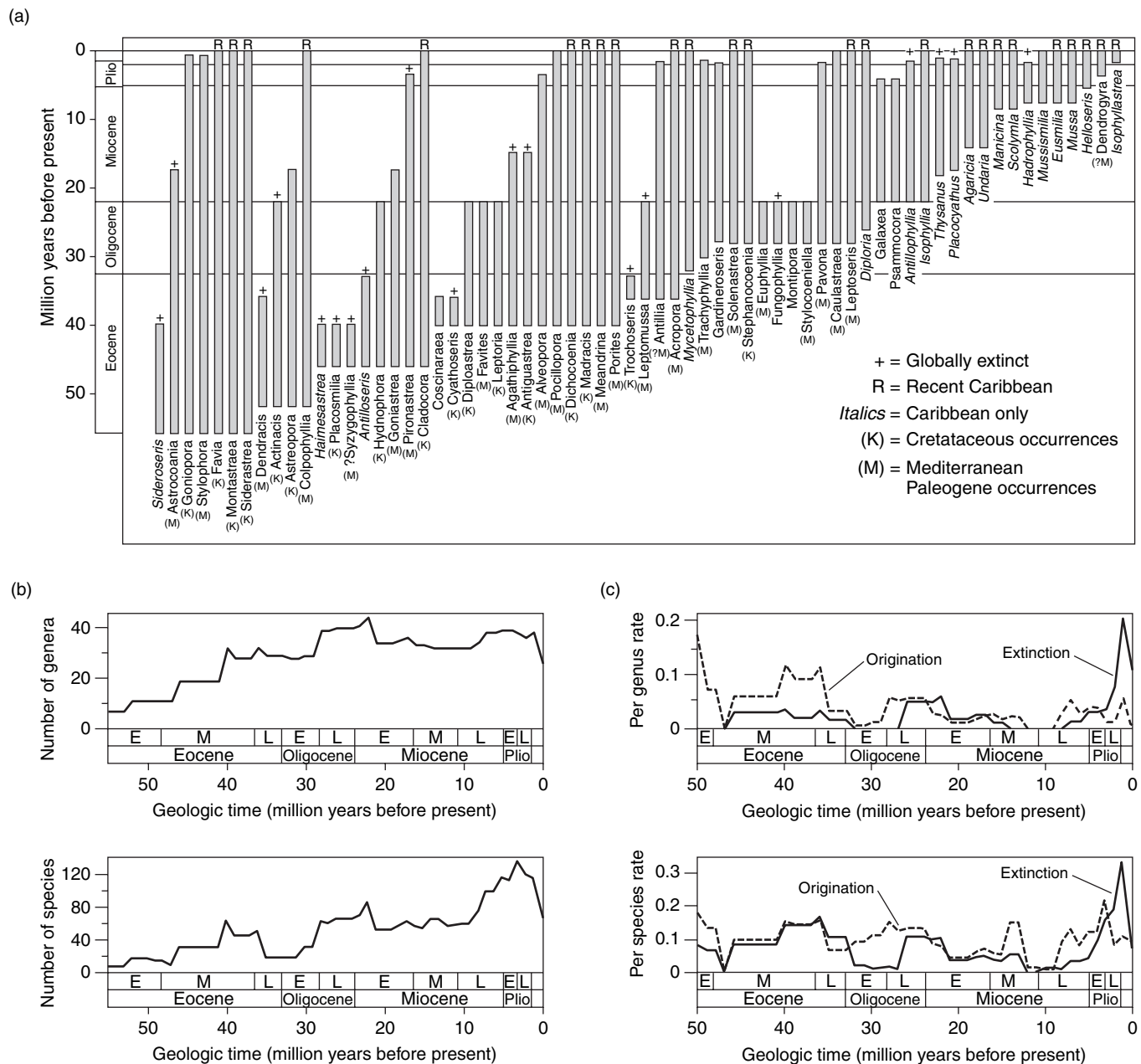


FIGURE 8.27 Budd's analysis of evolutionary rates among Caribbean corals during the Cenozoic.

(a) Composite chart of stratigraphic ranges for Caribbean coral genera from the Eocene to the Recent. (b) Diversity of coral genera (top) and species (bottom) from the Eocene through the Pliocene. (c) Origination and extinction rates for coral genera (top) and species (bottom) from the Eocene through the Pliocene. Origination and extinction were measured as proportional rates per million years (see Table 7.4). (Budd, 2000)

independent of each other to a fair extent after the Eocene, with evidence of elevated extinction near the end of each diversity plateau.

Despite a broad increase in total species diversity throughout the study interval, Budd found that the maximum number of species contained within individual assemblages had leveled off by the Late Eocene. She

suggested that stabilization in total numbers, if not composition (Figure 8.27a), may have been tied to the cessation of dispersal from the Mediterranean region during the Oligocene. Supporting this view is the observation that genera found in the Caribbean region from that time on were confined to the Caribbean, suggesting that they originated there rather than elsewhere.

