C h a p t e r   6

BIOSTRATIGRAPHY

Because it is an historical science, a central goal of pale-ontology is to determine the relative timing of any given set of events, even if the events took place in geograph-ic locations that were far apart. For example, if we want to know whether a time interval was characterized glob-ally by a mass extinction [SEE SECTIONS 8.6 AND 10.3], we must first figure out whether sets of extinction events recognized in different places around the world actually occurred simultaneously. The assessment of age relation-ships such as these is a major goal of **biostratigraphy,** the study of the geometry, biotic composition, and time relations of fossiliferous rocks.

Since its inception, biostratigraphy has relied on a set of basic principles concerning the stratigraphic ranges of taxa preserved in the fossil record, and these have per-mitted the development of a global geologic timescale. More recently, however, numerical methods have been developed that seek to combine information on the stratigraphic ranges of taxa contained at several separate localities, providing correlations at much finer scales of resolution than is generally possible by traditional bio-stratigraphic means.

Biostratigraphy has also been transformed in recent years by the advent of **sequence stratigraphy,** which focuses on the processes that produced sets of strata. Se-quence stratigraphers aim to recognize fundamental, re-peated units of stratigraphic architecture, **parasequences** and **sequences,** that can be used as bases for correlation in their own right. It has also been recognized that fossil distributions tend to be affected predictably by the same depositional processes that produce the sequences. These patterns must be diagnosed and understood if paleontol-ogists are to make full use of regional variations in the fossil content of rocks in studies of taxonomic origination and extinction.

We begin this chapter with a review of several fun-damental principles of biostratigraphy and their utility for constructing a global geologic timescale. Then we turn to the palette of quantitative techniques that have greatly enhanced the ability of biostratigraphers to cor-relate fossiliferous rocks at high resolution. Finally, we consider the new generation of stratigraphic models that help to diagnose the fundamental architecture of the fos-sil record and its effects on regional biotic patterns in space and time.

6.1 THE NATURE OF BIOSTRATIGRAPHIC DATA AND CORRELATION

All biostratigraphic methods require a detailed accounting of the occurrences and, in some cases, abundances of taxa within a set of strata under investigation. At any given out-crop, a worker can seek to determine the stratigraphic lim-its to the distribution of any fossil taxon that is present. We can refer to this interval as the **stratigraphic range** of the taxon, bounded at the base by the taxon's **first ap-pearance datum (FAD)** and at the top by its **last ap-pearance datum (LAD).** The FAD and LAD constitute the fundamental data for many approaches to biostratig-raphy. Of course, it is highly unlikely that this local strati-graphic range encompasses the entire global stratigraphic range of the taxon. In most cases, what we know about the
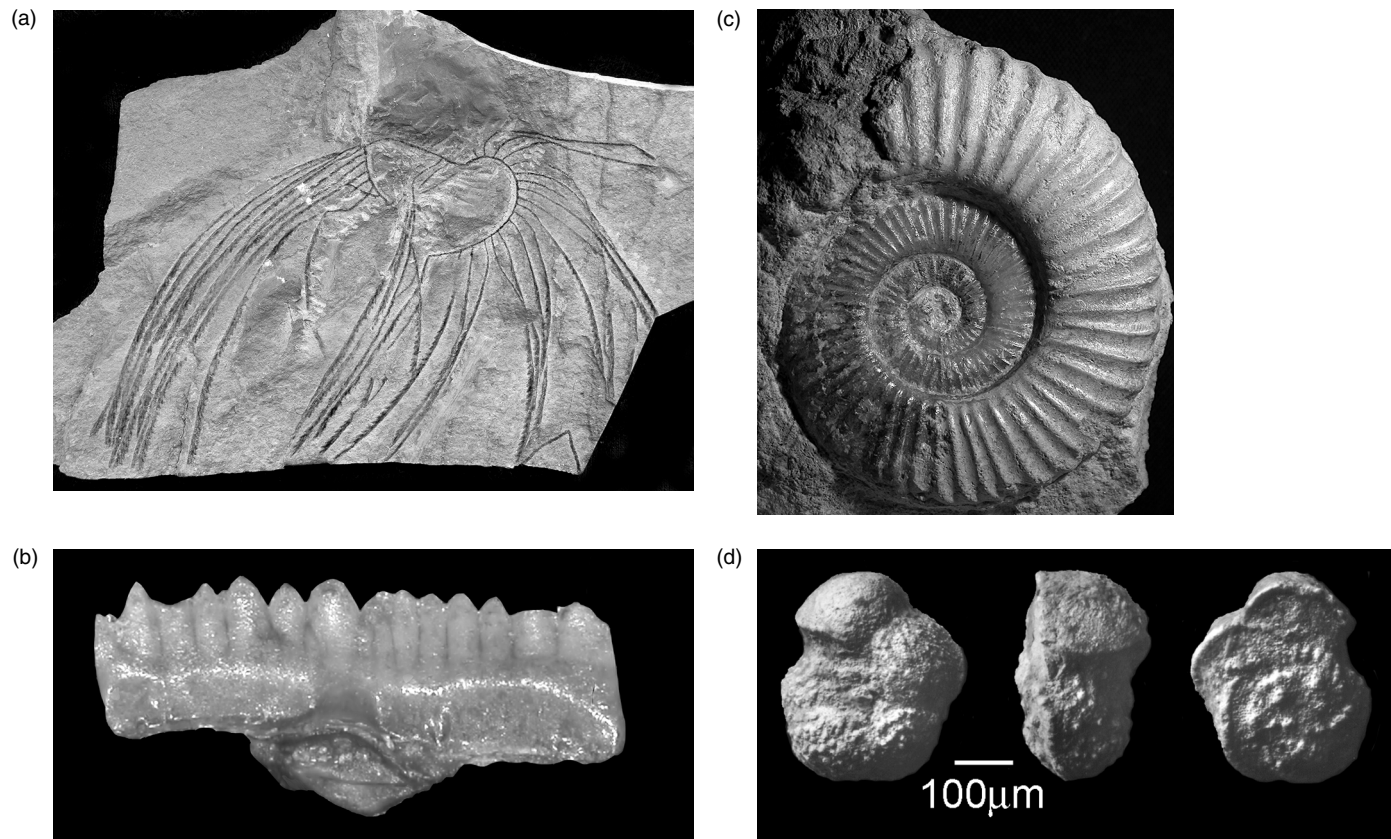
FIGURE 6.1 Examples of common index fossils from throughout the Phanerozoic. The sizes and nature of these examples are highly variable, but they were all associated with organisms that were capable of wide geographic dispersal. (a) A colony of the graptolite *Nemagraptus gracilis*, contained in a piece of the Ordovician Athens Shale, in Alabama (horizontal field of view is 12 cm). (b) An element of the conodont *Ozarkodina remscheidensis eosteinhornensis* (horizontal field of view is 1200 microns). (c) The ammonite cephalopod *Uptonia jamesoni*, from the Jurassic of France (approximate diameter is 9.6 cm). (d) The planktonic foraminiferan *Gansserina gansseri*, from the Late Cretaceous (note 100 micron scale at bottom). *(a: From Prem Subrahmanyam's online fossil gallery, www.premdesign.com/fossil.html; b: Museum of Natural History, London; c: Courtesy Hervé Châtelier's Jurassic and Cretaceous ammonite database, http://perso.wanadoo.fr/herve.chatelier/; d: Smithsonian National Museum of Natural History)*

global stratigraphic ranges of taxa is based on composites of information from several localities. Moreover, the preserved global stratigraphic range of a taxon is unlikely to preserve its entire true temporal range. Because the majority of individuals belonging to any species are not likely to be preserved in the fossil record, the true time of origination of any taxon almost certainly predates its first documented appearance in the fossil record, and the true time of extinction almost certainly postdates its last documented appearance.

Barring the intervention of post-mortem processes that disturb its stratigraphic position, the presence of the same taxon at any two localities permits a paleontologist to make a simple but important statement of **correlation** about the strata at these localities: The strata must have been deposited during the evolutionary lifetime of the taxon. Of course, this statement is of real value only if the taxon in question is confined to a small global stratigraphic range. In general, for correlating strata in this way, biostratigraphers endeavor to use taxa (generally species) that have two important properties: (1) They are of limited stratigraphic duration; and (2) they are geographically and environmentally widespread, ideally occurring in a variety of rock types worldwide.

Taxa with these properties, known as **index, guide,** or **zone** fossils, have been used widely in the correlation of Phanerozoic strata, and global biostratigraphic inter-
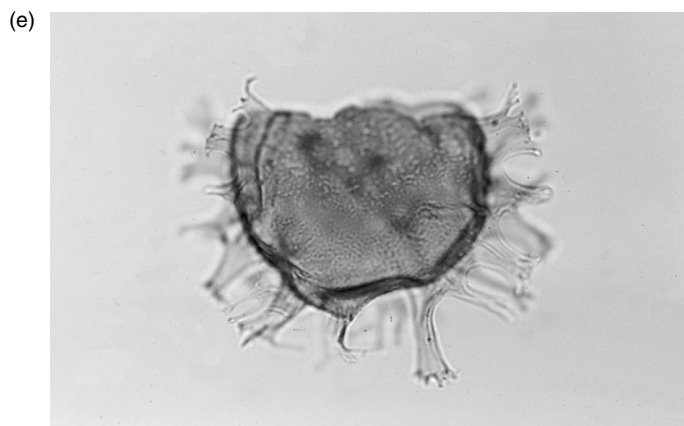
(e)

FIGURE 6.1 (*cont.*) (e) Walled cyst of the dinoflagellate *Chiropteridium galea,* from Oligocene sediments in a deep-sea core collected off the coast of Tasmania (approximate length from left to right of the main, dark shaded region is 60 microns). (*From Williams et al., 2003*)
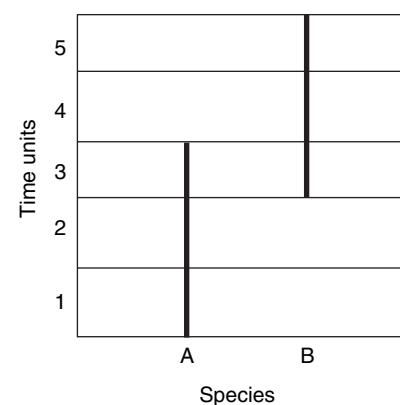

FIGURE 6.2 A simplified, hypothetical example that illustrates the use of overlapping ranges as a means to refine relative age determinations. In this **range chart,** the known stratigraphic ranges of two fossil species, A and B, are depicted, based on previous cataloguing of these species in strata from around the world. If a paleontologist found only individuals belonging to species A in a sedimentary stratum, she could assume that the stratum was deposited sometime in the range of time units 1 through 3 (barring post-mortem processes that affected the position of the fossil, relative to where it lived). If she found only species B in the stratum, then a time of deposition in the range of time units 3 through 5 would be implied. However, if she found that species A and B were *both* present, then the time range could be narrowed to unit 3 since this was the only interval during which species A and B are known to have coexisted (i.e., these species exhibited overlapping ranges encompassing only time unit 3).

vals have often been recognized on the basis of one or more pervasive, diagnostic fossil species. Formally, such an interval is referred to as a **zone** or **biozone.** In general, marine organisms that floated or swam in the water column, and terrestrial organisms that possessed components capable of windborne dispersal, are best suited as zone fossils because of the greater likelihood that they will be widespread (Figure 6.1).

In cases where the stratigraphic ranges of fossil taxa are too long for the taxa to be useful individually for correlation, they may nevertheless be useful *in combination* with the occurrences of other taxa. At its simplest level, this involves the diagnosis and use of **overlapping** (or **concurrent**) **ranges** among taxa (Figure 6.2). Even if two or more taxa exhibit long stratigraphic ranges, the interval of geologic time during which these taxa were extant *simultaneously* may have been far more limited. In such instances, the co-occurrence of these taxa permit correlations among strata in different venues that may be far more refined than what would be possible if only one of the taxa were present.

Primarily through the use of these biostratigraphic tools, a global geologic timescale has emerged (see inside front cover of this book). Whereas zones are demarcated based on the stratigraphic occurrences of individual fossil species or limited assemblages of species, more profound boundaries between **stages** and **series,** which tend to be local or regional in scope, as well as **systems** and **eras,** which are global in scope, are marked

by the near-simultaneous loss of larger numbers of taxa and their replacements by other taxa. In fact, as we will see when we consider the history of global biodiversity (Chapter 8), biotic changes can be particularly profound at system and, especially, era boundaries.

The absolute ages of important boundaries have been subsequently determined using radiometric dating techniques, which permit the calibration of geologic time intervals that correspond to the aforementioned stratigraphic intervals. Samples appropriate for radiometric analysis, which are typically volcanic in origin, have been difficult to obtain for many important boundaries, and the absolute calibration of the timescale has therefore not been straightforward. As researchers discover new materials from key horizons that are suitable for absolute dating and continue to refine methodologies used for absolute age determination, we can expect significant improvements to previous estimates of absolute ages, as well as the addition of age determinations for key boundaries that have heretofore not been dated.

For example, analyses in the past decade and a half of a suite of samples obtained from lowermost Cambrian rocks in northeastern Siberia by Samuel Bowring and colleagues (1993) have led to a recalibration, to 544 million years ago (Ma), of the Proterozoic–Cambrian boundary. This stands in contrast to previous estimates that generally depicted the boundary as some 30 million years older. In this case, the reason for the refined estimates was twofold: (1) The samples used for dating were linked more definitively to the boundary than previous suites of samples; and (2) the method used for dating, which relied on the decay of two different isotopes of uranium that could serve as cross-checks on each other, were more reliable than previous methods based on other isotopes.

