Ecosystem Structure and Stability: Middle Upper Ordovician of Central Kentucky, USA

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Cluster analysis reveals eight biofacies during a time of faunal turnover and regional oceanographic change in the middle Upper Ordovician of central Kentucky. These biofacies are arranged along a deep-water to shallow-water gradient, with the dalmanellid and the Sowerbyella *biofacies in offshore facies, the* Rafinesquina, *the atrypid, and the ramose trepostome biofacies in deep-subtidal to shallow-subtidal facies, the* Constellaria-Cyclonema *and the* Rhynchotrema *biofacies in the shallow-subtidal facies, and the* Solenopora-Hebertella *biofacies in sand-shoal facies. These biofacies are not discrete, but rather they share a large number of taxa suggesting that they are arbitrary subdivisions of a depth-related ecological gradient. Nonetheless, they are useful as a point of comparison with other studies of this time interval in the eastern United States. Previous lower and middle Upper Ordovician biofacies studies portray a similar pattern of plectorthines and rhynchonellaceans in the shallow subtidal, strophomenids in the deep subtidal, and dalmanellids and plectambonitaceans in the offshore, indicating an overall temporal consistency to many of these biofacies at suprageneric taxonomic levels. Similarly, values of preferred depth, depth tolerance, and peak abundance of most taxa are generally conserved, and this is particularly true for abundant taxa. Nonetheless, this 2-m.y. record also indicates temporal changes in the occurrence of some biofacies, in the relative abundances of taxa in some biofacies, in the species membership within biofacies, and in values of preferred depth, depth tolerance, and peak abundance for several taxa. Collectively these indicate a dynamic aspect to an ecosystem that otherwise displays several attributes of stability and underscore that ecologic stability should not be viewed as a simple dichotomy between stability and instability. The dynamic aspects of this ecosystem suggest that these biofacies were not governed by extreme degrees of species interactions that resulted in near constancy of biofacies structure. Continuous changes in water temperature, nutrient supply, and turbidity during this time may have been a contributing factor to changes within this ecosystem.*

INTRODUCTION

Almost since the recognition of communities, both in the recent and in the ancient past, biologists and paleontologists have commented on their widespread geographic distributions (e.g., Thorson, 1957) and their long geologic ranges (e.g., Walker and Laporte, 1970; Boucot, 1983; Ludvigsen et al., 1986; Brett and Baird, 1995). An emphasis on the stability of communities led to the formulation of models such as the turnover-pulse hypothesis (Vrba, 1985) and coordinated stasis (Brett et al., 1996), sometimes in conjunction with ecological models postulating extremely strong species-species interactions (Morris et al., 1995). Certain times and places may have fostered high levels of stability (e.g., Brett and Baird, 1995)—although this has been called into question recently (Bonuso et al., 2002a, b)—whereas other settings were characterized by much higher levels of faunal turnover (e.g., Westrop, 1996; Patzkowsky and Holland, 1997). Characterizing the conditions that promote varying degrees of stability, and developing means of characterizing and quantifying stability remain unsolved problems in paleoecology (Patzkowsky, 1999). Consensus on these conditions will not come from a single study such as presented here, but will require multiple studies from a wide range of geologic settings.

The Middle and Upper Ordovician of the eastern United States was a time of rapid faunal turnover, as indicated by origination and extinction rates (Patzkowsky and Holland, 1997). This interval of time consists of three blocks of moderate turnover, the M1–M4, M5–C3, and C4–C6 depositional sequences, separated by two times of heightened turnover, the M4–M5 and C3–C4 transitions (sequence nomenclature of Holland and Patzkowsky, 1996). Previous analyses of the M2 through C5 biofacies of the Nashville Dome in central Tennessee indicated long-term biofacies changes through successive depositional sequences in response to evolving paleoceanographic conditions in water temperature, turbidity, and nutrient supply (Patzkowsky and Holland, 1999). Well-exposed and highly fossiliferous complete sections through the M5, M6, and basal C1 sequences in central Kentucky offer an opportunity to build a comparative case study to examine the detailed structure of biofacies, their stratigraphic distributions, and their degree of stability. Here, biofacies of the middle Upper Ordovician of central Kentucky are documented, as is their relationship to depth-related lithofacies and sequence stratigraphic architecture. Despite an apparent large-scale stability of biofacies, not all biofacies are present at all times, changes in relative abundance of taxa occur within individual biofacies, species-level turnover is common within biofacies, and some genera significantly modify their autecological characteristics, specifically, their preferred depth, depth tolerance, and peak abundance.
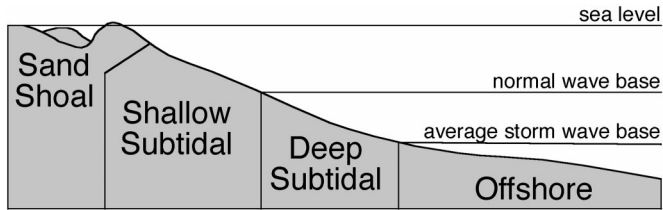
FIGURE 1—Lateral relationships of four principal lithofacies in the study interval.

FIGURE 2—Locality map depicting outcrop belt of Ordovician strata on the Cincinnati Arch. Most data in this study are from the Frankfort composite section, built from the Frankfort North (FN), Frankfort North Upper (FNU), and Peaks Mill (PM) sections; Frankfort city limits shaded in inset. Additional faunal samples were collected nearby at the Frankfort 421 (F421) and Swallowfield (S) sections and 60 km to the southeast at Clays Ferry (CF). Locality descriptions are given in Appendix 1.

REGIONAL BACKGROUND

The study interval includes the middle Upper Ordovician (Chatfieldian Stage) Lexington Limestone and overlying basal Clays Ferry Formation (Edenian Stage) of central Kentucky. Based on radiometric calibration (Sloan, 1987; Holland and Patzkowsky, 1996) of a conodont-based graphic correlation framework (Sweet, 1984), the study interval spans approximately 2 m.y.

The Lexington and Clays Ferry were deposited on a northward-dipping, storm-dominated, mixed carbonate-siliciclastic ramp in an epicontinental seaway at approximately 20° South latitude (Cressman, 1973; Holland, 1993; Pope and Read, 1997a). These rocks record major within-habitat environmental transitions, including a shift from tropical-type to temperate-type carbonates, an increase in phosphatization, and an increase in shale content, all driven by regional changes in oceanographic conditions triggered by the Taconic Orogeny to the east (Holland and Patzkowsky, 1997). The onset of these environmental changes coincided with the M4–M5 regional extinction (Patzkowsky and Holland, 1999).

