

The Use of Faunal Gradient Analysis for Intraregional Correlation and Assessment of Changes in Sea-Floor Topography in the Type Cincinnatian

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ABSTRACT

In paleobiology and stratigraphy, there is a growing need to develop high-resolution chronostratigraphic frameworks at regional scales, which would permit unprecedented assessments of spatiotemporal variation in preserved biotas. Here, we present an intraregional correlation for the Kope and lower Fairview Formations of the type Cincinnatian, on the basis of detrended correspondence analysis (DCA) of faunal census data; we believe that the method also holds promise as a tool of correlation in other fossiliferous venues. The data were collected directly in the field at closely spaced stratigraphic intervals but with relatively coarse taxonomic and quantitative data resolution. This approach is independent of lithologic assessments and does not require the delineation of sequence stratigraphic architecture in the study area. Faunal curves were constructed for each locality on the basis of stratigraphic changes in sample scores for DCA axis 1; the curves were smoothed to reveal a long-term signal of paleoenvironmental change recognizable at all localities. Several inflections on the curves provided lines of correlation from locality to locality. Moreover, comparisons of sample scores among three of the localities suggested notable changes through time in the relative paleoenvironmental attributes of locations arrayed across the Cincinnatian paleoramp, indicating that the sea floor was spatiotemporally dynamic.

Introduction

Several issues of current concern to paleobiologists and stratigraphers call for a dramatically improved understanding of the detailed texture of biotic patterns in space and time. This has placed a new premium on the development of high-resolution chronostratigraphic frameworks at regional scales: depositional sequences correlated across a region provide baselines against which biotic patterns can be mapped and assessed with respect to physical patterns apparent in lithological and geochemical data (e.g., Patzkowsky and Holland 1993, 1999). These data, in turn, are vital for the rigorous evaluation of issues ranging from the biotic responses of organisms in the face of abrupt physical perturbations (Miller 1998; Patzkowsky 1999) to the

changing topography of sea floors in regions under investigation (see below).

However, fine-scale correlation over even short distances may not always be accomplished easily. In the lowest portion of the type Cincinnatian Series (the upper Ordovician C1 and lower C2 third-order sequences of Holland and Patzkowsky [1996]), Holland et al. (1997) delineated approximately 50-m-scale, fifth-order cycles that can be recognized in outcrops throughout the region. While there is some stratigraphic variation in attributes from cycle to cycle, these variations are subtle at best (Miller et al. 1997), hindering correlations at the meter scale of resolution from outcrop to outcrop. Correlations at this scale are highly desirable, not only because they would provide a refined picture of regional-scale, background faunal variation down to the level of individual horizons, but also because they would open up the full potential of the highly fossiliferous type Cincinnatian as a natural laboratory for the investigation of patterns of faunal variation in space and time.

Manuscript received November 27, 2000; accepted April 20, 2001.

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We present here a method that holds promise for improvements in the precision of correlation from outcrop to outcrop, on the basis of multivariate analyses of faunal census data collected at outcrops throughout the Cincinnati area. While we cannot yet claim to have accomplished consistent, high-resolution correlations of individual horizons, if this is even possible (see below), we believe that the method provides a significant improvement in our ability to correlate intraregionally. The numerical methodology is not new (e.g., Cisne and Rabe 1978; Dattilo 1996; and especially Anstey et al. 1986 and Anstey and Rabbio 1989), but its success in this case, using data that were taxonomically and quantitatively coarse, suggests that it is broadly applicable not only to the continued correlation of Cincinnati strata, but also for the development of improved correlations in other regions.

The approach highlighted here is one of several currently under investigation for correlating among localities in the Cincinnati. In fact, the type Cincinnati has become something of a proving ground for the evaluation of various correlation methods. For example:

1. Brett and Algeo (1999) developed a stratigraphic framework for correlation of Kope Formation outcrops by laterally tracing prominent stratigraphic "bands" on the order of 10-m thick that are alternately rich in limestone or shale; this banding is a manifestation partly of the 20-m scale of cyclicity recognized by Holland et al. (1997). To further refine their correlations, Brett and Algeo (1999) were able to recognize and trace several distinctive horizons marked by unique physical and biological attributes.

2. Holland et al. (2000) correlated two outcrops using statistical cross-correlation techniques to compare the succession of meter-scale cycle thicknesses preserved at each outcrop. The occurrence of distinctive fossil suites permitted Holland et al. to choose among alternative correlations that would have otherwise been equally plausible on statistical grounds alone.