There are two operational limitations to the use of zone fossils or overlapping ranges as tools of correlation. First, it is appropriate to use biostratigraphic markers only in a positive way. If a stratum does not contain a fossil that is considered diagnostic of a particular stratigraphic interval, this does not necessarily imply that the stratum was not deposited during the interval in question. Even the most ubiquitous zone fossil is likely to be absent from a significant percentage of the strata deposited during the interval in which the taxon was extant, either because the taxon did not live at the locations represented by those strata or because it was removed after its death by taphonomic processes. In some important stratigraphic intervals (e.g., parts of the Ordovician System), it has been difficult to identify reliable and globally ubiquitous biostratigraphic markers; parts of the global timescale therefore remain in flux.

Second, there are limits to the degree of temporal resolution possible with these methods, owing to the simple fact that fossil species tended to persist for several million years [SEE SECTION 7.2]. For many paleobiological questions in which morphological and ecological patterns are assessed in space or through time, it would be useful to have a stratigraphic framework that permits much finer temporal acuity, at least on a regional basis.

6.2 COMPOSITE METHODS OF CORRELATION

Recognizing the need to develop timescales that are more highly resolved, biostratigraphers are adopting newer, more sophisticated methods that combine data on FADs and LADs from several outcrops into single, composite "sections." These composites can then be used as timescales that not only depict the order of all the events (i.e., the FADs and LADs) that they include, but can also serve as references for determining the probable stratigraphic placement of additional outcrops that are evaluated at some later date. In this respect, the methods we consider here have much in common, but they differ from one another in the ways that those data are assembled and treated to construct the composites. They are worth reviewing not only because of their growing usefulness, but because they illustrate well the jigsaw-puzzle-like challenge of piecing together information from a disparate set of localities.

Graphic Correlation

First proposed by Alan B. Shaw (e.g., 1964), the fundamental principles of graphic correlation can be illustrated by first considering the case of two outcrops, A and B, presented as examples in Figure 6.3. Using conventional biostratigraphic methods, a paleontologist would seek to correlate directly the FADs and LADs of taxa present jointly at *both* outcrops (taxa 5 and 9 in Figure 6.3a). However, several additional taxa are present uniquely at each outcrop, and it would obviously be desirable to combine all of the stratigraphic range information from the two outcrops so that we could know the relative order of *all* FADs and LADs preserved at the two outcrops. This is accomplished with graphic correlation by first developing a **line of correlation (LOC)** between the two outcrops based on the events that they share, and then superimposing onto the LOC the additional biological events from each outcrop. The methodology for determining the LOC is described in Box 6.1.

Once the LOC is defined, events that are unique to outcrop A can be projected onto outcrop B (Figure 6.3e), providing a composite of all of the biological events preserved at both localities, thereby resulting in a **composite standard reference section** or, more simply, the **composite standard (CS).** At this point, the power of graphic correlation becomes evident because the procedure is not limited to the two initial sections. It can be repeated indefinitely by correlating additional outcrops with the CS, which continues to mature so long as taxa not recognized previously continue to be incorporated graphically into the CS.

(a)

(b)

(c)

(d)

(e)
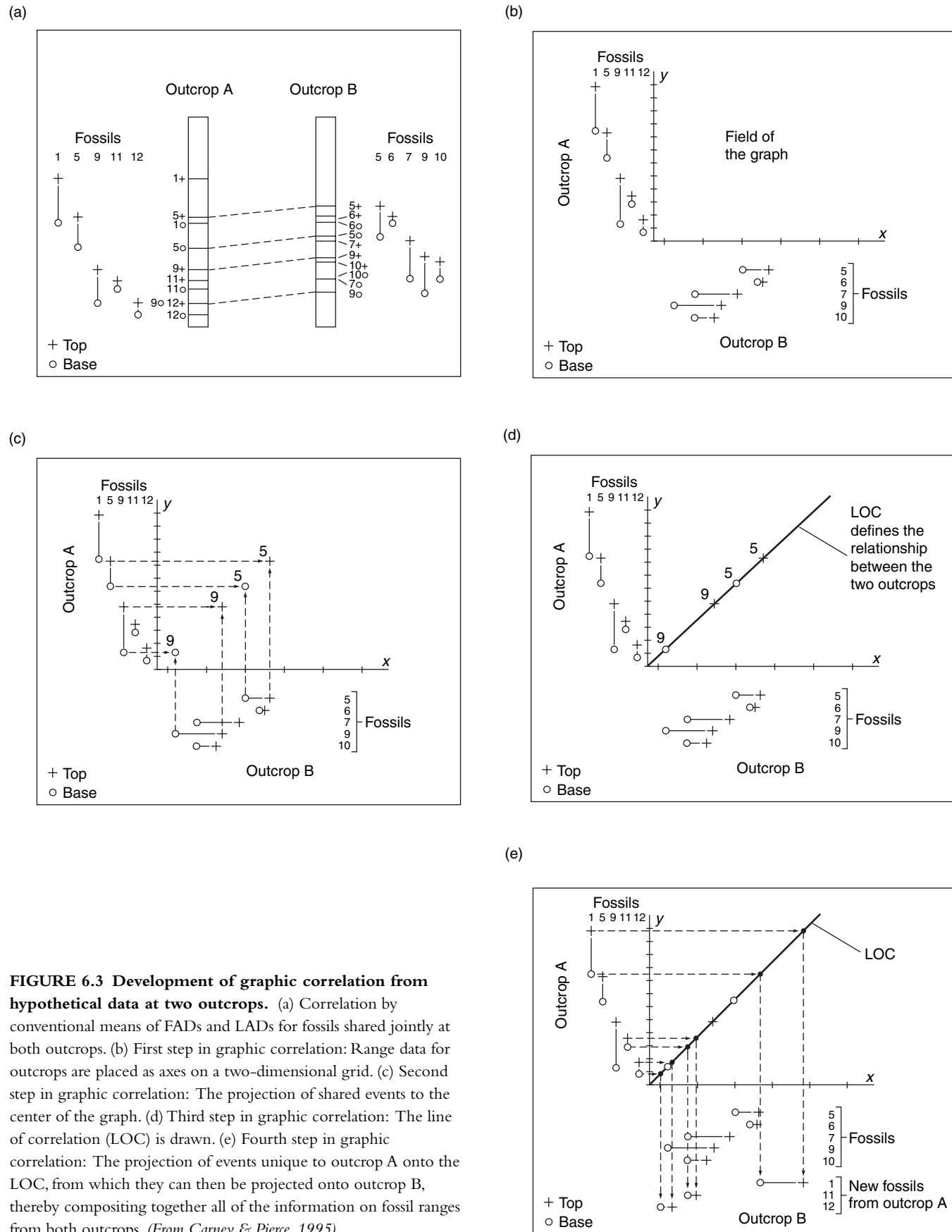
FIGURE 6.3 Development of graphic correlation from hypothetical data at two outcrops. (a) Correlation by conventional means of FADs and LADs for fossils shared jointly at both outcrops. (b) First step in graphic correlation: Range data for outcrops are placed as axes on a two-dimensional grid. (c) Second step in graphic correlation: The projection of shared events to the center of the graph. (d) Third step in graphic correlation: The line of correlation (LOC) is drawn. (e) Fourth step in graphic correlation: The projection of events unique to outcrop A onto the LOC, from which they can then be projected onto outcrop B, thereby compositing together all of the information on fossil ranges from both outcrops. *(From Carney & Pierce, 1995)*

Box 6.1

GRAPHIC CORRELATION

In graphic correlation, the stratigraphic–range data for each section are placed at right angles to one another, as axes of a two-dimensional grid, with distances along each axis corresponding to distances above the base of each section. By convention, the section with the greater number of events is placed along the *x* axis (Figure 6.3b)—although, in this example, outcrops A and B contain equal numbers of taxa. As a next step, the events common to both sections (i.e., the FADs and LADs of taxa 5 and 9) are projected, horizontally in the case of the section on the *y* axis and vertically in the case of the section on the *x* axis, to the center of the graph (Figure 6.3c). The points where the projections from the two axes meet on the graph define the LOC between the two outcrops (Figure 6.3d).

In the idealized example of Figure 6.3, note that the two outcrops are of equal thickness; thus, the LOC resides at a 45° angle to each axis. This is typically not the case, however. If one outcrop exhibits a greater thickness than the other outcrop for the

same stratigraphic interval, then the slope of the LOC will fall closer to the axis of the thicker outcrop than it will to that of the thinner one (Figure 6.4a). Moreover, in the real world, it is highly unlikely that all FAD and LAD events correlated among two outcrops will fall precisely on a straight line. For example, in cases where intermittent variations in stratigraphic thicknesses exhibited at one outcrop are not matched in corresponding intervals at the other outcrop, a connecting together of the "dots" representing joint FADs and LADs would result not in a straight line, but in a line that contains meanders (Figure 6.4b). Finally, because of preservational issues, the sequence of FADs and LADs for the same fossils (i.e., shared events) at two outcrops will not always be identical. The derived LOC might therefore have to accommodate contradictions among localities in the order of shared events. Numerous protocols have been proposed for numerically estimating the LOC in the event of these complications, some of which we discuss later.
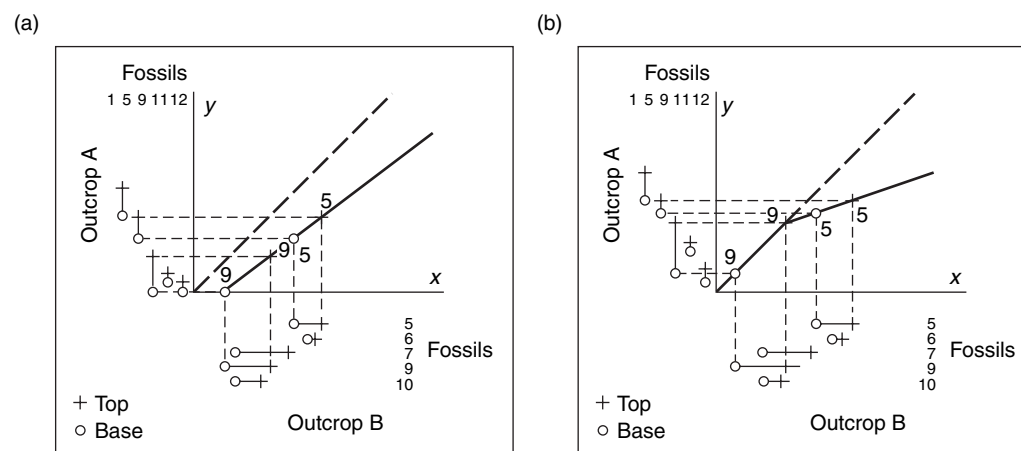
FIGURE 6.4 Deviations from the straight line of correlation (LOC), with a slope of 1, illustrated in Figure 6.3. (a) The stratigraphic thickness of outcrop A and the ranges of the fossil species that it contains are reduced relative to Figure 6.3. Outcrop B is unchanged. The resultant LOC (solid line) is shifted downward, and the slope decreases, relative to the original LOC (dashed line). (b) The lower portion of outcrop A remains the same as in Figure 6.3, but a localized decline in sediment accumulation rate coinciding with the FAD of species 5 results in a reduction of thickness thereafter. Outcrop B is unchanged. In this instance, the "true" LOC (solid line) deviates from the trajectory of the original LOC (dashed line) above the LAD of species 9.

This process is illustrated in Figure 6.5. By convention, the CS is placed along the *x* axis of the two-dimensional Cartesian grid, and the additional outcrop to be correlated to the CS is placed along the *y* axis. Note that the units designated along the *x* axis in this example do not correspond to distances above the base of a single outcrop but are reported as **composite standard units (CSUs).** The values for the CSUs in this example are derived from a timescale for Paleocene through Oligocene planktonic **FORAMINIFERIDA** developed by the former Amoco Oil Company. The global ranges of these species in the composite standard had already been established firmly in CSUs based on previous biostratigraphic analyses.

As before, the LOC is drawn based on the FADs and LADs of taxa present jointly at the outcrop and in the CS (taxa 1 and 9, as shown in Figure 6.5a). The ranges of two additional taxa present uniquely at the outcrop (taxa 2 and 4) are then projected onto the LOC (Figure 6.5b). On this basis, the outcrop has been correlated to the CS and, at the same time, the CS has matured further, through the addition of the FADs and LADs of two additional taxa. Therefore, as the CS for a given region continues to mature, it not only provides a means of correlating outcrops throughout the region with increased resolution, but it also provides a regional timescale, recording the order of biological events represented by the FADs and LADs of taxa. In practice, the events correlated graphically need not be biological and can include discrete physical events. For example, volcanic ash falls are sometimes preserved in the stratigraphic record as **bentonites,** clay layers that can be recognized at numerous localities, sometimes over broad geographic ranges.

Appearance Event Ordination

The procedure in graphic correlation of adding one locality at a time to the CS necessarily places greater weight on information added early in the process. If there were no contradictions in the information on stratigraphic ranges available from different localities, this would not be a problem. However, such contradictions are virtually inevitable because of preservational and lithological differences from locality to locality, and the CS becomes constrained increasingly as data from more and more localities are added to the composite, thereby favoring the information from localities added earlier. By contrast, the family of methods that we consider next all involve the simultaneous assessment of data from multiple localities.