Lexington and Clays Ferry strata preserve four main depositional environments (Cressman, 1973; Holland, 1993; Weir et al., 1984; Pope and Read, 1997a). The deepest-water environment is represented by offshore facies (Fig. 1), which were deposited below average storm wave base and are characterized by thin- to medium-bedded carbonate tempestites (mostly single-event) and varying proportions of siliciclastic mudstone and mudshale (*sensu* Potter et al., 1980). Fossil preservation in offshore facies is commonly excellent, with minimal breakage and abrasion, and with good preservation of fine detail. Deep-subtidal facies, deposited above typical storm wave base but below normal wave base, consist of medium-bedded carbonate tempestites, commonly amalgamated into multi-event beds or separated by very thin siliciclastic mudstones. Although fossil preservation can be good in this facies, breakage and abrasion are greater than in offshore facies. Shallow-subtidal facies, deposited above normal wave base, are characterized by highly bioturbated, wavy bedded to nodular skeletal packstone and fossiliferous siliciclastic mudstone. Abrasion, breakage, and disarticulation of fossils are common. Sand-shoal facies reflect a wide variety of carbonate sand environments, including beaches, tidal inlets, and subtidal sand belts, and are characterized by variably phosphatic and well-sorted crinoidal to skeletal grainstone. Fossil preservation is generally poor, with exceptionally high breakage and abrasion, although a few well-preserved shells may be found locally.
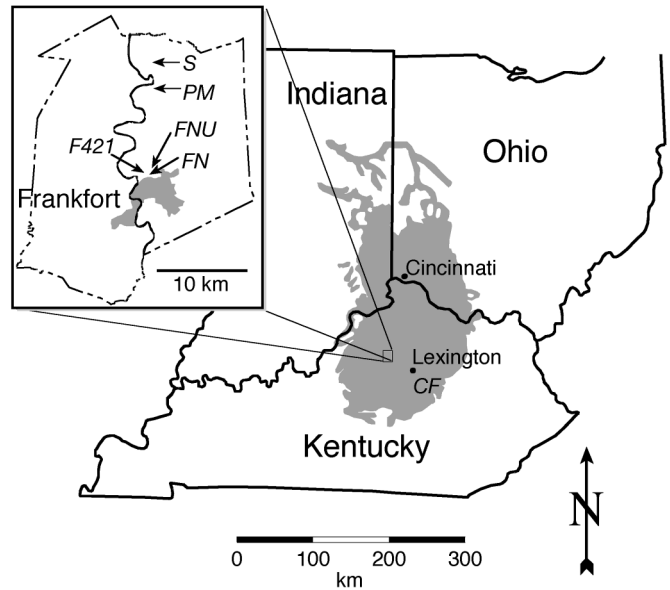
The sequence stratigraphy of the study interval previously has been well characterized (Pope and Read, 1997a, b) and our independent evaluation of the sequence architecture is in agreement. The study interval comprises the M5, M6, and basal C1 3rd-order sequences of Holland and Patzkowsky (1996). These 3rd-order sequences consist of alternating transgressive and highstand systems tracts. Moderate amplitude 4th-order cyclicity generated numerous 3–10 m cycles with repetitive gradual and abrupt facies transitions, which result in a complex lithostratigraphic nomenclature at the member and bed level (Cressman, 1973).

FIELD METHODS AND DATA SET

Field data are drawn primarily from a series of large road cuts in the Frankfort, Kentucky area (Fig. 2). The Frankfort North, Frankfort North Upper, and Peaks Mill sections (Appendix 1; Fig. 2) were described lithologically at a 10-cm level of resolution to build the 110-m Frankfort composite section from the uppermost Tyrone Limestone that immediately underlies the Lexington Limestone into the lowermost Clays Ferry Formation. A faunal survey was conducted in these sections and the abundances of individual taxa were recorded on a rank scale as rare, common, or abundant, where these categories correspond roughly to order-of-magnitude changes in abundance (Fig. 3). This survey was conducted on all exposed surfaces, including bedding planes and vertical faces, and was designed to provide qualitative information on faunal distributions where faunal counts, described below, could not be made.

Analyzed in this study is a series of faunal counts made on individual in-place bedding planes in the composite section, with supplementary counts made on two nearby out-
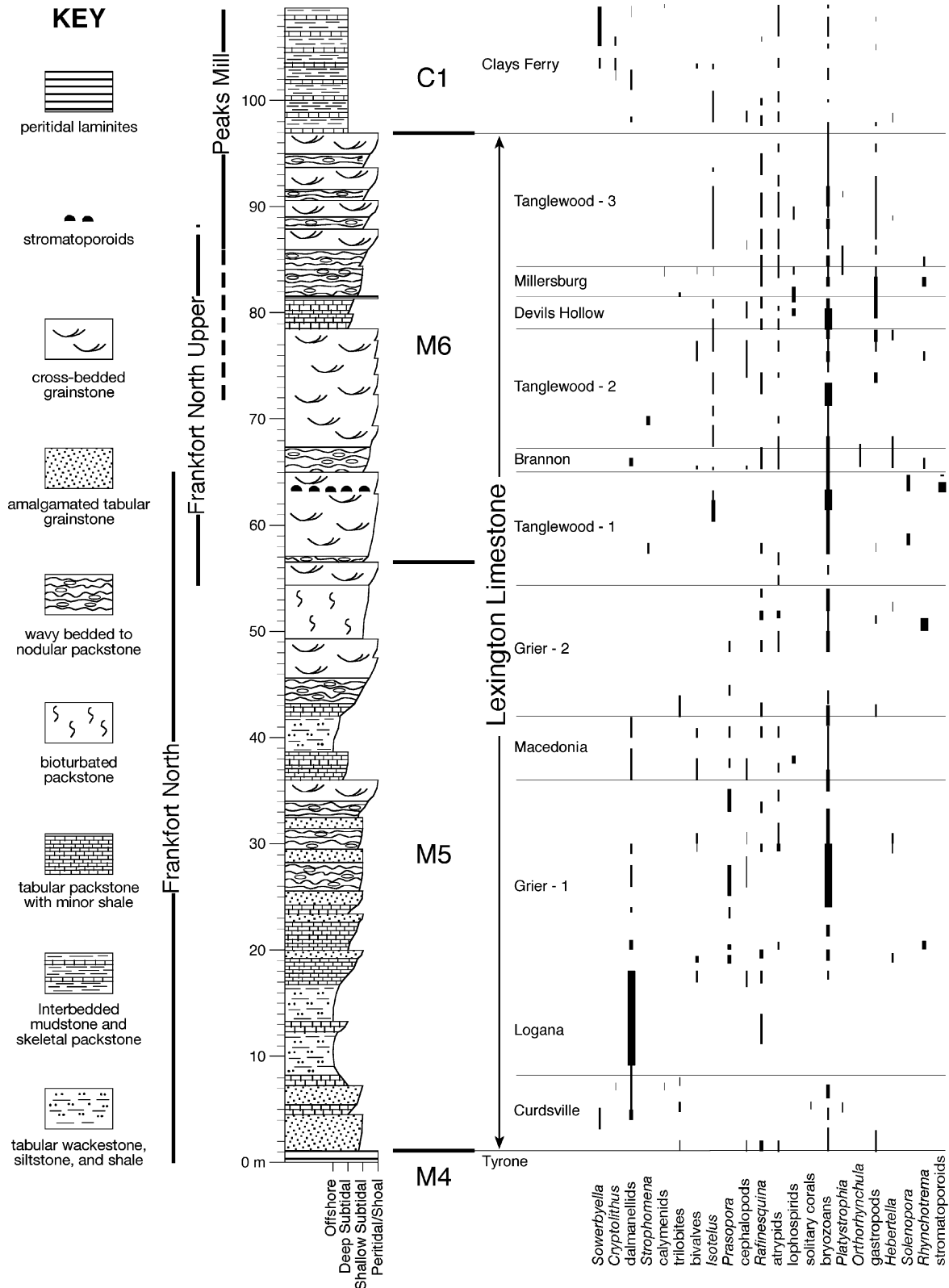
FIGURE 3—Frankfort composite section, illustrating the sequence stratigraphy, lithostratigraphy, and faunal abundances through the study interval. Boundaries of 3rd-order sequences of Holland and Patzkowsky (1996) are indicated with heavy lines to right of section, with more details of sequence stratigraphy shown on Figure 7. Lithostratigraphic nomenclature of Cressman (1973) is shown to right of sequence stratigraphic interpretation. Right half of figure shows faunal logs through the section, with the width of the line indicating relative abundance (rare is thin, common is medium, abundant is thick).