In addition, Budd ascribed the intense genus-level extinction in the Plio-Pleistocene to climatic deterioration. At the species level, elevated extinction rates in the Middle-Late Eocene, Late Oligocene-Early Miocene, and Plio-Pleistocene coincided with episodes of cooling in the first and third cases, and the onset of regional upwelling and turbidity in the second case. Interestingly, there is evidence that Pleistocene species in a variety of terrestrial and aquatic settings were able to survive significant climatic variations through shifts in their geographic ranges [SEE SECTION 9.6], and data on present-day coral species off the coast of Florida suggests that they, too, have undergone range shifts in response to recent climatic changes [SEE SECTION 10.6]. Thus, there is still much to learn about why some species appear to have been quite resilient to climatic changes, whereas others apparently were not.

Recoveries from Mass Extinctions

Global diversity rebounded rapidly in the aftermaths of several of the major extinctions of the Phanerozoic (Figure 8.5). Because the major mass extinctions were global in extent, it stands to reason that recoveries would also be observed on a global scale. However, there is no inherent reason to expect that the factors favoring the diversification of particular taxa should

also be global. As we saw with the Ordovician Radiation, the physical characteristics of different regions or environments can yield different diversification pathways and, thus, the nature and trajectory of biotic recovery may vary markedly from region to region.

In an analysis of biotic recovery from the K/T mass extinction, David Jablonski evaluated previous suggestions that the initial recovery in the Gulf Coast of North America was dominated by species belonging to so-called bloom taxa—very widespread species that were considered capable of diversifying unusually rapidly after the extinction. To test this suggestion, Jablonski (1998) compared molluscan diversification for the Gulf Coast against three other major regions. He found that, in proportion to other taxa, the diversity of species recognized by previous authors as bloom taxa, did *not* increase in the other regions (Figure 8.28). Not only does this call into question the global significance of bloom taxa, but it also shows that the recovery from the K/T extinction was far from a globally uniform process.

Because of the magnitude of the global diversity increase in the aftermath of the Late Permian mass extinction (Figure 8.5), this diversification has received considerable attention from paleontologists. In terms of the number of new taxa, this Mesozoic Radiation appears to have rivaled the Cambrian Explosion and

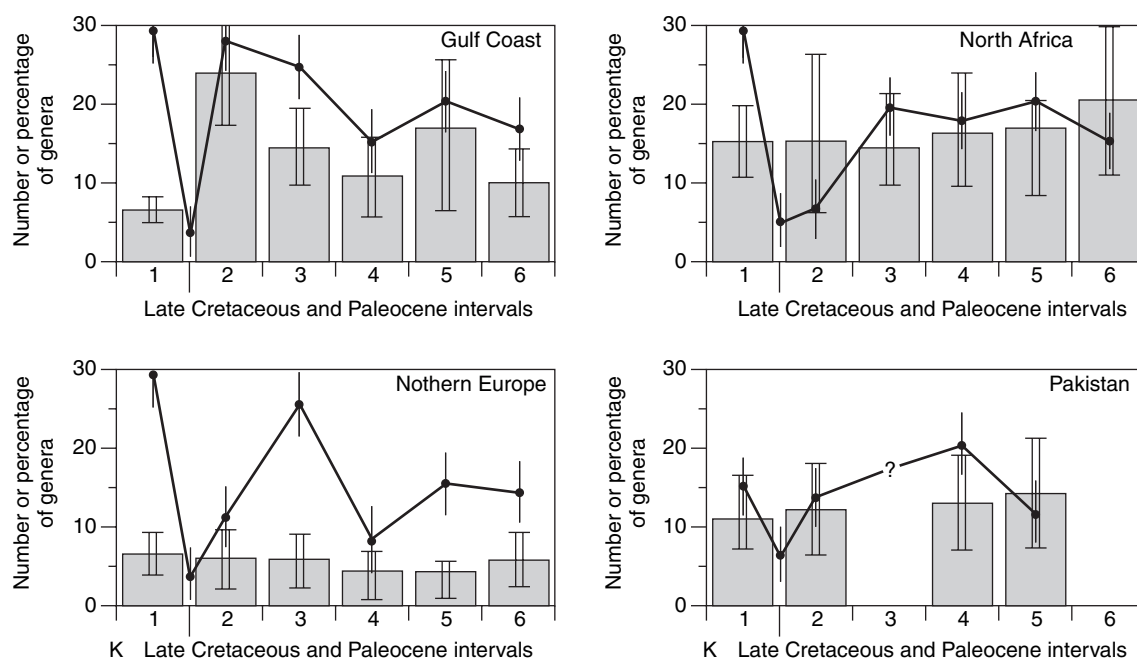


FIGURE 8.28 Jablonski's depiction of regional differences in the diversity of "bloom taxa" across the K/T boundary and into the Paleocene. Histograms depict percentages of total species diversity and points depict actual numbers of species. Among the four regions studied, the proportion of taxa categorized as bloom taxa increased following the mass extinction only along the North American Gulf Coast. (Jablonski, 1998)

