

Chapter 9

PALEOECOLOGY AND PALEOBIOGEOGRAPHY

Ecology is the study of interrelationships between extant organisms and the environments in which they live, so it follows that **paleoecology** is the study of the interrelationships between ancient organisms and the paleoenvironments in which they lived. Despite this distinction between the present-day and the geological past, it should be understood that ecological patterns are the consequences not only of present-day agents, but also of evolutionary processes that unfolded over millions of years. In this respect, paleontologists now recognize that the investigation of evolutionary transitions (or, in some cases, stability) through protracted intervals of geologic time, when melded with ecological perspectives, provides a dimension not available to ecologists working in the present day. The investigation of these long-term patterns and processes falls in the realm of **evolutionary paleoecology**.

On a parallel front, new analytical techniques, such as the geochemical assessment of skeletal compositions, have significantly improved the precision of paleoenvironmental and paleoclimatological reconstruction based on fossil material. These techniques have also enabled researchers to evaluate changes in ambient conditions at high resolution through extended intervals of geologic time. Thus, from a practical standpoint, paleoecology is now yielding data of importance to investigations that span a wide range of the geosciences.

In this chapter, we focus on several aspects of the ever-changing subdiscipline of paleoecology, emphasizing (1) the growing importance of the geologic time dimension to evolutionary paleoecology, and (2) new approaches to paleoenvironmental and paleoclimatological

reconstruction. Before doing so, however, it is important to review basic operational considerations and principles related to the development of **community paleoecology**, which was a significant, earlier focus of paleoecological research. The infusion of the community concept into paleoecology provided scientific and methodological foundations on which the development of evolutionary paleoecology was strongly dependent.

Paleobiogeography, the study of the ancient geographic distribution of life, also focuses on the spatial dimension. While paleontologists recognize fundamental differences between the environmental dimension that paleoecology highlights and geographic space, which is the focus of paleobiogeography, these differences are not always perfectly obvious. We will conclude this chapter by considering the relationship between environmental and geographic distributions and by discussing the role of paleobiogeography in assessing biotic distributions at regional and global scales.

9.1 THE NATURE OF PALEOECOLOGICAL DATA

In Chapter 1, we discussed general principles of sampling the fossil record, including the need to assess whether differences in the quality or volumes of fossiliferous samples affect our ability to detect meaningful biological differences among them. Because many paleoecological analyses involve direct comparisons of the biotic compositions of a set of samples, paleontologists often seek to standardize the method of data collection

used for any given study, to ensure that differences in sampling protocol are not, in themselves, responsible for measurable variations in sample composition. Given that the nature of preservation and accessibility of fossil material are highly variable throughout the fossil record, the methods used to extract, identify, and count fossils may differ appreciably from study to study.

The choice of sampling method is sometimes dictated by the nature of preservation, such as when a researcher encounters fossils in crystalline limestones or sandstones that are so hard that a jackhammer or dynamite blast is required to remove them (not that this necessarily stops an ambitious paleontologist!), or when fossils are located on public lands where removal of any material is illegal. These circumstances might call for an *in situ* census of fossil material. Moreover, even in cases where it is feasible to remove fossils, *in situ* methods may still be desirable when it is believed that the spatial arrangement of fossils at the outcrop reflects a true biological distribution rather than post-mortem transport (Figure 9.1a). Finally, when strata are not exposed at outcrops, samples may be obtained from a core collected during drilling

(Figure 9.1b). This has proven particularly useful for sampling the strata preserved beneath oceans and lakes.

In cases where samples are removed for fossil identification and counting, it is common practice to remove approximately the same volume of material for each sample—referred to as a **bulk sample**—to lessen the likelihood that differences among samples in the abundances of fossil elements are direct consequences of volumetric differences in the amount of sampled material. Another way to standardize the sizes of collections when working with fossils that are plentiful is to count the *same number* of individuals in each sample.

Although an *in situ* census is most easily conducted on a bedding plane (Figure 9.1a), a census can also be carried out on the lateral face of a stratum in wall-like exposures when bedding planes are not available. In the former case, a rectangular or square template, also known as a **quadrat**, can be placed directly on the bedding plane, and the individual fossils contained inside the template are identified and counted. If there is reason to believe that the spatial arrangement of fossils within the quadrat preserves a biologically meaningful pattern, a

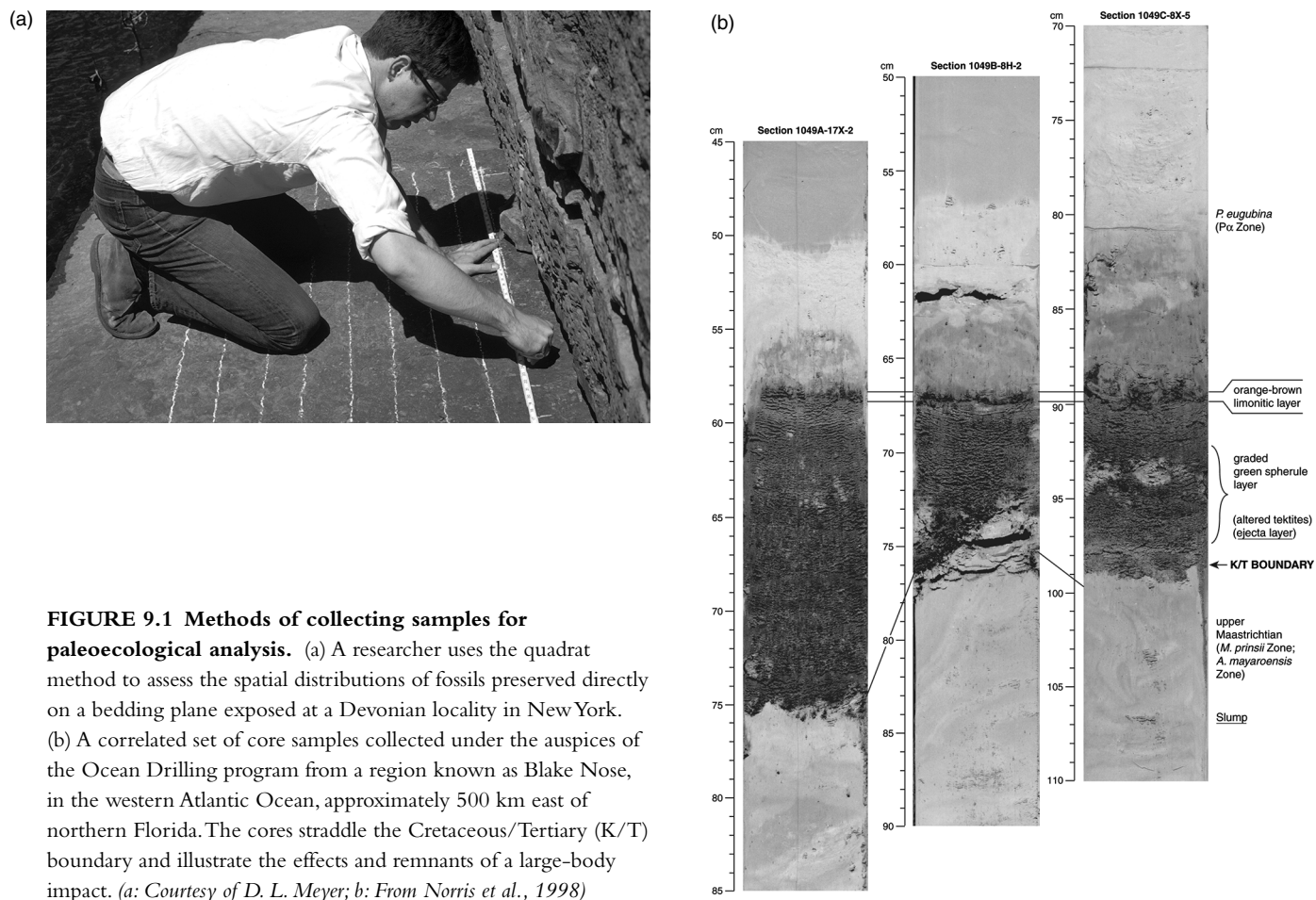


FIGURE 9.1 Methods of collecting samples for paleoecological analysis. (a) A researcher uses the quadrat method to assess the spatial distributions of fossils preserved directly on a bedding plane exposed at a Devonian locality in New York. (b) A correlated set of core samples collected under the auspices of the Ocean Drilling program from a region known as Blake Nose, in the western Atlantic Ocean, approximately 500 km east of northern Florida. The cores straddle the Cretaceous/Tertiary (K/T) boundary and illustrate the effects and remnants of a large-body impact. (a: Courtesy of D. L. Meyer; b: From Norris et al., 1998)

researcher might also develop a map of all the fossils contained in the quadrat.

An alternative to a quadrat, which can be used on a bedding plane or when conducting a census on the lateral face of a stratum, is a stretched line, also known as a **transect**. The abundances of taxa along the transect can be assessed by either counting up the number of individuals that the transect passes over or by direct measurement of the lengths of the transect covering each specimen. The latter approach yields estimates of how much of the tran-

sect is covered by each fossil taxon. It is particularly appropriate when working with clonal organisms such as corals, where the delineation and counting of “individuals” becomes problematic, so estimates of areal or volumetric coverage may instead be more appropriate.

Often paleontologists must also determine how many individuals in a sample contain disarticulated skeletal pieces—such as shell fragments, bones, or leaves—that may be derived from the *same* individual. Methods for making these determinations are considered in Box 9.1.

Box 9.1

DETERMINING THE NUMBER OF INDIVIDUALS IN A SAMPLE OF FRAGMENTED OR CLONAL SKELETAL ELEMENTS

When working with a sample that contains disarticulated skeletons, it is useful to consider whether there is reason to believe that multiple elements were derived from the same individual, and then to reduce the estimated abundances of these individuals accordingly to the minimum number of individuals that could have produced the elements in question. For example, when considering the preserved valves of bivalve molluscs, it is appropriate to determine the number of left and right valves present for a particular species. It can then be assumed, *at a minimum*, that the number of biological individuals of the species in the sample is equal to whichever of the abundances of the two valves is *greater*.

However, some researchers have viewed this kind of minimum approximation as too conservative, and instead advocate the opposite approach by assuming that every identifiable skeletal element is derived from a different individual. The number of individuals of a given taxon, then, is equal to the total number of identifiable elements of that taxon present in the sample. In our bivalve example, the number of individuals—a *maximum* estimate, really—would therefore be the number of left valves *plus* the number of right valves. While this would obviously be an inappropriate approximation in some cases—such as when the left and right valves of a bivalve are found as articulated pairs or when the bones that obviously comprise a single dinosaur skeleton are found adjacent to one another—there are many instances when the use of this approximation may actually be quite reasonable.

In fact, it has been shown statistically that, in cases where the elements that make up the skeleton of a taxon do not remain articulated to one another, there is a good possibility that all or most of the elements in a confined sample are derived from different individuals. While this may seem surprising, it is actually intuitive if one considers, for example, that the bivalve elements present in a typical bulk sample would likely have been derived from a living assemblage that covered a far larger volume of the sea floor. Given the taphonomic processes that we discussed in Chapter 1, once the two valves of a bivalve become disarticulated, it is highly *unlikely* that they will remain in close enough proximity to become part of the same two- or three-liter bulk sample, even if there has not been a significant amount of post-mortem transport.

When working with clonal organisms or highly disarticulated nonclonal organisms in a bulk sample composed of lithified material, an alternative to approximating the number of individuals is to estimate each taxon’s areal or volumetric coverage, through a technique known as **point counting**. One way to conduct a point count is to draw a rectangular or square Cartesian grid with a fixed number of points directly on a transparent sheet that can be overlain directly on the surface of the bulk sample. The number of grid points that overlie each fossil element can then be counted, providing estimates of the relative densities of the taxa that occur beneath at least one grid point. Because the same grid can be used for all samples in a given investigation, point counting can help standardize the collection of information from one sample to the next.

Our discussion of paleoecological data has focused on field-based assessments of the occurrences and abundances of taxa, which remain at the heart of many paleoecological studies. As we have already noted, however paleoecology in recent years has grown to include investigations that require other kinds of data and analyses, such as determination of the geochemical compositions of skeletal elements and the interpretation of the life habits and food preferences of fossil taxa that are encountered in a sample. We consider these additional sources of data later in the chapter.

9.2 COMMUNITIES

The development of paleoecology as a biologically based subdiscipline was dependent on the earlier research of biologists, working in isolation from paleontology. Thus, it is important to consider the scientific themes that emanated from this work and their eventual impact on paleontology.

While many researchers preceding him had been interested in the ways that environmental attributes affect the distributions of living organisms, the Danish biologist C. G. J. Petersen was among those who first applied the concept of a **community** to marine settings. Petersen's views emanated from his empirical observations and data collected while working on marine bottom faunas in Scandinavian waters, where he established a systematic program of faunal sampling and measurement of physical attributes of the sea floor along transects extending from the shoreline into waters several hundreds of meters deep. Petersen used bulk samples collected from the sea floor with a mechanical device dropped from a ship. His biological data consisted of lists of species identified from each sample, with abundances reported as both the number of individuals and the collective weight of these individuals.

Petersen recognized that, within his study area, species did not occur randomly in all possible combinations with one another. Rather, he observed that they could be found in a finite number of recurring assemblages and that similar sequences of such assemblages could be recognized from onshore to offshore in transects established at several locations (Figure 9.2). Based on his observations, Petersen viewed a community as a regularly recurring combination of numerically common species. He delineated communities in his study area based mainly on the species that were characteristic of a particular

suite of samples. In this regard, Petersen distinguished between *abundant* species, which were truly characteristic of an assemblage, and *attendant* species, which were also abundant but too widespread in their distributions to be diagnostic of a particular community.

In Petersen's view, the chief factor governing the distributions of bottom communities along depth gradients was not depth itself, but rather temperature changes associated with the transition to deep water. Petersen argued that this explained why the depth limitations of certain communities varied from transect to transect: At similar depths along different transects, water temperatures were not the same. He noted that other physical factors were also likely to be important in governing the distributions of species in his study area, and he acknowledged a possible role for biological interactions as well. Clearly, however, Petersen favored physical factors over biological interactions as explanations for the community patterns he delineated.

Although Petersen may have viewed the recognition of communities as straightforward from an operational standpoint, it is clear that among many of his contemporaries, the characterization of communities was controversial—and remains so even today. In particular, biologists have long debated whether the web of interactions that link species together (e.g., Figure 9.3) cause a community to function in some ways as a cohesive unit. Two end-member views, based on the study of terrestrial plants, illustrate the debate.

One was the **individualistic concept** championed by H. A. Gleason (e.g., 1926), who argued that plant species distributions were governed by two primary agents: (1) the migration of seeds and other propagules; and (2) local environmental conditions. Gleason noted that both factors were subject to substantial fluctuation and suggested, therefore, that chance plays a significant role in the assembly of associations (communities). To Gleason, it came as no surprise that species compositions in any two locations are unlikely to be the same, even in cases when the species in question might be considered representative of the same association, because no two locations are identical physically. Gleason downplayed the role of biotic interactions in effecting the distributions of species, and he questioned the proliferation of community classification schemes that, in his view, tended to mask differences among assemblages from place to place.

A decidedly different view was espoused by F. E. Clements (e.g., 1916), who wrote on the subject of **succession**, a general term for changes through time in the

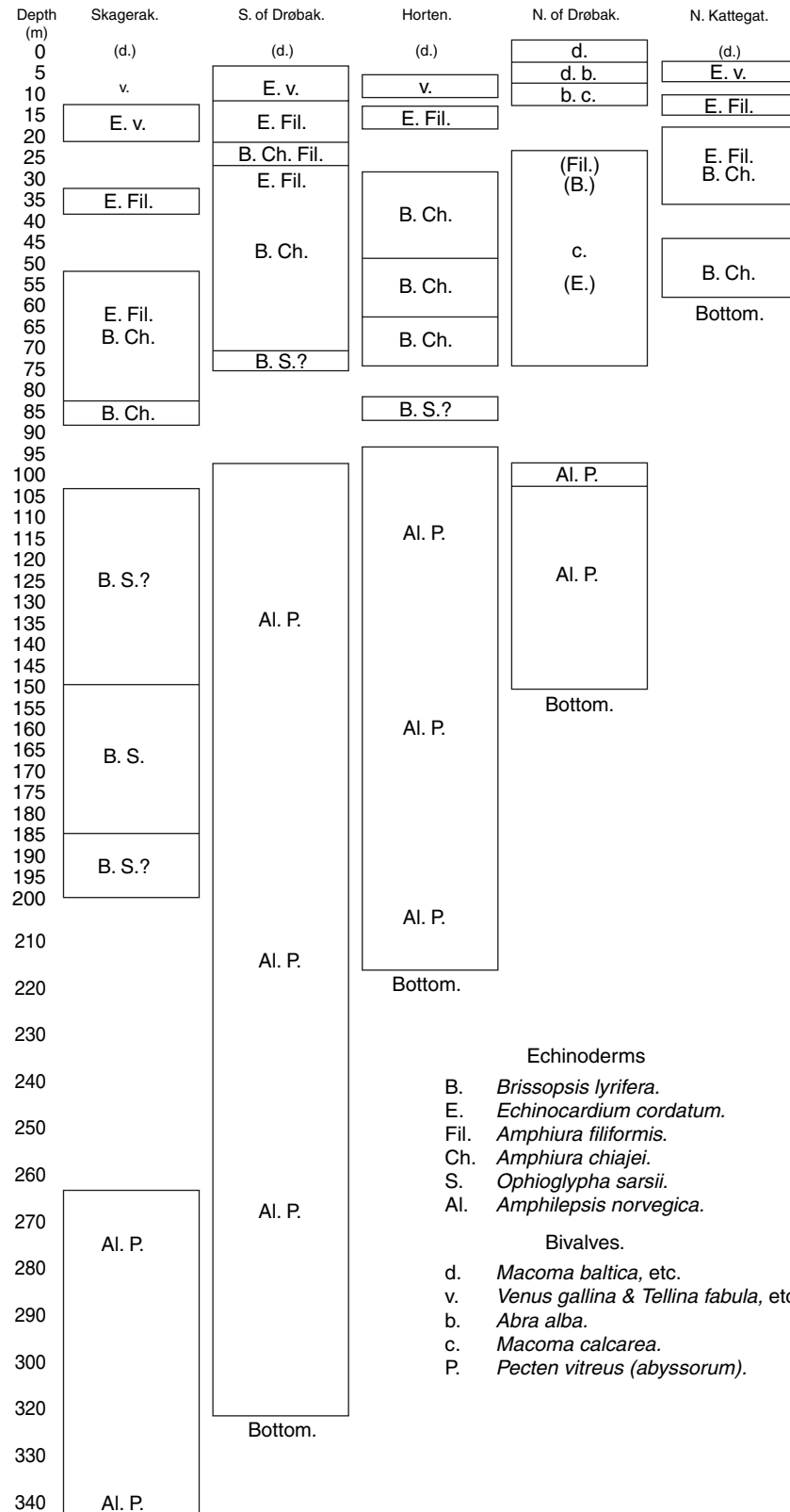


FIGURE 9.2 Distributions of marine communities along five underwater transects located in waters off the coast of Scandinavia. Communities are named for dominant bivalve and echinoderm species; a key to abbreviations is provided in the lower right-hand corner. Note that several of the transects exhibit similar, but not identical, patterns. (From Petersen, 1915)

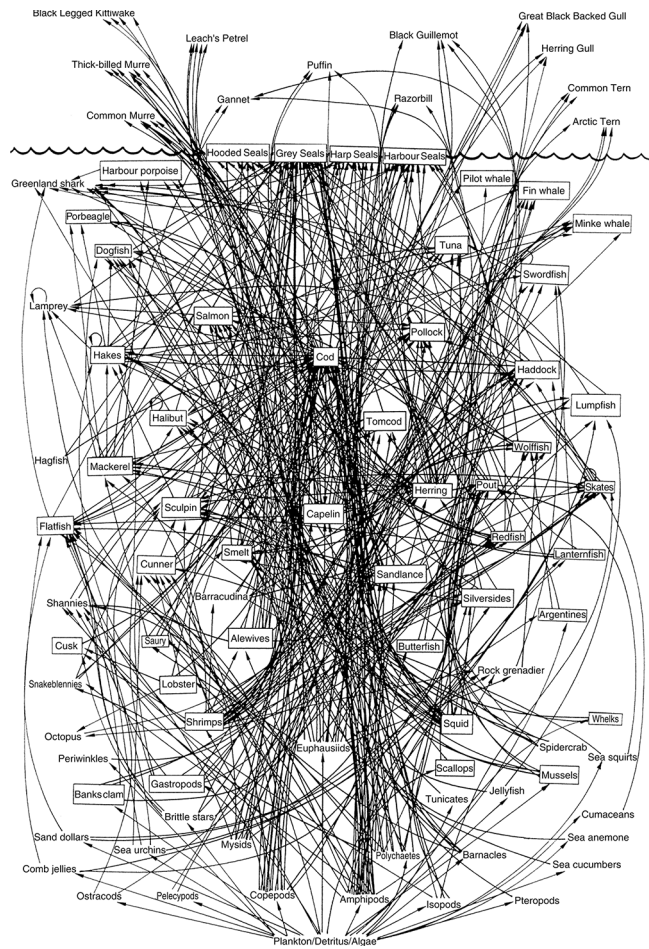


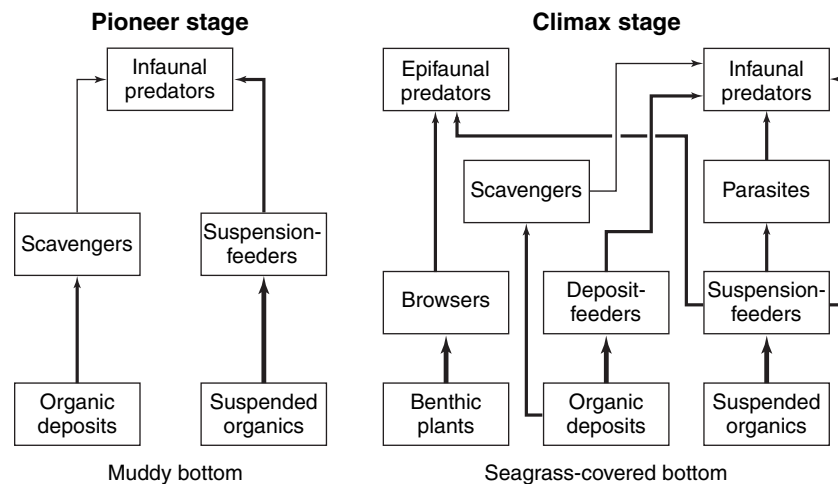
FIGURE 9.3 An example of a food web, for the northwest Atlantic Ocean, illustrating the complex set of pathways that link species to one another. Here and in Figure 9.4, arrows link food sources with the organisms that consume them, with the arrow pointed in the direction of the consumer. (From the International Marine Mammal Association, www.imma.org/codvideo/foodwebpic.html)

biological compositions of successive communities occupying a particular place. To some extent, the roster of species present at any given stage in a succession is thought to be a consequence of environmental changes caused by the organisms comprising earlier stages in the succession (Figure 9.4). However, the initiation of the first stage of a succession may depend either on physical events that remove much of the living biota from an area, such as a fire or hurricane, or on the geological development of new areas for colonization, such as a newly emergent oceanic island.