crops (Swallowfield and Frankfort 421; Fig. 2; Appendix 1) and at an additional exposure of the type Clays Ferry, approximately 60 km southeast of Frankfort. The surface area of rock included in each count was dictated largely by exposure availability, with a median area of 1800 cm^2. Fossils were identified to species wherever possible, although genus-level identifications were common. Because the diagnostic characters used for distinguishing closely related taxa (e.g., *Anazyga* and *Zygospira*) were not always visible in some samples, such taxa were lumped into coarser taxonomic units (e.g., atrypids) prior to analysis. Brachiopods and bivalves were counted if the beak of the shell was present, and the minimum number of individuals was calculated as the sum of the articulated shells, the greater of the number of brachial and pedicle valves (or left and right for bivalves), and one-half the number of indeterminate valves. Although some distinctive bryozoans were identifiable to genus (e.g., *Prasopora*, *Escharopora*, *Constellaria*), most bryozoans were identified only to order or morphological form (e.g., ramose, bifoliate, massive, encrusting). Each 1-cm length of bryozoan colony was counted as one individual to provide an internally consistent basis of measurement, although it is admittedly unclear how best to measure the abundance of colonial organisms relative to non-colonial organisms. For trilobites, all cranidia, pygidia, and librigenae were counted and a minimum number of individuals was calculated.

These counts produced an initial data matrix of 94 samples by 48 taxa. Taxa occurring in only one sample were removed because they supply no information linking samples and can distort relationships among samples and among taxa in multivariate analyses. In addition, seven samples were removed after initial multivariate analyses indicated that they behaved as outliers as a result of small sample size or the extraordinary abundance of a normally rare taxon. The resulting matrix analyzed in this study includes 87 samples and 40 taxa, with a total of 5754 individuals (data reposited online at <http://www.sepm.org/archive/index.html>).

STATISTICAL METHODS

Two-way cluster analysis was performed with PC-ORD 4.0 (McCune and Mefford, 1999) and was used to recognize groups of samples with similar faunal compositions (Q-mode) and groups of taxa that tend to co-occur (R-mode). Q-mode analysis was preceded by a percent transformation within samples to mitigate differences in sample size. R-mode analysis also was preceded by a percent transformation within samples, followed by a percent maximum transformation within taxa to correct for differences in abundance among taxa, where the transformed abundance (a_T) is equal to:

$$a_T = \frac{a_{ij}}{a\max_j}$$

Here, a_{ij} is the observed abundance of the taxon j in sample i and $a\max_j$ is the largest observed abundance of taxon j among all samples. Cluster analyses were performed on a dissimilarity matrix, calculated using the Sorenson distance, $D_{i,h}$:

$$D_{i,h} = \frac{\sum\limits_{j=1}^{p} |a_{ij} - a_{hj}|}{\sum\limits_{j=1}^{p} a_{ij} - \sum\limits_{j=1}^{p} a_{hj}}$$

In the Q-mode, $D_{i,h}$ is the distance or dissimilarity between samples i and h, measured among all p taxa. In the R-mode, it is the distance between taxa, measured among all samples. The Sorenson measure is also known as the Bray-Curtis coefficient and the Czekanowski coefficient, and is equal to one minus the quantified Dice coefficient (Sepkoski, 1974; McCune and Grace, 2002). The cluster analysis used group averaging as its linkage method, which is equivalent to the widely used UPGMA (unweighted pair-group method with arithmetic averaging, e.g., Springer and Bambach, 1985; Miller, 1988; Patzkowsky, 1995).

Biofacies are defined by a Q-mode cluster containing samples that share a distinctive association of taxa (cf. Ludvigsen et al., 1986). Commonly, Q-mode clusters share a large number of taxa indicating that biofacies are not discrete, but rather are arbitrary subdivisions of an ecological gradient (cf. Patzkowsky, 1995). Thus, biofacies are described in this study solely as a means of communicating faunal variation along an ecological gradient. For each biofacies recognized in the cluster analysis, species richness (S), Shannon's H, and Buzas and Gibson's E were calculated, with H based on natural logarithms (Hayek and Buzas, 1997).

In order to explore the gradient aspects of the biofacies in greater detail, the data set was ordinated with detrended correspondence analysis (DCA), also performed with PC-ORD. Ordination was preceded by a percent transformation within samples to correct for differences in sample size, followed by a percent maximum transformation within species to correct for differences in abundance of individual taxa. Default settings were used in the DCA, with rescaling axes (on), rescaling threshold (0), number of segments (26), and no downweighting of rare taxa.

CLUSTER ANALYSIS RESULTS

Q Mode

Q-mode cluster analysis results in eight primary clusters of samples with similar faunal compositions (Fig. 4; Tables 1–8 in Appendix 2). Cluster A defines the dalmanellid biofacies, and is dominated by dalmanellid brachiopods (chiefly *Dalmanella*, but also *Heterorthina*). Many samples include significant numbers of atrypid brachiopods (*Anazyga* and *Zygospira*) and ramose trepostomes. Modiomorphid bivalves are abundant in some samples, but these samples are the last to join cluster A. Relative to other biofacies in this study, the dalmanellid biofacies has a low mean diversity (S = 5.0) and a high evenness (E = 0.85).

Cluster B defines the *Sowerbyella* biofacies, and is composed primarily of the plectambonitacean brachiopod *Sowerbyella*, with abundant atrypids and ramose trepostomes. The trilobite *Cryptolithus*, bifoliate trepostomes, and dalmanellids occur commonly, but in lesser numbers. The *Sowerbyella* biofacies combines a high mean diversity (7.1) with moderate evenness (0.65).

Cluster C comprises the *Rafinesquina* biofacies, and is

dominated by the strophomenid brachiopod *Rafinesquina*. A diverse array of other taxa also occurs in many samples, including ramose trepostomes, the orthid brachiopods *Hebertella* and *Platystrophia*, and atrypids and dalmanellids. The *Rafinesquina* biofacies has the highest values of mean diversity (8.4) and evenness (0.91) in this study.

Cluster D defines the atrypid biofacies, and is dominated by exceedingly abundant atrypids. Many samples also contain ramose trepostomes, the asaphid trilobite *Isotelus*, and *Hebertella*. The atrypid biofacies is characterized by high diversity (8.0) and the lowest evenness (0.47) of all biofacies in this study.