Even in cases where there are no contradictions among a set of localities in the FADs and LADs of the

FIGURE 6.5 Projection of stratigraphic data from an additional outcrop onto the composite standard (CS). (a) Construction of the LOC between the new section (outcrop C) and the CS. (b) Projection of FADs and LADs for taxa unique to outcrop C (taxa 2 and 4) onto the CS. *(From Carney & Pierce, 1995)*

taxa that they share, the stratigraphic ordering depicted for some of these events in a composite section may nevertheless be incorrect. As a simple, if somewhat extreme, example, consider a case in which the evolutionary origination of some widespread taxon A preceded that of another widespread taxon B, but, simply by chance, depositional and taphonomic processes throughout an entire study area remove any evidence of taxon A in strata below those containing the FAD of taxon B. In such a case, the data from all localities would therefore be unanimous in depicting the FAD of taxon B in a position below that of taxon A, and a composite section would therefore depict incorrectly the first appearance of taxa B as preceding that of A.

More generally, if we consider the relative ordering of the FADs or that of the LADs for any pair of taxa preserved at an outcrop, it is always possible that additional sampling will reverse the ordering of either pair of events (Figure 6.6). However, if at some outcrop, we observe that taxon A occurs in strata that are below, or overlap with, strata that contain taxon B, there is one statement that will remain incontrovertible regardless of how much more sampling we conduct at the outcrop or anywhere else in the world (barring post-mortem reordering of taxa): The FAD and, indeed, the evolutionary first appearance of taxon A must predate the LAD and the
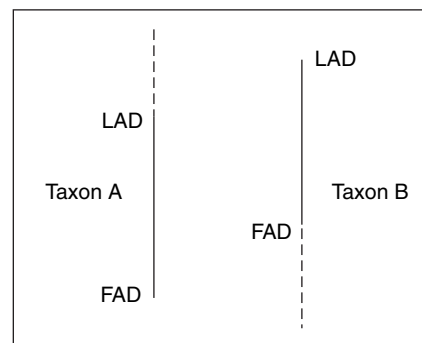
FIGURE 6.6 Schematic representation of the stratigraphic ranges of two hypothetical taxa at an outcrop. Solid lines depict the known ranges of each taxon. Based on these ranges, we can state that the FAD of taxon A precedes that of taxon B, and the LAD of taxon A precedes that of taxon B. However, if, with additional sampling, we extended the observed stratigraphic ranges of each taxon to include the dotted portions of each range, both of these statements would be overturned. By contrast, no amount of additional sampling at this locality or any other will overturn two additional statements that we can make: The FAD of taxon A precedes the LAD of taxon B, and the FAD of taxon B precedes the LAD of taxon A.

extinction of taxon B (Figure 6.5). This must be so because, while additional sampling could revise the FAD of taxon A down or the LAD of taxon B up, it cannot negate the overlap already observed in the ranges of the two taxa. Similarly, if taxon A overlaps stratigraphically with taxon B, it must also be true that the FAD of taxon B predates the LAD of taxon A.

John Alroy's (1994a) **appearance event ordination (AEO)** makes exclusive use of these incontrovertible observations, called **F/L statements.** Not all F/L statements will be preserved at all localities in a region under investigation, and AEO is designed to piece together a CS from the combination of information preserved at all localities. The basic principles of AEO are described in Box 6.2.

Note that, in the example presented in Box 6.2, the positioning of events in the CS is relative; no absolute indication is provided for the timing of these events. However, as with graphic correlation and the other methods we will consider, a CS generated by AEO can be calibrated to an absolute timescale based on correlations of some of the events to horizons from which absolute dates have been collected.

Constrained Optimization and Ranking and Scaling

While F/L statements are incontrovertible, this of course does not imply that other kinds of relationships observed among events are necessarily incorrect; the inclusion of these additional events, assuming that we can trust them, can obviously help to further refine a CS. **Constrained optimization (CONOP)** is a procedure that makes broader use than AEO of the stratigraphic events recognized collectively at a set of localities. As part of the procedure for CONOP, impossible solutions are first eliminated (constraint) and the best of all possible solutions is identified quantitatively (optimization).

At the outset, in constraining the roster of possible solutions, any solution can be viewed as impossible if it violates observations known to be incontrovertible. For example, it would obviously be inappropriate to establish a sequence in which the first appearance of any species is placed after its last appearance. Likewise, if the ranges of two species, A and B, are observed to overlap at any outcrop, we know from our discussion in the last section that the FAD of taxon A must precede the LAD of taxon B and the FAD of taxon B must precede the LAD of taxon A. Clearly, any solution that suggests otherwise would be incorrect.

Box 6.2

APPEARANCE EVENT ORDINATION (AEO)

As a first step in appearance event ordination (AEO), consider the three hypothetical localities in Figure 6.7a, depicting the stratigraphic occurrences of five species. Not all species are preserved at all localities, and species may occur in multiple horizons at any given locality. A list of F/L statements derived from the information at each locality is provided in Figure 6.7b. By convention, these statements are presented with a syntax of $X < Y$, which means that the FAD of taxon X predates the LAD of taxon Y.

For example, at section 1, we know that, because taxa 1 and 2 co-occur in the same horizon at locality 1, the following statements must be true: $1 < 2$ and $2 < 1$. Similarly, because taxon 3 occurs strati-graphically above taxon 1 at locality 1, we also know that $1 < 3$. However, it would not be appropriate to say that $3 < 1$ because taxon 3 does not occur at or below the horizon that contains taxon 1.

We can summarize the information from Figures 6.7a and 6.7b in the matrix presented in Figure 6.7c: Instances in which FADs (rows) predate LADs (columns) are designated with the symbol $<$. Although it is inevitable that the FAD of any taxon must predate its own LAD, we include these statements in the matrix because we will depict these events in our CS.

From the information in the F/L matrix, we construct a *composite event sequence* (really, the CS), as depicted in Figure 6.7d. We begin by first finding all taxa
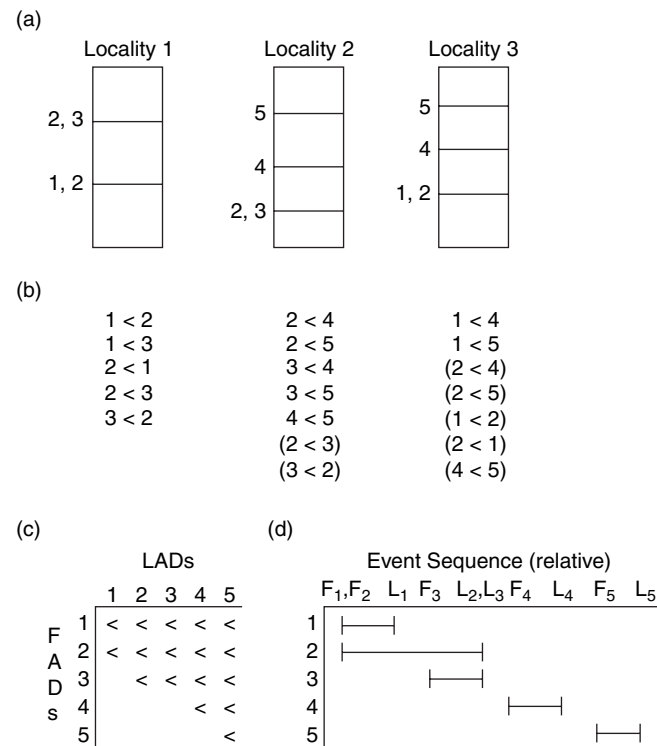

FIGURE 6.7 Illustration of the principles of appearance event ordination (AEO). (a) Occurrence data for five hypothetical taxa, numbered 1 through 5, at each of three hypothetical localities. Horizontal lines indicate the stratigraphic positions of collections at each locality, and the numbers to the left designate the taxa found in these collections. (b) A list of the F/L statements that can be made for each outcrop. Statements in parentheses repeat those already made at a previous locality. (c) A matrix that summarizes the information provided in part (b). (d) Composite event sequence for these taxa $(F_y = FAD_y; L_y = LAD_y)$. *(Based on an example presented by Alroy, 1994a)*

Box 6.2 (continued)

---

with FADs that predate the first LAD; in this instance, we recognize in Figure 6.7c that FADs 1 and 2 predate LAD 1, so we depict these events sequentially in Figure 6.7d (i.e., FAD 1 and FAD 2 together, followed by LAD 1). We then repeat this process, determining which FADs precede the subsequent LADs, until our entire event sequence is determined.

LAD 1 predates FAD 3 because there is no evidence of stratigraphic overlap between taxa 1 and 3, and the stratigraphic range of taxon 1 resides entirely below that of taxon 3. By contrast, there is a stratigraphic overlap between taxa 2 and 3, and, therefore, FAD 3 predates LAD 2 (i.e., 3 < 2). Note that LAD 2 and LAD 3 are grouped in tandem in the sequence because, based on the available evidence, we have no way of discriminating the relative timing of these two events (the same is true of FAD 1 and FAD 2). Their grouping should

therefore *not* be taken as a definitive indication that the two events took place simultaneously.

In perusing the CS, it might not seem clear, at first, how we can be certain of the sequence depicted. For example, how do we "know" that FAD 4 postdates LAD 3? The answer is that we can never be completely certain of this because it is always possible that, at some later date, we will find evidence, say, of stratigraphic overlap in the distributions of taxa 3 and 4. However, for the moment, all available events point to the stratigraphic range of taxon 4 entirely postdating that of taxon 3, so FAD 4 is depicted as occurring after LAD 3. While, as we noted earlier, individual F/L statements are incontrovertible, the sequence of FADs and LADs exhibited by a set of taxa may continue to evolve with the addition of new data, and therefore we may well add F/L statements in the future.

In developing an *optimized* solution, a CS is established for the events preserved in aggregate among all localities. When one works with a large number of taxa and localities, it is almost unavoidable that individual localities will preserve some events in an order different from that of the CS because, as we noted earlier, there will likely be some contradictions in the relative orders of FADs and LADs for taxa shared among localities. An additional objective, therefore, is to develop an optimal (re)ordering of events at each locality that maintains the order established for the CS in the first step. A schematic description of how this is accomplished is presented in Box 6.3.

In delineating the optimal ordering of events, it is useful to determine the abundance of a taxon throughout its observed range. All else being equal, the stratigraphic range of a taxon will more closely approximate its true range when it is ubiquitous throughout its observed range [SEE SECTION 6.5]. In such instances, a researcher can have confidence that additional specimens discovered at some later date are less likely to fall outside the observed range of the taxon. This is perhaps best understood by considering the extreme opposite case, in

which just a single specimen of a taxon is known from a locality, and, therefore, the FAD and LAD of the taxon coincide. In such a case, a researcher cannot be very confident that an additional specimen found at a later date will come from the same horizon as the first specimen. In fact, there is a strong possibility that the second specimen would come from a different horizon, thereby changing the FAD or LAD, depending on whether the second specimen is found stratigraphically below or above the first one. Thus, we would seek to weight the ranges of common taxa more heavily than those of rare taxa in deriving optimized solutions.

Continuing to build on these themes, a procedure known as **ranking and scaling (RASC)** can also be applied to stratigraphic data. The objective of RASC is to estimate the most *probable* ranges of taxa, under the assumption that inconsistencies among localities in the order of FADs and LADs result from some random combination of processes, such as those highlighted earlier, that potentially affect the stratigraphic ranges of taxa observed at any individual locality. In the simplest case, the relative orders of any given pair of events,

---

Box 6.3

CONSTRAINED OPTIMIZATION (CONOP)

Using CONOP, determination of an optimal ordering of events at a locality, and of the CS itself, involves the use of weighting coefficients, based on quantification of the likelihood that some observed FADs and LADs of taxa are more dependable than others. In particular, it is important to take into account the truncations of stratigraphic ranges that are virtually inevitable in association with unconformities and changes in lithology.

Conversely, there are also predictable tendencies for the preserved ranges of taxa to be extended beyond their initial (true) preserved ranges. For example, fossil specimens in drill cores often tend to be smeared downward by physical processes associated with drilling and extrusion of the core. This should cause a downward smearing of the FAD of any taxon whose stratigraphically lowest occurrences are affected in this way. By contrast, LADs of common taxa are less likely to be affected by this process because, while some specimens will be transported downward in the core, other specimens will remain at their original stratigraphic positions in the core, thereby preserving the LAD. Of course, if the taxon is rare, this increases the likelihood that all specimens will be smeared downward, thereby altering the LAD as well. In any case, when unconformities and dramatic lithologic transitions characterize the data from a locality, or when the data come from a core, these factors will result in the downweighting, or even the elimination, of certain classes of data.

A and B, are compared at all localities, and the order that occurs most commonly—either A above B or B above A—is deemed to be the most probable sequence. However, it is sometimes the case that contradictions will arise in determining pairwise orderings among three or more events; in these cases, a determination is made with RASC of the most probable order of events, as discussed in Box 6.4.