Clements viewed the final stage of a succession as the adult stage in the development of a kind of superorganism, which he termed a **seres**. Clements therefore considered a seres to be an entity that exhibits an ontogeny consisting of several highly predictable steps, following the physical emptying of a space and the initiation of recolonization of that space. Biotic interactions among individuals were seen by Clements as playing significant roles in this ontogeny, and he even suggested that different seres following similar developmental courses are bound together by something akin to phylogenetic relationships.

Against this backdrop, plant ecologists have gathered copious data on the spatial distributions of species in order to test different viewpoints on the intimacy of relationships between species within communities. Figure 9.5 illustrates the ways in which species distributions can speak to this issue. The abundance (“importance”) distributions of several hypothetical species are graphed along a hypothetical **environmental gradient**—a

FIGURE 9.4 Two stages in a succession recognized among ancient communities preserved in the Middle Miocene of Poland. It is thought that a sea floor covered initially by mud (pioneer stage) became colonized by seagrass (climax state). With this colonization came an increase in faunal diversity, in the complexity of the food web, and in the diversity energy pathways. (Based on Hoffman 1977, 1979)



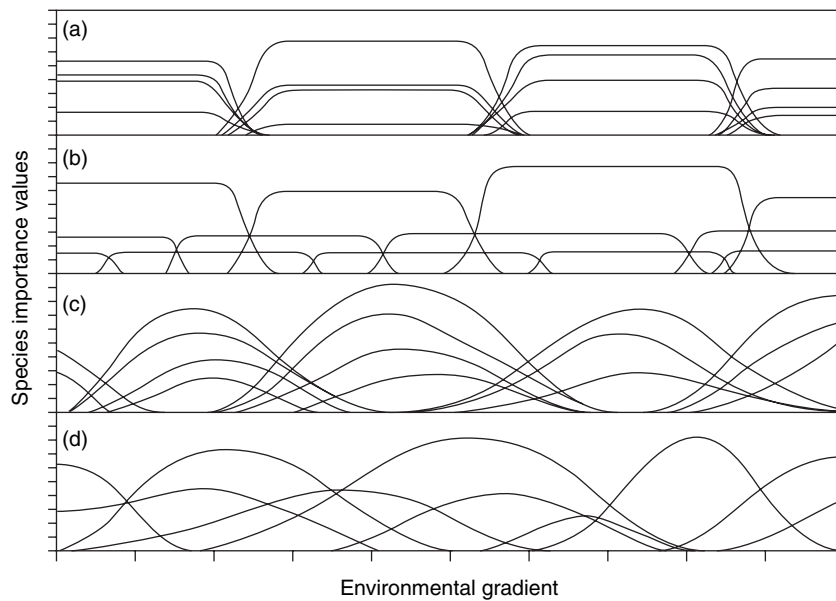


FIGURE 9.5 Schematic depictions of species abundance distributions along a hypothetical environmental gradient.

Models range from a scenario in which the distributions of species were highly dependent on one another (top) to one in which they were independent of one another (bottom). See text for descriptions of parts (a) through (d). (From Whittaker, 1975)

transect along which environmental transitions are gradual and continuous rather than abrupt. In Figure 9.5a, despite the gradual environmental transitions, there is distinct zonation of species along the gradient, with well-defined, sharply bounded communities of species that develop close associations with one another, as evidenced by their parallel abundance patterns. Boundaries between communities are sharpened by **competitive exclusion**, which relates to the hypothesized tendency of closely related, potentially interactive species to avoid competing with one another for resources by cordoning off from one another different portions of ecological space.

In Figure 9.5b, competitive exclusion causes the distributions of individual species to be sharply bounded, but there is no tight linkage of individual species within communities. In Figure 9.5c, there is little competitive exclusion among species, so their abundance distributions are not sharply bounded, and abundances fall gradually away from presumed zeniths somewhere along the transect, where environmental conditions are most ideal for the species to thrive. However, biotic interactions do produce parallel abundance relationships among some species. Finally, in Figure 9.5d, biotic interactions do not govern the development of parallel relationships of species distributions to one another, nor do they serve to sharpen boundaries between species through competitive exclusion.

Thus, the four panels in Figure 9.5 illustrate a spectrum of possible scenarios, ranging from a system governed strongly by biotic interactions [part (a), a “Clementsian”

perspective] to one in which species respond individually to physical attributes of the gradient [part (d), a “Gleasonian” perspective]. Empirical data from plant communities appear to suggest that Figure 9.5d is by far the most common of the four scenarios observed in nature (Figure 9.6). Based on these observations, the biologist R. H. Whittaker (1975) concluded:

It is useful to recognize life-zones. . . . But the zones are continuous with one another. . . . The zones are kinds of communities [that humans] recognize . . . , mainly by their dominant plants, within the continuous change of plant populations and communities along the elevation gradient. The zones can be compared to the colors [humans] recognize . . . , and accept . . . as useful concepts, within the spectrum of wavelengths of light which are known to be continuous. [pp. 116–117]

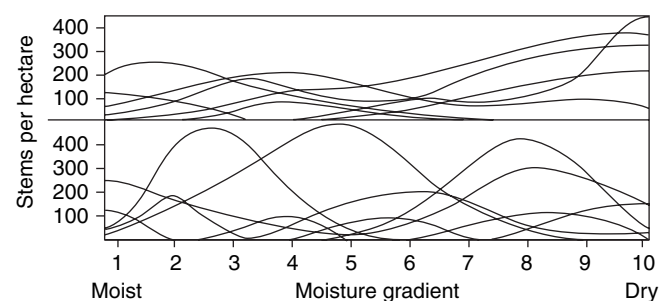


FIGURE 9.6 Real distributions of plant species abundances along two moisture gradients in Oregon (top) and Arizona (bottom). These patterns appear to mimic closely the hypothetical scenario illustrated in Figure 9.5d. (From Whittaker, 1975)

The metaphor of a continuous color spectrum does not apply in all instances, but it can be said with some confidence that there is little evidence in the present day for the kinds of biotic units implied by Figure 9.5a.

9.3 PALEOCOMMUNITIES

Distributions of Fossil Taxa within and among Paleocommunities

As we have already suggested, the central prerequisite for most paleoecological investigations is identification and quantification of the organisms present at particular places in space and time. For this reason, paleontologists have long been interested in knowing whether it is possible to meaningfully recognize ancient communities in the fossil record. Of course, in most cases, direct information about the soft-bodied taxa present in an ancient community will not be available, thereby precluding an understanding of the entire roster of taxa present in most preserved paleoenvironments. Nevertheless, even when

limited to studying the skeletonized portion of the biota, paleontologists have discovered that it is possible—and worthwhile—to identify and characterize the taxa that lived in ancient environments. And while we might not be able to determine definitively the soft-bodied taxa present in a paleocommunity, we can often infer the broad presence of certain groups that are not preserved, such as phytoplankton in marine paleocommunities throughout the Phanerozoic.

During the 1960s, Alfred Ziegler sought to recognize paleocommunities preserved in Silurian strata of Wales and elsewhere. He began by distinguishing five brachiopod-rich paleocommunities in the Welsh borderland that were arrayed from nearshore to deep water (Table 9.1; Figure 9.7), for which he recognized *characteristic* (i.e., abundant) and *associated* (i.e., usually present but less abundant) species. The similarity to the approach advocated earlier by Petersen in the study of present-day organisms is unmistakable. In fact, Ziegler noted that “it is clear that the animal community technique of the ecologists is applicable to fossil assemblages” (p. 272).

TABLE 9.1
Lists of the Principal Taxa Contained within Each of Five
Communities Recognized in Silurian Strata of the Welsh Borderland

Community Name	Characteristic Species	Associated Species
<i>Lingula</i>	<i>Lingula pseudoparallela</i> “ <i>Camarotoechia</i> ” <i>decemplicata</i> “ <i>Nucula</i> ” <i>eastnori</i>	“ <i>Hormotoma</i> ” sp. “ <i>Pterinia</i> ” sp. <i>Cornulites</i> sp.
<i>Eocoelia</i>	<i>Eocoelia</i> spp. “ <i>Leptostrophia</i> ” <i>compressa</i> <i>Dalmanites weaveri</i>	<i>Howellella crispa</i> <i>Salopina</i> sp. “ <i>Pterinia</i> ” sp.
<i>Pentamerus</i>	<i>Pentamerus</i> spp. <i>Atrypa reticularis</i> <i>Dalejina</i> sp.	<i>Eocoelia</i> spp. <i>Howellella crispa</i>
<i>Stricklandia</i>	<i>Stricklandia</i> spp. <i>Eospirifer radiatus</i> <i>Atrypa reticularis</i>	<i>Resserella</i> sp.
<i>Clorinda</i>	<i>Clorinda</i> spp. <i>Diocoelosia biloba</i> <i>Cyrtia exporrecta</i> <i>Skenidioides lewisi</i>	<i>Plectodonta millinensis</i> <i>Coolinia applanata</i> <i>Plectatrypa marginalis</i>

SOURCE: Ziegler (1965), Adapted from Table 1

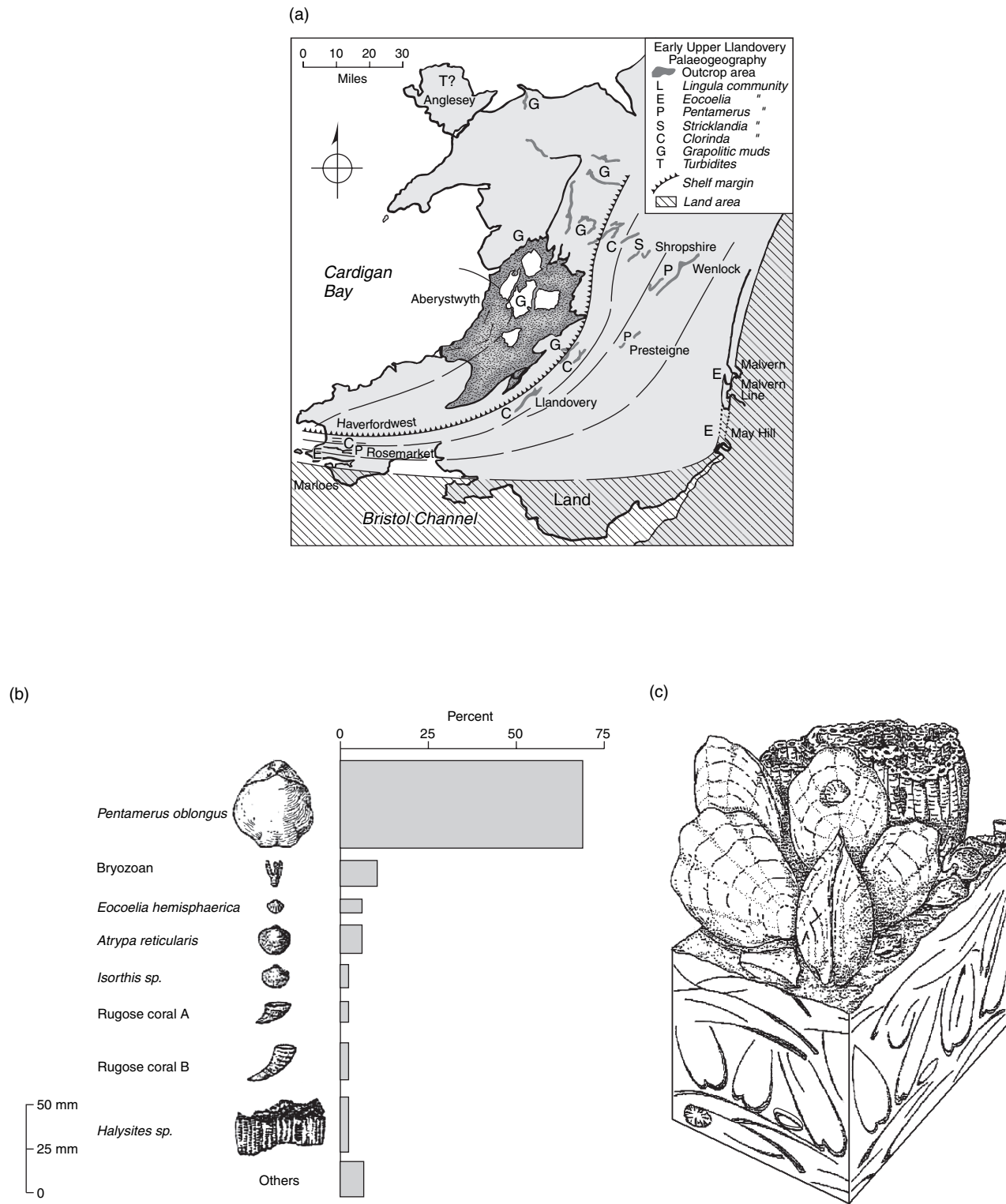


FIGURE 9.7 Ziegler's delineation of Silurian communities, in the Welsh borderland and elsewhere.

(a) A paleogeographic map depicting the communities from the shoreline (lower right) into deep water (middle).

(b) A bar graph illustrating the relative abundances of major taxa in a fossil assemblage that preserves the *Pentamerus*

community, at a locality in Wales. (c) A sketch of the *Pentamerus* community, based on data from assemblages

preserved in North American strata. (a: From Ziegler, 1965; b, c: From Ziegler et al., 1968)

Ziegler followed this by demonstrating that suites of paleocommunities that were rather similar to those documented in Wales could be recognized in Scandinavia and North America. This provided further credence to the view not only that paleocommunities could be recognized dependably, but also that they were coherent, repeatable units of organization.

Paleontologists now routinely analyze quantitatively the spatial distributions of ancient organisms within and among paleocommunities. As a result, they have observed patterns in the fossil record that conform closely to those recognized along present-day environmental gradients. In Chapter 6, we described the application of multivariate techniques to paleoecological

Box 9.2

GRADIENT ANALYSIS IN THE FOSSIL RECORD

Figure 9.8 highlights the diagnosis of biological gradients in the fossil record and an illustration of the sometimes subtle effects that the choice of numerical techniques can have on our perception of the distributional patterns exhibited by taxa. In Figure 9.8a, cluster analysis (see Box 3.2) is applied to paleoecological data collected through bulk sampling of a stratigraphic interval of the Ordovician Martinsburg Formation at a locality in southwestern Virginia. Cluster analysis has been used widely in paleoecology for assessing variations among samples in their biological compositions (a so-called Q-mode analysis), as well as variations among taxa in their occurrences within samples (an R-mode analysis).

Computationally, the set of methodological steps is very similar to that applied to morphological data in the *Stegoceras* example presented in Chapter 3, except that in this case, the starting point is a set of samples, each containing taxa for which abundances were reported, rather than a set of specimens for which measurements of multiple morphological features are reported (see Box 3.2). The main output of cluster analysis is a dendrogram, a kind of graphical tree on which samples or taxa that are in close proximity have distributions that are more similar to one another than those that are comparatively remote from one another. The two dendrograms placed at right angles to one another in Figure 9.8a illustrate the tendency for

certain clusters of taxa to recur within certain clusters of samples. In fact, as illustrated with the lettering of the sample clusters and the lines between them, it might be reasonable to view each lettered cluster as representing a separate paleocommunity, given the high level of consistency in taxonomic composition exhibited among the samples in each cluster.

However, paleontologists have come to appreciate that, because of its inherent tendency to produce discrete groupings of samples on a dendrogram, as well as the reduction of what may be complex relationships among samples down to the single dimension of a dendrogram, cluster analysis tends to mask what are actually more gradational transitions in the compositions of samples and the distributions of taxa comprising each community. This is illustrated in Figures 9.8b and 9.8c. In Figure 9.8b, the samples illustrated in the dendrogram were compared using *polar ordination* (PO), an ordination technique that is similar in intent to *detrended correspondence analysis* (DCA) (see Box 6.5).

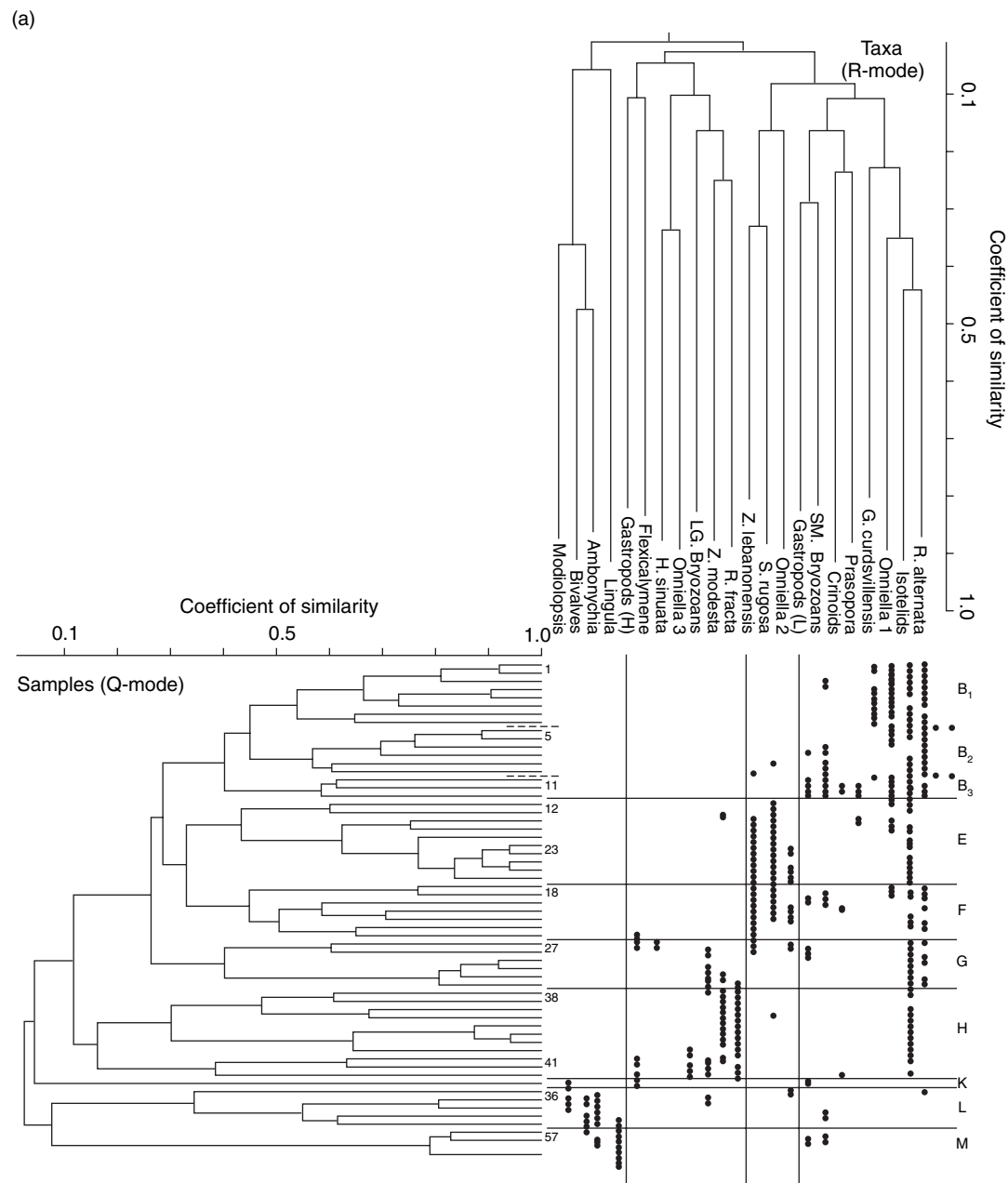
In this example, the samples are arrayed as points in a two-dimensional space, determined by simultaneous consideration of the abundances of all the taxa that are present in the samples. Like DCA, PO seeks to identify the main axes of variation among samples, based on a numerical combination of taxa rather than a single taxon. Thus, the way in which samples are

FIGURE 9.8 Gradient analysis of fossil assemblages in the Upper Ordovician Martinsburg Formation at a locality in southwestern Virginia. (a) A two-way cluster analysis, depicting the tendency of certain taxa to be present in particular clusters of samples collected at one locality. The dendrogram on the left compares samples based on their taxonomic compositions. The dendrogram at top compares taxa based on their occurrences within samples. In the middle grid, dots denote the presence of a taxon in a sample. Letters along the side denote major cluster of samples (see Figure 9.8b). (From Springer & Bambach, 1985)

data as a means of achieving high-resolution, regional correlations among localities. This approach was predicated on the recognition that boundaries between adjacent paleocommunities tend to be gradational rather than discrete, and, as we noted, the evaluation of taxonomic distributional patterns among communities is known as **gradient analysis**. A discussion of the diag-

nosis and interpretation of gradients in the fossil record is presented in Box 9.2.