Through its reliance solely on quantitative analysis of faunal data, the techniques advocated here remove an interpretative step relative to previous correlation methods, in that delineation and matching of cycles or lithological packages is not an integral part of our method. Further, because the fossil organisms preserved in Kope strata appear to be more sensitive to environmental variation than the sediments that encase them (Holland et al. 2001), subtle stratigraphic variations in faunal content provide objective means of correlation that, in

some instances, would not be possible on lithologic grounds (Cisne and Rabe 1978). Finally, in addition to their utility in correlation, these techniques may permit the diagnosis of changes in sea-floor topography within the study area that have not been documented previously.

The Study Interval

The study interval includes the Kope and lower Fairview Formations in the vicinity of Cincinnati, which constitute the entire C1 sequence of Holland and Patzkowsky (1996 emended) and the base of the C2 sequence. Details of this interval are provided by Holland et al. (1997, 1999) and Miller et al. (1997) and will be summarized here only briefly.

The Kope Formation consists of some 70 m of strata dominated by siliciclastic mudstone, with interbedded skeletal limestones, siltstones, and calcisiltites. The siliciclastic components were derived from eastern sources uplifted during the Taconic Orogeny. The basal 8–9 m of the Fairview Formation, which constitute the upper limit of this investigation, are characterized by a significant increase in the ratio of limestone to shale: 3-ft intervals of the Kope have an average siliciclastic content of 86%, whereas those of the Fairview average 64% (Ford 1967). Notably, the transition associated with the formal lithologic boundary between the Kope and Fairview (Ford 1967; Tobin 1986) does not coincide with a fundamental biotic transition (Caster et al. 1961), which instead occurs some 3 m higher in the section.

The Kope and Fairview Formations were deposited on a northward-dipping ramp (but see "Results and Discussion" below) subjected to appreciable storm activity (Kreisa et al. 1981; Tobin 1982; Jenette and Pryor 1993). Storm proximity concepts (Aigner 1985) applied to these strata have permitted the development of an increasingly refined delineation of relative fluctuations in sea level and other perturbations related to a hierarchy of cycles (Holland et al. 1997, 1999). These include the aforementioned third- and fifth-order sequences, as well as an intermediate (20-m) scale of cyclicity manifested in the Kope Formation by changes in the relative spacing of the amalgamated packstone and grainstone ledges that cap successive meter-scale cycles. Intervals in which these ledges are spaced widely alternate with those in which they are bundled more closely (see fig. 12 of Holland et al. 1997; Brett and Algeo 1999).

Because there are four 20-m cycles within the Kope, and the meter-scale cycles that constitute them differ from one another in ways that are rather

subtle (Holland et al. 1997), high-resolution correlation at the meter scale based on cycle architecture appears problematical from a lithological standpoint. However, the study interval is richly fossiliferous, and its faunal composition has been shown previously to vary stratigraphically, at least in a broad sense (Anstey and Rabbio 1989; Diekmeyer 1998). Our motivation here was to determine (1) whether faunal compositions varied in a net sense at relatively fine stratigraphic scales through the Kope interval, and (2) whether the same stratigraphic pattern of variation was repeated at different localities, thereby permitting its use for correlation.

Methods

The field and analytical methods used here are described in detail in a companion article (Holland et al. 2001); salient aspects are summarized here. The backbone of this analysis was a faunal database collected at five localities arrayed throughout the Cincinnati area (fig. 1). The K445 locality has been highlighted in several of our previous investigations (Holland et al. 1997, 1999, 2000, 2001; Miller et al. 1997) and will be the focus of our initial discussion of faunal patterns; this locality includes all but the basal 10 m of the Kope Formation and spans the lower portion of the overlying Fairview. The locality at Holst Creek, some 50 km to the east-southeast of K445, is more extensive stratigraphically than K445 in that it includes the entire Kope Formation, but a large, central interval at this locality is poorly exposed and difficult to sample. While the entire interval at Holst Creek was included in our analyses, only the well-sampled portion that includes the upper half of the Kope and the lower Fairview is reported here. The other localities at Aurora, Miamitown, and Hume are stratigraphically less extensive, covering limited portions of the Kope Formation and/or the lower Fairview.

The localities span an appreciable portion of the Ordovician paleoramp. Thus, they provide an appropriate testing ground for the methodology presented here: the stratigraphically "shorter" localities at Aurora, Miamitown, and Hume were already known to overlap stratigraphically with some portions of the more extensive K445 locality. Moreover, given their areal coverage, it was possible to assess paleoenvironmental overprints on stratigraphic faunal patterns related to changes in basin geometry (see below).