Despite their differences, there is no reason to expect that any of the methods just highlighted should

---

Box 6.4

RANKING AND SCALING (RASC)

As an example of the use of RASC in a case in which contradictions might arise in the apparent order of three or more events, consider the ordering of events A, B, and C at several localities. It might be observed that event A occurs most frequently below event B, and B most frequently below C. Therefore, it should follow that event A occurs below event C. Nevertheless, it is possible that, at some localities, event C will be observed to occur below event A. When these kinds of contradictions occur, the probability of pairwise event sequences are ranked, with greater weight given to event pairs that occur most commonly among the localities under investigation. In our three-event pair example, therefore, if observations of events A above B and B above C occur more frequently among the sampling localities than the observation of event C above A, then C above A is discounted in establishing the most probable sequence.
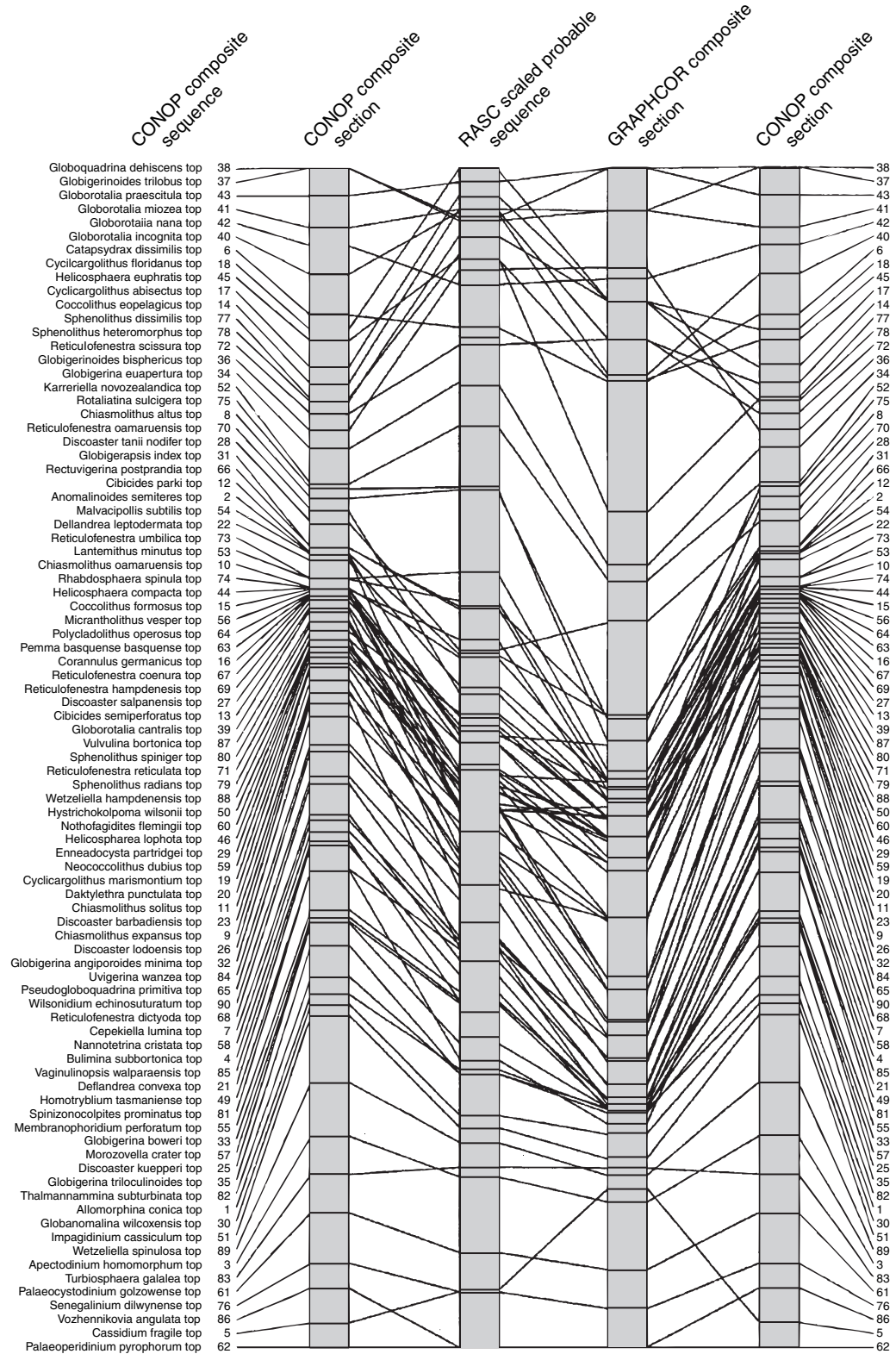
FIGURE 6.8 Comparison of results from constrained optimization (CONOP), ranking and scaling (RASC), and graphic correlation (GRAPHCOR), applied to a set of eight cores from the Taranaki Basin of New Zealand. A composite sequence of events (the sequence of species LADs, or "tops," at the left) and their spacing (the adjacent column, labeled "CONOP composite section") were determined for a culled data set that eliminated "questionable" events, including all FADs, because of concern that these were subject to downward smearing in the sample cores. The crossing of lines indicates instances in which there were contradictions from one technique to the next; note that these are concentrated most heavily in the central portion of the interval, where events are spaced most closely. *(From Cooper et al., 2001)*

produce wildly contradictory results when applied to the same data. A comparison presented by Roger Cooper and colleagues (2001) of GRAPHCOR (graphic correlation), CONOP, and RASC is illustrated in Figure 6.8, based on fossil data collected from eight wells in the Taranaki Basin of New Zealand, encompassing a complex set of Paleocene to Miocene strata. Since the data came from cores, the authors decided to exclude all FADs from the analyses because of the possibility of downward smearing, for reasons that were discussed in Box 6.3. Results generated with each method exhibit strong similarities, and, not surprisingly, most differences are concentrated in a central portion of the interval where there are many, narrowly spaced events.

The CONOP sequence was easily correlated directly to an existing regional timescale (Figure 6.9) because most of the events depicted in Figure 6.8 are well known outside the Taranaki Basin, and their broader stratigraphic significance throughout New Zealand had already been determined. Thus, based on these events, it was possible to correlate each of the localities individually to the regional timescale, as well as to one another (Figure 6.9).

6.3 REGIONAL CORRELATION WITH GRADIENT ANALYSIS

In Chapter 9, we discuss how fossil data are used in the spatial delineation of ancient ecological communities. Because the analytical approaches we will describe have also proven valuable for high-resolution correlation, we now briefly take up these methods before returning to them later in the context of paleoecology.

Paleontologists now recognize that, like biological communities in the present day, ancient communities did not consist of tightly interlocked sets of species separated by discrete boundaries [SEE SECTION 9.3]. Instead, just as environmental transitions along a marine transect or down the side of a mountain may be gradational, boundaries among the communities contained in these spaces are also gradational because species tend to be linked closely to the environments in which they are capable of living. The analysis of spatial variations in biotic composition has therefore come to be known as **gradient analysis,** which typically involves statistical comparisons of paleontological samples collected from different locations arrayed along a hypothesized gradient. While many

different numerical techniques have been used in gradient analysis, they are similar in comparing samples on the basis of the occurrences—and, typically, the relative abundances—of the taxa they contain. Data reduction techniques like those discussed in Chapter 3 are then used to order the samples in a multidimensional space that reflects their compositional similarities. Samples with similar positions or *scores* in this space have similar biotic compositions.

The same analytical techniques can also be used to assess faunal variation through time rather than in space. Samples are collected from a series of horizons arrayed stratigraphically at a given locality, and the resulting sample scores from gradient analysis can be graphed in stratigraphic order. This paints a picture of temporal variations in biotic composition at a locality that may be related directly to paleoenvironmental transitions. An example of how these variations can then be used to accomplish high-resolution regional correlations is presented in Box 6.5 (on page 164), for a portion of the fossil-rich Upper Ordovician strata in the Cincinnati, Ohio, region.

Because changes in water depth relate in some (though certainly not all) instances to global fluctuations in sea level, one might expect that gradient analyses could be used for global-scale correlations. However, although local and regional stratigraphic patterns are partly influenced by global variations in sea level, this by no means suggests a one-to-one correlation of these variations with regional trends in water depth or other biologically significant environmental variables that are also expressed on a regional level. Individual regions are characterized by environmental factors (e.g., the availability of a source area for terrigenous sediments or the evolution of basin topography) that produce unique biotic transitions. Thus, while gradient analysis is a powerful tool for high-resolution correlation at the regional scale, it does not have much potential for global correlation.

6.4 SEQUENCE STRATIGRAPHY AND THE DISTRIBUTION OF FOSSILS

Earlier, we noted that post-mortem processes, or simply the tendencies of taxa to live in some environmental settings and not in others, make it highly unlikely that any two correlative intervals at different localities will contain
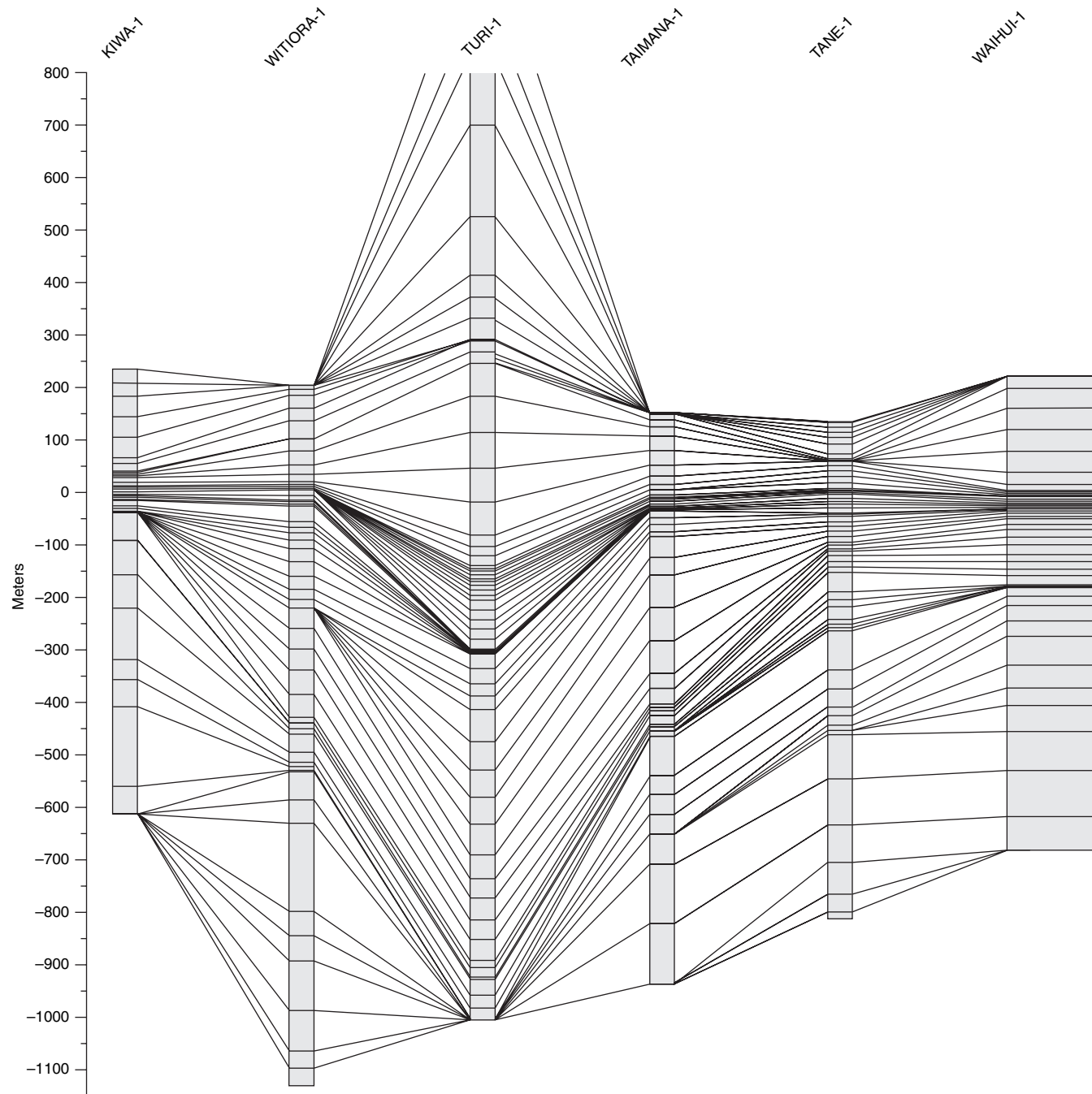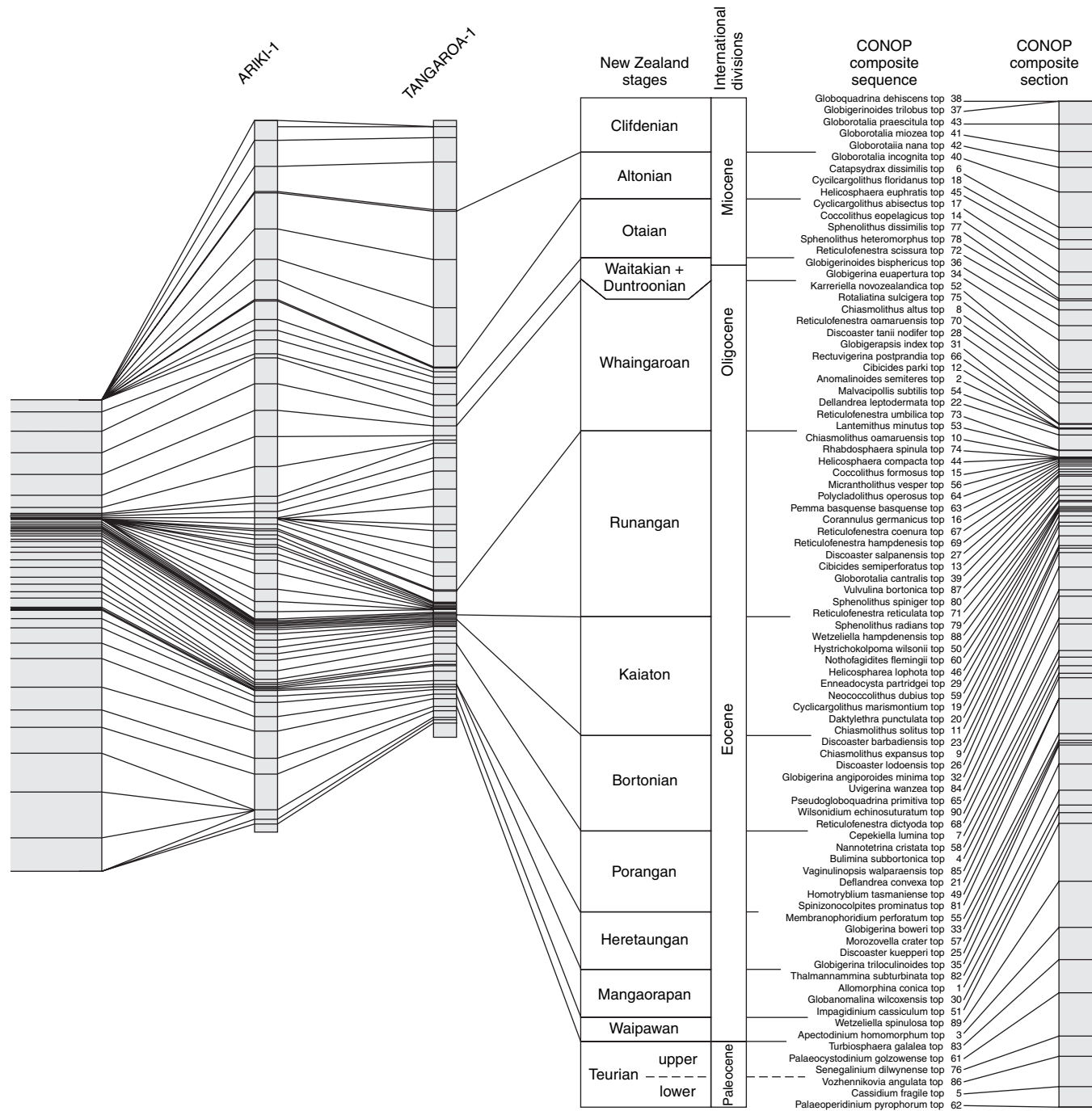
FIGURE 6.9 Correlations for eight Taranaki Basin cores from New Zealand, based on CONOP. The
stratigraphic positions of events in each well were adjusted from their actual locations, based on the outcome of
the procedure. *(From Cooper et al., 2001)*