Ordovician Radiation combined. However, the Mesozoic Radiation was arguably less profound from an evolutionary standpoint than its Paleozoic counterparts. During the Mesozoic, there was comparatively little origination of phyla and classes among marine taxa (Figure 8.29). Two principal explanations for this have been offered. First, by the end of the Paleozoic, genetic pathways may have become channeled to an extent that prevented the kind of “experimentation” that appears to have been rampant during the Late Precambrian and Early Paleozoic [SEE SECTION 10.2]. Second, despite the severe diversity decline of the Late Permian extinction, the actual ecospace occupied by the remaining taxa did not contract substantially, relative to pre-extinction levels.

Therefore, in marked contrast to the Early Paleozoic diversification—which was accompanied by the advent of organisms exhibiting a variety of novel modes of life above, at, and below the sea floor [SEE SECTION 9.4]—the amount of unoccupied ecospace available for the development of novel lifestyles in the early Mesozoic may have been more limited. Clearly, these two explanations are not mutually exclusive and may have acted together to inhibit the origination of phyla and classes after the most extensive mass extinction in the history of life.

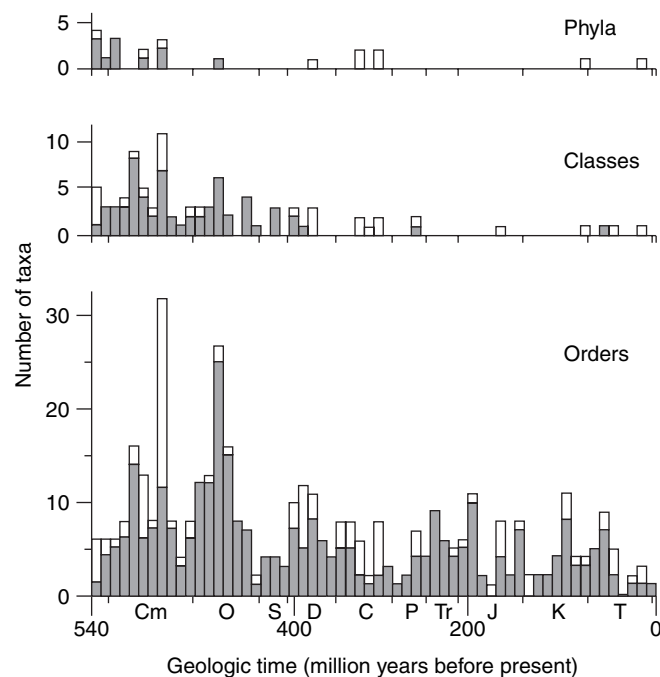


FIGURE 8.29 Erwin et al.’s depiction of the time of origination of well-skeletonized (solid bars) and lightly skeletonized or unskeletonized (open bars) marine taxa.

Note that the vast majority of phyla and classes originated early in the Paleozoic. (Erwin et al., 1987)

8.9 A SCHEMATIC OVERVIEW OF BIOLOGICAL TRANSITIONS

As suggested throughout this chapter, paleontologists have proposed a variety of explanations for the major global transitions in taxonomic composition observed throughout the Phanerozoic. Typically, these have involved the classification of two or more groups with respect to biological attributes that give one group an advantage over the other through geologic time. In some cases, like that of cyclostome and cheilostome bryozoans [SEE SECTION 8.4], competition has been invoked to explain the long-term diversification of the “later” group at the apparent expense of the “earlier” group. As we have noted, however, this approach is typically not fruitful because it is difficult to demonstrate definitively that one higher taxon enjoyed a long-term competitive advantage that would be sufficient to cause biotic replacement through geologic time.

The topic of biotic transitions is explored further in Chapter 9, in our discussion of paleoecology. For the moment, to help summarize the variety of ideas proposed to explain the replacement of one group by another through geologic time, it is useful to consider the schematic diagram prepared by Michael Benton, illustrated in Figure 8.30. Explanations range from gradual replacement brought on by interactions in which one group outcompetes another over the long term (Type 1, left side of the figure) to rapid replacement fueled by fortuitous survival—or the lack thereof—in the wake of a mass extinction, accompanied by the rapid radiation of survivors into the ecospace vacated by organisms that became extinct (Type 5, right side of the figure). Intermediate scenarios involve the advent of morphological or functional innovation (a “key adaptation”) in group B that affords it a competitive advantage over group A, but, to varying degrees in Types 2, 3, and 4, a mass extinction or perturbation plays a significant role in the transition by removing incumbents.