At all five localities, in conjunction with bed-by-bed measurement of the sections, faunal censuses

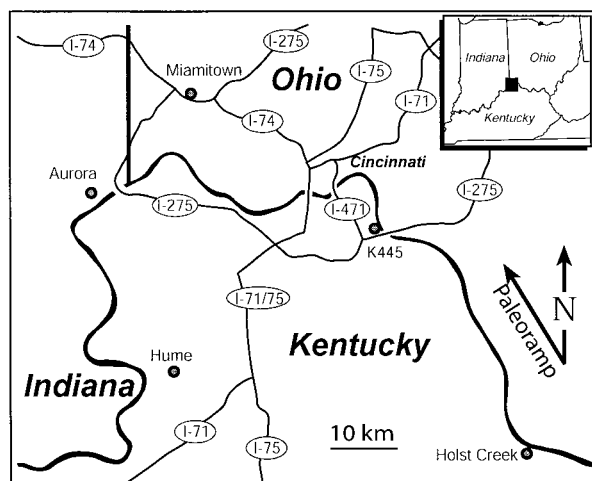


Figure 1. Map of sampling localities; detailed locality descriptions are provided by Holland et al. (2001). The direction of approximate dip of the ramp during the Ordovician is indicated on the map.

were conducted during fieldwork that included the body and trace fossils in every horizon observed to contain fossils. In all, within the 255 m of section logged in aggregate at the five localities, 1949 such censuses were conducted, for a mean density of one census per 13 cm of section.

Censuses on limestones and siltstones were conducted by exposing a piece of the surface of the bed to be censused and cleaning it if necessary; siliclastic mudstones were censused by splitting pieces apart to expose skeletal material. The need to rapidly conduct numerous censuses necessitated two logistical compromises, however. First, the taxonomic resolution of the censuses was fairly coarse; some faunal elements, including the most common brachiopods and crinoid columnals, were identified to genus or species (many of the genera are known to be monospecific within the study interval), but others were categorized only to class (e.g., cephalopods) or by growth form (e.g., "thick ramose bryozoans"). Second, abundances were assessed using a three-fold categorization as "rare" (~1–2 specimens per 1000 cm²), "common" (~3–10 specimens per 1000 cm²), or "abundant" (>10 specimens per 1000 cm²); in effect, this constituted an effort to estimate biovolume, and no attempt was made to distinguish between solitary and colonial organisms, nor between solitary organisms that disaggregated readily upon death (e.g., trilobites) and those that were less likely to do so (e.g., brachiopods). For subsequent quantitative analyses, these classes were assigned values of 1 (rare), 6 (common), and 12 (abun-

dant) to reflect the approximate midpoints, and relative abundances, of the three classes.

Before quantitative analysis, the data were culled to exclude: (1) taxa that occurred in only one census and (2) censuses that contained only a single taxon. This eliminated 11 taxa and 612 censuses, resulting in a final data matrix of 1337 samples and 46 taxa; a complete listing of these 46 unique taxonomic designations is provided in table 1. This matrix was then evaluated using detrended correspondence analysis (DCA), a multivariate ordination technique that simultaneously determines scores for samples and taxa on axes found analytically to capture major vectors of variation in the data. The computer package PC-ORD 3.0 (McCune and Meford 1997) was used here, using default settings for rescaling of axes (on), rescaling threshold (0), and the number of segments into which axes are divided for the detrending algorithm (26). In addition, rare taxa, defined by PC-ORD as any taxon with an overall abundance of less than one-fifth that of the most abundant taxon, were downweighted in proportion to their abundances.

Samples that yield high scores on a DCA axis tend to be similar in taxonomic composition, dominated by taxa that score highly on that axis; samples that yield low scores also tend to be comparable to one another, dominated by taxa with low scores on that axis.

Results and Discussion

Throughout this discussion, we will focus on sample scores for axis 1, which exhibit robust stratigraphic trends recognized at all localities analyzed herein. It has been demonstrated elsewhere (Holland et al. 2001) that these scores provide proxies for environmental attributes most likely correlated with water depth, including the degree of energy, and the concomitant percentages of siliciclastic and carbonate mud, on Cincinnatian sea floors. The justification for this interpretation, and its paleoecological significance, are discussed extensively by Holland et al. (2001). It is based partly on the recognition that samples scoring highly on axis 1 are rich in taxa characteristic of shallower-water assemblages in the upper Ordovician of the eastern United States, whereas those with lower scores are dominated by taxa associated with deeper-water facies. However, it should be emphasized that the correlation framework presented here is not contingent on the definitive determination of paleoenvironmental attributes. The only prerequisite is that long-term, stratigraphic trends in these scores be reflected basinwide, as discussed below.