While spatial variation within individual horizons (i.e., during a confined time interval) was not assessed in the study illustrated in Box 9.2, it has been assessed elsewhere. Figure 9.9 illustrates an investigation of variations in the compositions of bulk samples of fossil



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Box 9.2 (continued)

arrayed along an axis may reflect variations in the abundances of not just a single taxon, but several taxa that vary similarly in their presence and abundance among samples. Moreover, different axes may highlight different aspects of variation of the data. Although only two axes are illustrated here, it is generally possible to derive additional axes for a data set that contains a large number of samples and taxa.

We can observe in Figure 9.8b that the samples identified by cluster analysis are not arrayed as discretely as suggested by the sample dendrogram in Figure 9.8a. Furthermore, when the abundances of several

of the important taxa are graphed through the sampling interval (Figure 9.8c), a pattern is observed that is reminiscent of that depicted earlier for the spatial arrangement of plants along present-day environmental gradients (Figure 9.6). In both cases, there is broad overlap in the distributions and abundances of taxa rather than discrete boundaries. While the depiction in Figure 9.8c is stratigraphic instead of spatial, the broad distributions of these taxa suggest that this pattern would also be reflected in the spatial distributions among the communities that coexisted at any given time during the interval under investigation.

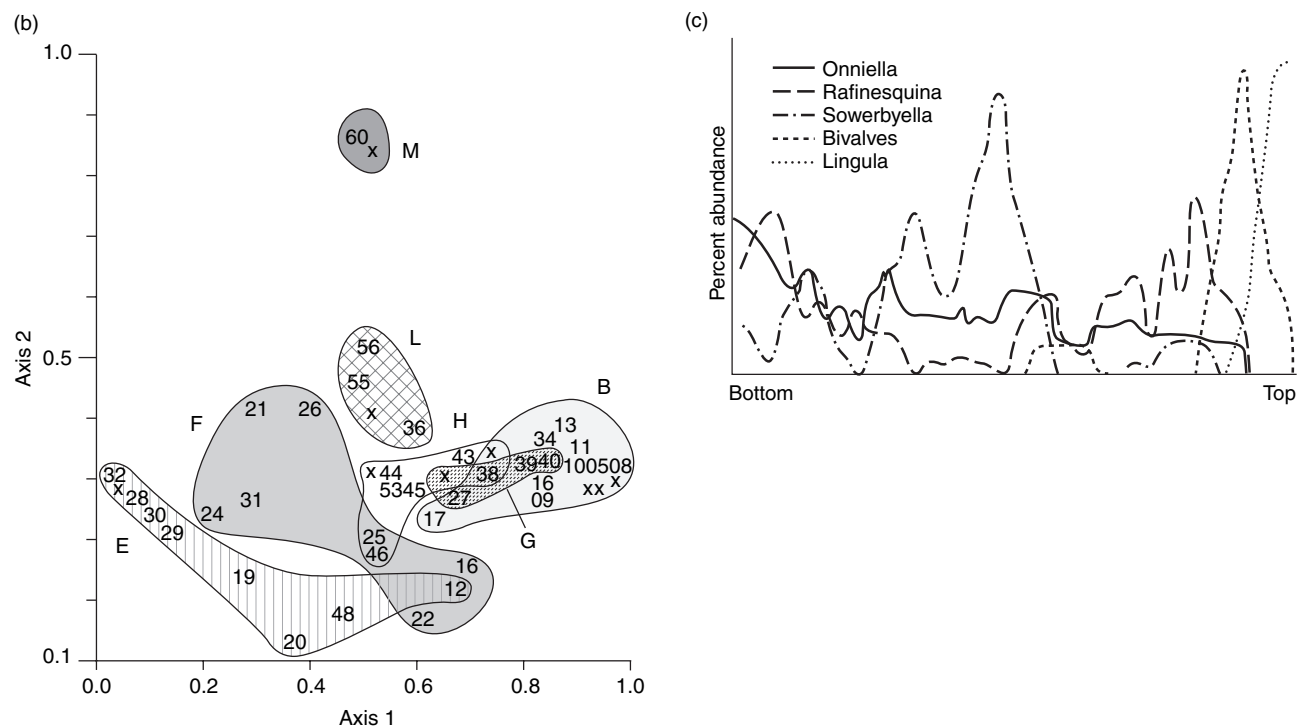


FIGURE 9.8 (cont.) (b) An ordination analysis of the same samples as in part (a). Individual samples are denoted with numbers; x's mark the overlap of two or more samples. Lettered, demarcated groups of samples correspond to the lettered clusters in Figure 9.8a. Note the broad overlap among the groups of samples depicted in the dendrogram.

(c) Stratigraphic depictions of variations in the abundances of major taxa at the locality. Note the tendencies of the five taxa to vary individually. (From Springer & Bambach, 1985)

oysters collected at several spatial scales in a single horizon of the Upper Cretaceous Navesink Formation in New Jersey. The two localities were approximately 10 km apart, and, at each locality, outcrops

were spaced several tens of meters apart. Four samples were collected from each outcrop, and adjacent samples were no more than a few meters apart (Figure 9.9a). The taxonomic data collected from each

sample indicate that the abundances of taxa contained in adjacent samples were highly variable (Table 9.2). This suggests a pattern known as **patchiness**, which appears to be a general feature of spatial distributions within communities and paleocommunities at small scales. It may reflect the interplay of multiple factors, including the tendency of some species to aggregate in clumps, coupled with chance spatial variations in local environmental factors—such as the availability of substrates suitable for the settlement of larvae, seeds, spores, or other early developmental stages of organisms.

Ecologists have become interested in understanding the nature of interactions and genetic communication among members of the same species that are semi-isolated from one another in different patches or subpopulations. They now understand that the ecological persistence of a metapopulation [SEE SECTION 3.1]—the collective set of subpopulations—and the evolutionary persistence of the species itself may be contingent on the nature and extent of genetic interaction among the subpopulations.

While paleoecologists have begun to embrace metapopulation theory, particularly as it relates to the evolutionary persistence of species, the incorporation of metapopulation dynamics into paleoecology is still in its

infancy. In part, this is because paleoecologists are still attempting to develop means of determining assuredly that the patchiness preserved in most fossil assemblages reflects actual biological patchiness in the once-living community of species rather than simply a combination of time averaging and post-mortem transport. Among marine biotas, there are indications from a few investigations that biological patchiness can persist through several generations of skeletal accumulation on a sea floor, even in the face of severe storms. But it remains to be determined whether this is a general feature of the fossil record.

Whatever its cause, the pervasiveness of patchiness points to the need to collect multiple samples at local scales because of the possibility that a single sample will provide a misleading sense of the overall biotic composition of the area. For example, of the 20 *Gryphaeostrea* individuals that were counted in the illustrated study (Table 9.2), 18 came from a single sample! Had this been the only sample collected at the locality, it would have obviously provided a misleading sense of the relative importance of *Gryphaeostrea* at the locality. That said, when the samples at each locality are averaged together to determine locality-wide abundances (Figure 9.9b), the aggregate biotic compositions of the two localities are remarkably similar despite the 10-km distance between them.

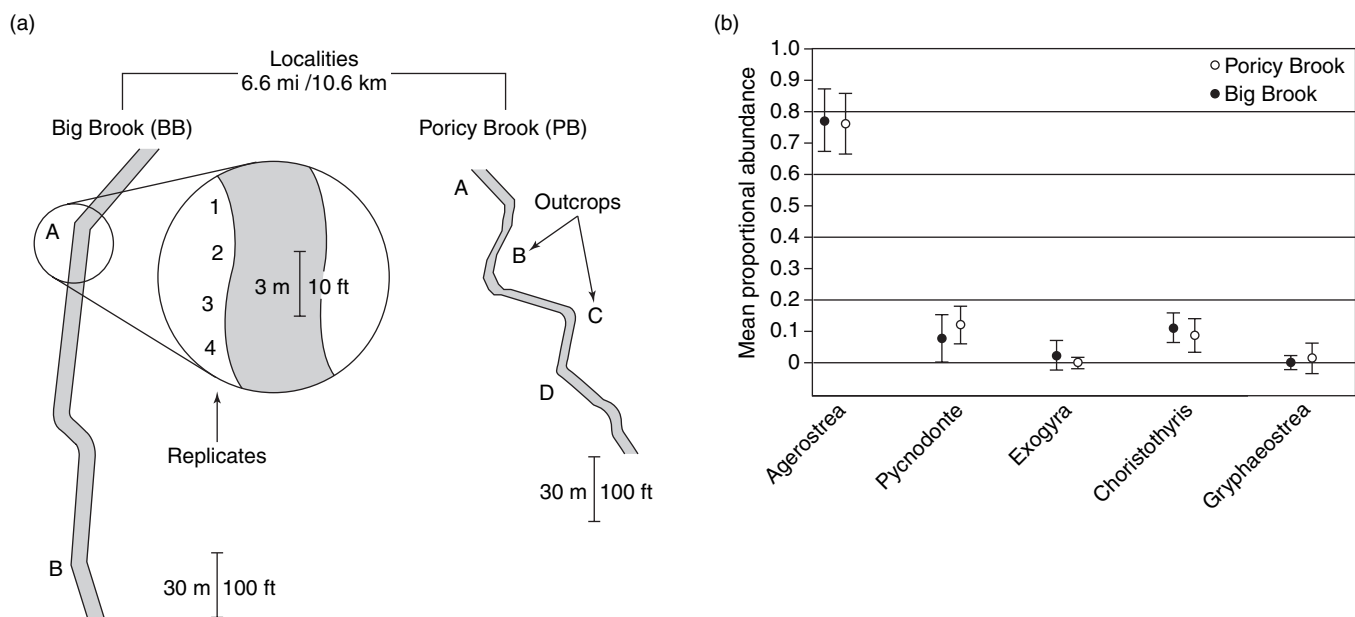


FIGURE 9.9 An assessment of variation in the faunal contents of samples collected at several different spatial scales, in Upper Cretaceous strata of New Jersey. (a) Samples were collected in replicates that were a few meters apart at outcrops spaced several tens of meters apart at two localities that were about 10 km apart. (b) Although the compositions of adjacent replicates were sometimes highly variable in composition (see Table 9.2), aggregate abundances for the two localities were comparable to one another for the five main species found in the study. (From Bennington, 2003)

TABLE 9.2
Faunal Data Matrix for a Set of Samples
Collected from Upper Cretaceous Strata in New Jersey

Sample ID	<i>Agerostrea</i>	<i>Pycnodonte</i>	<i>Exogyra</i>	<i>Choristothyris</i>	<i>Gryphaeostrea</i>	Total
BBA1	35	7	4	9	1	56
BBA2	5	6	0	1	0	12
BBA3	3	7	0	0	0	10
BBA4	27	5	5	2	0	39
BBB1	46	4	1	8	0	59
BBB2	77	3	1	6	0	87
BBB3	65	1	0	11	0	77
BBB4	75	2	0	12	0	89
PBA1	46	5	0	7	1	59
PBA2	22	13	0	0	0	35
PBA3	21	5	0	1	0	27
PBA4	59	14	0	10	0	83
PBB1	42	10	1	0	0	53
PBB2	69	10	1	11	0	91
PBB3	124	6	1	10	0	141
PBB4	25	6	1	13	0	45
PBC1	57	20	1	24	0	102
PBC2	45	6	0	9	0	60
PBC3	121	4	0	6	0	131
PBC4	106	5	0	6	0	117
PBD1	15	9	0	0	0	24
PBD2	63	6	0	0	0	69
PBD3	21	9	0	0	0	30
PBD4	22	12	0	2	18	54
Total	1191	175	16	148	20	1550

SOURCE: Bennington (2003), Table 3

NOTE: These data were used to assess the degree of compositional variability evident among samples collected at different spatial scales. Key to sample ID: Localities: BB (Big Brook), PB (Pocoy Brook); Outcrops: A, B, C, D; Replicate Samples: 1, 2, 3, 4.

Regional Stratigraphic Distributions of Fossil Taxa

The study of paleocommunities has provided a biologically based foundation for the further development of paleoecology as a subdiscipline. Methods of data collection and analysis pioneered in this research have become standard practice for paleoecologists, and their importance has become particularly

evident in the investigation of ecological dynamics associated with regional patterns of diversification and extinction.

In numerous investigations of stratigraphic transitions among regional biotas, a common theme seems to have emerged: A large percentage of the appearances and disappearances of taxa tend to be concentrated in narrow intervals that punctuate broader intervals of relatively stable composition. For example,

Carlton Brett and Gordon Baird (1995) investigated stratigraphic patterns of regional biotic change in Silurian and Devonian strata located across a large, interior portion of New York State. Brett and Baird compiled species-level faunal lists and found that biotas within several stratigraphically consecutive, region-wide intervals exhibited a high degree of compositional stability at the species level, with some 60 to 80

percent of species persisting through a typical interval (Table 9.3a).

These intervals each lasted some 3 to 7 million years and appear to have been punctuated by much shorter intervals during which there were dramatic transitions in species composition throughout the basin, with compositional turnovers on the order of 80 percent from one interval to the next (Table 9.3b). Lithological changes

TABLE 9.3
Calibration of Taxonomic Turnover Metrics for Silurian and Devonian Ecological Evolutionary (e-e) Subunits in the Appalachian Basin of New York

(a) Persistence and Extinction Values of Four Well-Characterized Faunas of the Silurian to Middle Devonian Interval

Fauna	e-e Subunit	Duration (m.y.)	Persistence (%)	Extinction (%)
Hamilton	10	5–6	80	5
Onondaga	9	6–7	78	< 10
Helderberg	6	7–8	70	< 10
Up. Clinton–Lockport	3	7–8	66	32

SOURCE: Brett & Baird (1995), Table 9.2

NOTE: The degree of persistence and extinction within four well-characterized e-e subunits. Persistence is measured as the percentage of species that range from the lowest to the highest parts of the e-e subunit. Extinction is measured as the percentage of species that disappear prior to the end of the subunit. Note that the majority of species persist through each of the subunits.

(b) Appalachian Basin Silurian and Devonian Faunas, Showing Holdover and Carryover Indices

e-e Subunit	Fauna	Age	Duration (m.y.)	Carryover	Holdover
10	Hamilton–Tully	Givetian	6–7	30/335 (9%)	32/335 (10%)
9	Onondaga	Eifelian	5	32/200 (16%)	37/200 (18%)
8	Schoharie	Emsian	5	37/125 (30%)	10/125 (8%)
7	Oriskany	Pragian	2	10/94 (11%)	25/94 (26%)
6	Helderberg	Gedinnian	6	25/130 (19%)	7/130 (5%)
5	Keyser–Bertie	Pridolian	2	7/54 (13%)	14/54 (26%)
4	Salina	Late Ludlovian	3–4	14/48 (16%)	7/48 (15%)
3	Up. Clinton–Lockport	Late Llandovery–Wenlock	7–8	7/146 (5%)	30/149 (20%)
2	Lo. Clinton	Mid-Llandovery	4	30/87 (34%)	48/87 (55%)
1	Medina	E. Llandovery	5	48/139 (34%)	?

SOURCE: Revised from Brett & Baird (1995), Table 9.5

NOTE: The degree of holdover and carryover from one e-e subunit to the next in the Appalachian Basin. Carryover is measured as the proportion of species within a subunit that carries over to the subsequent subunit. Holdover is measured as the proportion of species within a subunit that appeared in the subunit that preceded it. Note that, for the most part, these values tended not to exceed 25 percent, suggesting that there were substantial biotic transitions from one e-e subunit to the next.

associated with the turnover events suggest that the broad pattern of turnover was controlled by major, region-wide environmental transitions. The details of these transitions, including a determination of whether some or all of them are correlated with global-scale changes, are currently being investigated.

To underscore the potential significance of these intervals, Brett and Baird called them **ecological evolutionary (e-e) subunits**, a name derived from a set of broader designations known as **ecological evolutionary units** that some researchers had used previously to subdivide Phanerozoic diversity on a global scale. While there has been only limited evaluation of the morphological attributes of species within e-e subunits, it has been suggested that species morphologies remained fairly static from the bottom to the top of each e-e subunit, producing a pattern that was dubbed **coordinated stasis**—in recognition of the suggestion, if not the documentation, that biotic compositions within communities and the morphologies of constituent species remained fairly static throughout an e-e subunit.

The diagnosis of coordinated stasis is not a claim that biotic composition at any given location remained the same through the entire duration of an e-e subunit. Brett and Baird were careful to point out, for example, that several episodes of sea-level increase and decrease took place *during* the intervals represented by most e-e subunits, and that a range of paleocommunities inhabited environmental gradients that varied spatially as well as temporally. The main point, however, was that throughout a given e-e subunit interval, the compositions of biotas associated with paleocommunity gradients remained fairly stable. Therefore, when environmental conditions at a given locality reverted to an earlier state, a paleocommunity returned to the locality that was fairly indistinguishable from the earlier occurrence, provided that both occurrences were contained in the same e-e subunit.

The coordinated stasis hypothesis has been scrutinized carefully since its introduction, and several questions have arisen about the biological significance of the pattern. From a sampling standpoint, the rate of compositional change across e-e subunit boundaries may be artificially inflated because of the overprint of sequence stratigraphic architecture on the stratigraphic distributions of fossils [SEE SECTION 6.4]. It is

probable that many transitions between e-e subunits coincided with boundaries between depositional sequences, which would tend to exaggerate the number of first and last appearances associated with these boundaries. In addition, while species composition may remain fairly stable, it has been shown that the relative abundances of species sometimes shift dramatically within the confines of an e-e subunit.

Finally, the extent to which appearances and disappearances within the Appalachian Basin constitute true originations and extinctions of **endemic** (localized) species, as opposed to the regional appearances and disappearances of widespread species that persist elsewhere, remains to be determined. Needless to say, this information is crucial for understanding the evolutionary significance of coordinated stasis. However, such data are not easy to acquire because they must be underpinned by definitive species-level identification.

Paleontologists have also sought to determine whether the pattern recognized by Brett and Baird transcended brachiopod-dominated faunas of the Silurian and Devonian of New York. Results have been mixed, even when considering other Paleozoic marine settings that were dominated taxonomically by a similar suite of organisms. In many cases, a broad pattern of relative compositional stability *has* been recognized for intervals that were somewhat protracted, in comparison to bounding intervals during which changes apparently took place more rapidly. However, the actual extent of stability within e-e subunits, the durations of e-e subunits, and the taxonomic levels at which stability is exhibited have all been shown to vary widely.

Because regional patterns of biotic variation are currently being investigated for a range of settings and taxa, there is reason to expect that paleontologists might soon be in a position to determine whether particular environments, biotas, or time intervals are characterized by their own unique levels of stability and turnover. This kind of cataloguing, in turn, will be useful for determining whether evolutionary rates vary in a predictable fashion as a function of environment. For example, it has been suggested that marine e-e subunits exhibit greater stability in shallow settings than in deeper settings. If this proves generally to be the case, then it would indicate that rates of taxonomic origination and extinction are greater in deep-water settings.