exactly the same roster of taxa preserved in the same strati-
graphic order. To some extent, these factors are expressed
randomly in space and time: There is no telling precisely
where a taxon will turn up in the fossil record through-
out its paleogeographic, paleoenvironmental, or strati-

graphic extent. However, there are also nonrandom factors
that tend to produce a high concentration of taxonomic
occurrences, particularly FADs and LADs, in specific kinds
of horizons that are laterally extensive. In fact, stratigraph-
ic patterns of first and last appearances, regionally and per-

haps globally, may relate predictably to the physical stratigraphic record. The delineation of these relationships emanates directly from sequence stratigraphy.

A fundamental goal of sequence stratigraphy is to diagnose a hierarchy of stratigraphic units and the boundaries between them. Because the processes that produced these patterns were regional or, in some cases, global in scope, it follows that the units, or at least the boundaries between them, should be correlative over broad areas. To the extent that this is the

Box 6.5

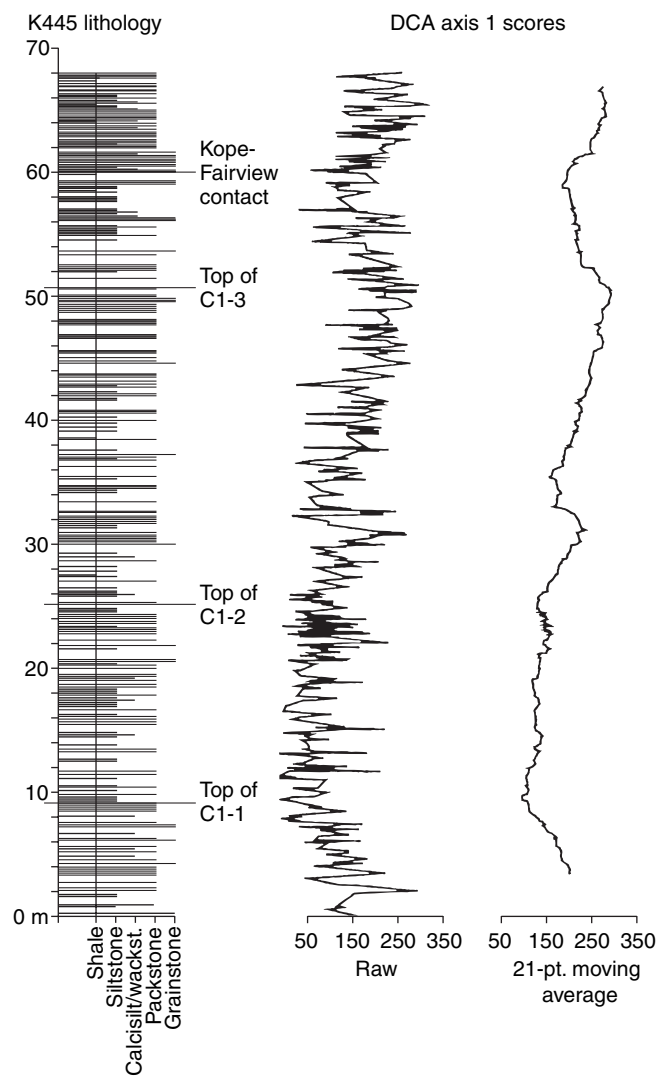# HIGH-RESOLUTION CORRELATION WITH GRADIENT ANALYSIS

The use of gradient analysis as a method of correlation is illustrated in Figures 6.10 and 6.11. In Figure 6.10, samples from the study area near Cincinnati are compared using a data-reduction technique called *detrended correspondence analysis* (DCA). Here, scores are graphed stratigraphically as a simple x–y line plot in the middle column, for faunal census samples collected from every fossiliferous horizon at a locality in northern Kentucky. A smoothed version of these data, presented in the right column, is a moving average of the same data, constructed by averaging together for each horizon the scores of several of contiguous horizons (21, in this case) centered on the horizon in question.

In developing the moving average, there is no definitive guideline for deciding how many contiguous points to average together. As with the diagnosis of periodicity in harmonic analysis (see Box 2.2), the objective is to make it easier to see longer-term trajectories in the curve, while removing higher-frequency fluctuations that hinder the researcher's ability to recognize the broader pattern; typically, there is some trial and error involved in determining a suitable number of points to average. In the moving average curve, there are several broad "meanders" to the left (lower scores)

FIGURE 6.10 Results of detrended correspondence analysis (DCA) of faunal census data collected bed by bed through a section of the Upper Ordovician Kope and Lower Fairview Formations, located in northern Kentucky (K445). The column on the left summarizes the lithological variation through the section; the central column depicts the census scores from axis 1 of DCA; and the rightmost column is a smoothed version of the middle curve, based on a 21-point moving average. The value for each point on the smoothed curve is the average of the actual value at that horizon, plus those of the 10 sample horizons immediately below it and the 10 immediately above it. *(From Miller et al., 2001)*

and right (higher scores) that are associated with significant changes to the faunal compositions of samples.

Samples with higher scores are dominated by large, robust brachiopods and branching bryozoans.

case, it has motivated an intriguing pair of questions for paleontologists: (1) Are FADs and LADs concentrated at these boundaries, and, if so, (2) can these boundaries be taken as evidence for rapid evolutionary transitions? As we will see, an affirmative answer to the

first question does not necessarily imply an affirmative answer to the second.

A depositional sequence can be defined as a cyclical unit bounded at its base and top by a **sequence boundary (SB),** which is marked by a marine or subaerially

Based on previous studies of their natural histories, these are known to have been associated in the study region with shallow, relatively turbulent waters, in which fine-grained sediments generally did not settle permanently on the sea floor. Samples with lower scores are dominated by smaller, more fragile brachiopods, as well as trilobites that were associated with quieter water and muddier (i.e., finer-grained) sea floors.

Therefore, inflections on the smoothed curve record transitions from intervals of deepening to intervals of shallowing, or vice versa, at the locality. Because these broad transitions were at least regional in scope, the inflection points can be correlated among localities throughout the region. This approach is illustrated for the Cincinnati-area localities in Figure 6.11. Here, the smoothed curve from the locality illustrated in Figure 6.10 was placed in the middle, and inflection horizons recognized in curves for several other localities were correlated directly to this curve. The correlations are supported by close correspondence to several distinctive horizons and surfaces that were already known on the basis of independent evidence to be correlative throughout the study area.
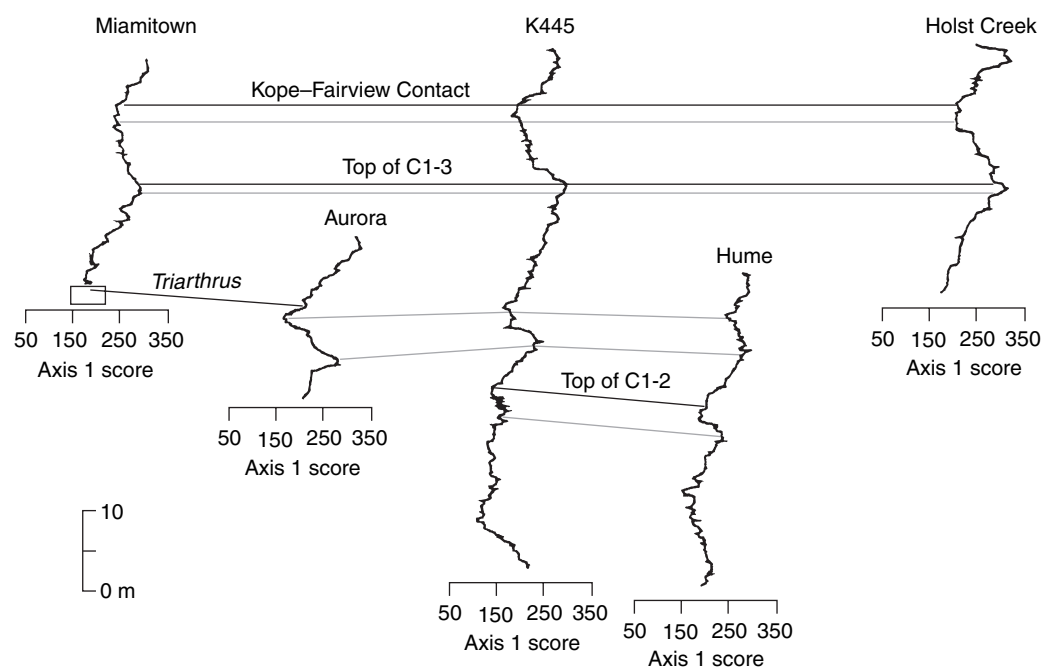

FIGURE 6.11 High-resolution correlation based on DCA scores on axis 1 (smoothed curves) for Upper Ordovician localities in the Cincinnati, Ohio, area. Gray lines indicate correlations based on major inflections at multiple localities (K445 is in the middle). Solid lines are independent correlations, for comparison, based on the tops of recognized stratigraphic cycles (labeled as "Tops of *C*1-2, *C*1-3"), the Kope–Fairview formational contact, and a unique stratigraphic occurrence of the trilobite *Triarthrus*. *(From Miller et al., 2001)*

exposed erosional surface (i.e., a hiatus), or a noneroded interval that correlates to a hiatus recognized at other localities (Figure 6.12a). Sequence boundaries are caused by relative falls in sea level. The internal architecture of sequences, in turn, may be controlled by several factors, including global fluctuations in sea level, the rate at which these fluctuations take place, local changes in water depth, tectonic controls on the geometry of the depositional basin, and the availability of sediment. Of all these factors, global sea level may have an overriding
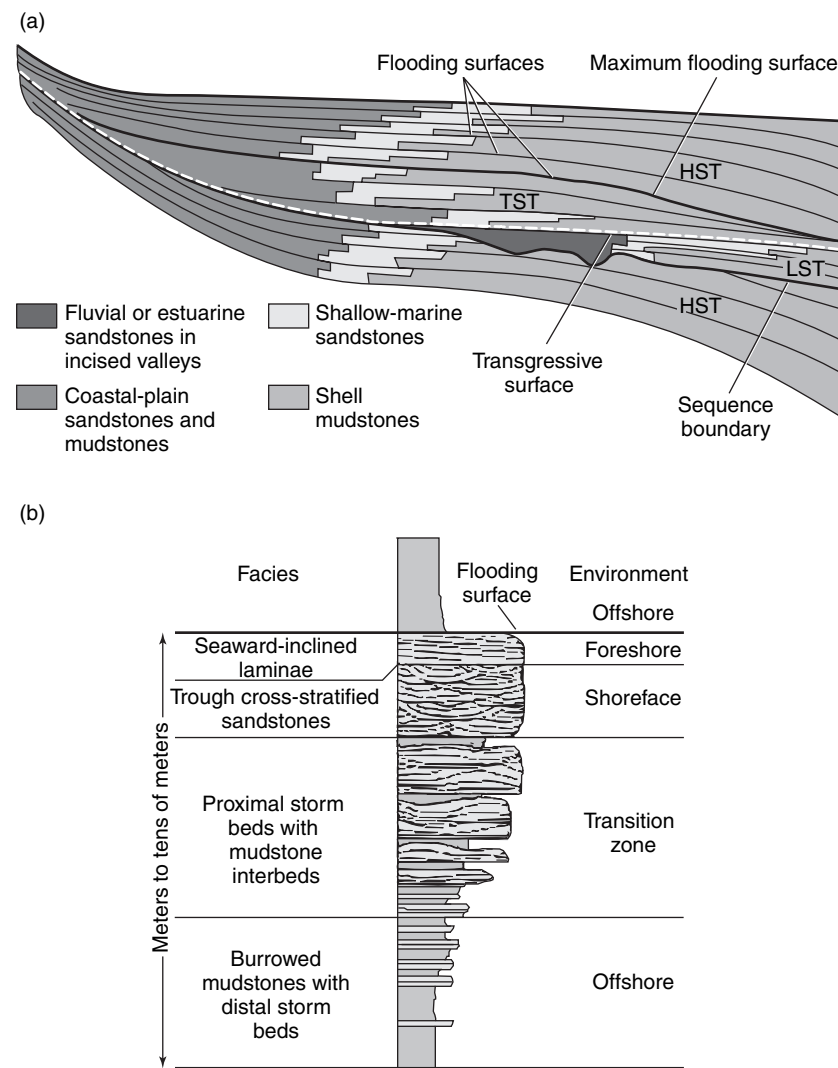
(a)