Table 1. The 46 Taxa Included in the Detrended Correspondence Analysis (DCA) Presented in This Article

Articulate brachiopods:
<i>Dalmanella</i>
<i>Platystrophia</i>
<i>Plectorthis</i>
<i>Rafinesquina</i>
<i>Sowerbyella</i>
<i>Strophomena</i>
<i>Zygospira</i>
Inarticulate brachiopods:
<i>Craniops</i>
<i>Pseudolingula</i>
<i>Schizocrania</i>
Bryozoans:
<i>Aspidopora</i>
<i>Escharopora</i>
<i>Parvohallopora</i>
<i>Prasopora</i>
<i>Stomatopora</i>
Cryptostomes
Fenestellids
Encrusters
Thick bifoliate
Thick ramose
Thin bifoliate
Thin ramose
Annelida:
<i>Cornulites</i>
Scolecodonts
Trilobites:
<i>Acidaspis</i>
<i>Ceraurus</i>
<i>Cryptolithus</i>
<i>Isotelus</i>
<i>Proetidella</i>
Calymenids
Bivalvia:
<i>Ambonychia</i>
<i>Modiolopsis</i>
Nuculoids
Univalved molluscs:
<i>Cyclonema</i>
<i>Cyclora</i>
Indeterminate gastropods and monoplacophorans
Cephalopods
Crinoidea:
<i>Cincinnatiocrinus</i>
<i>Ectenocrinus</i>
<i>Iocrinus</i>
<i>Merocrinus</i>
<i>Glyptocrinus</i>
Other:
Graptolites
Hydrozoans
<i>Lepidocoleus</i>
Ostracods

To assess stratigraphic patterns of variation in sample scores for axis 1, the scores were plotted with respect to their stratigraphic positions initially at the K445 locality (fig. 2). One obvious char-