9.4 EVOLUTIONARY PALEOECOLOGY

The question of coordinated stasis, and the broader analysis of regional biotic patterns, reflect a growing focus in paleontology on the investigation of paleoecological changes through geologic time. Paleontologists have embraced this perspective in recent years, melding evolutionary and paleoecological approaches together in the study of evolutionary paleoecology. It is probably no coincidence that evolutionary paleoecology has blossomed in conjunction with the growing focus on Phanerozoic diversification, which was highlighted in Chapter 8. In fact, a prime objective of this research has been to explain the biotic transitions recognized in global diversity compilations.

Ecospace Utilization through Time

As we noted earlier, it is not clear whether it is possible in most cases to reconstruct the fine-scale, spatial distributions of taxa in paleocommunities. However, if we can establish the life habits of these taxa based on principles discussed in Chapter 5, then it is possible to determine the ecospace within the local habitat that was likely utilized by the taxa in a paleocommunity.

In this context, an ecospace is a setting in which ecological conditions are suitable for the subsistence of a particular taxon or group of taxa. For example, in considering the fossils contained in strata that preserve a sand-covered sea floor, in many cases it is possible to determine, based primarily on their morphological characteristics, whether taxa occupied positions above, at, or below the surface of the sediment. Because they provide direct indications of the kinetic activity of individuals, trace fossils are also particularly helpful in making these assessments, especially with respect to activity at or below the sediment surface.

Among the striking features of Phanerozoic marine diversity are the biotic transitions among the three evolutionary faunas [SEE SECTION 8.4], each of which apparently achieved successively greater levels of total diversity. Given that the three faunas were characterized by rather different sets of animals, we might expect that, in a broad sense, they were living their lives in different ways. With this in mind, we can ask whether successive evolutionary faunas achieved higher levels of diversity than their predecessors because, collectively, their con-

stituents occupied greater portions of ecospace. This issue can be addressed by attempting to categorize the different modes of life represented by the taxa extant at any given point in time and then determining whether there were changes through time in the number and variety of such modes. For this purpose, it has been convenient to use a unit of categorization known as a **guild**, which can be thought of here as a group of taxa that exploit the same class of environmental resources in a similar way without regard to taxonomic position.

Richard Bambach (1983, 1985) sought to calibrate the number of guilds represented within Phanerozoic communities, which he did by identifying and tabulating the number of guilds in some 193 fossil collections from the Ordovician, Silurian, Devonian, Carboniferous, and Neogene. His determination of guild membership for each species in a collection was based on (1) its basic physiological and morphological characteristic (i.e., its body plan); (2) its food sources; and (3) its space utilization (Figure 9.10).

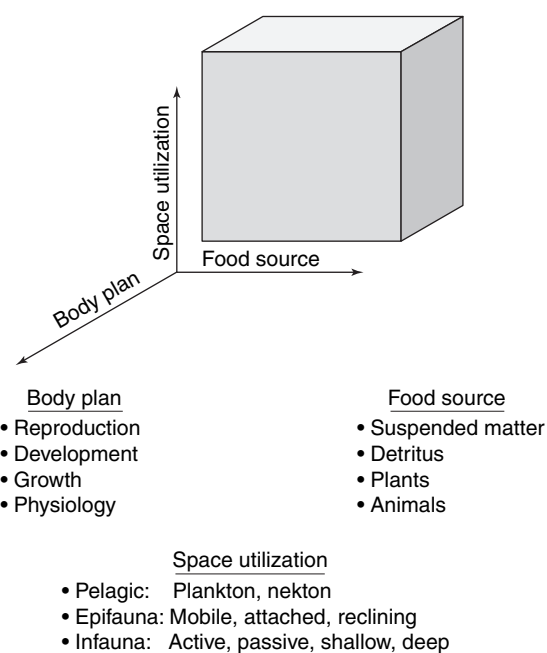


FIGURE 9.10 Bambach's schematic representation of the three dimensions and related criteria that he used to categorize the ecological characteristics of taxa throughout the Phanerozoic. He delineated guilds of organisms as taxa that were concentrated in a confined portion of this space because they possessed similar features based on the criteria listed on the diagram. (From Bambach, 1983)

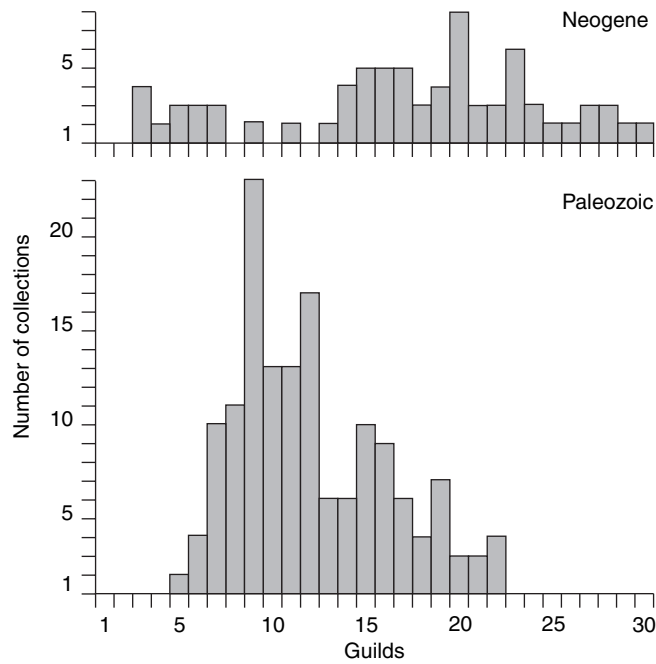


FIGURE 9.11 Histograms comparing the number of guilds represented in Paleozoic collections, versus those in Neogene collections. (From Bambach, 1983)

Bambach's results are summarized in Figures 9.11 and 9.12. Figure 9.11 indicates that the degree of ecospace utilization increased through the Phanerozoic: The median number of guilds grew from 11 in his Paleozoic assemblages to 18 in his Neogene assemblages. As Figure 9.12 indicates, this was associated with an increase in the variety of adaptive strategies exhibited by successive evolutionary faunas. Thus, it is plausible that the increasing level of diversity was indeed based ecologically on the growing amount of available ecospace.

A related pattern is recognized in the nature of tiering through the Phanerozoic among marine organisms that live on soft substrates, such as muddy, silty, or sandy bottoms. A **tier** is thought to be a fairly discrete level above, at, or below the sea floor where there is a concentration of organisms. In the case of infaunal organisms that live beneath the sea floor, it is possible to distinguish between deep and shallow sediment burrowers, which would therefore occupy deeper or shallower infaunal tiers. These assessments can be made based on the style and extent of active burrowing as indicated by trace fossils (Figure 9.13a) and the morphological features of preserved organisms (Figure 9.13b). For epifaunal organisms, which occupy the surface of the sea floor, skeletal features, such as the length

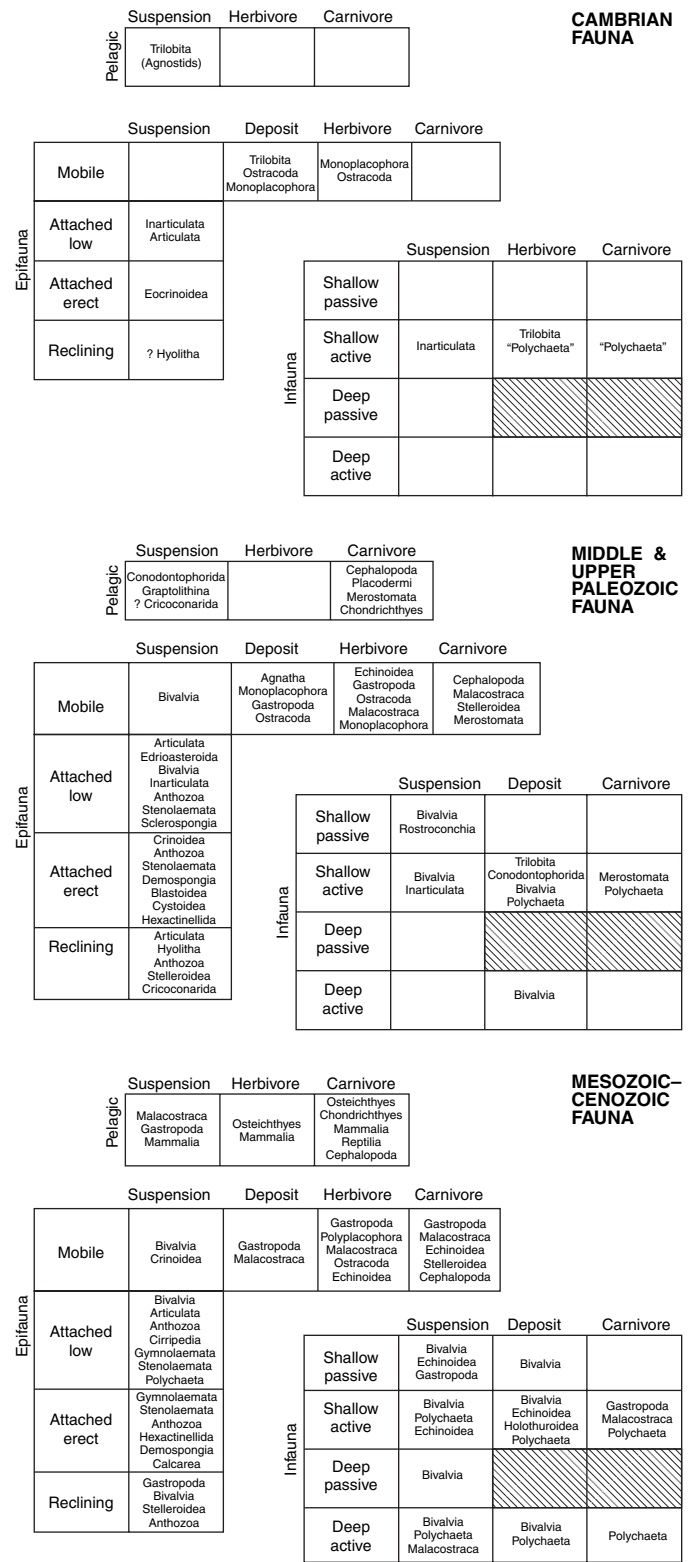


FIGURE 9.12 Charts depicting the adaptive strategies of taxa that comprised biotas during the Cambrian, the Middle and Upper Paleozoic, and the post-Paleozoic. Note the increasing diversity of strategies exhibited successively from one interval to the next. (From Bambach, 1983)

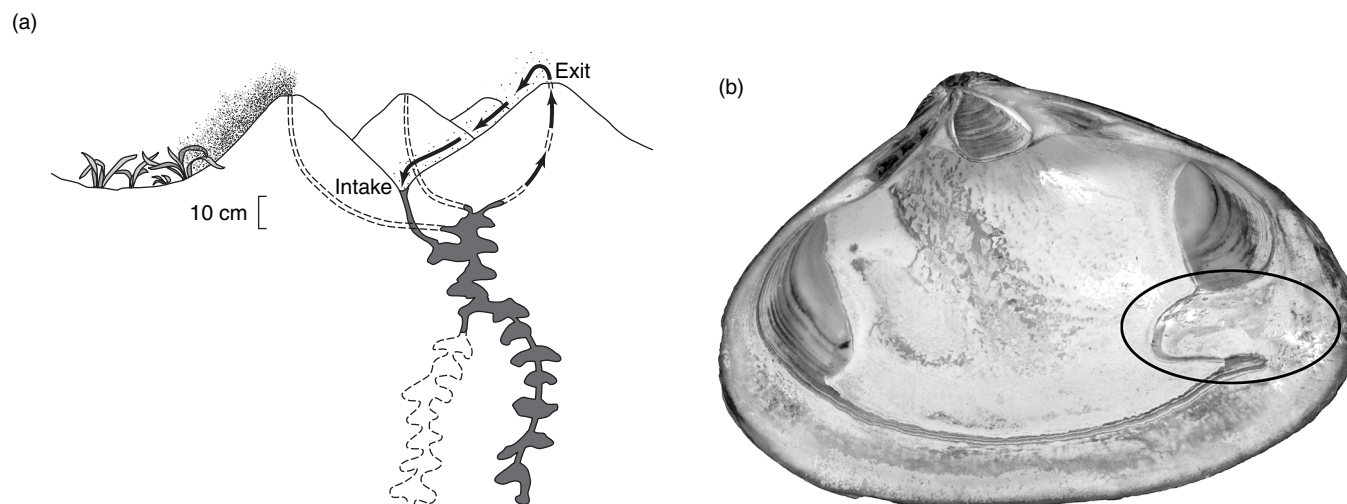


FIGURE 9.13 Indications of an active, burrowing lifestyle. (a) The burrow structure of *Callianassa rathbunae*, an active bioturbating shrimp that lives in Caribbean sea floors. Sediment enters the living chamber of the organism intake tubes located between mounds. *C. rathbunae* strips food off of these sediment grains and expels fine-grained sediment back to the sediment surface. These expelled sediments form the distinctive, volcano-shaped mounds that are illustrated here. (b) The interior of the shell of the bivalve *Spisula*, illustrating the position of the pallial sinus (circled), marking the position to which the siphons of this species are retracted. The possession of siphons, as well as other features of the shell, indicate that this species lives beneath the sediment–water interface. (a: From Suchanek, 1983; b: The Academy of Natural Sciences)

of the stem of an attached crinoid, can indicate occupancy of epifaunal tiers. There were several transitions in the extent of tiering among infaunal and epifaunal organisms throughout the Phanerozoic that, in some cases, appear to have paralleled changes in marine taxonomic diversity (Figure 9.14), [SEE SECTIONS 8.3 AND 8.4].

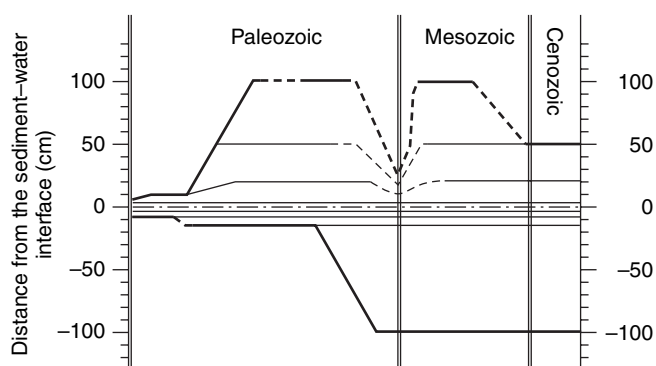


FIGURE 9.14 A depiction of the history of epifaunal and infaunal tiering on soft substrates throughout the Phanerozoic. Note that the pattern appears to parallel, in some respects, the Phanerozoic history of global marine diversity (Figure 8.5). Solid lines are based on direct observations and measurements of fossil organisms; dotted lines are inferred patterns, based on interpolation between solid lines. (From Bottjer & Ausich, 1986)

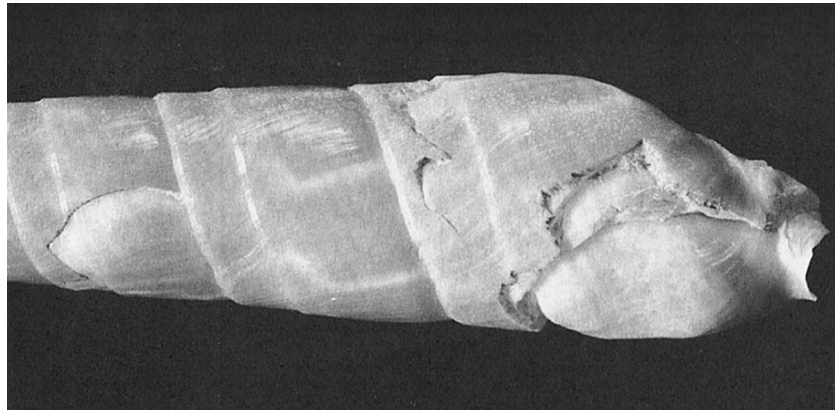
Some paleontologists have questioned whether marine organisms really were, or are, distributed into discrete tiers. It is clear, however, that the maximum distance above the sea floor occupied by epifaunal organisms and the maximum depth of infaunal penetration increased from the Cambrian to the mid-Paleozoic. It is also clear that the maximum depth of burrowing increased further during the Mesozoic. Interestingly, the maximum reach of attached, sedentary organisms above the sea floor appears to have decreased during the Cenozoic, which may relate to an increase in predation intensity. These organisms would have been particularly vulnerable to attack by a diversifying array of mobile predators, the importance of which we consider more fully below.

Evolutionary Transitions Associated with Ecological Interactions

Ecologists have come to recognize that interactions among present-day organisms play significant roles in determining their distributions and abundances. Prominent among these are predator–prey interactions, which are governed by complex cycles of booms and busts in the abundances of predators and the organisms on which they prey. These relationships, and the interwoven

FIGURE 9.15 A specimen of the gastropod *Terebra dimidiata*, from Guam.

This specimen preserves in its whorls the scars of several instances of nonlethal predation by shell-peeling crabs, followed by repairs to the shell. (From Vermeij, 1987)



strategies of predators and prey that govern them, are assuredly the products of extended intervals of evolution, and paleontologists have therefore assumed that similar kinds of interactions have been a pervasive part of ecosystems for as long as there have been predatory organisms. This, in turn, has motivated a general question for paleoecologists: Do the ecological interactions that can be shown to mediate the distributions and abundances of organisms in the present day also play significant roles in the mediation of evolutionary trends that we can observe through geologic time?

In the case of predator-prey interactions, one straightforward expectation is that if there is a diversification of predatory taxa that prey on a particular set of organisms, then in the course of evolution, morphological characteristics might evolve among prey taxa that increase their chances of surviving predatory attacks. Geerat Vermeij (1977, 1987) investigated this possibility extensively and has compiled evidence suggesting that these “arms races” between predator and prey lineages may be pervasive features of evolution. Among the most compelling cases are those involving gastropods and the predators that crushed their shells, which Vermeij tracked through the Mesozoic and Cenozoic Eras. He referred to the collective transitions associated with these arms races as the **Mesozoic Marine Revolution**.

There is ample evidence, in the form of damage and/or repair features on gastropod shells (Figure 9.15), that many gastropods are subjected to repeated episodes of predation during their lifetimes. Has this always been the case? As far back as the Devonian, there was a notable increase in the diversity of marine taxa capable of breaking shells, but, from the early Cretaceous through the Neogene, the diversification of these shell crushers appears to have been particularly pronounced, increasing

at the family level by a factor of about 2.5 (Figure 9.16). This rate of increase was greater than that for marine animal families as a whole (see Figure 8.4a), which, for well-preserved organisms, increased by a factor of about 1.3 during the same interval. Therefore, even if the apparent rate of increase was amplified by the Pull of the Recent [SEE SECTION 8.3], the *percentage* of the marine biota that was made up of shell crushers appears to have increased substantially during the late Mesozoic and Cenozoic eras.

While gastropods were also apparently undergoing a significant diversification at that time, certain morphological features exhibited by gastropod taxa were in decline. For example, Vermeij noted that gastropods

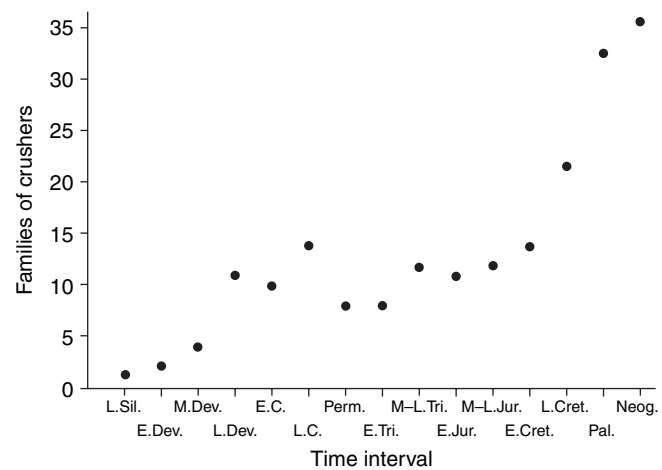


FIGURE 9.16 A depiction of the Phanerozoic diversity of marine families with members that were capable of crushing shells. Note the moderate increase in the mid-Paleozoic, followed by a sharp increase in the Late Mesozoic. This increase in diversity appears to exceed that of the biota as a whole during the same interval. (From Vermeij, 1987)

possessing an umbilicus—a hollow cavity associated with the axis of coiling (Figure 9.17a)—declined markedly as a percentage of total gastropod diversity in the Mesozoic and Cenozoic (Figure 9.17b). Vermeij also investigated the changing morphologies of gastropod apertures, the

openings at the margins of gastropod shells. He documented a Mesozoic and Cenozoic increase in the percentage of gastropods with apertures that were narrow, or in which the shell region surrounding the aperture was notably thickened (Figures 9.17c and 9.17d).