Flooding surfaces   Maximum flooding surface

HST

TST

LST

HST

Transgressive
surface

Sequence
boundary

Fluvial or estuarine
sandstones in
incised valleys

Coastal-plain
sandstones and
mudstones

Shallow-marine
sandstones

Shell
mudstones

(b)

**FIGURE 6.12 Schematic illustrations of
the major features of stratigraphic
sequences and parasequences.** (a) Sequence
architecture, including a lowstand systems tract
(LST), a transgressive systems tract (TST), and a
highstand systems tract (HST). (b) An idealized
parasequence in a terrigenous setting, consisting
of a shallowing-upward succession of strata,
bounded at the top by a marine flooding
surface. *(Modified from Van Wagoner et al., 1990,
from an online guide to sequence stratigraphy,
maintained by Steven Holland,
www.uga.edu/~strata/sequence/seqStrat.html)*

Facies

Flooding
surface

Environment

Offshore

Seaward-inclined
laminae

Foreshore

Trough cross-stratified
sandstones

Shoreface

Proximal storm
beds with
mudstone
interbeds

Transition
zone

Burrowed
mudstones with
distal storm
beds

Offshore

Meters to tens of meters

effect, at least among large-scale sequences that may be
several tens to thousands of meters thick; the factors con-
trolling smaller-scale sequences have been more open to
question. The anatomy of an idealized sequence is de-
scribed in Box 6.6.

For our purposes here, the essential message of se-
quence stratigraphy is that the record preserves a hierar-
chical set of paleoenvironmental variations, and, within
this hierarchy, it is possible to recognize particular hori-
zons that mark significant gaps in the deposition of sed-
iments and fossils. Any taxonomic first or last occurrence
that took place during an unpreserved interval at a par-
ticular location cannot possibly be recorded in the fossil
record at that location. Therefore, it stands to reason that
the LAD of any taxon whose last occurrence falls dur-
ing such an interval should be observed somewhere be-
neath the gap, and the FAD of any taxon whose first

occurrence took place during such an interval should be
observed somewhere above the interval. Moreover, FADs
and LADs may be concentrated in a given section at
times of rapid environmental change, when taxa that
already exist follow their preferred environments and
migrate into or out of the area where the section
accumulated.

With these points in mind, Steven Holland has been
investigating the relationship between the deposition of
sequences and the stratigraphic distributions of fossils.
Holland (1995) developed a set of models that simulate
important depositional and taphonomic processes, and
how they interact with the paleoecological properties of
individual taxa to produce patterns that can be observed
in the fossil record. Holland's models have two main facets.
First, an environmental gradient [SEE SECTION 9.3] is sim-
ulated in which each modeled taxon is randomly assigned

Box 6.6

THE ANATOMY OF A SEQUENCE

Because of the interplay of factors that control sedimentation, the nature of a sequence varies throughout its stratigraphic extent, and stratigraphers have designated three major sequence components. In stratigraphic order, working upward, these are the **lowstand systems tract (LST), transgressive systems tract (TST),** and **highstand systems tract (HST).** All three of these units, in turn, are built of sets of **parasequences** (Figure 6.12b). A parasequence is a shallowing-upward cycle that is bounded at its top by an abrupt deepening event, preserved as a **flooding surface,** which also defines the base of the next parasequence.

The LST consists of a progradational (i.e., net seaward stacking) set of parasequences or sequences that lie above the sequence boundary. Because the relative rate of sea-level rise during this initial transition is slow, the land-derived sediments that are deposited in shallow conditions—and the successive set of parasequences or higher-order sequences that are produced by these sediments—tend to build seaward, away from the shoreline (Figure 6.12a).

By contrast, during the subsequent deposition of the TST, an increase in the rate of sea-level rise causes successive parasequences, or higher-order sequences, to migrate landward—a pattern known as retrogradation (Figure 6.12a). The sea-level rise continues, but at a slower rate, in the early part of the HST. Because of the slowing rate, the stacking pattern reverses in the HST back to progradation. The late part of the HST is characterized by a relative fall in sea level.

Aptly, the boundary between the TST and the HST is referred to as the **maximum flooding surface,** which records the greatest water depth in the sequence and marks the transition from retrogradational to progradational stacking. As indicated by our discussion of the HST, the maximum flooding surface does not mark a cessation of sea-level rise; it forms at some point following a decrease in the rate of sea-level rise, when this rate is balanced by the rate of sedimentation. Thereafter, the rate of sedimentation exceeds the rate of sea-level rise, and progradation ensues.

To understand how this can be so, it is important to keep in mind that water depth is not synonymous with sea level. Although it may seem paradoxical, water depth can actually decrease in a situation where the sea level is rising if a significant amount of sediment is flowing into an area, which is what occurs during progradation. And, in fact, much of the sedimentary record is deposited under regional conditions of rising sea level. As progradation continues and sea level ultimately does begin to fall in the later stages of the HST, the area may become exposed, producing a hiatus that marks the next sequence boundary.

It should be kept in mind that the patterns illustrated in Figure 6.12 describe an idealized situation. The exact nature of any sequence may vary considerably from this model, contingent on such factors as the timescale over which the variations are observed; the nature of global sea-level changes; regional variations in water depth and the extent, if any, of subaerial exposure; the shape of the depositional basin; the rate of tectonic subsidence; and the availability of various kinds of sediments. For example, a rather different pattern than that illustrated here might be expected in the absence of terrigenous sediments.

---

attributes that define its abundance and environmental preferences in the landscape. In all, three numerical characteristics are used that govern the abundance of each taxon along a simulated water-depth gradient, with a distribution of individuals for the taxon that approximates a normal (i.e., bell-shaped) curve (Figure 6.13): a **preferred depth,** the center of the distribution where the taxon will exhibit its greatest probability of collection; a **peak abun-**

dance, the maximum abundance achieved at the preferred depth; and a **depth tolerance,** the degree of spread in the distribution of the taxon. The latter variable is in keeping with the recognition that some taxa are highly tolerant of environmental variation and can subsist over a broad environmental region, whereas others cannot.

The second facet of the model simulates the occurrences of modeled taxa in a sequence stratigraphic
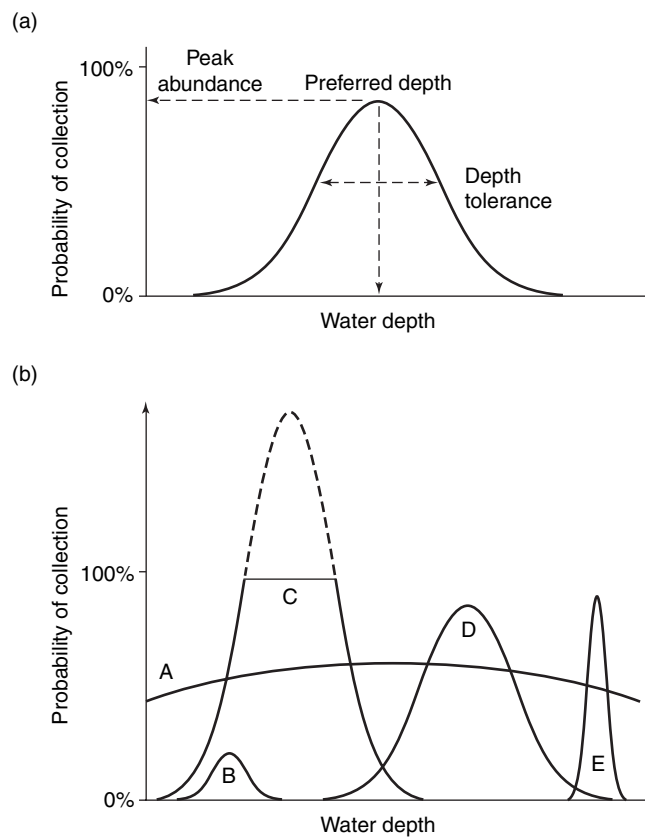
(a)

(b)

FIGURE 6.13 Holland's protocol for determining the positions and collection probabilities of taxa included in his simulation of the preserved record of FADs and LADs in a sequence stratigraphic context. (a) Each taxon is modeled to have a bell-shaped abundance distribution along a simulated water-depth gradient. Three characteristics are defined for each taxon: preferred depth, peak abundance, and depth tolerance. (b) Illustrations of the potential variability among different taxa, based on differences in these parameters. *(From Holland, 1995)*

context, based on their attributes as defined in the previous step. In Holland's model, two shallow-water sequences are simulated: Each has a duration of 3.5 million years, the scale of a typical regional sequence, and is broken into time steps that last 50,000 years. The time steps conform approximately to stratigraphic cycles recognized by field research; these are about 1 meter thick and compose the larger-scale sequences. Additional details of the model are described in Box 6.7.

In thinking intuitively about how the model works, it is useful to consider the depth (i.e., environmental) preferences of any taxon in the context of the water depth preserved in the strata. For a given taxon to be preserved in a stratum, one prerequisite is that the stratum represent

a paleodepth in which the taxon could have occurred, based on its model parameters. However, this by no means guarantees that the taxon will be found in the stratum. If the taxon is comparatively rare, it will exhibit a probability of collection that is substantially less than 100 percent even at its preferred depth. If the taxon is common, it will nevertheless be encountered less frequently in a stratum representing a paleodepth near the fringes of the depth range that it can tolerate.

As Holland demonstrated, even fairly common, widespread taxa will not be encountered in every stratum that could potentially house them; rarer taxa will inevitably be distributed spottily throughout their stratigraphic ranges. And, as implied elsewhere, one outcome of this spotty distribution is that the preserved FADs and LADs of taxa will almost certainly be truncated, relative to the true intervals in which they first and last occurred. While this truncation will, on average, be especially acute for rare taxa, there is likely to be some degree of range truncation for virtually all taxa.

In this respect, the overprint of sequence architecture becomes particularly relevant. If the lower- or uppermost portion of the temporal range of a taxon coincides with a depositional hiatus, an inevitable outcome, noted earlier, is that the LAD or FAD will be truncated directly by the hiatus. Importantly, what Holland's model demonstrates is that we would expect LADs and FADs to coincide with the horizons immediately below (for a LAD) or immediately above (for a FAD) the hiatus. Thus, even in an interval where diversity remains stable and the true temporal ranges of taxa are not concentrated significantly at any horizon, we would expect to see a concentration of FADs and LADs at or near sequence boundaries. This is precisely what Holland observed as an outcome of his model.

In Figure 6.14, note the significant concentrations of observed first appearances through each TST at each of the first three flooding surfaces (horizons of rapid deepening). These mark the flooding surfaces at the bases of parasequences (Figure 6.12). The taxa that form these concentrations were of two basic types: (1) shallow-water taxa that originated during the preceding lowstand but were first observed in the section when the appropriate deposits are found for the first time during the transgression; or (2) deep-water taxa that also originated during the preceding lowstand *or earlier* in the shallow portions of the upper HST of the previous sequence, where they would not have been preserved because deep-water lithologies were not preserved at this location.

Box 6.7

ADDITIONAL ASPECTS OF HOLLAND'S MODEL

Because of its relative proximity to shoreline, a shallow-water sequence often lacks the LST. Shallower areas will be subaerially exposed during lowstands, provided that tectonic subsidence rates are low. If subsidence rates are high, subaerial exposure will not occur and the LST will be preserved.

Holland's model excluded deposition during the LST (Figure 6.14) because much of the fossil record comes from slowly subsiding areas. In each of the two modeled sequences, the TST consisted of two parasequences and the HST consisted of six. In the case of the TST, its transgressive nature can be seen by the deepening (leftward), sawtooth pattern exhibited by the two parasequences; this conforms to the retrogradational pattern illustrated for the TST in Figure 6.12. In the case of the HST, a shallowing (rightward) pattern was exhibited, owing to the slowing and reversal of sea-level rise and the infilling of the basin with sed-

iment; this conforms to the progradational pattern exhibited for the HST in Figure 6.12.