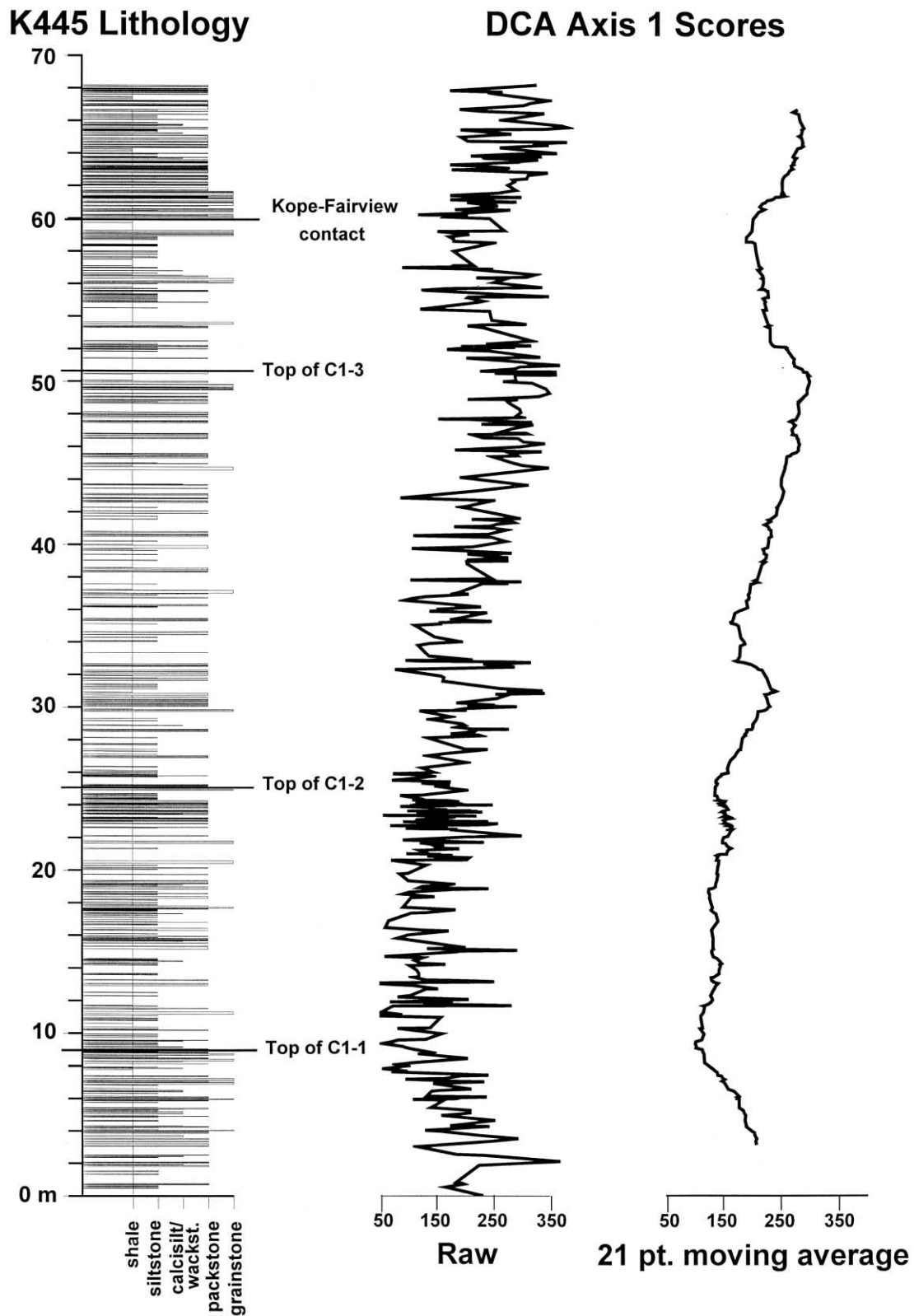


Figure 2. Stratigraphic depiction of DCA axis 1 sample scores for the K445 locality, plotted next to a lithologic summary of the locality for comparison. The curve on the right was prepared using a 21-point moving average, as described in the text. Major lithologic horizons are noted to the right of the stratigraphic column; these include the tops of 20-m cycles and the Kope/Fairview formational contact.

acteristic of the resulting curve is substantial high-amplitude fluctuation at and below the meter scale. It is possible that the fluctuations reflect variations at that scale among the paleoenvironments preserved at K445, or they might simply record random fluctuations in the biota; to address this issue, an assessment of the fine-scale variations is ongoing (Webber et al. 2000; A. J. Webber, unpub. data).

For present purposes, however, our focus was on the diagnosis of broader trajectories through the study interval. It was determined empirically that these trajectories could be recognized more readily by smoothing the raw curve with a 21-point moving average: this extent of smoothing was sufficient to suppress high-frequency variation, preserving longer-term trends in the data. Its effects are illustrated in figure 2 (these averages cannot be computed for the uppermost and lowermost 10 samples, which are therefore not depicted on the smoothed curves). The amplitudes of the fine-scale fluctuations are dampened significantly, and a longer-term background pattern emerges. If these sample scores provide proxies for water depth, or paleoenvironmental attributes correlated with water depth, the exposure at K445 records an initial episode of deepening, followed by several alternating episodes of shallowing and deepening, related partly to the 20-m scale of cyclicity recorded in these strata (Holland et al. 1997), and culminating in the shallowing interval associated with the transition from the Kope Formation into the lower Fairview. It should be emphasized, however, that the correlations presented below are contingent on neither the delineation of cycles through the study interval nor the interpretation of a relationship between axis 1 sample scores and water depth. They are dependent only on the recognition of robust stratigraphic trends in sample scores that emerge through the study interval at all localities, and the implication that major inflections on these curves reflect basinwide, simultaneous environmental transitions of some kind, whether they are produced by changes in water depth or some other mechanism(s) (Dattilo 1996).

Smoothed stratigraphic trajectories of axis 1 sample scores are presented in figure 3 for all five localities. Several similarities are apparent among different localities in curve trajectories as determined by the positions and stratigraphic durations of major inflections. This is especially apparent in the upper portion of the study interval, preserved at Miami town, K445, and Holst Creek. On the basis of these similarities, as well as additional similarities among Aurora, K445, and Hume in the lower

portion of the interval, several lines of correlation were drawn between sections, depicted with the dotted lines in figure 3.

To provide independent "checks" of these correlations, we established several additional lines of correlation among localities, primarily on the basis of prominent stratigraphic boundaries that can be recognized easily in the field: the Kope-Fairview contact and the tops of two 20-m cycles in the Kope (Holland et al. 1997). Our objective in doing so was to provide independent tie-ins for each locality to at least one other locality. Because the base of the Aurora section lies very close to the top of 20-m cycle C1-2, and the top of the section sits below the top of cycle C1-3, another tie-in had to be used in this case. During our fieldwork, we confirmed the findings of earlier workers (Caster et al. 1961) that the ptychopariid trilobite *Triarthrus* was extremely rare in the study interval and that, excluding the lowermost Kope, it was limited to a single horizon. Because it occurred at Aurora and Miami town, we established an independent line of correlation between these two localities using this horizon.

In all instances, it can be seen that the correlations based on the DCA axis 1 trajectories were corroborated by the independent correlations, providing confidence that the method yields a dependable, objective means of correlation among sections. Moreover, the established correlations should be valid not only for the major inflections linked by the dotted lines but also for much of the interval surrounding them (but see below).

Despite the apparent success of the method in establishing correlations among sections, several issues must be addressed before it can be claimed that the method provides a practical means of high-resolution correlation in the Cincinnati or elsewhere:

First, for the method to be viable, there must be net paleoenvironmental change within the confines of the study interval. In the case of the Kope and lower Fairview, there is evidence of overall shallowing through the interval (Tobin 1982; Jenette and Pryor 1993; Holland et al. 1997), and the faunal expression of the 20-m-scale cycles varies from cycle to cycle: the slope of the curve for DCA axis 1 becomes more pronounced near the top of cycle C1-2, and the shapes and absolute values of its major inflection intervals also change substantially upsection. However, if there was no net paleoenvironmental change through the interval, then the smoothed faunal curve might have taken on the appearance of a sine curve or some other regularly repeating signal, making it more difficult