Among the examples that we have considered in this chapter, Sepkoski’s coupled logistic model, and its use to explain the transition from cyclostome to cheilostome bryozoans, would be classified as a Type 1 replacement. Gould’s (1985) view of mass extinctions as overarching arbiters of long-term transitions is a Type 5, and Rosenzweig and McCord’s scenario for transitions from stiff- to flexible-necked turtles falls somewhere in between. Although Benton and others have sought to determine the extent to which each of these five models appropriately describes Phanerozoic biotic transitions, we are still a long way from knowing

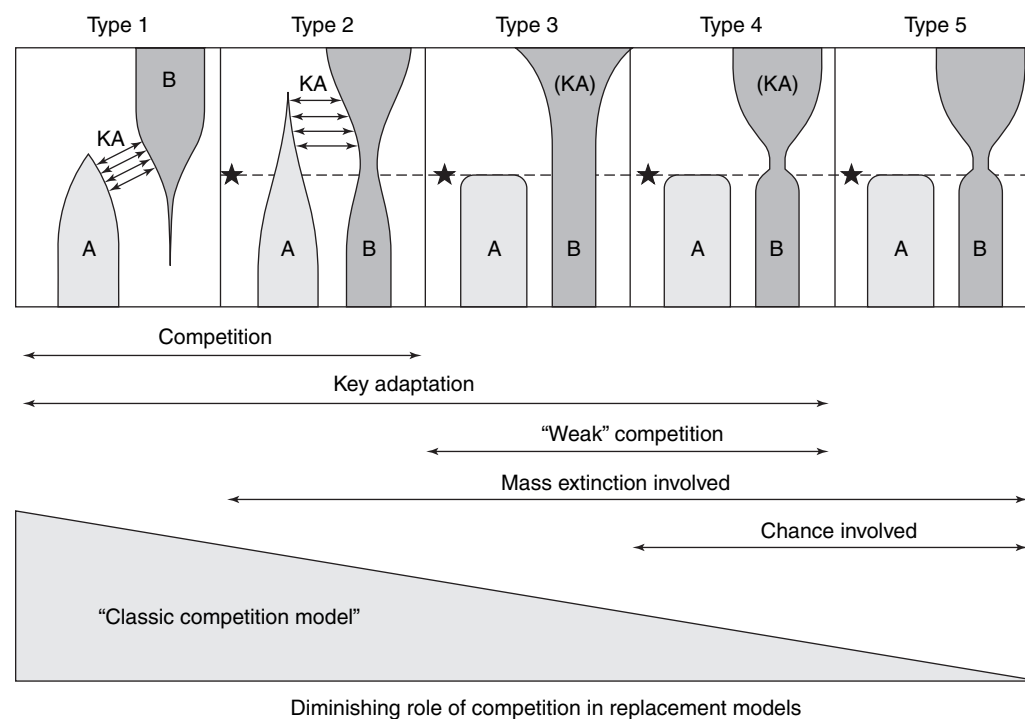


FIGURE 8.30 A series of schematic models depicting possible modes of biotic replacement of one clade by another. The role of competition diminishes, and that of physical perturbation increases, from left to right. The star in four of the figures denotes a mass extinction, and “KA” denotes a “key adaptation.” (From Benton, 1996)

whether any of these models has dominated the history of life. However, there is reason to be optimistic that the approaches described throughout this book will ultimately help us to make these determinations.

8.10 MORPHOLOGICAL DIVERSITY

Our discussion of diversity has so far focused strictly on taxonomic diversity or richness. Yet many questions raised in this chapter involve morphological differences between species. These differences, which are referred to as **disparity**, represent another important aspect of biological diversity.

Because species in the fossil record are recognized on the basis of their form, it is natural to ask whether taxonomic and morphological diversity really are different for paleontological species. To illustrate the distinction between these two aspects of diversity, Figure 8.31 depicts morphological data for a number of specimens of blastoid echinoderms. The measurements are the x -, y -, and z -coordinates of selected homologous landmarks on the theca, as shown in Figure 2.8b. Because there are

more measurements than can easily be visualized, the data have been converted to synthetic principal components [SEE SECTION 3.3]. In Figure 8.31, the specimens of