Cluster E represents the ramose trepostome biofacies, and is dominated by ramose trepostomes, which are abundant to some degree in nearly all biofacies. The brachiopods *Rafinesquina*, *Hebertella*, dalmanellids, and atrypids occur in many cluster E samples. The ramose trepostome biofacies has a high mean diversity (7.6) and moderate evenness (0.70).

Cluster F defines the *Constellaria-Cyclonema* biofacies and is a distinctive association of ramose trepostomes, the cystoporid bryozoan *Constellaria*, the gastropod *Cyclonema*, and atrypids. Although not included in the analysis, crinoid columns and ossicles are locally abundant in this biofacies. The *Constellaria-Cyclonema* biofacies is moderate in mean diversity (6.0) and evenness (0.71).

Cluster G defines the *Solenopora-Hebertella* biofacies, and consists of an association of crinoid ossicles, ramose trepostomes, the red alga *Solenopora*, and *Hebertella*. *Rafinesquina* and the rhynchonellid brachiopod *Rhynchotrema* are also common in some samples. The *Solenopora-Hebertella* biofacies has moderate mean diversity (5.8) and high evenness (0.81).

Cluster H represents the *Rhynchotrema* biofacies, and is correspondingly dominated by *Rhynchotrema*, with lesser numbers of ramose trepostomes, *Hebertella*, and atrypids. The *Rhynchotrema* biofacies has the lowest mean diversity (4.5) of any biofacies, coupled with a low evenness (0.64).

Three samples do not fall within any cluster. Samples 20 and 70 contain abundant specimens of the bryozoan *Prasopora*, as well as elements of the dalmanellid biofacies. The limited number of samples suggests caution in recognizing this as a biofacies, but with additional samples, a separate *Prasopora* biofacies might be recognized. Sample 39 joins supercluster E-F-G and is characterized by abundant ramose trepostomes, *Rafinesquina*, and atrypids.

R Mode

R-mode cluster analysis leads to the recognition of three clusters linked at relatively low-levels of similarity, as is generally common for ecological data (Fig. 4). Cluster I is composed of *Strophomena*, *Conularia*, modiomorphid bivalves, and two lingulid brachiopod genera (*Pseudolingula* and *Lingulella*). It is found largely in samples from cluster A and represents a distinctive assemblage within the offshore Logana Member in the C5 sequence.

Cluster II is composed of the brachiopods *Eridorthis*, *Petrocrania*, and *Sowerbyella*, trilobites (odontopleurids and *Cryptolithus*), and the graptolite *Geniculograptus*. It is found principally within samples from cluster B, and represents a distinctive assemblage within the offshore Clays Ferry Formation of the C1 sequence.

Cluster III consists of nearly all of the remaining taxa (except gastropods and the bryozoans *Prasopora* and *Escharopora*), and is found within all sequences and all Q-mode clusters. Chaining is conspicuous within this cluster; consequently, taxa could be crudely ordered from deep-water forms on the left to shallow-water forms on the right.

Although cluster analysis is useful for recognizing samples that are faunally similar and taxa that tend to co-occur, the interpretation of such clusters can be ambiguous (Springer and Bambach, 1985; Bonuso et al., 2002). The clustering algorithm itself insures that clusters will be produced from any data set, regardless of whether the data are truly clumped. Distinct clusters of samples can arise when samples are obtained from distinct communities, but they can also arise from uneven sampling of a continuous ecological gradient. Many of the taxa in this study span several biofacies, indicating that these biofacies are best interpreted as divisions of an ecological gradient, rather than as distinct entities (cf., Miller, 1988; Bambach and Bennington, 1996). For this reason, cluster analysis is used here to define biofacies solely as a means of communicating faunal change along a continuous ecological gradient.

DCA RESULTS

Axis 1 Sample Scores

Detrended correspondence analysis was used to reconstruct the positions of samples and taxa along environmental gradients and to relate biofacies to those gradients. This gradient approach is significant in that it avoids generating the perception that biofacies are distinct entities with sharp boundaries in the way that cluster analysis can. As is common in analyses of marine data sets (e.g., Rabe and Cisne, 1980; Patzkowsky, 1995; Holland et al., 2001; Olszewski and Patzkowsky, 2001), DCA axis 1 in this study is correlated with water depth. Samples from sand-shoal and shallow-subtidal facies, as determined from lithologic criteria alone, have high DCA axis 1 scores (Fig. 5). Samples from deep-subtidal facies have intermediate axis 1 scores and samples from offshore facies have low axis 1 scores. The partial overlap in axis 1 scores of samples from adjacent depositional environments likely reflects faunal patchiness (Holland, 2003) and the difficulties of distinguishing some depositional environments, which are expected when sampling an ecological gradient.