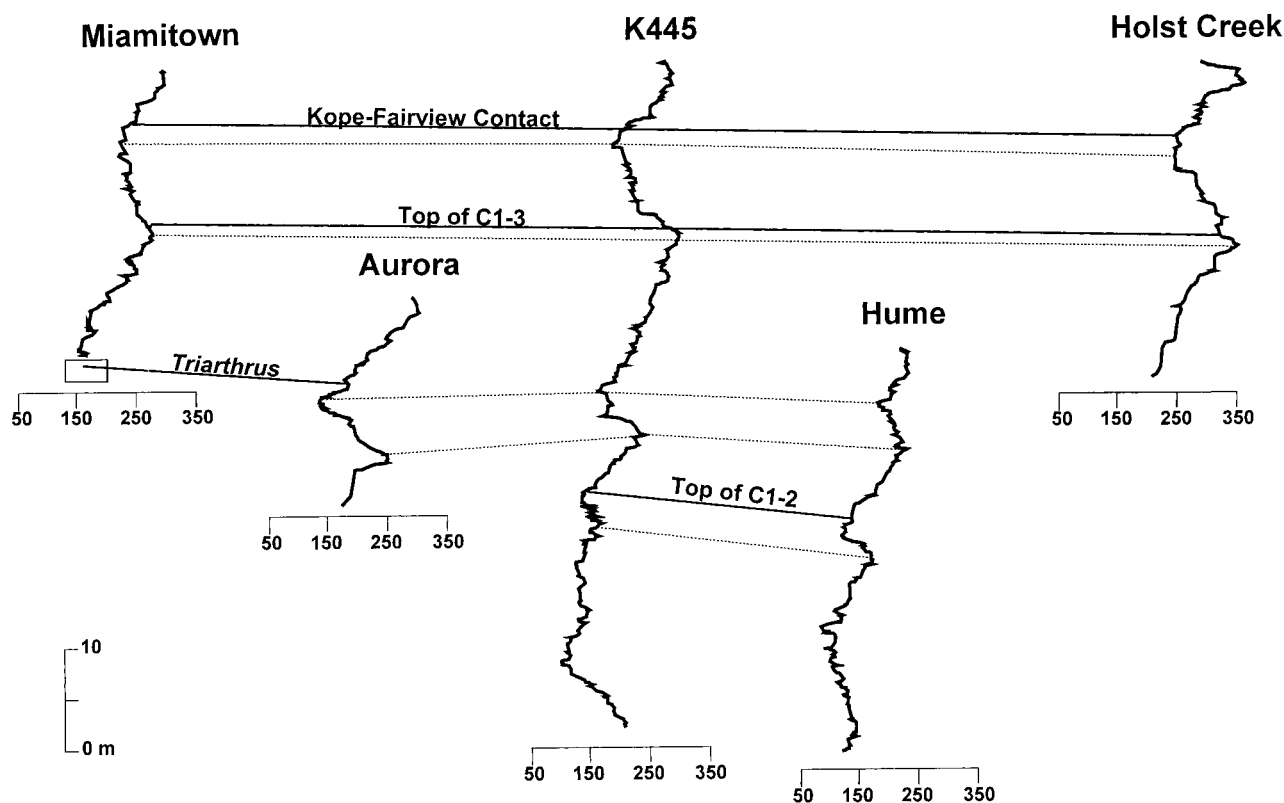


Figure 3. Correlations among the five localities, based on the 21-point moving-average curves from sample scores on DCA axis 1. Dotted lines depict correlations based on major inflections in the curves recognized at multiple localities. Solid lines depict independent correlations, for comparison, based on 20-m cycle tops, the Kope/Fairview formational contact, and a unique stratigraphic occurrence of the trilobite *Triarthrus*.

to confidently correlate two sections without independent, corroborating evidence. Ironically, in the Cincinnati, an ambiguity of this kind was demonstrated by Holland et al. (2000) with respect to the stratigraphic pattern of meter-scale cycle thicknesses, rather than with the biotic pattern. In fact, in that case, faunal data permitted an unambiguous choice between three alternative correlations that would have been equally plausible on the basis of cycle thickness data alone.

Second, while the correlations appear highly constrained, this is not tantamount to suggesting that correlation down to the meter scale has been achieved or that one can recognize the same bed at different localities. Indeed, even at individual outcrops, single limestone layers commonly vary in thickness and may be observed to pinch out entirely or bifurcate laterally. The extent to which individual beds persist within and between outcrops is currently under active investigation (e.g., Barbour 1999; Brett and Algeo 1999; Webber et al.

2000), and it is likely that the extent to which single horizons can be identified at multiple outcrops will be understood better in the future. For the moment, it appears that the best candidates for inter-outcrop correlations of individual layers are the prominent grainstone ledges that cap many of the meter-scale cycles in the study interval.