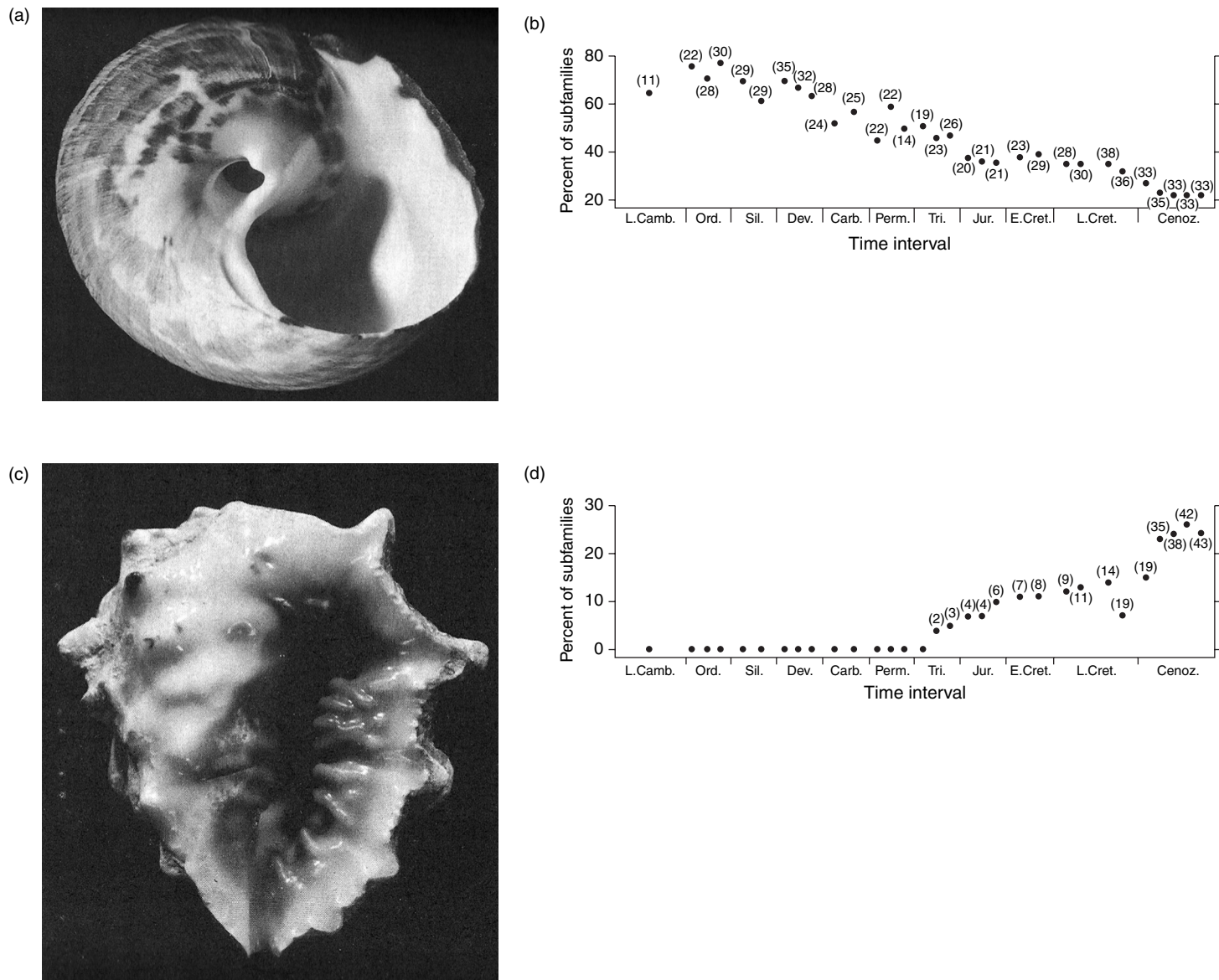


FIGURE 9.17 Phanerozoic transitions in the morphology of gastropods. (a) *Cittarium pica*, from Panama, a species with an umbilicus, a broad aperture, and a thin wall surrounding the aperture. These features are thought to render this species vulnerable to predation by shell crushers and peelers. (b) The percentage of gastropod species that were umbilicate, as a function of geologic time, in assemblages representing warm-water settings. (c) *Drupa morum*, from the northern Mariana Islands, a species with a narrow aperture and thickened walls surrounding the aperture. These and other features are thought to render this species less vulnerable to predation by shell crushers and peelers. (d) The percentage of species with thickened or narrowed apertures, as a function of geologic time. In (b) and (d), numbers in parentheses are the number of assemblages sampled. (From Vermeij, 1987)

Vermeij attributed all of these transitions to the diversification of predatory organisms, particularly crustaceans that possessed hammerlike appendages capable of crushing shells or strong claws capable of peeling them open. The possession of an umbilicus renders a gastropod more vulnerable to crushing [SEE SECTION 5.3], whereas the possession of a broad aperture associated with a thin shell renders it more vulnerable to being peeled open. Therefore, the patterns among gastropods illustrated in Figure 9.17 are precisely what one would expect in the face of increasing predation.

Morphological transitions do not constitute the only potential macroevolutionary responses to increased predation. Another possible response is for organisms to become restricted to physical environments that are beyond the reach of their predators. Just such a response has been suggested in the restriction during the Mesozoic and Cenozoic Eras of stemmed crinoids to deep water in association with the diversification of teleost fish and other organisms that prey on them (Meyer & Macurda, 1977). In the Paleozoic, stemmed crinoids were among the most prolific organisms in shallow-water marine communities. Today, however, mobile crinoids, which can take refuge in cracks and crevices on reefs and other hard substrates, tend to predominate in shallow water, particularly in reef settings. Moreover, the decline in the maximum height above the sediment surface of epifaunal tiering (see Figure 9.14) appears to be related to the loss of the longest-stemmed crinoids in shallow, marine settings, which may have been particularly vulnerable to predation.

Onshore–Offshore Patterns of Diversification

It stands to reason that changes through time in the diversity of any group might be related closely to environmental transitions exhibited by the group. For example, we might expect the diversification of a higher taxon to be accompanied by an expansion in the range of environments occupied by its constituents, whereas we might expect environmental contraction to accompany a diversity decline. However, we should not take these kinds of associations for granted. It is certainly plausible that a taxon undergoing a major radiation could simply accommodate more individuals within the settings that it already occupies, particularly if other taxa have become extinct in those settings.

Jack Sepkoski and Peter Sheehan (1983) investigated the environmental signatures of the Cambrian Explo-

sion and Ordovician Radiation, the global aspects of which were discussed in Chapter 8, by compiling a database of 102 species- and genus-level faunal lists from published data sources. These lists were all representative of faunal assemblages collected from Cambrian and Ordovician rocks in North America, and they were accompanied by sedimentological data that permitted broad determinations of the paleoenvironmental settings in which each assemblage was thought to have lived. In addition, it was possible to determine the stratigraphic position of each assemblage within the Cambrian or Ordovician. Based on this information, Sepkoski and Sheehan placed the assemblages on a two-dimensional grid, known as a **time–environment diagram**, on which the vertical dimension depicts time and the horizontal dimension depicts environmental position on a very broad, simplified gradient that ranges from intertidal to deep-water settings (Figure 9.18).

From the faunal data, Sepkoski and Sheehan assembled a matrix at the taxonomic level of order by tabulating the species richness of each order within each assemblage. Assemblage compositions were then compared using cluster analysis, the results of which showed that most assemblages could be classified in the resultant dendrogram into two broad clusters, with a much smaller number of assemblages contained in each of two other clusters (Figure 9.19). The compositional differences among the assemblages in each cluster were clear, with the two main clusters dominated by elements of the Cambrian (lower large cluster) and Paleozoic (upper large cluster) evolutionary faunas. The small cluster at the base of the dendrogram was dominated by a unique Early Cambrian biota, whereas the four samples in the cluster at the top of the diagram were rich in bivalves (i.e., elements of the Modern evolutionary fauna).

When the assemblages were demarcated on the time–environment diagram based on their membership in the four clusters (Figure 9.18), an onshore–offshore pattern emerged: The Cambrian Fauna appeared to have become restricted offshore through the Ordovician, while the Paleozoic Fauna diversified initially in nearshore settings and subsequently expanded offshore. This was thought to suggest a kind of paleoecological cohesiveness to the Cambrian and Paleozoic evolutionary faunas, given their apparent segregation from one another on Paleozoic sea floors. These findings were further amplified by extending the analysis of North American fossil assemblages to the rest of the Paleozoic (Sepkoski & Miller, 1985). In these later analyses, there were

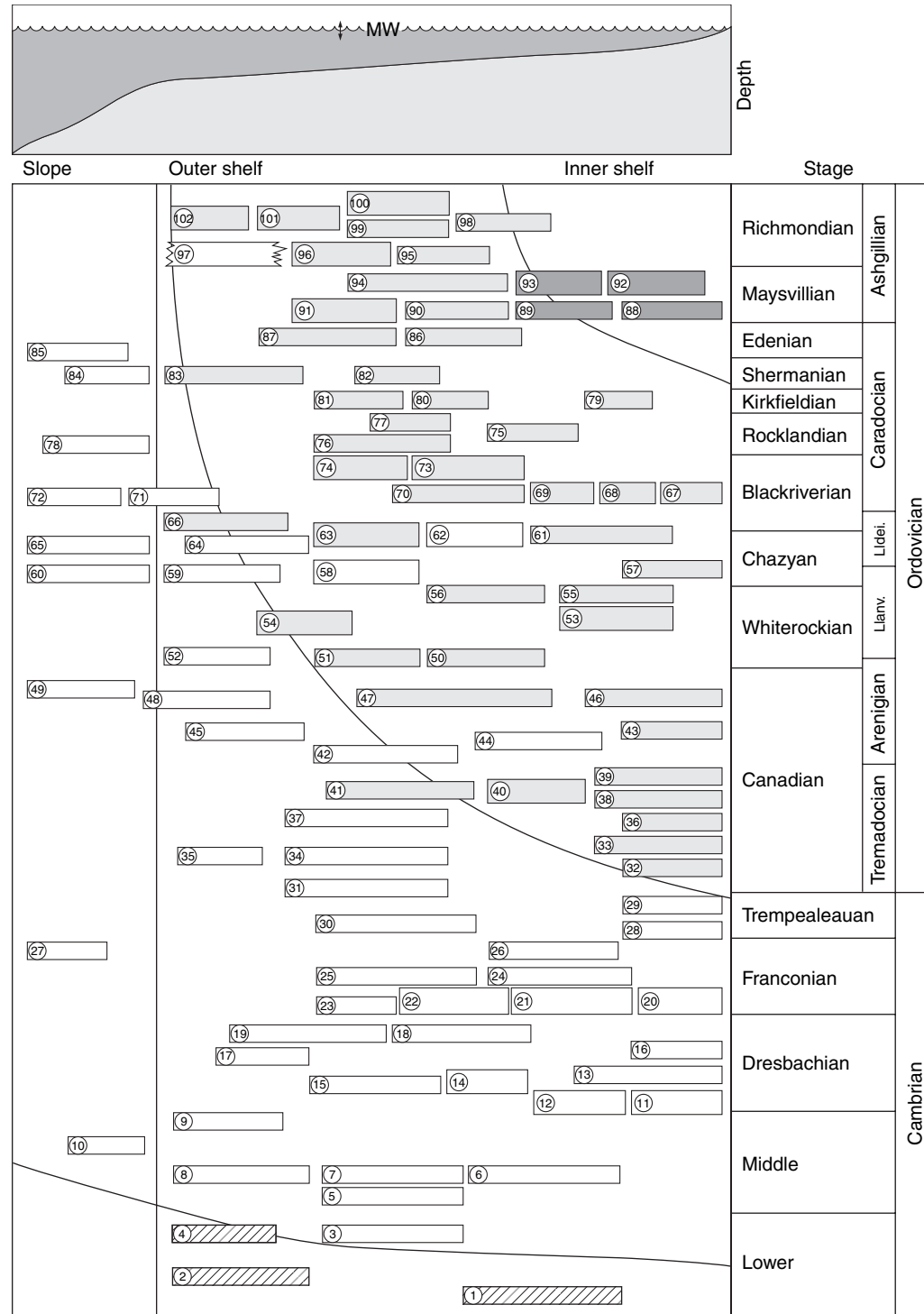


FIGURE 9.18 Time–environment diagram depicting the positions in space and time of the 102 community-level samples from North America compiled by Sepkoski and Sheehan. Note that the environmental dimension is a simple onshore–offshore scheme. Rectangles vary in width, according to the environmental breadths of the samples depicted and, in some cases, uncertainties thereof. Information on cluster membership from Figure 9.19 was superimposed using different stippling patterns on the rectangles. Note specifically that a cluster of samples in which trilobites were particularly diverse became limited mainly to deep-water settings during the Ordovician, as samples rich in articulated brachiopods and other elements of the Paleozoic evolutionary fauna dominated settings closer to shore. (From Sepkoski & Sheehan, 1983)

indications that the Modern Fauna expanded slowly and irregularly offshore throughout the mid- to late Paleozoic, as the Paleozoic Fauna became restricted primarily to settings away from the shoreline.

The general suggestion of an onshore–offshore vector to the diversification of higher taxa was extended to the Mesozoic and Cenozoic eras in a series of time–environment studies conducted by David Jablonski and David Bottjer (1983). Jablonski and Bottjer found that “Paleozoic-type” organisms living on the surface of soft sediment substrates—including inoceramid bivalves, oysters, and other nonbivalve elements—became restricted offshore, while a more “modern” biota, dominated by bivalves that burrowed beneath the sediment surface, diversified and expanded closer to shore. Subsequently, Jablonski and Bottjer (1991)

conducted case studies for several other taxa, demonstrating some form of onshore–offshore diversification in various groups of bivalves, bryozoans, crinoids, and trace fossils. In addition, and perhaps most interestingly, Jablonski and Bottjer conducted an aggregate analysis of post-Paleozoic orders, recently updated by Jablonski (2005). They found that the first appearance of orders, considered to be a kind of taxonomic proxy for the origination of evolutionary novelties, took place overwhelmingly in nearshore through middle-shelf settings and were rare in outer-shelf and deep-water settings (Figure 9.20). Interestingly, there was no indication of environmental bias in origination at lower taxonomic levels, suggesting that the origination of orders is a distinct phenomenon from the origination of lower taxa.

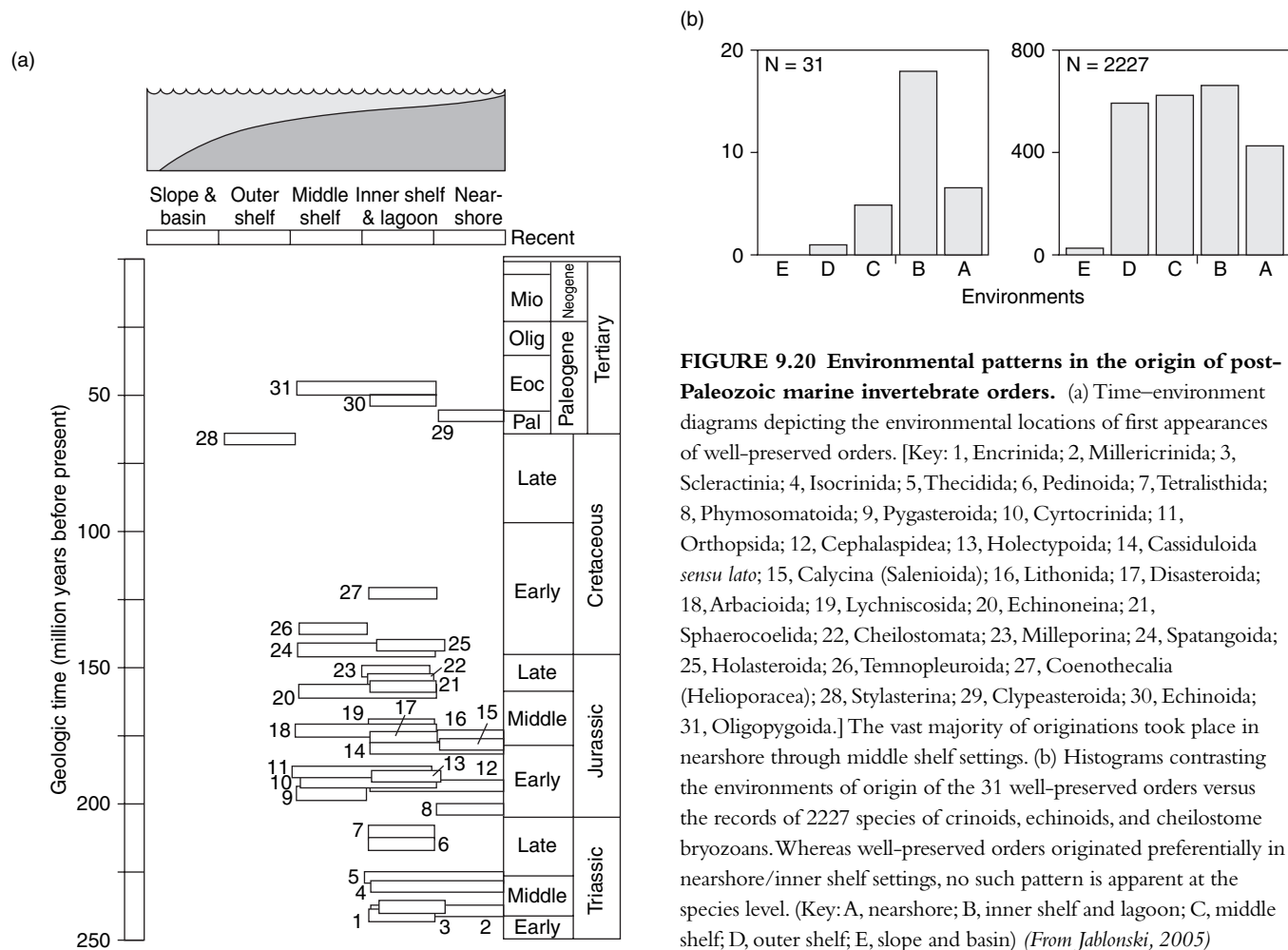


FIGURE 9.20 Environmental patterns in the origin of post-Paleozoic marine invertebrate orders. (a) Time–environment diagrams depicting the environmental locations of first appearances of well-preserved orders. [Key: 1, Encrinida; 2, Millericrinida; 3, Scleractinia; 4, Isocrinida; 5, Thecidida; 6, Pedinoida; 7, Tetralisthida; 8, Phymosomatoida; 9, Pygasteroida; 10, Cyrtocrinida; 11, Orthopsida; 12, Cephalaspidea; 13, Holecypoida; 14, Cassiduloida *sensu lato*; 15, Calycina (Salenioida); 16, Lithonida; 17, Disasteroida; 18, Arbacioida; 19, Lychniscosida; 20, Echinoneina; 21, Sphaerocoelida; 22, Cheilostomata; 23, Milleporina; 24, Spatangoida; 25, Holasteroida; 26, Temnopleuroida; 27, Coenothecalia (Helioporacea); 28, Stylasterina; 29, Clypeasteroida; 30, Echinoida; 31, Oligopygoida.] The vast majority of originations took place in nearshore through middle shelf settings. (b) Histograms contrasting the environments of origin of the 31 well-preserved orders versus the records of 2227 species of crinoids, echinoids, and cheilostome bryozoans. Whereas well-preserved orders originated preferentially in nearshore/inner shelf settings, no such pattern is apparent at the species level. (Key: A, nearshore; B, inner shelf and lagoon; C, middle shelf; D, outer shelf; E, slope and basin) (From Jablonski, 2005)

Collectively these studies argue for the existence of a paleoecologically mediated mechanism that transcends individual taxa and promotes both the origination of novelty and the initial diversification of higher taxa in nearshore environmental settings. That said, the onshore–offshore approach has motivated many studies intended to assess in greater detail the patterns just summarized, and to explore further the question of whether unique mechanisms are actually needed to explain the observations. With respect to the Paleozoic patterns that we described earlier, it has been demonstrated that neither the environmental segregation between evolutionary faunas nor the cohesiveness of individual evolutionary faunas is as straightforward as suggested in earlier research. For the most part, trilobites, which were major components of the Cambrian evolutionary fauna, did not actually become restricted to deep water during the Ordovician; rather, their numbers were “diluted” nearshore by elements of the diversifying Paleozoic Fauna (Westrop & Adrain, 1998). Similarly, the Ordovician distribution of bivalves was not limited to shallow water but was controlled largely by the distribution of terrigenous sediments [SEE SECTION 8.8], which sometimes extended into offshore settings.

Despite these caveats, it is clear that the investigation of diversification in an environmental context has begun to provide a significant conceptual advance to paleontology by treating the space dimension as an emergent characteristic of taxa that, like morphology, is subject to evolution. More generally, this research has motivated paleontologists to incorporate information about paleoenvironments directly and routinely into evolutionary analyses, and data relevant to these assessments are now compiled in large-scale paleontological databases [SEE SECTION 8.7].