Plotting cluster membership of samples against DCA axis 1 and 2 scores is useful for relating biofacies to environmental gradients (Fig. 6). All *Sowerbyella* biofacies samples were collected from offshore facies, as were a majority of samples from the dalmanellid biofacies. Both of these biofacies plot at low DCA axis 1 scores and fix this end of axis 1 as indicating deeper-water settings. Samples from the *Rafinesquina*, atrypid, and ramose trepostome biofacies are nearly evenly split between deep-subtidal and shallow-subtidal facies. These three biofacies plot at intermediate axis 1 scores. All samples from the *Solenopora-Hebertella* biofacies are from sand-shoal facies and all samples from the *Constellaria-Cyclonema* and *Rhynchotrema* biofacies were collected from shallow-subtidal facies. These three biofacies plot at high axis 1 scores and
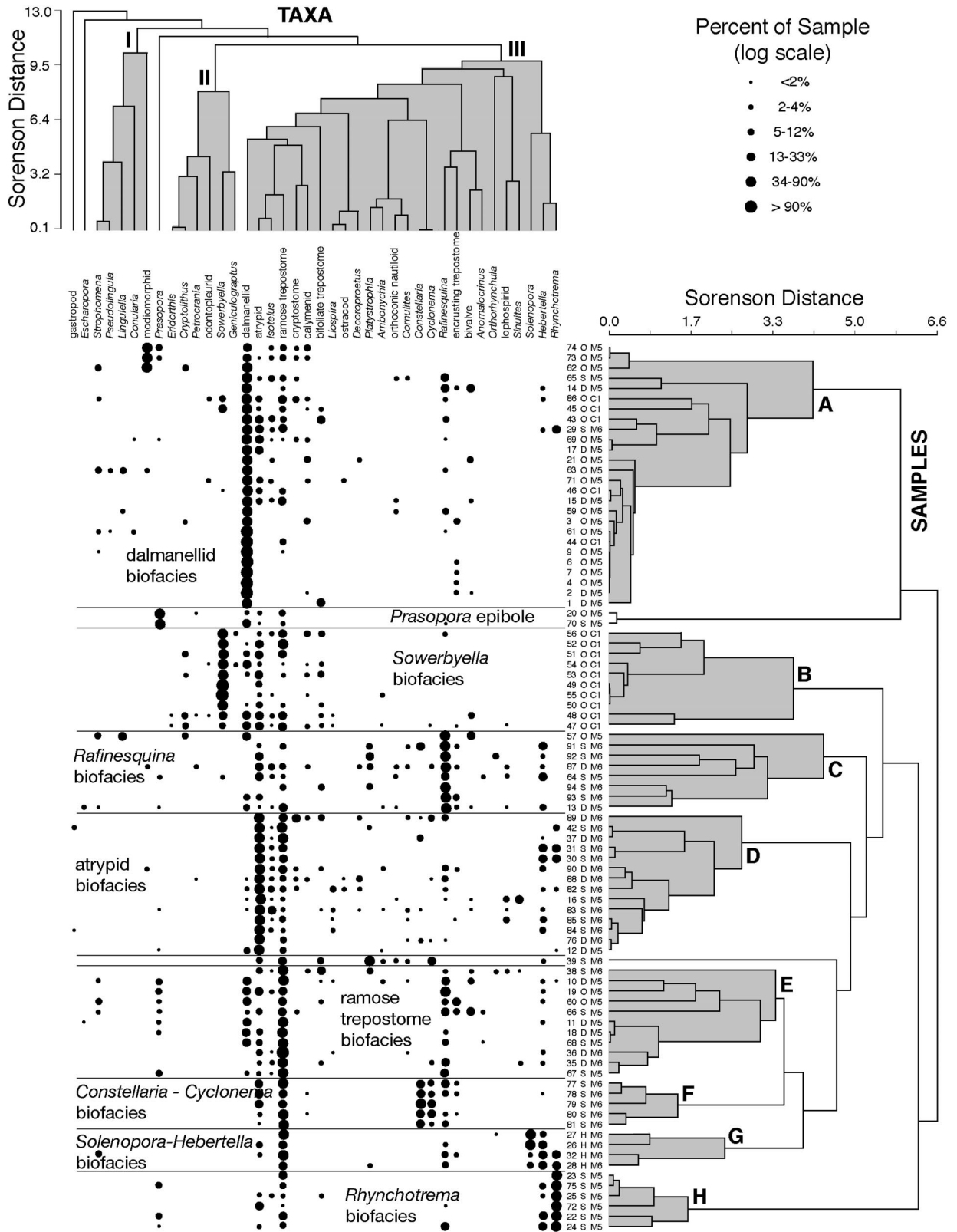
FIGURE 4—Two-way cluster analysis of faunal counts. Size of dots corresponds to relative abundance of taxon in a sample, expressed on a log scale. Sample numbers correspond to data table reposited online at <http://www.sepm.org/archive/index.html>. Depositional environment and sequence are listed next to each sample number. O: offshore; D: deep subtidal; S: shallow subtidal; H: sand shoal.
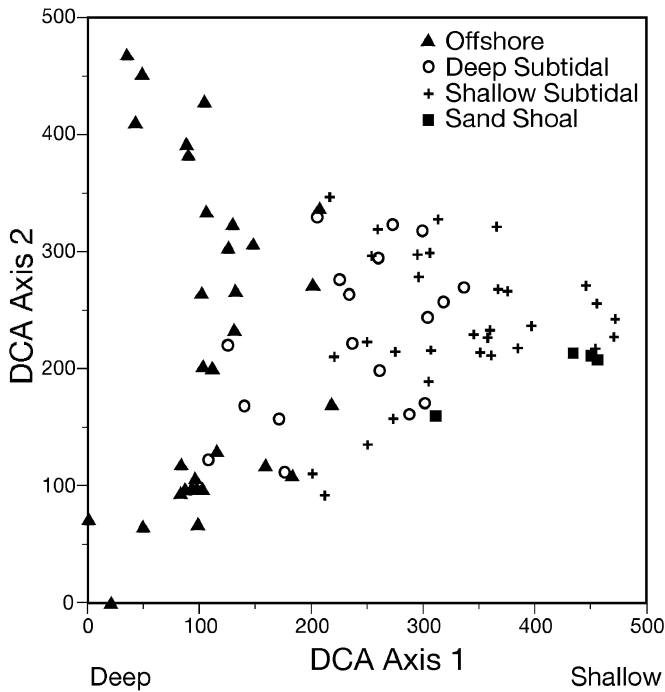
FIGURE 5—DCA axis-1 and axis-2 sample scores labeled according to depositional environment as determined solely from lithologic criteria. See text for characteristics of depositional environments.
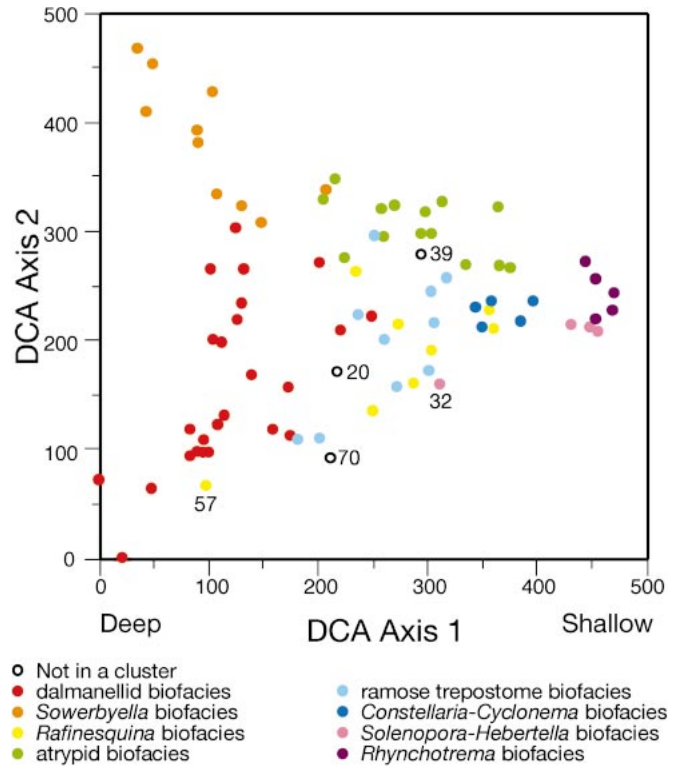

FIGURE 6—DCA axis-1 and axis-2 sample scores labeled according to biofacies membership shown in Figure 4. Outlier samples and samples not belonging to any cluster are labeled with their sample numbers.

anchor this end of axis 1 as reflecting shallow-water habitats.

In the ordination, two samples (57 and 32) are marked outliers from their respective biofacies. Sample 57 is transitional in composition between the dalmanellid and *Rafinesquina* biofacies (Fig. 4), and although it happened to cluster with the *Rafinesquina* biofacies, the DCA ordination shows its equal similarity to the dalmanellid biofacies (Fig. 6). Sample 32 plots at a much lower axis 1 score than other samples from the *Solenopora-Hebertella* biofacies because of its unusual inclusion of *Strophomena*, commonly found in somewhat deeper-water facies in this study interval.