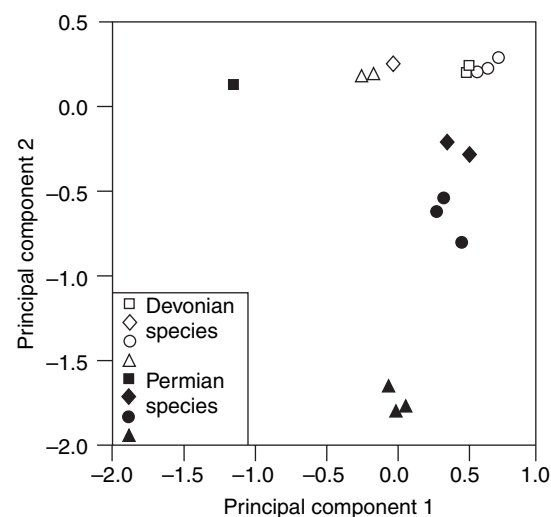


FIGURE 8.31 Principal component scores for a sample of Devonian and Permian blastoids. Each time period is represented by several specimens belonging to four species; thus, species richness is the same in these two periods. The Permian forms are more dispersed, however; they have greater disparity. (Data from Foote, 1991)

each species cluster together and tend to be separated from other species. This is not a circular exercise, since the species were not originally recognized on the basis of the measurement data shown here.

Figure 8.31 shows several species from the Devonian and Permian, with 1–3 specimens per species. Each period is represented by four species, but the Permian

forms are more widely dispersed—they have greater disparity. As this simple example demonstrates, richness and disparity measure quite different aspects of diversity. How they relate to each other is one of the primary questions addressed by evolutionary studies of disparity. Box 8.3 describes some approaches to measuring disparity.

Box 8.3

MEASURING DISPARITY

Studies of disparity typically start by measuring differences among related species within an interval of time. To illustrate this, Figure 8.32 portrays the mean of each species from Figure 8.31. One obvious way to measure the disparity of a sample of species would be to measure the area covered by the points in this figure—or the volume or “hypervolume,” if there were three or more dimensions. This area is shown for the Permian sample by the hatched lines. This approach, while having a clear intuitive appeal, creates one problem, espe-

cially for paleontological studies: The area covered by the points depends on how many species are sampled. Thus, apparent disparity may reflect the completeness of sampling. If only half the species in Figure 8.32 had been sampled, the spread of points would have been considerably smaller.

Another way to measure disparity is to extend the univariate measure of variance that we considered in Chapter 3. This is illustrated for the Permian species in Figure 8.32. Recall that, for a single trait, x , measured on n species and having mean \bar{x} , the sample variance is defined as $s^2 = \sum (x - \bar{x})^2 / (n - 1)$. With two or more traits, we first compute the mean of each variable and then plot the position of the resulting bivariate or multivariate mean, shown as the cross in Figure 8.32. The straight-line distance d of each species from this mean is then calculated [SEE SECTION 3.2]. The bivariate or multivariate variance is the average of the squared distances from the mean: $\sum d^2 / (n - 1)$. Like the univariate variance, this measure of disparity is generally unbiased by sample size.

Yet another way to measure disparity is to compute the squared distances between all pairs of species, as shown for the Devonian forms in Figure 8.32, and to take the average of these distances. (The average squared distance is in fact directly proportional to the variance.) This approach must be used when the traits are categorical or ordinal rather than continuous [SEE SECTION 3.2]. This is because the mean and variance make sense only for continuous variates. There are many ways to measure a distance between two species using discontinuous characters. One approach is simply to tabulate the total number of traits for which the two species have a different trait value.

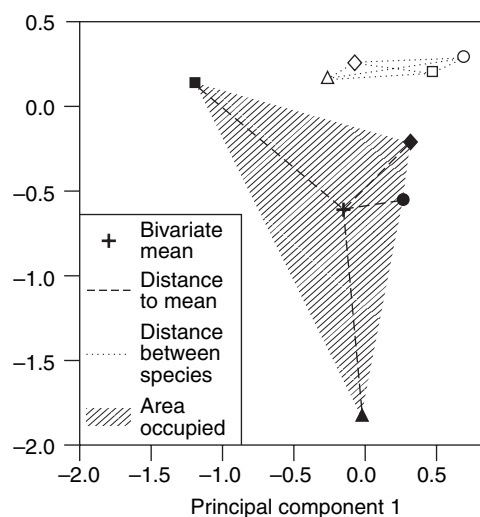


FIGURE 8.32 Three ways to measure disparity. The points represent the species means from Figure 8.31. (1) The hatched region shows the area occupied by the Permian species. (2) The dashed lines show the distances from these same species to the overall Permian average; the mean of the squared distances measures disparity. (3) The dotted lines show the distances between the Devonian species; the mean of these squared distances also measures disparity. (Data from Foote, 1991)