Third, whereas the general lack of lateral variation in interval thickness provides confidence that intervals between inflection points on the DCA axis 1 curves are correlatable, there are instances in which thickness appears to vary between localities (e.g., the portion between the dotted lines at Aurora vs. K445). In such cases, correlation away from inflection points is problematical. This issue may be amenable to solution if the high-amplitude fluctuations apparent for each locality in the raw, unsmoothed DCA axis 1 curves ultimately prove useful for correlation. A. J. Webber (unpub. data) has developed a stratigraphic binning procedure

that should help to diagnose the veracity of patterns down to the meter scale.

Finally, it might reasonably be asked whether it is practical to collect the data required for the method to be utilized. Censuses can be conducted rapidly, but our experience thus far has relied on data collected bed-by-bed for significant stratigraphic intervals (at least 15–20 m) at each locality, which requires more than just a casual exploration of a locality. However, it is possible that a useful stratigraphic signal would emerge with some relaxation of the bed-by-bed sampling protocol. We are currently investigating the extent to which stratigraphic sampling density can be reduced, while still maintaining essential elements of the curves depicted in figures 2 and 3.

We believe that these data are worth obtaining, not only because of their utility for correlation, but also because they may prove to be vital for other purposes, including the detection of subtle basin attributes or biotic transitions of evolutionary and paleoecological significance. For example, in the case of our study interval, our data demonstrate that paleoenvironmental attributes of the Cincinnati sea floor were more variable spatially and temporally than envisaged previously. In the past, for example, the regional sea floor has been characterized as a ramp that dipped to the north-north-west. While it has been recognized that the direction and extent of dip were somewhat dynamic (Tobin 1982; Weir et al. 1984; Holland 1993; Jenette and Pryor 1993), the impression has emerged nevertheless that ramp topography was relatively featureless. Thus, given the direction of dip on the ramp, it might fairly be expected that a line from Holst Creek through K445 to Miamitown would have always traced a deepening trend during the Cincinnati.

However, the overlays provided in figures 4 and 5 provide a rather different impression of ramp geometry. In comparing the Miamitown locality directly to K445 (fig. 4), faunal data suggest that near the top of cycle C1-3, there was a transition in the topographic relationships of the two localities. Before the transition, Miamitown was located at a greater water depth than K445, perhaps as expected on the basis of previous interpretations of the region. However, following the transition, the relative depths of the two sections changed, and Miamitown appears to have been shallower than K445! In a comparison of Holst Creek with K445 (fig. 5), a dynamic pattern emerges as well: the “expected” depth relationship of Holst Creek to K445 only emerged near the top of C1-3. Before that, the depths of Holst Creek and K445 appear to have been

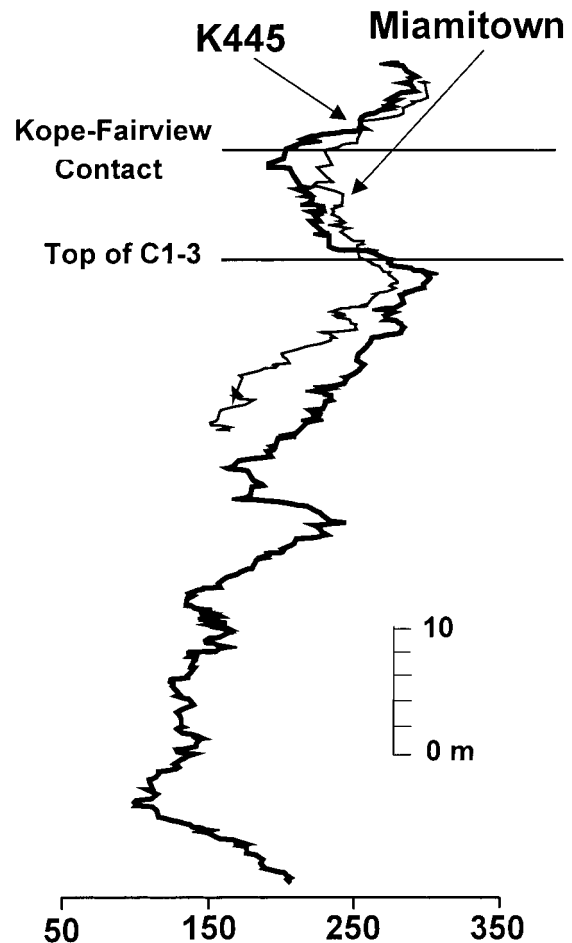


Figure 4. The 21-point DCA moving-average curve for Miamitown superimposed on the corresponding curve for K445. Note the transition in relative values on the two curves, suggesting a change in sea-floor topography through the sampling interval; initially, water depth was greater at the Miamitown locality, but later in the interval, it appears that the depth was greater at K445.

comparable, at least for the interval portrayed here. On the basis of calculations presented by Holland et al. (2001), these relative changes in water depth among localities were less than 10 m.