Stratigraphic Patterns in Axis 1 Scores

Because these axis 1 scores reflect facies arrayed along a water-depth gradient, they can be used to reconstruct the water-depth history of a stratigraphic section (Rabe and Cisne, 1980; Springer and Bambach, 1985; Holland et al., 2001). Axis 1 sample scores in the M5 sequence record a slow shallowing upward, with a rapid shift to shallow-water conditions in the upper portion of the sequence (Fig. 7; 40–50 m), consistent with the overall progradational stacking in the highstand systems tract, which dominates the M5 sequence (Pope and Read, 1997a). A lack of samples near the base of the sequence (0–7 m) results in poor development of a deepening-upward trend within the lowest part of the transgressive systems tract. However, logs of faunal abundance (Fig. 3) demonstrate the shift from a relatively diverse shallow-water assemblage containing bryozoans, *Rafinesquina*, and atrypids in the Curdsville Member to the dalmanellid-dominated assemblage in the Logana Member. Faunal logs also indicate the subsequent

shallowing through the M5 highstand systems tract by the return to a diverse assemblage of brachiopods and bryozoans, culminating in a *Rhynchotrema*-dominated interval near the top of the sequence (52 m).

Sample scores in the M6 sequence record a basal deepening in the transgressive systems tract, but poorly record any trend within the subsequent highstand systems tract, again owing to a lack of sample availability (Fig. 7). Faunal logs (Fig. 3) indicate aggradational to weakly progradational stacking in the highstand systems tract, a pattern corroborated by the repetitive cycles capped by sand-shoal facies from 85–95 m (Fig. 7).

The basal C1 sequence displays an abrupt shift to low axis 1 scores and deeper-water conditions. A suggestion of a net deepening-upward trend, consistent with a transgressive systems tract, is present in the basal C1, but only the lowest portion of the sequence was sampled (Fig. 7).

Modeling the Autecology of Taxa

In addition to displaying the relationship of taxa and samples along environmental gradients, DCA axis 1 scores also can be used to estimate the distribution of individual taxa with respect to the primary environmental gradient (Holland et al., 2001). In this way, the preferred habitat of a taxon, its degree of stenotopy or facies restriction, and its abundance can be teased apart and compared to other taxa. The distribution of each taxon with respect to environment is modeled with three parameters as a Gaussian curve that describes the probability of collection
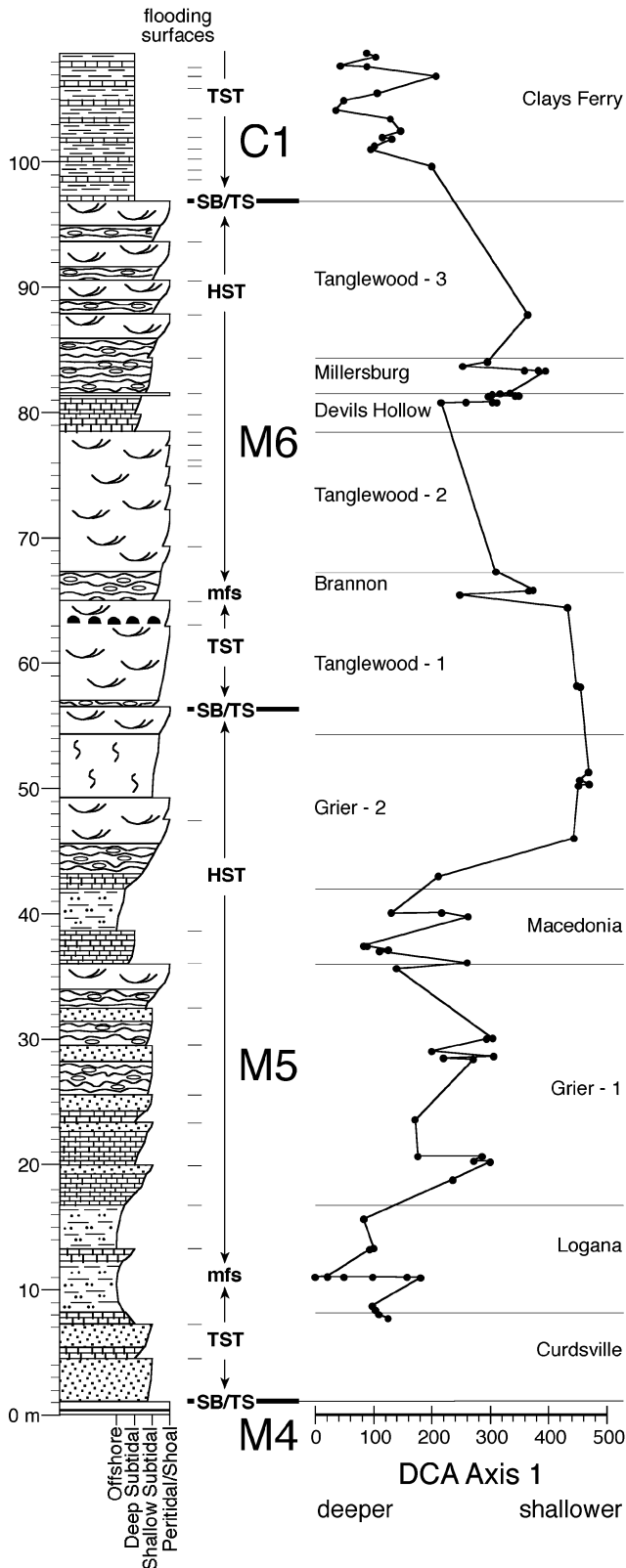
FIGURE 7—DCA axis-1 sample scores plotted against the Frankfort composite section; mfs: maximum flooding surface; TST: transgressive systems tract; HST: highstand systems tract; SB/TS: combined sequence boundary and transgressive surface.

of a taxon as a function of water depth, using DCA axis 1 scores as a proxy for depth (Holland, 1995). Preferred depth (PD) is the mean value of the Gaussian curve and describes the water depth (or DCA axis 1 value) at which the taxon is most likely to be collected. Depth tolerance (DT) is the standard deviation of the Gaussian curve and characterizes the extent to which a taxon is present outside of its preferred facies. Peak abundance (PA) is the height of the Gaussian curve at the preferred depth of the taxon and is the maximum probability of occurrence of a taxon (i.e., the probability of occurrence of the taxon in a sample collected from the preferred depth).

The values of these three parameters for each taxon can be calculated using the original data matrix, the taxon axis 1 scores, and the sample axis 1 scores (Holland et al., 2001). PD is given, by definition, as the axis 1 score for the taxon. DT is calculated as the standard deviation of axis 1 scores of all samples containing the taxon. PA is calculated by the percentage of all samples within 1 DT of the PD that contain the taxon, multiplied by the ratio of the peak height of the Gaussian curve to the average height of the Gaussian curve within 1 DT of the PD (a ratio approximately equal to 1.186). More details on the method, its justification, and its relation to similar approaches in ecology can be found in Holland et al. (2001).

The broadly overlapping curves calculated for taxa in this study underscore that the taxa are distributed along a gradient (Fig. 8; tabulated results reposited online at <http://www.sepm.org/archive/index.html>). Taxa do not appear to be clustered into discrete communities along DCA axis 1, nor are there obvious zones of elevated faunal turnover along DCA axis 1.