The entire depth range represented in the preserved portion of each modeled sequence was 65 m. Against this backdrop, standing taxonomic diversity was held constant at 1000 taxa, with a random extinction probability of 0.0125 in each 50,000-year time step. This corresponds to an empirically calibrated mean species duration of 4 million years [SEE SECTION 7.2]. To hold diversity fixed, each extinction was matched by the origination of a new taxon during the subsequent time step. Upon origination, each taxon was randomly assigned a preferred depth ranging from 0 to 65 m, a peak abundance ranging from a 25 to 100 percent probability of being collected, and a depth tolerance ranging from 1 to 21 m. This combination of model parameters produced the pattern of first and last occurrences illustrated in Figure 6.14.
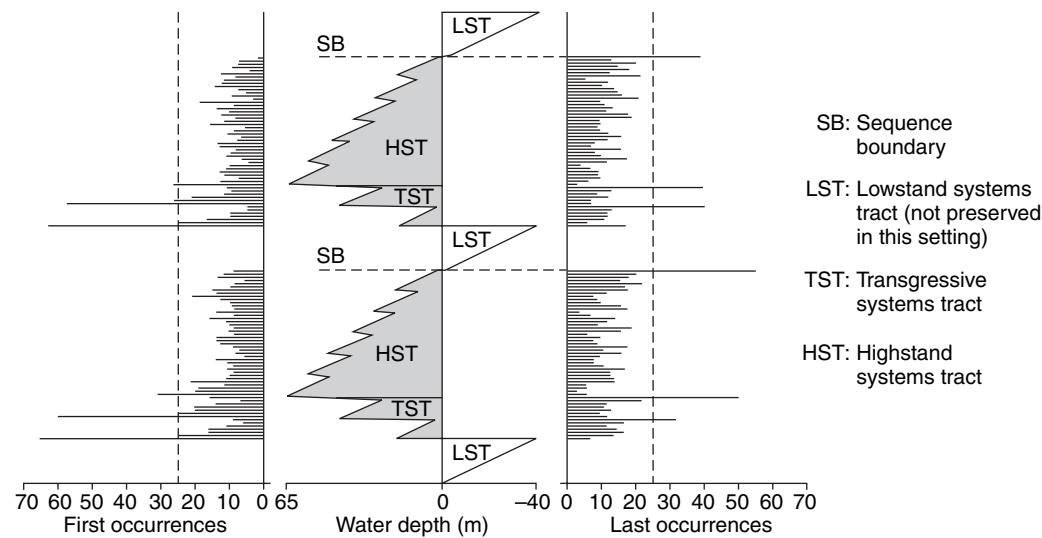

FIGURE 6.14 Results from Holland's (1995) simulation of the preserved record of FADs and LADs in a sequence stratigraphic context. Each TST consists of two parasequences, and each HST consists of six parasequences. The vertical dashed lines designate the threshold for statistical significance of peaks in first or last occurrences (see Figure 6.16 for more on statistical significance). *(Modified from Holland, 1995)*

Similarly, there is a significant concentration of observed LADs at the top of each sequence (the top of each HST). This is because taxa whose true time of extinction coincided with the sequence boundary or with the sub-

sequent, unpreserved lowstand had their observed ranges truncated at the boundary. In addition, LADs are concentrated immediately beneath flooding surfaces in the TST. These represent shallow-water taxa with narrow

depth tolerances that must have become extinct at some point after the deepening but prior to the recurrence of environments sufficiently shallow to house them.

Given the pervasiveness of sequence architecture in the stratigraphic record at several scales, it therefore becomes imperative to assess the possibility that observed local, regional, or global peaks in taxonomic origination or extinction may be inflated artificially by their association with sequence boundaries or by the loss of key paleoenvironments. For example, Daniel Goldman and colleagues (1999) reevaluated the stratigraphic zonation of graptolites in the Middle Ordovician strata of New York. Their analysis involved more extensive sampling than that of earlier work on these rocks, and they were able to place their biotic data in a stratigraphic framework developed independently using a network of volcanically derived K-bentonites (potassium-rich bentonites).

Comparison with the K-bentonites reveals that the boundaries between graptolite zones are fairly isochronous. At the same time, many common graptolite species were restricted to particular paleoenvironments, with some species occurring preferentially in shallow water and others in deep water. With respect to potential sequence stratigraphic overprints, this finding is particularly important because, as we saw when considering Holland's model, the restriction of species to certain environments enhances the likelihood that their ranges will be concentrated artificially at or near sequence or systems tract boundaries.

Indeed, this is precisely what Goldman and colleagues found, as illustrated in Figure 6.15. There is a clear association in the study interval of FADs with systems tract boundaries. Moreover, stratigraphic gaps in the observed ranges of some species are recognized in association with the loss, followed by the return, of appropriate paleoenvironments. In fact, in some instances, because of their extensive sampling, Goldman and his colleagues found several occurrences of key taxa in beds significantly below and above their previous known stratigraphic ranges. Thus, although the traditional zonation is upheld, there is

FIGURE 6.15 Comparison of the stratigraphic ranges of graptoloid species to depictions of relative sea level and sequence-stratigraphic architecture in the Middle Ordovician Utica Shale of New York. (Abbreviations for portions of sequences are as in Figure 6.14.) Solid lines indicate observed ranges, and dotted lines show inferred occurrences. Note the concentration of FADs at systems tract boundaries, and the gaps in the distributions of some species that relate to the availability of appropriate lithologies and the paleoenvironments they represent. *(From Goldman et al., 1999)*
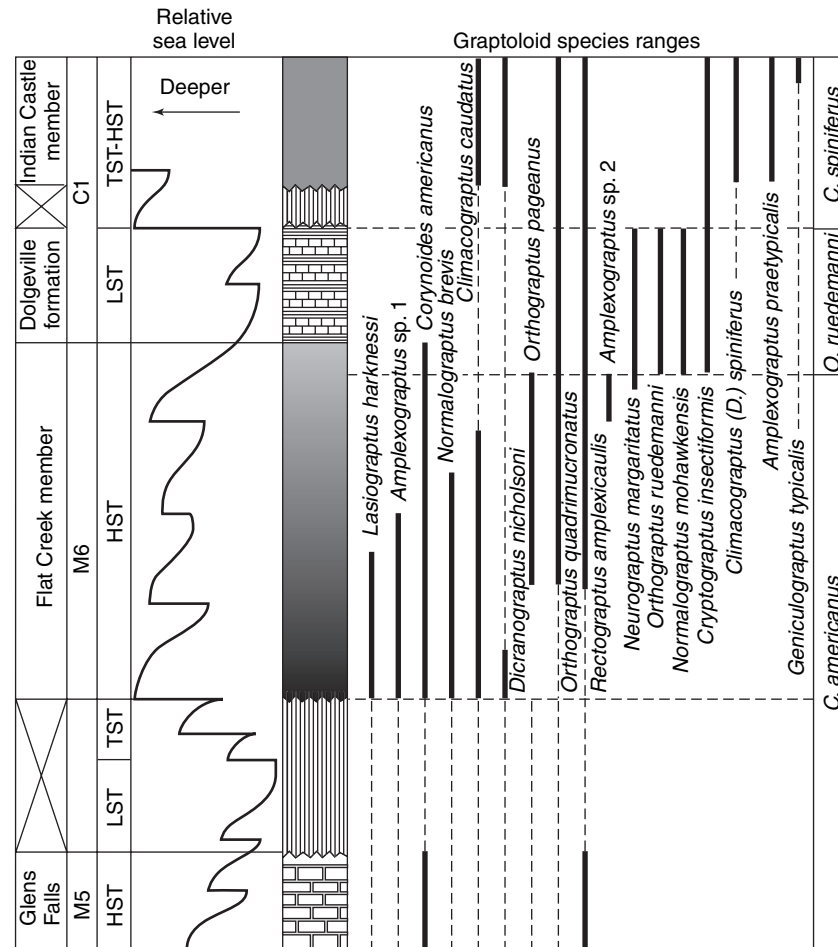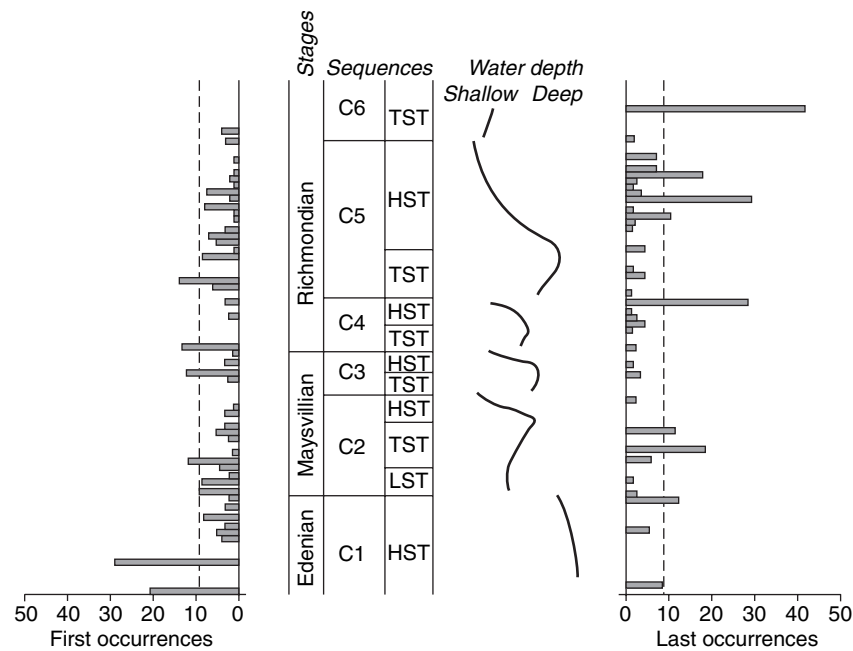
FIGURE 6.16 Sequence stratigraphy and first and last appearances of species within a section from the Upper Ordovician of Indiana. C1 through C6 denote sequences of the Cincinnatian Series. The vertical dashed lines indicate the statistical limits of how strongly clustered the FADs and LADs could appear to be if they were not in fact clustered; the probability is less than 0.001 that a spike would exceed the dashed lines if the first and last appearances were distributed randomly throughout the section. Some clusters of events occur where predicted by the sequence stratigraphic model (e.g., LADs at the ends of HSTs), but others cannot be easily explained by this model and are therefore more likely to reflect biologic events (e.g., LADs within the HST of sequence C5). *(From Holland, 1995)*

much more facies dependence and sequence-stratigraphic overprint than had previously been appreciated.

Sequence stratigraphy can aid paleontology much more positively than might be suggested by these notes of caution. When FADs and LADs cluster at levels where they would not be expected as artifacts based on position in the sequence, then they represent strong candidates for true biological turnover events. Figure 6.16 shows examples from an Upper Ordovician (Cincinnatian) section in Indiana. C1 through C6 in this figure denote sequences. Several clusters of events appear where they would be expected based on Holland's models—for example, the spike of LADs at the end of the HST of sequences C1 and C4. Others, however, appear where they are not predicted by the model and are therefore more likely to mark biological turnover—for example, the spike of LADs within the highstand of sequence C5.

Beyond the clustering of FADs and LADs, other paleobiological patterns are associated intimately with sequence stratigraphic architecture. For example, the nature of fossil preservation can vary significantly through a stratigraphic sequence, and even within a parasequence, because of variations in sedimentation rates, turbulence, geochemical conditions, and other parameters. With respect to correlation, these variations can be quite valuable: Beds marked by unique styles of preservation, or even a unique biotic composition produced by unusual depositional conditions, may be trace-able throughout a region, providing an additional means of high-resolution, regional correlation.

6.5 CONFIDENCE LIMITS ON STRATIGRAPHIC RANGES

The recognition that depositional environments and their associated facies vary, and that the probability of collecting fossils of a given species varies with facies, can also be turned to advantage to estimate the probable size of the gap between the observed LAD and the true time of extinction, or between the observed FAD and the true time of origination. To see how this is possible, first consider the overly simplified situation in which the probability of sampling is assumed to be constant over time. Figure 6.17 depicts the stratigraphic range of a hypothetical species. There are 50 time increments between its first and last appearance, and it is actually represented by fossils in five of these increments. Thus, the estimated sampling probability of the species is $5/50$ or 0.1 per time increment. Let us step 1 time increment beyond its observed last appearance and ask: How likely is it that the species was still alive at this time but simply was not preserved? The probability is $(1 - 0.1)$, or 0.9—a high enough value that it is quite reasonable to suppose that the species was still alive.