Although there is no definitive explanation for the changes to Cincinnati sea-floor topography depicted here, there is ample evidence that the region was tectonically active at that time, reflecting earthquake activity focused mainly to the east (Pope et al. 1997) coupled with reactivation of a fault system associated with an antecedent rift basin (Drahovzal et al. 1992). Alternatively, these changes in depth could simply reflect local differences in the rate of sedimentation. Arguably, the

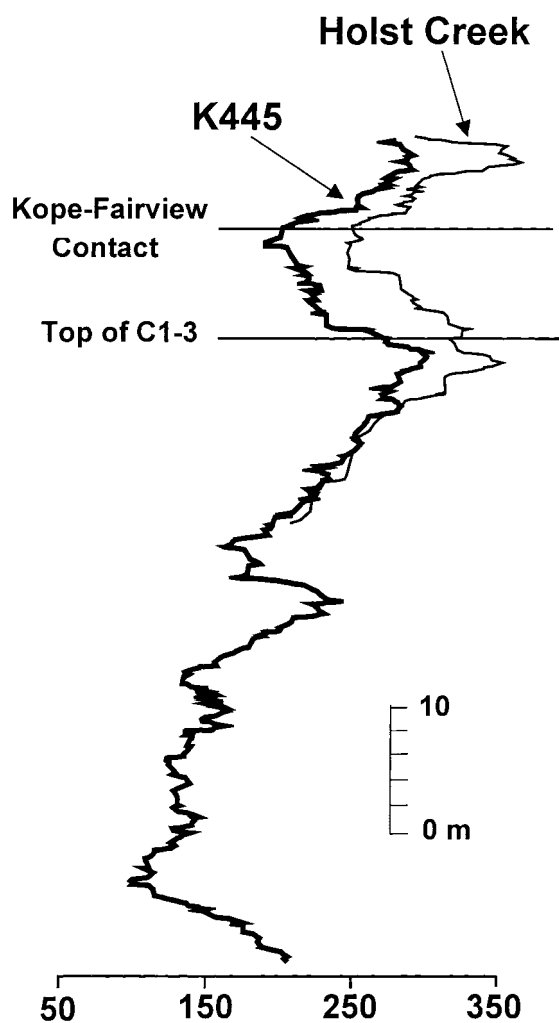


Figure 5. The 21-point DCA moving-average curve for Holst Creek superimposed on the corresponding curve for K445. As in figure 4, note the transition in relative values on the two curves, suggesting a change in sea-floor topography through the sampling interval: initially, water depth at the two localities was roughly comparable, but the divergence of the two curves higher in the interval suggests that Holst Creek became shallower than K445.

continued acquisition and analysis of the kinds of data highlighted herein will permit the development of a highly resolved, three-dimensional perspective on the evolution of regional sea-floor topography. This, in turn, would permit a firmer linkage to the processes that produced them.

This interpretation of basin geometry is contingent, of course, on the argument that DCA axis 1 scores provide proxies for water depth or paleoenvironmental attributes related to water depth (Holland et al. 2001). If this is not the case, however, and axis 1 instead summarizes biotic responses to something else (e.g., paleoclimatic fluctuations; Holland et al. 1999; A. J. Webber, unpub. data), it would nevertheless be true that paleoenvironmental relationships among localities were subject to dramatic changes during the Cincinnati.

These results serve to further illustrate the general value of the procedures advocated herein. Although the primary objective in acquiring these data was to develop a more precise framework for correlation, it is clear that the data will have utility for the diagnosis of a suite of paleobiological and physical attributes within the region under investigation.

Conclusions

1. Detrended Correspondence Analysis (DCA) of taxonomically and quantitatively coarse faunal data collected bed-by-bed from the Kope and lower Fairview Formations of the type Cincinnati reveals a stratigraphic pattern of variation in the faunal contents of individual horizons that remains consistent from locality to locality.

2. Because of their geographic consistency, major inflections in curves for DCA axis 1 provide bases for improved correlations among localities.

3. In addition to their utility as tools of correlation, curves for DCA axis 1 provide a means of detecting changes in sea-floor topography throughout the study interval, indicating relative shifts in water depth among localities.

4. Because these procedures do not rely on species-level taxonomic identifications or precise quantitative-abundance data, they should be readily applicable beyond the immediate study area.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation grants EAR-9204916 to A. Miller and D. Meyer and EAR-9204445 to S. Holland. We thank S. Diekmeyer and T. Reardon for field and laboratory assistance and A. Webber for reviewing an earlier draft of this manuscript.

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