Ecological Interactions and Mass Extinctions

In Chapter 8, we considered the roles of mass extinctions in mediating major changes in taxonomic composition through the removal and replacement of incumbent taxa [SEE SECTION 8.6]. Given these changes, we might also expect major transitions in the nature of ecological interactions. To assess this possibility, Conrad Labandeira and colleagues (2002) investigated transitions in insect–plant interactions across the Late Cretaceous–Paleocene (K/T) mass-extinction boundary.

Although the record of insect body fossils is rather limited throughout the study interval, there is abundant evidence of the presence and behavior of insects preserved on the fossil leaves of woody plants found in paleofloral assemblages. Labandeira and colleagues focused on assemblages preserved in southwestern North Dakota, in which they examined more than 13,000 fossil leaf specimens for signs of insect damage.

In these and other studies, Labandeira and his colleagues have been able to recognize more than 50 unique damage types caused by insects that can be grouped into eight categories, several of which are illustrated in Figure 9.21. In addition, by determining the degree of plant–host specificity observed for the same damage types in the present day, Labandeira and colleagues classified these damage types into three categories—generalized, intermediate, and specialized—reflecting the degree to which insects were selective in their choice of food.

When they partitioned their data to analyze stratigraphic transitions in leaf damage (Figure 9.22), Labandeira and colleagues found a significant decrease across the K/T boundary in the percentage of leaves damaged and in the number of damage types. Moreover, the decline in leaf damage was significantly greater among damage types classified as intermediate or specialized than among generalized damage types.

Importantly, Labandeira and colleagues observed a substantial Paleocene recovery near the top of their study interval in the number of damage types and in the percentage of leaves in a given assemblage that showed some form of damage. However, the recovery was far more pronounced among generalized damage types than among intermediate or specialized types, suggesting that: (1) Insects specialized for feeding on particular plant hosts were affected more profoundly than generalists during the K/T mass extinction; or (2) the plant hosts associated with specialized insects were strongly affected by the extinction; or (3) both. These findings are of obvious relevance to discussions about the biological selectivity of mass extinctions, discussed in Chapter 8 [SEE SECTION 8.6].

In addition to demonstrating a significant transition in the nature of ecological interactions in association with the K/T mass extinction, the study by Labandeira and colleagues also illustrates the general importance of fossil leaves as treasure troves of information about the evolution and behavior of herbivores throughout the Phanerozoic. We consider another example of the use of leaf-damage data in Chapter 10 [SEE SECTION 10.4].

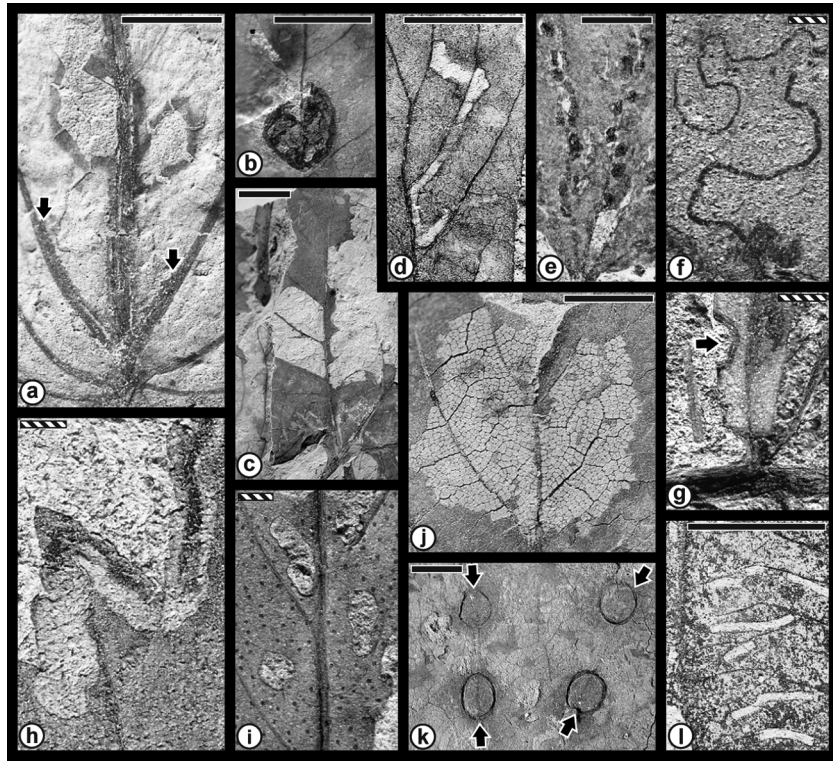


FIGURE 9.21 Examples of damage to leaves caused by insects, from the K/T boundary interval in southwestern North Dakota. Black scale bar, 1 cm; striped scale bar, 0.1 cm. (a) Two linear leaf mines, with oviposition (egg laying) at the sites of the arrows. (b) A gall (a bump caused by irregular tissue growth after damage by an insect). (c) Free feeding. (d) Skeletonization (chewing damage). (e) Multiple galls. (f) Serpentine leaf mine. (g) Cusped margin feeding. (h) Serpentine leaf mine. (i) Hole feeding. (j) Skeletonization. (k) Insect impressions at sites of arrows. (l) Slot hole feeding. (From Labandeira et al., 2002)

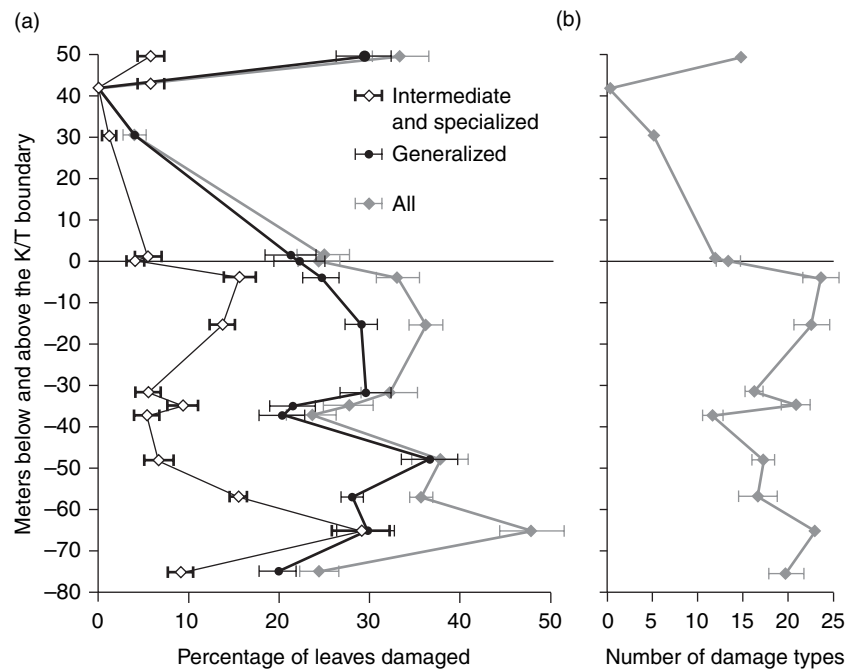


FIGURE 9.22 Declines in the extent and diversity of insect-induced leaf damage across the K/T boundary in southwestern North Dakota, for horizons containing at least 200 leaf specimens.

(a) Decline in the percentage of leaves showing evidence of damage. Note that the decline is greater for damage caused by intermediate and specialized feeders. (b) Decline in the number of different damage types, in aggregate, exhibited across the K/T boundary. To make the comparison equitable from horizon to horizon, all samples have been rarefied (see Box 1.2) to 200 specimens. (From Labandeira et al., 2002)

9.5 NEW APPROACHES TO PALEOENVIRONMENTAL AND PALEOCLIMATIC RECONSTRUCTION

An underlying theme throughout this chapter has been the question of paleoenvironmental interpretation. While the characteristics of enclosing sediments can help us determine the environmental conditions that prevailed at the time that the sediments were deposited, there are many ways in which fossils can be used directly as data for reconstructing paleoenvironments.

At a basic level, determining the range of guilds represented by the constituents of a fossil assemblage may

help us constrain the properties of the paleoenvironment represented by the strata in which fossils are found. For example, if it is determined that the majority of taxa preserved in an assemblage of fossil organisms were sedentary organisms with structures or skeletal features indicative of attachment to the substrate, this would imply that the substrate in question, be it on a sea floor or a forest floor, was firm enough to support this lifestyle.

The differing properties of fossil assemblages in close stratigraphic proximity may be diagnostic of important paleoenvironmental transitions, such as the degree of oxygenation on ancient sea floors. This approach was pioneered by Charles Savrda (1995) in the study of trace fossils, as illustrated in Figure 9.23. Savrda established a

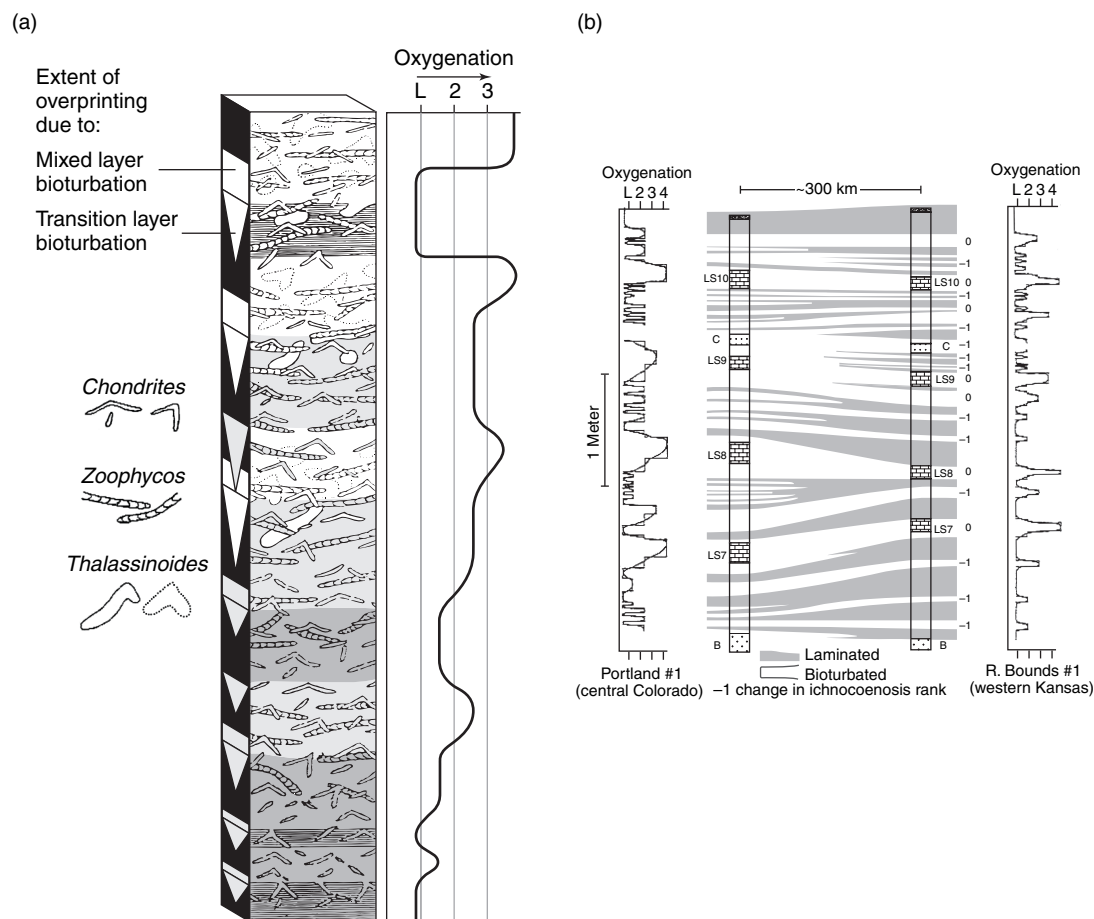


FIGURE 9.23 The use of trace fossils to diagnose oxygenation levels on a sea floor. (a) Hypothetical stratigraphic column illustrating variations in the concentration and nature of trace fossil assemblages in association with the degree of oxygenation of the sea floor. At low oxygen levels (L on the schematic graph), lamination is preserved, and only the producers of the trace fossil *Chondrites* survive. As oxygenation increases, the number and complexity of trace fossils also increase. (b) Oxygenation curves for two localities of the Lower Bridge Creek Limestone (Cretaceous) in western Kansas. The two localities have been correlated on the basis of two bentonites (preserved volcanic ash fall), marker beds (B and C), and a series of limestone beds. In general, the degree of bioturbation and associated oxygen levels decrease eastward (i.e., to the right). An eastward increase in the thickness and frequency of laminated intervals can also be observed. (From Savrda, 1995)

framework that relates the presence of particular trace fossils, and the general extent of bioturbation, to the amount of oxygen available in sea-floor sediments (Figure 9.23a).

Sediments in which there was little or no oxygen are characterized by the preservation of fine-scale horizontal features of primary bedding, known as laminations. With increasing levels of oxygenation, a more complex bottom fauna burrows through the sea floor (see Figure 1.20), obliterating laminations and generating a diverse set of trace fossils. This framework has been shown to be applicable broadly to the geological record (e.g., Figure 9.23b) and has been useful for recognizing fine-scale transitions in oxygenation levels, both stratigraphically and geographically.

$\delta^{18}\text{O}$ and the Mg/Ca Ratio

Beyond the characterization of the ecological properties of the taxa preserved within a fossil assemblage, paleontologists are now making use of a sophisticated set of geochemical techniques that evaluate directly the isotopic

properties of growth increments, or bands, preserved in the hard parts of many organisms. While these analyses are, of course, limited to the subset of preserved hard parts that have not been altered chemically after the death of the organism, the temporal resolution of the paleoenvironmental transitions diagnosed with these procedures is unmatched by any other paleontological method.

In many instances, it is possible to analyze samples collected with a microscopic coring device, within and across the annual growth increments of an organism. There can be environmental and geographic variation among the individuals of a species in the yearly emplacement of the “lighter” and “darker” bands that make up an annual increment in many organisms (Figure 9.24a). However, the geochemical transitions measured across these bands are often unmistakable.

We have already seen an illustration of the utility of oxygen isotopic techniques in Chapter 2, in the analysis of heterochrony in the Jurassic oyster *Gryphaea* [SEE SECTION 2.3]. This analysis depended on the ability of

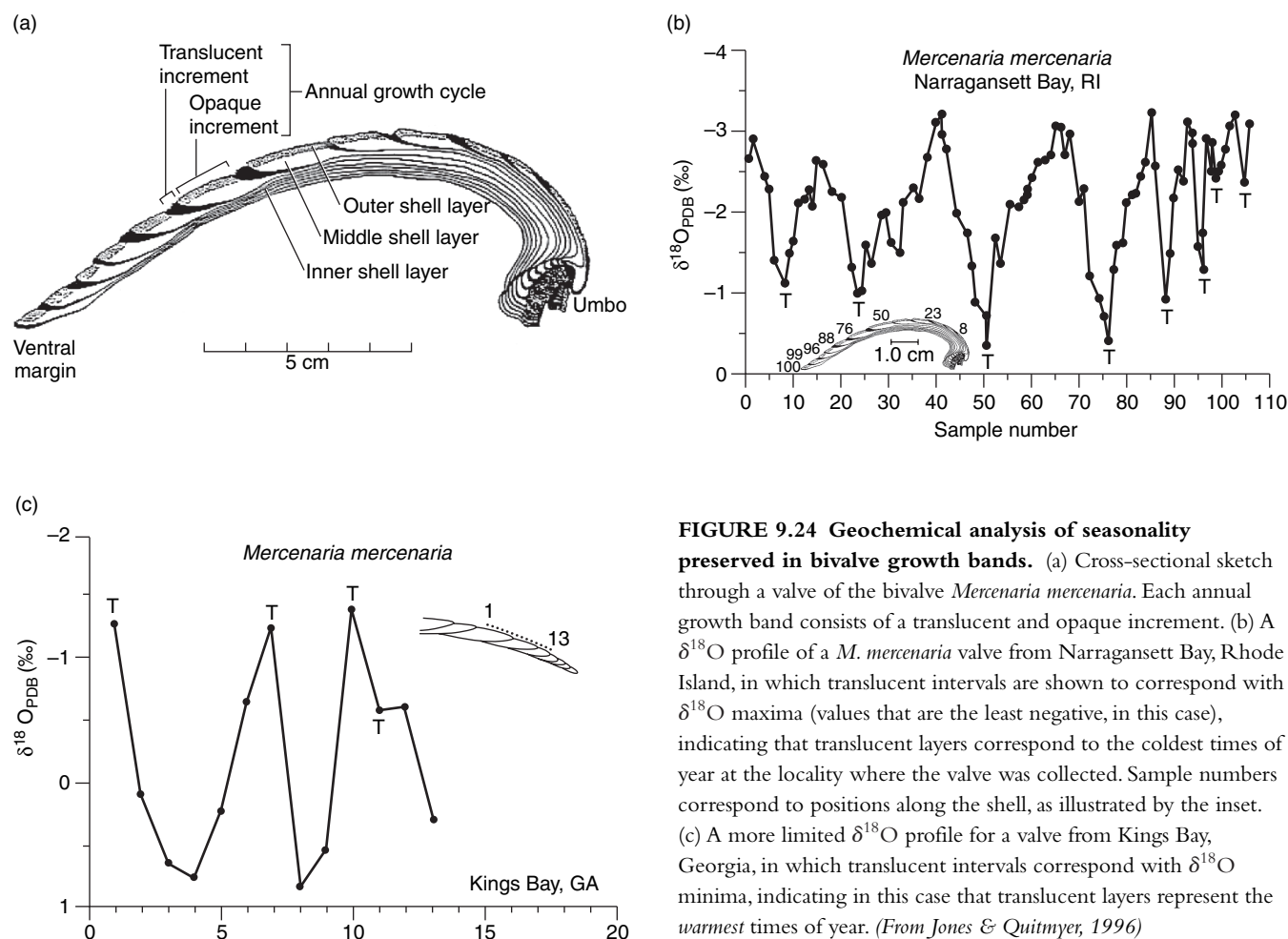


FIGURE 9.24 Geochemical analysis of seasonality preserved in bivalve growth bands. (a) Cross-sectional sketch through a valve of the bivalve *Mercenaria mercenaria*. Each annual growth band consists of a translucent and opaque increment. (b) A $\delta^{18}\text{O}$ profile of a *M. mercenaria* valve from Narragansett Bay, Rhode Island, in which translucent intervals are shown to correspond with $\delta^{18}\text{O}$ maxima (values that are the least negative, in this case), indicating that translucent layers correspond to the coldest times of year at the locality where the valve was collected. Sample numbers correspond to positions along the shell, as illustrated by the inset. (c) A more limited $\delta^{18}\text{O}$ profile for a valve from Kings Bay, Georgia, in which translucent intervals correspond with $\delta^{18}\text{O}$ minima, indicating in this case that translucent layers represent the warmest times of year. (From Jones & Quitmyer, 1996)

paleontologists to recognize seasonal and annual growth increments based on variations in the relative concentrations of two naturally occurring isotopes of oxygen, ^{16}O and ^{18}O , which can be measured with an instrument known as a mass spectrometer. Although the concentrations of these two isotopes in skeletal material may be affected by several factors, there is a measurable association of the ratio of these two isotopes with the temperature in surrounding waters at the time of skeletal accretion.

Isotopic ratios are generally reported in terms of their deviations from standard substances, in parts per thousand (‰), as defined in the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where δX is the enrichment (if positive) or depletion (if negative) of any high-mass isotope X (e.g., ^{18}O , in comparisons of ^{18}O and ^{16}O), and R is the high-mass to low-mass isotopic concentration ratio. Standard substances with which samples are compared in oxygen isotopic assessments include a belemnite cephalopod collected from the Upper Cretaceous Peedee Formation of the eastern United States (PDB) and present-day standard mean ocean water (SMOW).

Equations have been developed empirically for calcitic and aragonitic material that enable a researcher to estimate changes in the ambient temperature of a marine setting based on the $\delta^{18}\text{O}$ value determined for the sample. In a relative sense, a higher value for $\delta^{18}\text{O}$ (i.e., enrichment in ^{18}O relative to ^{16}O) corresponds to a lower temperature at the time of skeletal accretion. As an example, the annual record of oxygen isotopic variation can be observed in a specimen of a Recent bivalve, *Mercenaria mercenaria*, collected from Narragansett Bay, Rhode Island, as illustrated in Figure 9.24b. Here, translucent (dark) increments correspond dependably to colder portions of the year, as evidenced by the enrichment in ^{18}O associated with these increments. Elsewhere, however, translucent increments have been shown to correspond to the warmest portions of the year (see Figure 9.24c), suggesting that paleontologists should be cautious in assessing the significance of light and dark banding. Nevertheless, the oxygen isotopic pattern appears to record faithfully the temperature profile on an annual basis, regardless of timing during the year of light and dark increments.