Probability that species is still extant but not sampled

$0.9^7 = 0.48$

$0.9^6 = 0.53$

$0.9^5 = 0.59$

$0.9^4 = 0.66$

$0.9^3 = 0.73$

$0.9^2 = 0.81$

$0.9^1 = 0.9$

LA

Stratigraphic level

Species sampled (5 times between FA and LA)

Species not sampled (45 times between FA and LA)

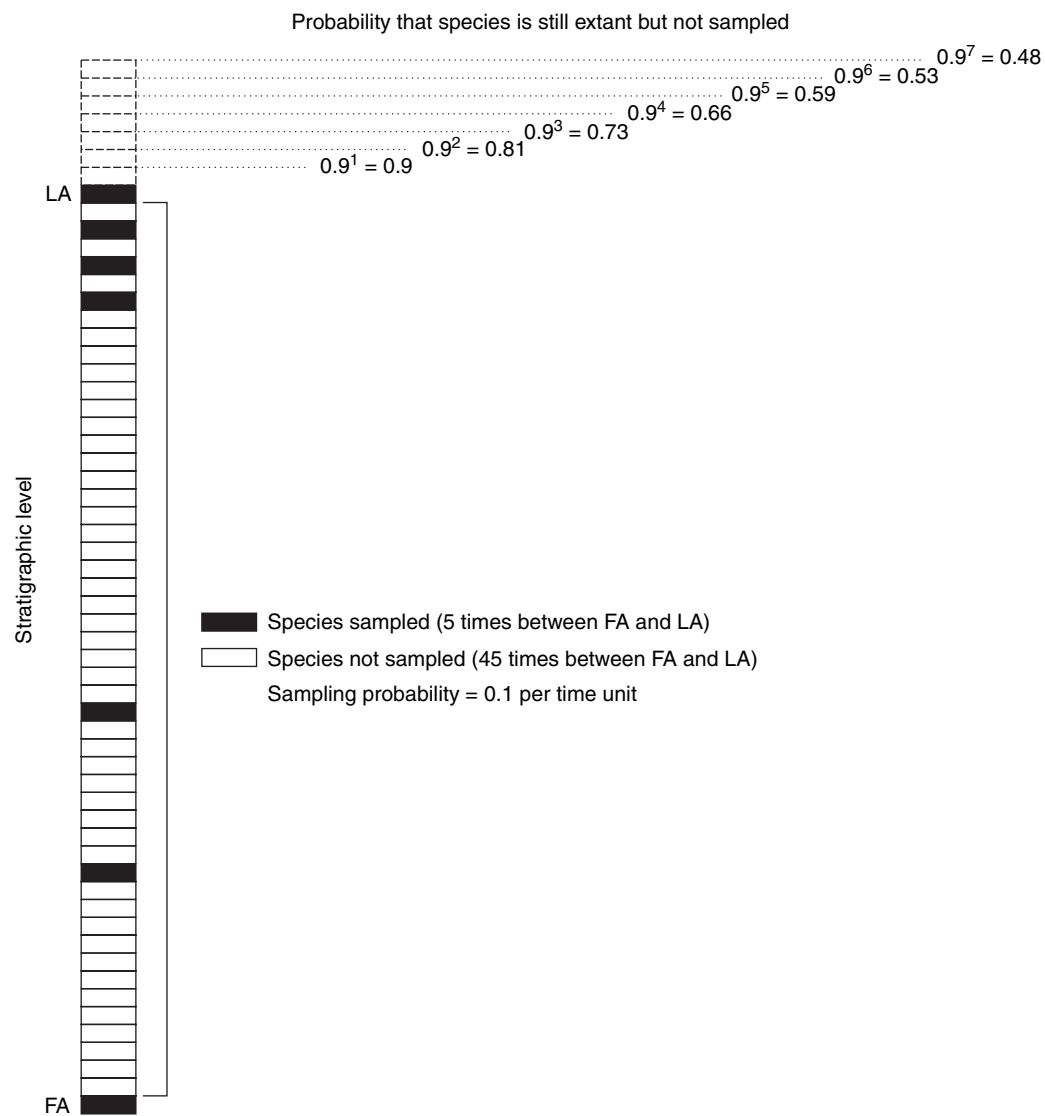Sampling probability = 0.1 per time unit

FA

FIGURE 6.17 Hypothetical example of confidence limits on the time of a species' extinction, assuming constant sampling probability. FA and LA denote the first and last appearance. Filled boxes show time intervals in which the species is sampled; empty boxes show times when it is not sampled. The farther above the last observed appearance, the smaller is the probability that the species is still alive but simply has not been sampled.

If we go 2 time increments past the last appearance, then the probability that it was still alive but simply not preserved is equal to 0.9^2, or 0.81. In other words, there is an 81 percent chance that the species is still alive and only a 19 percent chance that it has already become extinct. In this particular example, the probability that a species will fail to be preserved in seven successive time increments is 0.9^7, or 0.48. At this point, it is about equally likely that the species is still alive as it is that it has already become extinct. The point in time at which the odds are even in this way is referred to as the 50 percent confidence limit; it is essentially a best guess for the true time of extinction. The size of the confidence interval varies from case to case, being smaller when the sampling probability is higher. Wider confidence limits, say 95 percent, can also be constructed if one wants to be even more certain that the true extinction falls somewhere between the last appearance and this limit. Confidence limits can be developed in the same way for first appearances.

The approach of confidence limits sketched out in Figure 6.17 is valid only if we can assume that the average sampling probability does not change significantly, as it might if the last appearance of the species coincided with a change in facies. If we knew how the probability of sampling varied with facies, we could easily substitute these variable probabilities into Figure 6.17. Box 6.8 illustrates one way that this can be done.

6.6 CONCLUDING REMARKS

Rather than accepting the stratigraphic record of fossil occurrences at face value, paleontologists are coming to understand why a particular fossil is likely to occur at a particular place in the record. And, just as important, they are developing methods to help reconcile differ-ences in the stratigraphic distributions of taxa from locality to locality. Not only is this permitting more sophisticated approaches to high-resolution correlation; it is also a prerequisite to understanding the causes of many of the paleontological patterns described through-out this book.

For example, it is possible that the physical transitions responsible for sequence architecture and sequence boundaries were also capable of inducing real extinction and significant biotic turnover. However, as Holland's model illustrated for us, the *rate* at which these transitions are observed to have taken place in the stratigraphic record can exaggerate significantly the true rate of bio-logical turnover. Recognizing these relationships, re-searchers are now developing methods that incorporate preservation criteria directly into the calibration of tax-onomic origination and extinction rates.

CONFIDENCE LIMITS ON STRATIGRAPHIC RANGES WITH VARIABLE SAMPLING PROBABILITY
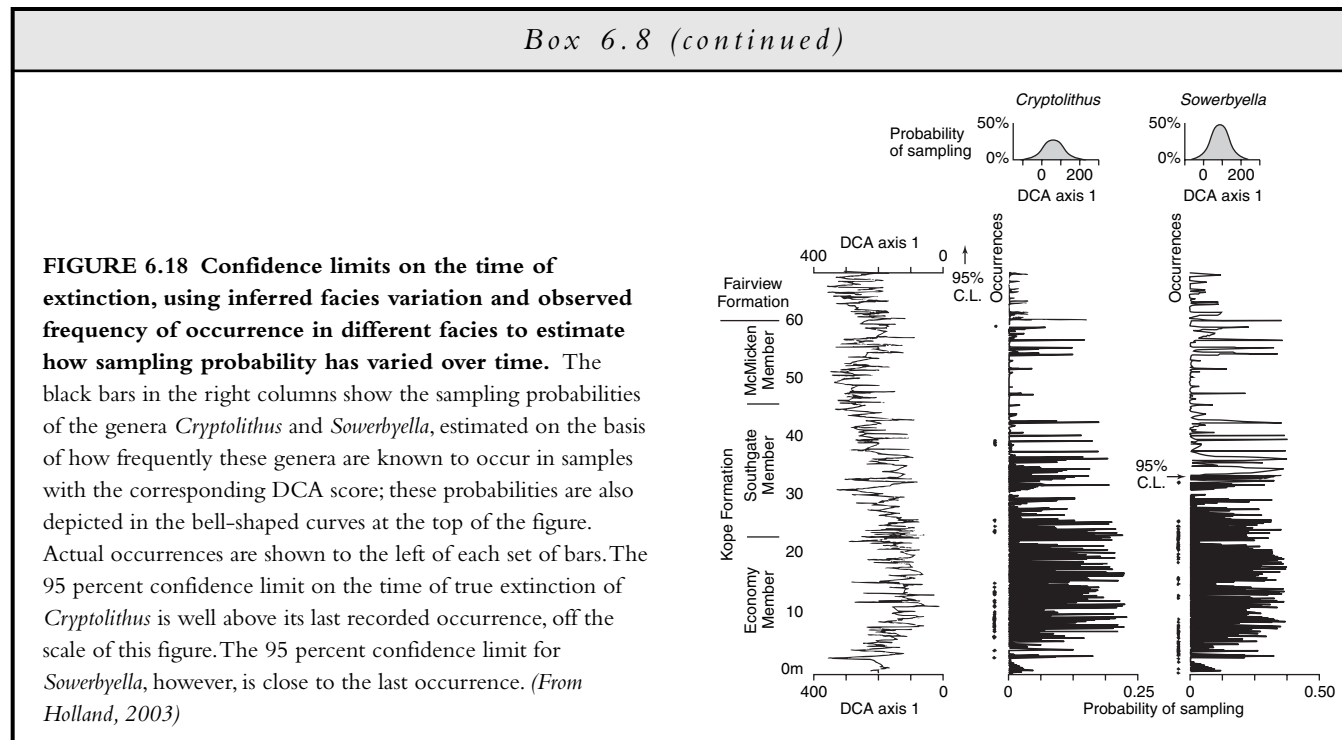
The curve on the left in Figure 6.18 shows estimated water depth through the Upper Ordovician Kope and Lower Fairview Formations; it is the same as the curve in Figure 6.10, with the *x* axis reversed so that deeper facies are to the right.

The bell-shaped curves in the upper part of Fig-ure 6.18 depict estimated sampling probabilities for the trilobite *Cryptolithus* and the brachiopod *Sower-byella*, relative to inferred water depth. These are anal-ogous to the hypothetical sampling curves in Figure 6.13, but they are based on the actual frequency with which each genus is found in each environment. *Cryptolithus* preferred slightly deeper water than *Sowerbyella*, and overall its probability of sampling is only about half that of *Sowerbyella*. Knowing how water depth varies and how sampling probability varies with water depth, it is straightforward to deter-mine how sampling probability varies through the section; this is indicated by the black bars. For exam-ple, *Sowerbyella* has its highest sampling probability, just under 50 percent, in relatively deep waters corre-sponding to a detrended correspondence analysis (DCA) score of about 100. Thus, whenever the left-hand curve hits 100, the sampling curve for *Sower-byella* hits its maximum.

The dots in Figure 6.18 show stratigraphic levels at which *Cryptolithus* and *Sowerbyella* were actually sam-pled. The last appearance of *Cryptolithus* is at about 59 m in the section, and that of *Sowerbyella* is at about 32 m. The disappearance of *Cryptolithus* comes at a time of low sampling probability corresponding to water depths at which it did not prefer to live. It is therefore quite likely that its disappearance is not a true extinc-tion. If the variable sampling probabilities are applied as in Figure 6.17, the 95 percent confidence limit is well beyond the top of the section. *Sowerbyella*, by contrast, disappears from the record despite the persistence of facies in which it would have a reasonably high prob-ability of being sampled if it were still alive. It is there-fore likely that the true extinction is close to the last appearance. Accordingly, the 95 percent confidence limit is just a short distance above the last appearance.

Box 6.8 (continued)

FIGURE 6.18 Confidence limits on the time of extinction, using inferred facies variation and observed frequency of occurrence in different facies to estimate how sampling probability has varied over time. The black bars in the right columns show the sampling probabilities of the genera *Cryptolithus* and *Sowerbyella*, estimated on the basis of how frequently these genera are known to occur in samples with the corresponding DCA score; these probabilities are also depicted in the bell-shaped curves at the top of the figure. Actual occurrences are shown to the left of each set of bars. The 95 percent confidence limit on the time of true extinction of *Cryptolithus* is well above its last recorded occurrence, off the scale of this figure. The 95 percent confidence limit for *Sowerbyella*, however, is close to the last occurrence. *(From Holland, 2003)*

SUPPLEMENTARY READING

Brett, C. E. (1995) Sequence stratigraphy, biostratigraphy, and taphonomy in shallow marine environments. *Palaios* **10:**597–616. [An overview of the relationship of sequence stratigraphy to biostratigraphy and taphonomy.]

Brett, C. E. (1998) Sequence stratigraphy, paleoecology, and evolution: Biotic clues and responses to sea–level fluctuations. *Palaios* **13:**241–262. [A follow-up to Brett (1995) that considers the paleoecological and evolutionary ramifications of sequence stratigraphy.]

Gradstein, F. M., Ogg, J. G., and Smith, A. G. (eds.) (2004) *A Geologic Time Scale 2004.* New York, Cambridge University Press, 589 pp. [A comprehensive overview and presentation of the latest geologic timescale.]

Holland, S. M. (2000) The quality of the fossil record: A sequence stratigraphic perspective. *Paleobiology* **26** (Supplement to No. 4): 148–168. [An extensive discussion of the relationship between sequence architecture and the stratigraphic distributions of fossils.]

Mann, K. O., and Lane, H. R. (eds.) (1995) *Graphic Correlation. SEPM Special Publication* **53,** 263 pp. [An overview of graphic correlation and related techniques; includes the papers by Kemple et al., and Carney & Pierce, cited in the bibliography.]

SOFTWARE

Holland, S. M. (1999) *Biostrat 1.7.* [A program for modeling the stratigraphic distributions of fossils within depositional sequences [SEE SECTION 6.4]. The program and documentation are available at www.uga.edu/~strata/software/Software.html.]

Sadler, P. M. (2003) *CONOP9, version 6.5.* [This program performs Constrained Optimization [SEE SECTION 6.2] on a user-defined data set. The program and documentation are available at www.usask.ca/geology/classes/ geol246/CONOP9.htm. A web-hosted version is currently under development at http://portal.chronos. org/gridsphere/gridsphere;jsessionid=A90316B3AF52 C245C61C98C8B497ABAE?cid=tools_conop9.]