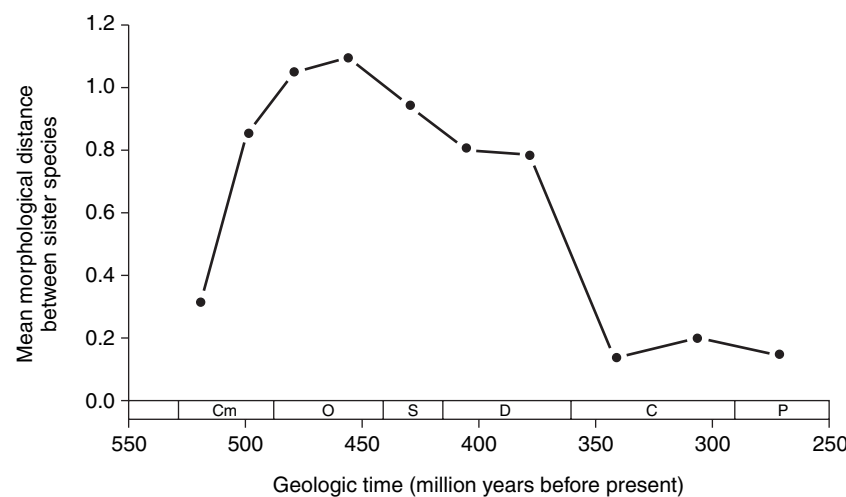


FIGURE 8.33 Mean morphological distance between sister species of blastozoan echinoderms. Larger distances imply larger evolutionary transitions. (Data from Wagner, 1995)

Examples of Disparity Analysis

Morphological Changes during Evolutionary Radiation Many paleontologists over the years have noted a general tendency for morphological changes to be relatively large during the early stages of diversification of a biologic group, and to become smaller as the evolutionary radiation proceeds. This pattern has generally been interpreted to reflect major morphological changes associated with the occupation of new ways of life. The tendency has been questioned, however, in part because it has sometimes been inferred from a subjective assessment of the morphological differences between taxa. Analysis of morphological data allows patterns of early radiation to be assessed more explicitly.

Echinoderms are one of the groups commonly thought to have undergone large evolutionary transitions in form early in their history. As an example, Figure 8.33 shows results of a study of the echinoderm subphylum Blastozoa, based on about 65 discontinuous morphological characters. Several phylogenetic analyses, all of them conducted independently of this study, were combined to produce a cladogram [SEE SECTION 4.2]. The size of morphological changes was estimated by computing the morphological distance between sister-species pairs on the cladogram [SEE SECTION 4.2]. Of all the species sampled, sister species are most closely related, so the distances between them should reflect evolutionary changes. Consistent with the conventional view, the size of morphological transitions in blastozoan echinoderms is high in the Cambrian and Ordovician, and it declines over the rest of the Paleozoic.

In many cases, phylogenetic relationships within a group are not known; therefore, the direct measurement of evolutionary changes is not possible, as it was in the case of blastozoans. However, disparity among species, irrespective of their phylogeny, can be useful as an indirect guide to transition sizes. To infer the nature of transitions without phylogenetic information, it is necessary to rely on additional assumptions in the form of evolutionary models.

Figure 8.34 compares two highly idealized models of the diversification process. In the first (Figure 8.34a), the average size of morphological steps between ancestor and descendant does not change over time. As a result, the evolutionary tree continues to spread out as it branches and accumulates new taxa; thus, disparity and richness increase together. In the second model, morphological steps are substantially larger early in the radiation than later (Figure 8.34b). The evolutionary tree

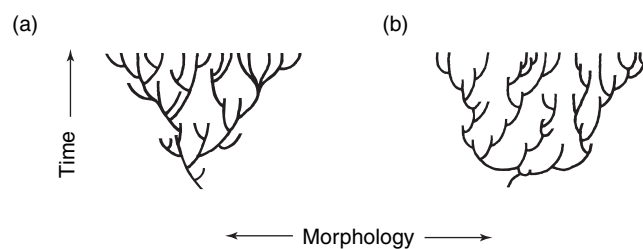


FIGURE 8.34 Models of richness and disparity during an evolutionary radiation. (a) The average size of evolutionary transitions between ancestor and descendant is constant over time. As a result, disparity and richness increase together. (b) The size of transitions is large early and small later. As a result, disparity initially increases more rapidly than richness. (From Foote, 1993)

spreads rapidly at first, then more slowly, and therefore disparity initially increases more rapidly than richness.