The utility of oxygen isotope profiles for assessing seasonality can be seen further in the example illustrated in Figure 9.25, which records $\delta^{18}\text{O}$ and temperature pro-

files based on the microsampling of successive growth bands of fish otoliths (ear stones) collected at localities spanning the Eocene–Oligocene boundary in the Gulf Coast region of the United States. A comparison by Linda Ivany and colleagues (2000) of otolith profiles for Eocene versus Oligocene specimens suggests that, while there was little change in summer temperatures across the boundary, there appears to have been a significant decrease in winter temperatures, indicating an overall increase in seasonality. It remains to be determined whether this apparent paleoclimatic change was associated with a major extinction that took place at that time, but the coincidence is intriguing.

Geologists are now making routine use of isotopic analyses in the study of ancient environments. Among the other isotopic suites that are of particular importance to paleontologists are the $^{13}\text{C}/^{12}\text{C}$ suite, which is useful for diagnosing the presence of photosynthetic activity [SEE SECTION 10.5], and the $^{34}\text{S}/^{32}\text{S}$ suite, which provides an indication of the degree of oxygenation.

The use of $\delta^{18}\text{O}$ as a paleo-thermometer is not limited to assessment of temperature variations recorded in the growth bands of individual skeletons or skeletal elements. It can also be used to diagnose an extended record of temperature change in a region based on intraspecific stratigraphic variations in the average isotopic compositions of samples of skeletal elements. Researchers typically assess $\delta^{18}\text{O}$ trends for more than one species because different species sometimes exhibit different stratigraphic $\delta^{18}\text{O}$ trends through the same interval. As we will see in Chapter 10 [SECTION 10.4], the demonstration of a similar stratigraphic pattern among several species provides compelling evidence that the pattern transcends taxonomic bias.

Complications in the interpretation of $\delta^{18}\text{O}$ trends can arise for other reasons, including variations through time in the volume of ice occurring on the earth. Because ^{16}O is lighter than ^{18}O , water molecules containing ^{16}O evaporate more readily than those containing ^{18}O , and it follows that ^{16}O will occur preferentially in the precipitation derived from evaporated water. Given that the growth of glaciers depends on the water supplied by this ^{16}O -enriched precipitation, it stands to reason that ^{16}O will be sequestered preferentially in glacial ice, thereby causing a global enrichment in ^{18}O in sea water (i.e., increased $\delta^{18}\text{O}$) during intervals of increased glaciation. Of course, we would expect the earth to be cooler globally during an interval of glacial advance, and this cooling might be reflected in a positive excursion in $\delta^{18}\text{O}$ at a given locality. However, it is possi-

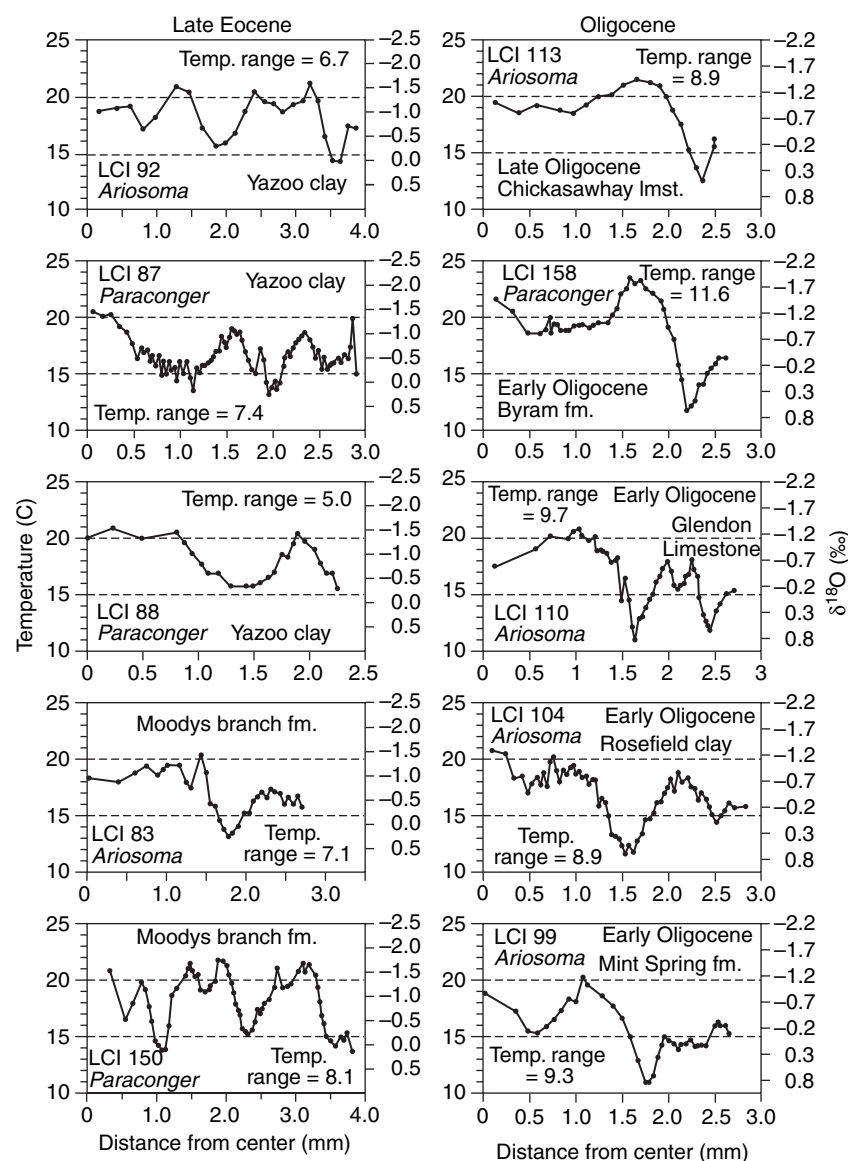


FIGURE 9.25 Temperature records, based on $\delta^{18}\text{O}$ profiles from microsampling of several Late Eocene and Oligocene fish otoliths. Note the tendency of Oligocene profiles to exhibit greater amplitudes, primarily because of colder temperatures during the winter. Summer temperatures remained fairly constant from the Late Eocene into the Oligocene. (From Ivany *et al.*, 2000)

ble that excursions related to changes in ice volume will overwhelm patterns that would otherwise reflect local or regional temperature variations that did not parallel the advance or retreat of glaciers.

With this in mind, additional methods for estimating ancient temperatures have been developed that use other elements preserved in fossil skeletons. These should be viewed as supplements to assessments based on $\delta^{18}\text{O}$. One of the more promising of these approaches uses the

ratio of magnesium to calcium (Mg/Ca) preserved in the skeletons of foraminifera. While not entirely free of its own complications, a strong empirical association with temperature has been recognized in the Mg/Ca ratios of several present-day benthic foraminiferal species. In general, the Mg/Ca ratio preserved in benthic foraminifera increases exponentially with increased temperature (Figure 9.26); temperature changes through time can therefore be diagnosed by this alternative means.

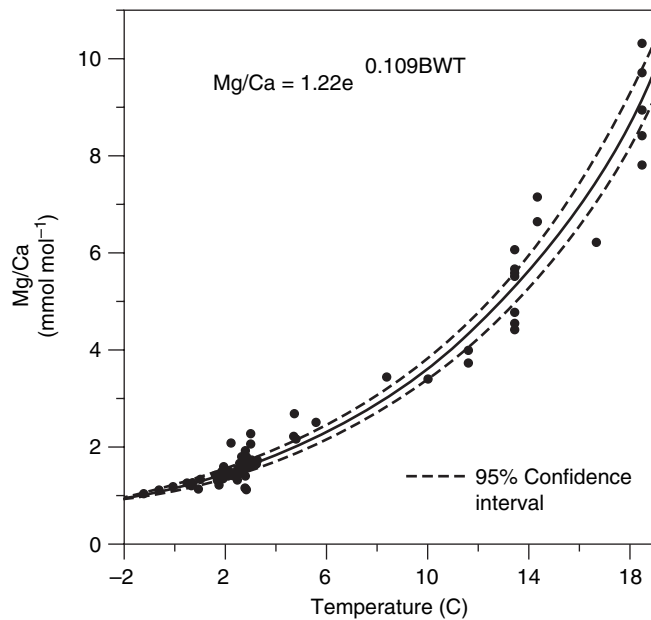


FIGURE 9.26 An illustration of the strong empirical relationship between Mg/Ca ratios in the benthic foraminiferal genus *Cibicidoides* and present-day water temperature, based on an analysis of specimens collected from the tops of cores collected at several deep-sea locations.

An equation is fitted by statistical methods to the data, as illustrated here, which can then be used to estimate bottom-water temperature (BWT) based on Mg/Ca ratios observed for this taxon in older samples. (From Martin et al., 2002)

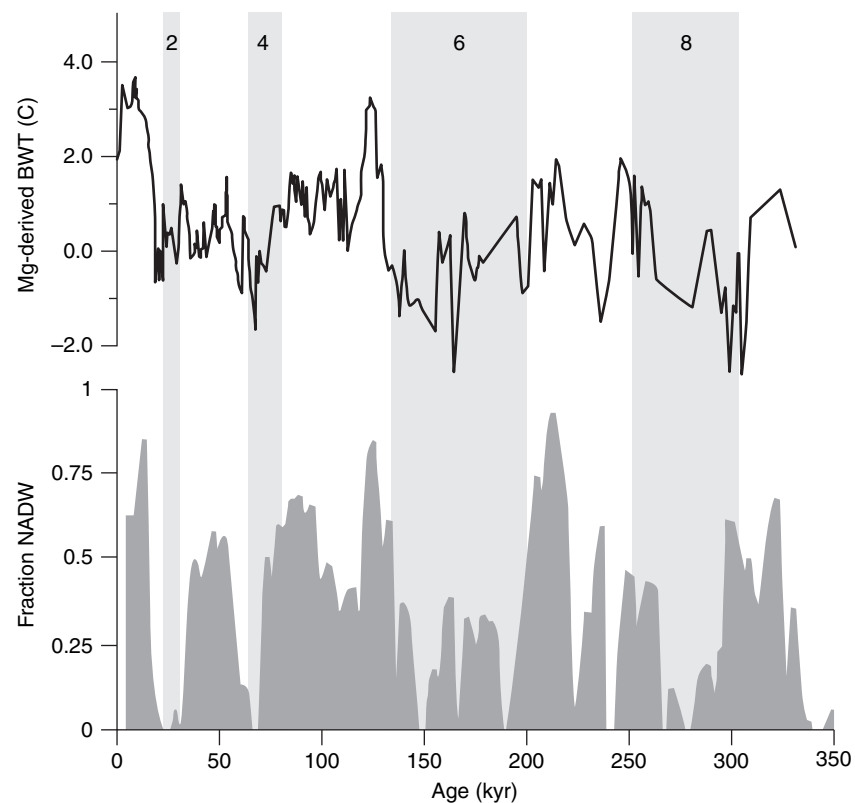
Pamela Martin and colleagues (2002) demonstrated a clear relationship between changes in bottom-water temperature estimated by this method and glacial–interglacial cycles during the past 350,000 years. Interestingly, for one deep-sea location in the tropical Atlantic, Martin and her colleagues were able to diagnose the interplay of two different water masses in association with glacial–interglacial cycles. Intervals of cooling coincided with regional decreases in the fraction of North Atlantic deep water (NADW) relative to the contribution of Antarctic bottom water (AABW; Figure 9.27).

Paleoclimatic and Paleoatmospheric Estimates from Fossil Plants

The anatomical features of leaves are highly responsive to changes in ambient climatic and even atmospheric conditions. Taking advantage of several of these features, paleontologists have established a set of novel methods that provide unique information about ancient paleoenvironments. Collectively, these methods illustrate the amazing array of information available through the thoughtful analysis of fossil specimens.

Leaf margin analysis (LMA) and leaf area analysis (LAA) relate to the observation of significant, present-day

FIGURE 9.27 A comparison of bottom-water temperatures, based on Mg/Ca ratios, and the percentage contribution of North Atlantic deep water (NADW) relative to Antarctic bottom water (AABW) in the deep eastern tropical Atlantic Ocean. Age is depicted in thousands of years (kyr). Changes in the contribution of NADW are estimated from stratigraphic variations in $\delta^{13}\text{C}$ [SEE SECTION 10.4], given the observation that NADW and AABW are characterized by different $\delta^{13}\text{C}$ values. Vertical shading denotes glacial (gray) and interglacial (white) intervals of the past 350,000 years. Note that temperature decreases tend to be associated with decreases in the contribution of NADW. (From Martin et al., 2002)



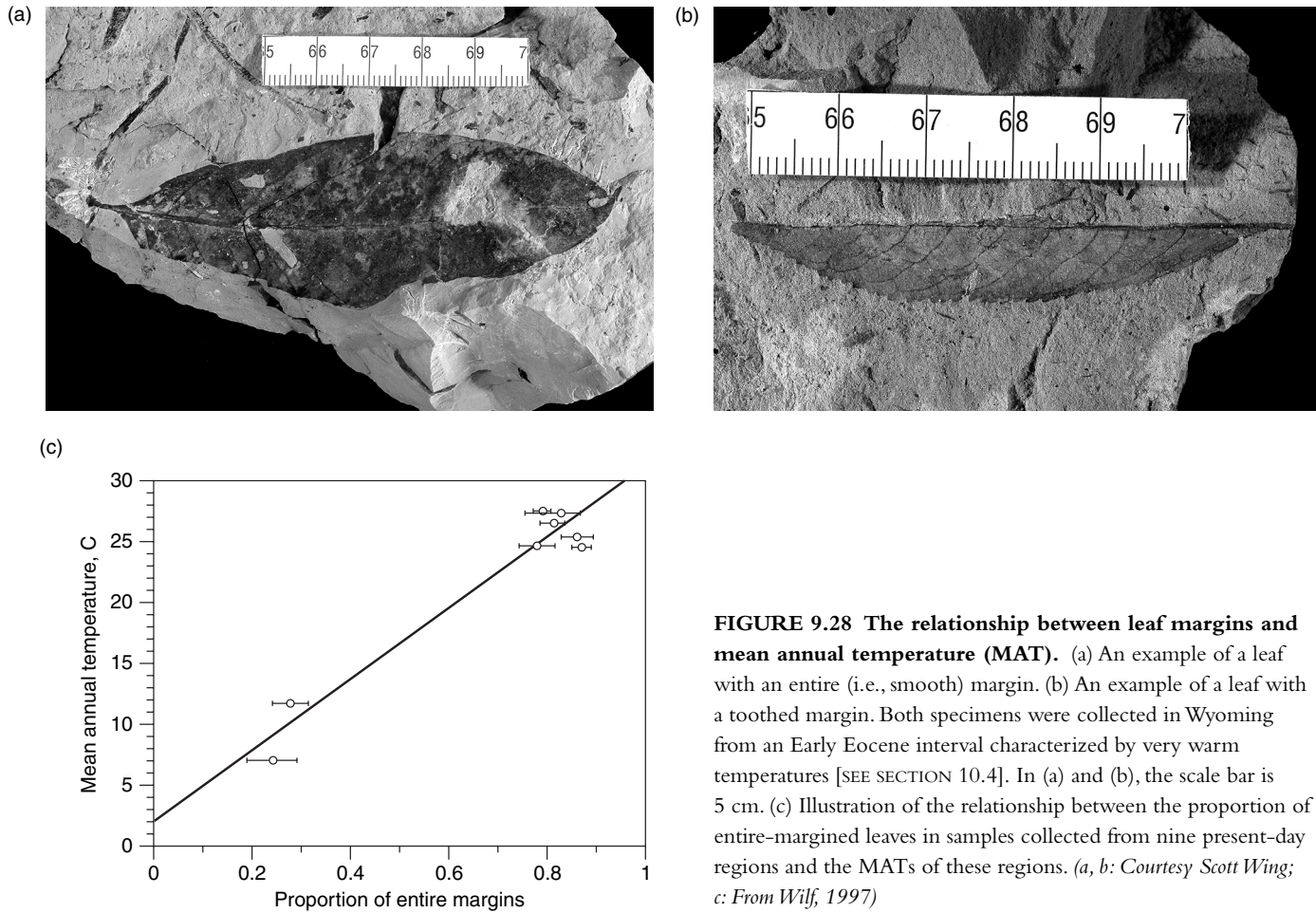


FIGURE 9.28 The relationship between leaf margins and mean annual temperature (MAT). (a) An example of a leaf with an entire (i.e., smooth) margin. (b) An example of a leaf with a toothed margin. Both specimens were collected in Wyoming from an Early Eocene interval characterized by very warm temperatures [SEE SECTION 10.4]. In (a) and (b), the scale bar is 5 cm. (c) Illustration of the relationship between the proportion of entire-margined leaves in samples collected from nine present-day regions and the MATs of these regions. (a, b: Courtesy Scott Wing; c: From Wilf, 1997)

relationships between variations in leaf morphology and climate. LMA is based on the recognition of a consistent, positive relationship between mean annual temperature (MAT) in a given region and the proportion of leaves in the flora of the region that have smooth, untoothed margins (so-called **entire-margined** leaves; Figure 9.28). Inversely, as MAT decreases, the proportional representation in the flora of leaves with toothed margins increases.

While more sophisticated methods have been developed for paleoclimatological reconstruction that make use of a much larger array of leaf characteristics, Peter Wilf (1997) has presented a compelling case that simple LMA is at least as effective as methods that rely on the broader array of characteristics. Similarly, Wilf and colleagues (1998) illustrated a strong positive relationship between mean (average) leaf area and mean annual precipitation (MAP) for a set of 50 samples collected from locations around the world (Figure 9.29), suggesting that LAA can be applied to fossil leaves to estimate paleoprecipitation. An application of LMA and LAA to the fossil record is discussed in Chapter 10 [SECTION 10.4].

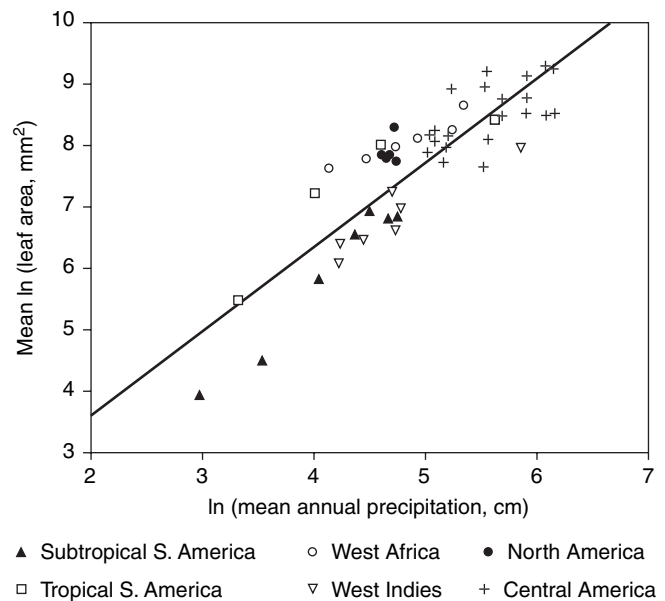


FIGURE 9.29 Illustration of the relationship between mean annual precipitation (MAP) in several regions worldwide and the mean areas of the leaves contained in 50 samples from these regions. (From Wilf et al., 1998)

Finally, botanists have discovered through empirical observations and experiments that the density of **stomata** (tiny pores involved in gas exchange) on the undersides of leaves is sensitive to CO₂ levels in the atmosphere: The number of stomata per unit area decreases as CO₂ levels increase. Given concerns that global warming in the present day is linked to elevated atmospheric CO₂ levels, researchers have investigated historical changes in stomatal density (SD) and have discovered that, indeed, SD has decreased substantially during the past 200 years (Figure 9.30).

Given the relationship between SD and CO₂, paleobotanists have used SD as well as a related metric, the stomatal index (SI), to estimate changes to paleo-CO₂ levels during critical intervals in the Phanerozoic. The SI is measured as $SD / (SD + \text{epidermal cell density}) \times 100$ and is less sensitive than simple SD to potential extraneous factors unrelated to CO₂. Generally, paleobotanists report both values, since the SI is derived directly from SD.