Roughly seven taxa, including dalmanellids, *Isotelus*, *Rafinesquina*, atrypids, ramose trepostomes, *Hebertella*, and *Rhynchotrema*, are truly abundant, with peak abundances greater than 50%, indicating a greater than 50% chance of the taxon occurring in a sample collected from that taxon's preferred depth. An additional twenty-four taxa have PA values between 10% and 50% and would be regarded as moderately common in their preferred facies. Only three taxa have PA values less than 10%, likely reflecting the limited number of samples. With a greater number of samples, rare taxa would have been collected more often and could have been included in the DCA necessary for calculating these parameters.

The mean depth tolerance of all taxa is 78 axis-1 units, compared to the nearly 500 axis-1 units over which samples were collected (Fig. 5). In comparison, individual lithofacies range over 200–300 axis-1 units (Fig. 5). Because changes in faunal abundance along this depth gradient occur at a finer scale than changes in lithofacies, faunas reflect environment more sensitively than do lithofacies (Miller, 1988; Brett, 1998; Holland et al., 2001).

Axis 2 Sample Scores

Like other eigenvalue-eigenvector ordination methods, DCA produces a series of axes, each explaining progressively less variance in the data set. DCA is known to distort gradient relationships on axes 2 and higher, often making their interpretation difficult and prohibiting any quantitative interpretations as is possible with axis 1 (Kenkel and Orlóci, 1986; Minchin, 1987). In this study,
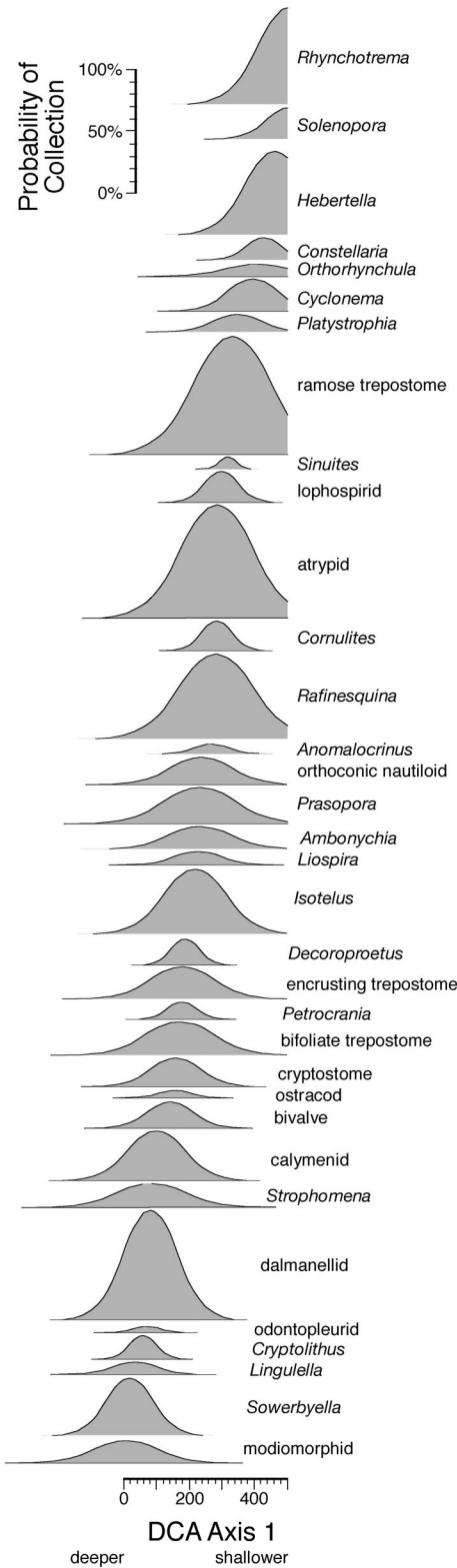
FIGURE 8—Modeled distributions of taxa in the study interval relative to DCA Axis 1 using the model of Holland (1995). Taxa are sorted by their preferred depth (PD), with shallower-water taxa at the top of the figure and deeper-water taxa at the bottom. The extension of many of these curves beyond the sampled DCA interval (0–500, shown at bottom) represents a prediction of the parameter-fitting procedure. Because the shallowest-water environments in the study would have
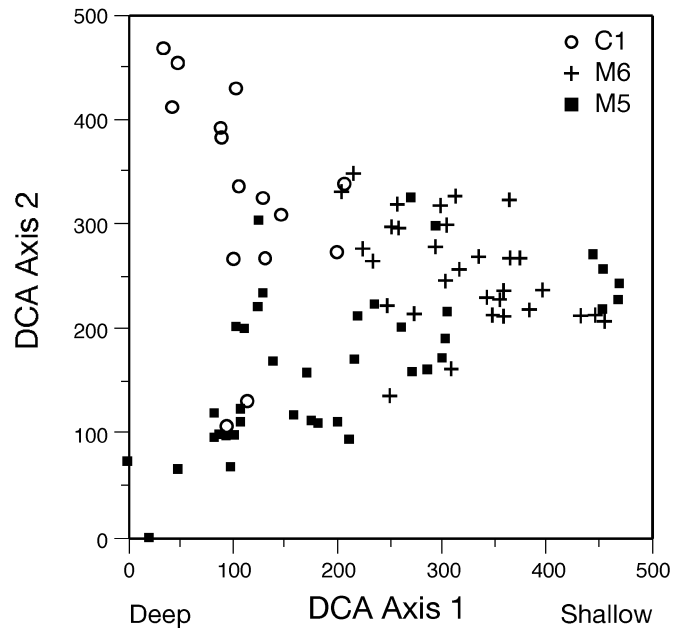

FIGURE 9—DCA axis-1 and axis-2 sample scores labeled according to depositional sequences of Holland and Patzkowsky (1996).

however, DCA axis 2 does reflect temporal changes in the biofacies that are present at any point along the water-depth gradient (Figs. 6, 9). Sorting of samples along axis 2 by depositional sequence is best developed at low values of axis 1 (0–150). Here, low values on axis 2 correspond to samples from the M5 sequence and high values correspond to samples from the C1 sequence. Most of this segregation along axis 2 is the result of the restriction of the *Sowerbyella* biofacies to the C1 sequence. At intermediate axis-1 scores (150–350), M5 samples typically have lower axis-2 scores than those from the M6. Because the *Rafinesquina*, atrypid, and ramose trepostome biofacies are not restricted to individual sequences, such segregation of sample scores along axis 2 suggests temporal differences in the relative abundance of taxa within individual biofacies. At the highest axis-1 values (350–500), the *Rhynchotrema* biofacies is limited to the M5 sequence, with both the *Constellaria-Cyclonema* and the *Solenopora-Hebertella* biofacies restricted to the M6 sequence (Figs. 5, 9). In short, axis 2 reflects not only the sorting of some biofacies through time, but also temporal changes in the abundance structure of taxa within other biofacies.