With these models in mind, let us return to the blastozoan data. These are depicted in another form in Figure 8.35a, as the average distance between all species extant within an interval of time rather than just between sister species. Like the distances between sister species,

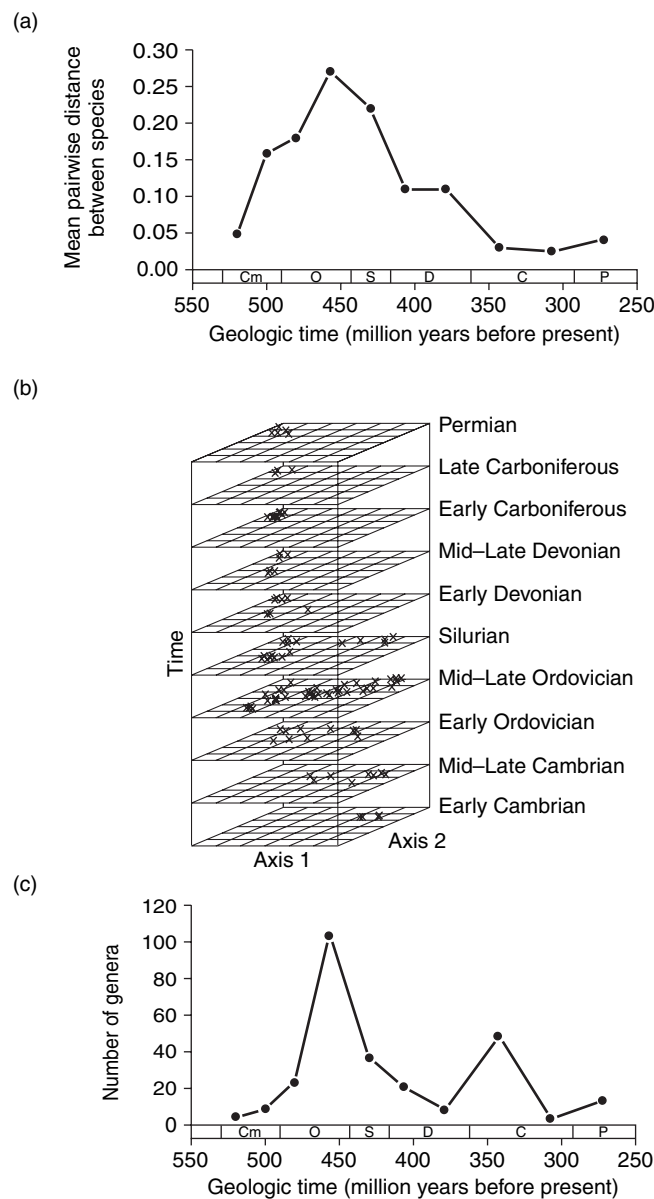


FIGURE 8.35 Disparity and richness in blastozoan echinoderms. (a) Disparity, measured as the average squared distance between species. (b) Scatterplots of species through time, showing a wide spread of points at times of high disparity. (c) Richness, measured as the number of genera. Note that disparity and richness do not change in the same way over time. (Data from Foote, 1992)

these distances increase through the Cambrian and Ordovician and then decline. Yet another way to display the data is as a series of scatterplots of the species, sorted by time interval (Figure 8.35b). Here each scatterplot represents synthetic variables similar to principal components. As suggested by Figure 8.35a, the dispersion of points increased through the Cambrian and Ordovician, declined through the Silurian and Devonian, and was largely stable through the Carboniferous and Permian.

The idealized models in Figure 8.34 suggest that it is helpful to interpret the evolution of disparity in relation to taxonomic richness. For comparison with blastozoan disparity, Figure 8.35c depicts the number of blastozoan genera. Evidently, disparity increased much more rapidly than richness during the Cambrian and Early Ordovician. In light of the model in Figure 8.34a, this suggests that morphological transitions were larger early in the history of blastozoans—which is exactly what was found by measuring transitions directly on the cladogram (Figure 8.33). Thus, the indirect and direct approaches largely agree in this example.

Morphological Selectivity in Extinction The richness and disparity histories of blastozoans show a curious feature. There was a pronounced drop in richness from the Ordovician into the Silurian, yet disparity barely changed at this time. We can make some sense of this discordance with additional idealized models (Figure 8.36). During a decline in richness, if lineages are lost at random with respect to morphology, then the observed range of form, which is correlated with the number of species sampled, will decrease (Figure 8.36a). However, the branches of the tree will be thinned out rather than pruned back, and the average distance among them will largely be maintained. As a result, disparity, measured as variance, will not drop as severely as richness. If, on the other hand, extinction selectively removes certain main branches of the evolutionary tree, as in Figure 8.36b, then disparity may drop along with richness.