In an analysis of samples collected from southern Sweden and eastern Greenland that span the Triassic–Jurassic boundary, Jennifer McElwain and colleagues (1999) found significant decreases in SD and the

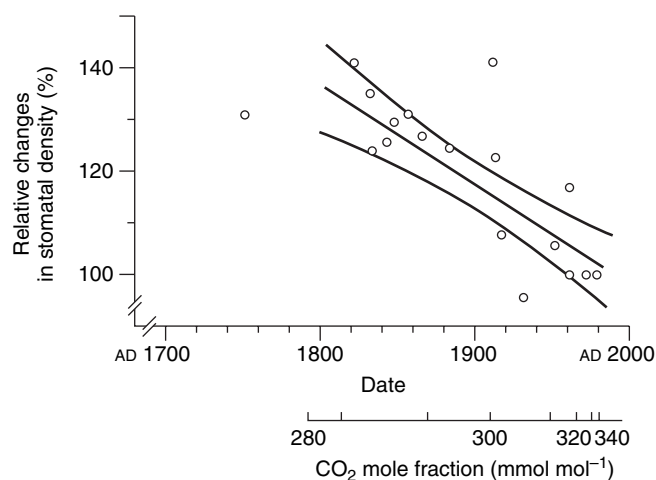


FIGURE 9.30 Illustration of changes through historical time in the stomatal densities of individual specimens for leaves of five different plant species. Measurements illustrated in the graph were collected from specimens that had been stored and dried in a herbarium over the past 200 years. The values are reported as percentages of present-day densities. The two outer lines are 95 percent confidence intervals on the central line, which were fitted to the data. Estimated changes in atmospheric CO₂, based on analyses of ice cores, are also presented in parallel with the x (time) axis to illustrate the relationship with the decline in stomatal densities. (From Woodward, 1987)

SI through the Late Triassic and into the earliest Jurassic (Figure 9.31). Based on the extent of the decrease, McElwain and her colleagues estimated a CO₂ increase that, given the known effects of CO₂ as a **greenhouse** gas, implies a temperature rise of 3° to 4°C. This suggests a role for global warming in a major extinction and turnover of floral species recognized across the Triassic–Jurassic boundary.

The application of LMA, LAA, and stomatal analysis is not problem-free. For example, MAT may be underestimated when LMA is conducted on the leaves of plants that lived adjacent to rivers and lakes (Burnham et al., 2001). With the growing awareness of these biases, however, adjustments to analytical results can be made to account for them.

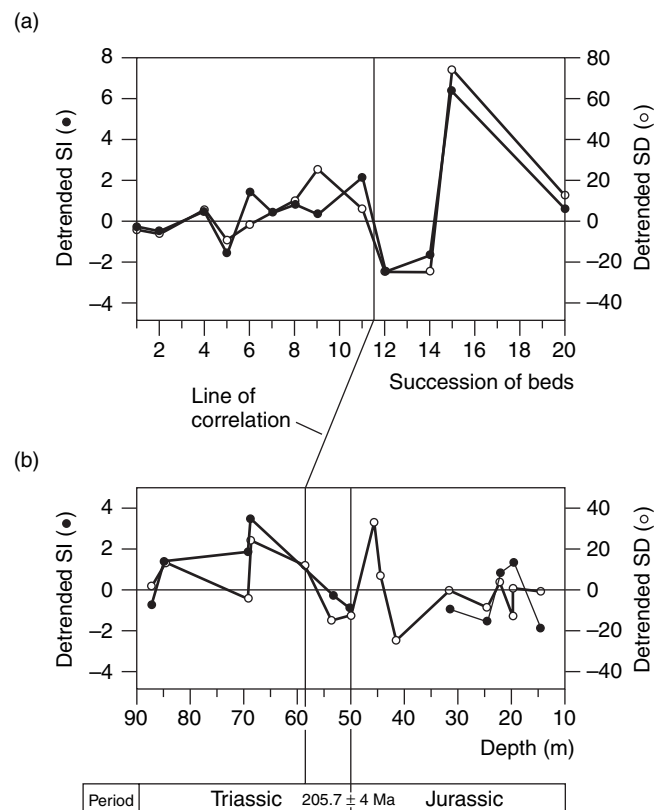


FIGURE 9.31 Changes in stomatal density (SD) and the stomatal index (SI) in samples of fossil leaves collected across the Triassic–Jurassic boundary in (a) southern Sweden and (b) East Greenland. A line of correlation is illustrated between the two regions and is based on the first occurrence of a new flora found in both regions. For both metrics, “detrended” values, which reflect deviations from the overall mean values of the genera analyzed in a given sample, are used in order to overcome bed-to-bed variations in the taxa analyzed. Ma signifies millions of years ago. (From McElwain et al., 1999)

9.6 PALEOBIOGEOGRAPHY

When we consider the environment in which an organism lives, it should be understood that we are speaking mainly of the physical and biological conditions of a particular space, rather than the geometric outlines or location of the space. It is common for an ecologist or paleoecologist to make reference, say, to a mud-covered sea floor or a rocky cliff face, and we expect these and other environments to be characterized by communities of organisms that are or were adapted for life in those settings. Of course, any environment is characterized not by a single physical or biological variable, but by a multitude of variables that interact synergistically. Thus, from an environmental standpoint, no two mud-covered areas of a sea floor are likely to be identical because, even if they are covered by mud of precisely the same grain size and mineralogy, other variables that define these settings, such as temperature or water depth or salinity, are likely to differ at least to some degree. Following the logic of H.A. Gleason that we discussed earlier, we should therefore not expect the taxonomic compositions of the communities present at any two locations to be identical.

In the same vein, we should not expect the species in any community to have identical geographic distributions. It stands to reason that the inherent uniqueness of every species would imply that the environmental requirements, and therefore the geographic distributions of each species, differ at least to some extent.

Assessments of the geographic, as opposed to environmental, distributions of taxa preserved in the fossil record bring us into the realm of paleobiogeography. Given the dynamism through time of the earth from a physical standpoint, we might expect the geographic distribution of any species to be equally dynamic throughout its evolutionary lifetime. In cases where the stratigraphic record provides opportunities to observe changes through time with very high stratigraphic-temporal resolution, this dynamism is, in fact, quite evident.

For example, paleobotanists have studied the stratigraphic records of plant pollen preserved in lake sediments deposited during the late Quaternary Period throughout the world. The abundance records for several species in a 160-m-thick sequence are depicted in Figure 9.32. While these patterns appear to resemble the stratigraphic relationships that we observed earlier for brachiopods in the Ordovician (Figure 9.8c), the temporal duration of the interval covered by the Quaternary data is far shorter, and the temporal resolution is much

finer. In fact, it has been suggested that there is sufficient temporal resolution in these Quaternary sediments to recognize fine-scale ecological transitions. Note, for example, that times of dominance by trees, such as pines (*Pinus*) and oaks (*Quercus*), tend also to be characterized by reduced abundances of grasses (e.g., Gramineae),

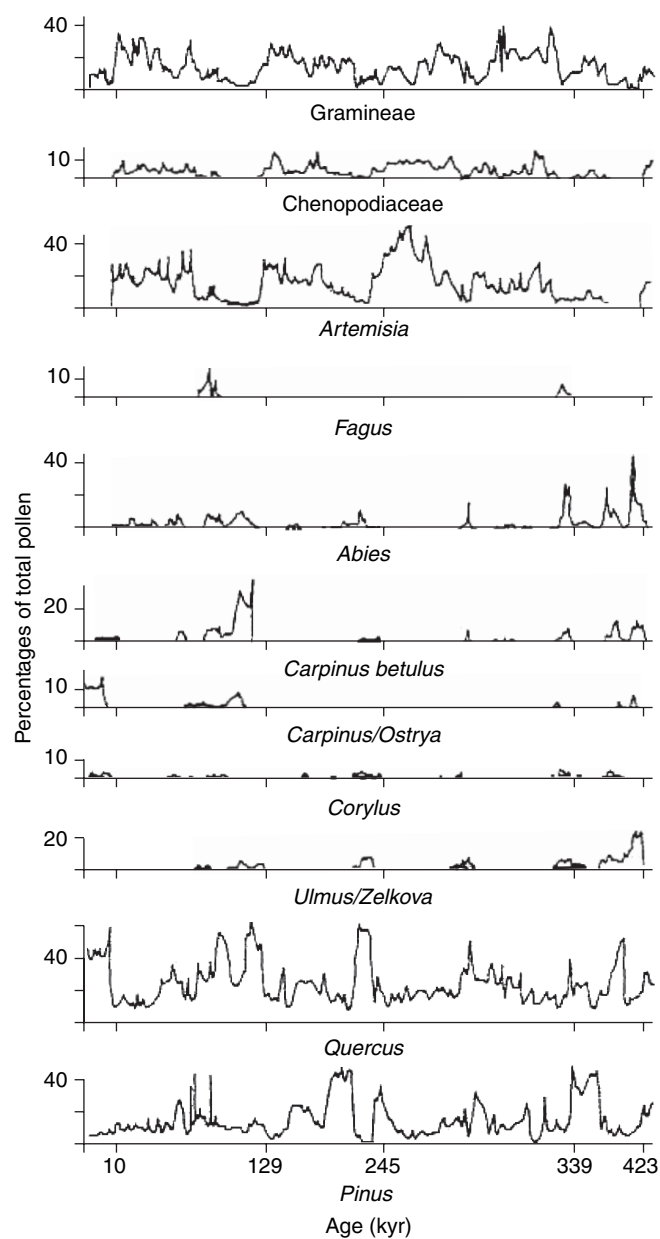


FIGURE 9.32 Abundance records for several different pollen types on a 160-m sequence of Quaternary lake sediments, spanning some 400,000 years, collected in northwestern Greece. Age is depicted in thousands of years (kyr). Note, in particular, the nearly opposite abundance tendencies of *Quercus* (oaks) and *Pinus* (pines). (From Bennett, 1997)

herbs, and shrubs (e.g., *Chenopodiaceae* and *Artemisia*). One such interval occurred just after 245,000 years ago. At other times, trees were subordinate to other groups, at least as indicated by the relative abundances of their pollen.

The dramatically shifting abundances through time apparent at the locality in Greece hint at significant geographic dynamism among the species preserved there. This is particularly evident in the mapping of plant distributions based on pollen data from Holocene sediments preserved throughout Europe, an example of which is shown for oak trees in Figure 9.33. In general, where the fossil record affords opportunities to investigate changes in the geographic ranges of species with resolutions finer than a few thousand years, these ranges have proven to be so dynamic that they have been likened by Keith Bennett, who has evaluated these patterns extensively, to the kneading of dough. By this, Bennett meant that the response of species to a major climatic shift was almost assuredly *not* to be reduced in abundance to the point of extinction, but to exhibit a kind of plasticity in their geographic ranges in rapid response to geographic shifts in climatic belts. Analyses of other biotas, including terrestrial vertebrates and marine molluscs, suggest not only that this is a common phenomenon among species, but also that the ranges of species tend to change independently of one another.

Given this dynamism and independence in the geographic ranges of species, we might be tempted to infer that the geographic ranges of different species are *never* similar to one another at *any* geographic scale. However, it can be demonstrated easily that this is not the case. Consider the Isthmus of Panama, the narrow land bridge that connects North and South America. Because it is a fully emergent feature (or at least was, until the construction of the Panama Canal), it serves as a very effective barrier to migration of marine species between the Atlantic and Pacific sides of the Isthmus. Thus, there is obviously a strong coincidence in the westernmost boundaries of the geographic ranges of many species that abut the Isthmus on the Atlantic side, just as there is a close relationship among the easternmost boundaries of species on the Pacific side.

Geologists who have studied the history of the Isthmus of the Panama know that it was not fully emergent until some 4 to 5 million years ago. Although the emergence was not like the rapid flipping of a switch—prior to which there was free interchange among marine biotas and after which there was a completely opaque barrier to movement between the two sides—it is certainly true that, once the barrier formed, populations and subpopulations of species were cut off from one another. This has resulted in suf-

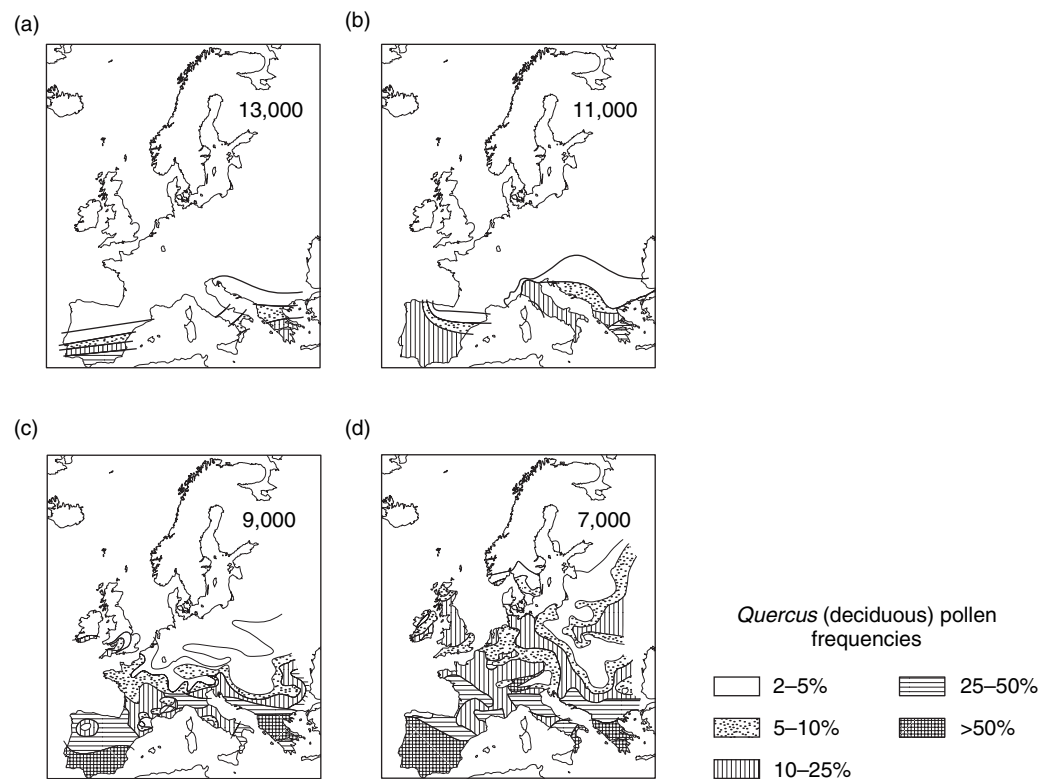


FIGURE 9.33 Map of western Europe, showing the changing distribution and abundance of oak trees, as recorded in pollen records covering a span from 13,000 years ago to 7,000 years ago. (From Bennett, 1997)

ficient divergence on opposite sides of the Isthmus to cause the evolution of sister species.

The Isthmus of Panama is an example of a barrier to the migration and dispersal of organisms that simultaneously affects a large number of species. These kinds of barriers are quite common in nature and are not limited to land bridges that inhibit the movement of marine organisms. In fact, the *lack* of land bridge or some other connection among land masses effectively isolates terrestrial organisms from one another, particularly if they are incapable of airborne dispersal through flight or if they do not possess a developmental stage, such as a pollen or spore stage, during which dispersal by wind is possible.

Throughout the history of life, there are many well-documented examples of cases in which barriers to the movement of terrestrial organisms have come and gone. Some barriers involve the in-place development or loss of waterways through tectonic activity or changes in sea level. Well-known examples include the waterway between North and South America that existed prior to the formation of the Isthmus of Panama, or the waters that currently isolate several islands from one another off the coast of Southeast Asia, but which were previously part of a single landmass when sea level was lower during the Pleistocene.

Other barriers, however, have come and gone as a direct consequence of the movement of continents throughout geologic time. When land masses rift apart, as they have repeatedly in earth history, they carry with them terrestrial biotas that become isolated from one another. What may be less obvious, but is no less true, is that these same land masses are surrounded by shallow marine environments containing organisms that can also become isolated from one another because of the sheer distance that develops among regions that diverge geographically. This is particularly true among marine organisms that become separated by deep ocean basins, especially if they are bottom-dwellers that do not pass through planktonic larval stages during which they might be carried over large distances by ocean currents.

The development of barriers, whatever their scales or causes, results in the formation of **provinces**—groups of taxa with similar geographic ranges that, owing to the presence of the barriers, are geographically separated from other provinces that are similarly bounded. One of the main goals of paleobiogeography has been to understand the history of **provinciality**. Because of differences in the ecological characteristics of various taxa, including their abilities to disperse widely, it should be understood

that at any given time, different taxa may be characterized by different degrees of provinciality; this must be taken into account when mapping out faunal provinces.

Nevertheless, from a practical standpoint, the delineation of ancient provinces has proven to be a valuable tool in determining the relative paleogeographic positions of ancient continents and smaller land masses known as **terranes**. As an example, there is a region in present-day Argentina known as the Precordillera, which contains a suite of Ordovician rocks and fossils that is unique in comparison to the strata contained in adjacent areas. Interestingly, this interval contains in its oldest portions a biota that is similar taxonomically to that preserved in rocks of the same age in parts of present-day North America. However, younger intervals in the Precordillera contain a biota that exhibits growing taxonomic similarities with strata preserved nearby, in present-day South America (Figure 9.34a). These data support the still-controversial view that the Precordillera was a terrane that became separated from the paleocontinent of Laurentia (an ancient portion of present-day North America) and subsequently moved southward, where it collided with the ancient Gondwanan supercontinent, which included South America (Figure 9.34b).

9.7 CONCLUDING REMARKS

Admittedly, this chapter has covered much ground, but there is a simple explanation for this: The subdiscipline of paleoecology has been expanding at a remarkable rate. In the 1960s, the study of paleocommunities was the major conceptual theme in paleoecology, but this was supplemented in the 1970s and 1980s by evolutionary paleoecological investigations that incorporated the geologic time dimension. During the 1980s and 1990s, paleoecology expanded again with the infusion of an ever-growing palette of techniques that provide sophisticated means for high-resolution paleoenvironmental reconstruction. Given the excitement generated by the continued development of these new methods, it is tempting to downplay the earlier themes. However, beyond the desire to describe the intellectual roots of the subdiscipline, there is another reason to consider anew paleocommunities and related topics: These remain as important conceptual themes in paleontology.

For example, the study of metapopulations, which we discussed briefly in this chapter, requires an understanding

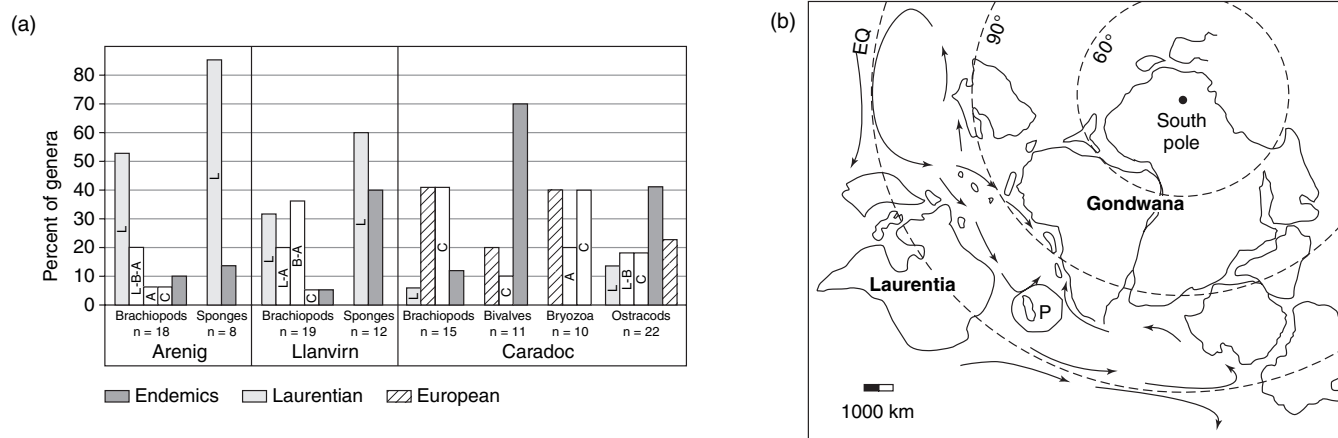


FIGURE 9.34 An assessment of the paleobiogeography of the Precordillera region of South America. (a) The changing biogeographic affinities of taxa preserved in the Precordillera region of South America from the Arenig (Early Ordovician) to the Caradoc (Middle and Late Ordovician). Note, in particular, the decreasing affinity with Laurentian forms. [Key to locations of genera (see Figure 8.25 for a complete depiction of these paleocontinents): L = Laurentia; L-A = Laurentia and Avalonia; L-B = Laurentia and Baltoscandia; L-B-A = Laurentia, Baltoscandia, and Avalonia; C = **cosmopolitan**] (b) Paleogeographic map for the Early Ordovician, depicting the position of the Precordillera (P, circled) roughly midway between Laurentia and the portion of Gondwana that includes present-day South America. (From Benedetto et al., 1999)

of the extent to which the fine-scale spatial distributions of organisms preserved in the fossil record can be shown to reflect a biological signal rather than post-mortem processes. As we have suggested in this chapter, there are reasons to believe that the patchiness evident in biological communities can be preserved in the fossil record, but

we still have a long way to go before we can estimate the extent to which this is the case among taxa that lived in a variety of marine and terrestrial settings.

As we will see in Chapter 10, another unique new paleoecological theme is emerging in the study of recent, human-induced changes to present-day settings.

SUPPLEMENTARY READING

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