Returning to the blastozoan data of Figure 8.35 with these models in mind, the transition from the Ordovician to the Silurian suggests a loss of lineages that is largely nonselective. From the Silurian to the Devonian, on the other hand, the drop in richness is accompanied by a large decline in disparity, suggesting that certain branches of the evolutionary tree are selectively removed. In fact, by the Carboniferous, all classes of blastozoans except the blastoids had become extinct. Thus, disparity is lower in the Carboniferous than in the Devonian, even

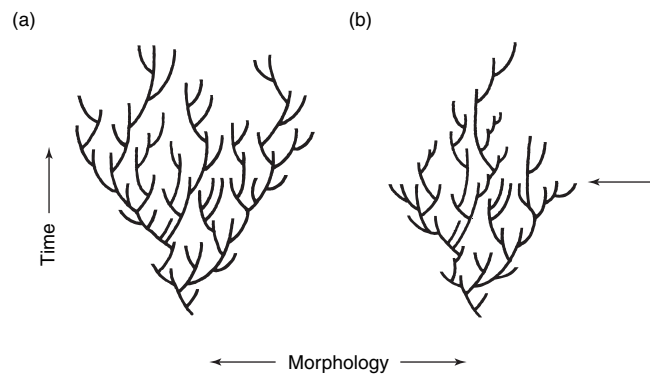


FIGURE 8.36 Models of richness and disparity during a decline in richness, which begins at the point in time marked by the arrow. (a) Lineages are lost at random with respect to morphology. As a result, disparity is largely maintained. (b) Morphologically extreme lineages are lost preferentially. As a result, disparity and richness drop together. (From Foote, 1993)

though there was in fact a major increase in genus richness in the Carboniferous (Figure 8.35c).

Therefore, whether or not disparity and richness decline together provides an indirect test for morphological selectivity in extinction. It is important to bear in mind that selectivity depends to some extent on the scale of analysis. In saying that extinction from the Ordovician to the Silurian appears to be nonselective, we do not mean that there is no good reason, related to particular details of their form, why some species survived and others did not. We mean instead that there is not a simple, overarching relationship between survival and form, such that one could have predicted the survivors based on where they lie in a scatterplot like Figure 8.35b.

8.11 CONCLUDING REMARKS

It should be evident from the topics covered in this chapter that the paleontological study of global biodiversity is still in its formative stages, even though it has been a focal point of extensive paleontological research for more than a quarter century. To be sure, several topics that we considered in this chapter, such as the causes of global taxonomic transitions and mass extinctions, remain controversial. At the same time, perhaps more than any other themes in paleontology, these issues have captured the interests and imaginations of a wide array of geoscientists, biologists, and even astronomers.

In this context, one of the more promising developments in the past few years has been the growth in cross-disciplinary collaborations among researchers interested in understanding the causes of biological transitions throughout earth history. Databases such as NMITA and the PBDB are outgrowths of this interest, as paleontologists have come to recognize the importance of understanding how local and regional diversity trends combine to produce the patterns observed at the global level. Beyond the assessment of diversity as an end in itself, however, highly resolved regional and taxonomic data can be coupled with information on morphology, lithology, and geochemistry to develop a more intricate picture of the relationship between biological and physical transitions throughout earth history. Clearly, this is one of the major growth areas in paleontology, several examples of which are highlighted in Chapters 9 and 10.

SUPPLEMENTARY READING

- Foote, M. (1997) The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28**:129–152. [A review of research on morphological diversity, emphasizing paleontological examples.]
- Hallam, A., and Wignall, P. B. (1997) *Mass Extinctions and Their Aftermath*. Oxford, U.K., Oxford University Press, 320 pp. [Chapter summarizing each of the major mass extinctions in the history of life.]

- Jablonski, D., Erwin, D. H., and Lipps, J. H. (eds.) (1996) *Evolutionary Paleobiology*. Chicago, University of Chicago Press, 484 pp. [A collection of papers emphasizing broad approaches to the study of macroevolutionary patterns.]
- Rosenzweig, M. L. (1995) *Species Diversity in Space and Time*. Cambridge, U.K., Cambridge University Press, 436 pp. [An overview of large-scale patterns of species

- diversity and the factors that govern it, with an emphasis on the present day.]
- Ryder, G., Fastovsky, D., and Gartner, S. (eds.) (1996) *The Cretaceous–Tertiary Event and Other Catastrophes in Earth History*. *Geological Society of America Special Paper 307*, 569 pp. [A comprehensive collection of papers on mass extinction; a successor to Silver & Schulz, 1982.]
- Silver, L. T., and Schulz, P. H. (eds.) (1982) *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*. *Geological Society of America Special Paper 190*, 528 pp. [A collection of papers focused on early research spurred on by the Alvarez et al. impact scenario for the K/T extinction.]
- Valentine, J. W. (ed.) (1985) *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton, N.J., Princeton University Press, 441 pp. [A collection of papers that consider a variety of features of Phanerozoic diversification in marine and terrestrial settings.]
- Wills, M. A. (2004) Morphological disparity—A primer. In J. M. Adrain, G. D. Edgecombe, and B. S. Lieberman (eds.), *Fossils, Phylogeny and Form: An Analytical Approach*. New York, Kluwer Academic/Plenum Publishers, pp. 55–144. [A detailed overview of methods and applications of disparity analysis.]