DISCUSSION

The stability of biofacies has long been a central question in evolutionary paleoecology (e.g., Thorson, 1957; Valentine, 1973; Boucot, 1983; Brett et al., 1996). Instead of approaching the question of ecological stability as a simple dichotomy, ecological stability in the middle Upper Ordo-

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been close to the shoreline, these modeled distributions are truncated near the shallowest end of the gradient (high axis-1 scores).

vician of central Kentucky is evaluated here in three distinct ways: (1) the geographic and temporal extent of biofacies; (2) the constancy of taxonomic composition of these biofacies; and (3) changes in the autecology of the component taxa along a depth-correlated gradient.

Geographic and Temporal Extent of Biofacies

Studies on coeval strata from elsewhere in the eastern United States have recognized a similar bathymetric distribution of biofacies (Appendix 3). Within M5–C2 strata (Chatfieldian–Maysvillian Stages) of southwestern Virginia are six faunal associations (Springer and Bambach, 1985): (1) *Onniella* sp. 1 (a dalmanellid)/*Rafinesquina alternata*; (2) large ramose bryozoan; (3) *Sowerbyella rugosa/Zygospira lebanonensis*; (4) *Onniella* sp. 3/*Rafinesquina fracta*; (5) small ramose bryozoans/*Hebertella sinuata/Zygospira modesta*; and (6) *Lingula*/bivalve. Comparable depositional environments in central Kentucky are known for the first four of these, in that they are found within storm-dominated mixed carbonate-siliciclastic deposits. These four associations correspond respectively to our dalmanellid, ramose trepostome, *Sowerbyella*, and *Rafinesquina* biofacies. The fifth bears a strong similarity to the *Solenopora-Hebertella* biofacies of central Kentucky, but lacks *Solenopora*. From M5–M6 strata of New York, Cisne and Rabe (1978) described offshore facies rich in *Sowerbyella*, *Paucicrura* (a dalmanellid), and *Flexicalymene*, similar to our *Sowerbyella* biofacies. From M5–C1 strata of central Tennessee, Patzkowsky and Holland (1999) described an *Anazyga* biofacies, a *Ctenodonta* biofacies, and a *Dalmanella* biofacies. The *Anazyga* and *Dalmanella* biofacies of central Tennessee are highly similar to their counterparts in central Kentucky. The *Ctenodonta* (now *Deceptrix*) biofacies occurs in a narrow stratigraphic interval of central Tennessee and is not recognized in central Kentucky as a distinct biofacies, although *Deceptrix* does occur in the same facies and stratigraphic interval.

Several aspects of this biofacies pattern are even more geographically and temporally extensive. For example, a *Sowerbyella-Dalmanella* community occurs in offshore environments and a diverse brachiopod community with strophomenids and *Platystrophia* occurs in somewhat shallower-water settings in the Welsh Borderland (McKerrow, 1978; Lockley, 1983). Younger strata (C1–C3; Edenian–Maysvillian Stages) of central Tennessee contain a *Platystrophia* biofacies in shallow-subtidal habitats that includes abundant *Hebertella*, *Rafinesquina*, *Zygospira*, and *Rhynchotrema*, similar to the *Hebertella-Solenopora* and the *Rhynchotrema* biofacies of central Kentucky (Patzkowsky and Holland, 1999). Older strata (Whiterockian to Turinian Stages) of the eastern United States contain a similar onshore to offshore array of biofacies (Patzkowsky, 1995): (1) a lingulid biofacies; (2) a *Rostricellula-Doleroides* biofacies; (3) a *Strophomena* biofacies; (4) a *Sowerbyella* biofacies; (5) a *Paucicrura*-plectambonitacean biofacies; and (6) an inarticulate biofacies.

Methodological differences in these studies hamper any detailed comparisons of biofacies. Furthermore, the standard practice of communicating biofacies by the one or two most dominant taxa hinders comparisons by hiding the relative abundances of all taxa within the biofacies. Nonetheless, a similar overall pattern appears to be present in these studies at the suprageneric level, with rhynchonellaceans (*Rostricellula*, *Rhynchotrema*, and *Orthorhynchula*) and plectorthines (*Doleroides* and *Hebertella*) dominating the shallow subtidal, strophomenids (*Strophomena* and *Rafinesquina*) characterizing the deep subtidal, and dalmanellids (*Dalmanella* and *Paucicrura*) and plectambonitaceans (*Sowerbyella*, *Eoplectodonta*, and *Bilobia*) typifying the offshore. Such a pattern of apparent similarity in biofacies distribution is consistent with placing Middle and Late Ordovician faunas within a single Ecological-Evolutionary Unit (Boucot, 1983; Sheehan, 1996).

Although such a coarse-scale consistency in biofacies is clear, aspects of this study demonstrate that any perceived ecological stability is not absolute. For example, the *Sowerbyella* biofacies is restricted to the C1 and the *Rhynchotrema* biofacies is restricted to the M5. In both cases, this restriction occurs despite the availability of suitable lithofacies at other times. For example, the *Sowerbyella* biofacies is found in the offshore facies of the C1 sequence, but the *Sowerbyella* biofacies is absent from the offshore facies of the M5 sequence. Similarly, the sand-shoal facies in which the *Rhynchotrema* biofacies is found is also present in the M6, but the *Rhynchotrema* biofacies is absent. In addition to such absences, several midshelf biofacies display within-biofacies temporal sorting of samples along DCA axis 2 (Fig. 9), indicating changes in the relative abundance structure within individual biofacies over geologic time.

Taxonomic Composition of Biofacies

Although a full picture of taxonomic changes within these biofacies awaits long-needed taxonomic and phylogenetic reevaluations, existing taxonomic work indicates a widespread pattern of species-level turnover, even within the eponymous genera of the central Kentucky biofacies. For example, dalmanellids of the M5 sequence consist of *Dalmanella fertilis*, *D. sulcata*, and *Heterorthina macfarlani*, whereas those in the C1 are primarily *D. multisecta* and *D. bassleri* (Walker, 1982). Sowerbyellids in the M5 belong to *Sowerbyella curdsvillensis* and *S. grierensis*, whereas those of the C1 are *S. rugosa* (Howe, 1979). Midshelf, *Rafinesquina trentonensis* in the M5 gives way to *R. winchesterensis* in the C1 (Cressman, 1973). At the shallow end of the gradient, *Hebertella* is represented in the M5 by *H. frankfortensis*, but by *H. parksensis* and *H. occidentalis* in the M6 (Walker, 1982). Some taxonomic changes are at the genus level, such as the transition among the atrypids from *Anazyga* in the M5 to *Zygospira* in the C1 (cf., Copper, 1977). Some taxonomic changes occur within a single sequence such as the transition from *Rhynchotrema kentuckiensis* to *R. increbescens* within the M5 (Cressman, 1973). Because each of these sets of related species is found in the same lithofacies, the taxonomic differences are likely to be real and not just ecophenotypic variation. This list is not exhaustive, even considering just the brachiopods, and many other taxa have similar potential for turnover (e.g., calymenid trilobites). Although such a compilation is admittedly anecdotal, these examples do suggest that species-level turnover may be common within these biofacies, even given the relatively short duration (2 m.y.) of the study interval (*contra* Brett et al., 1996).

Degree of Autecological Stability

In some cases, changes in the ecological preferences of individual taxa over time can be diagnosed easily, such as

Preferred Depth (PD)
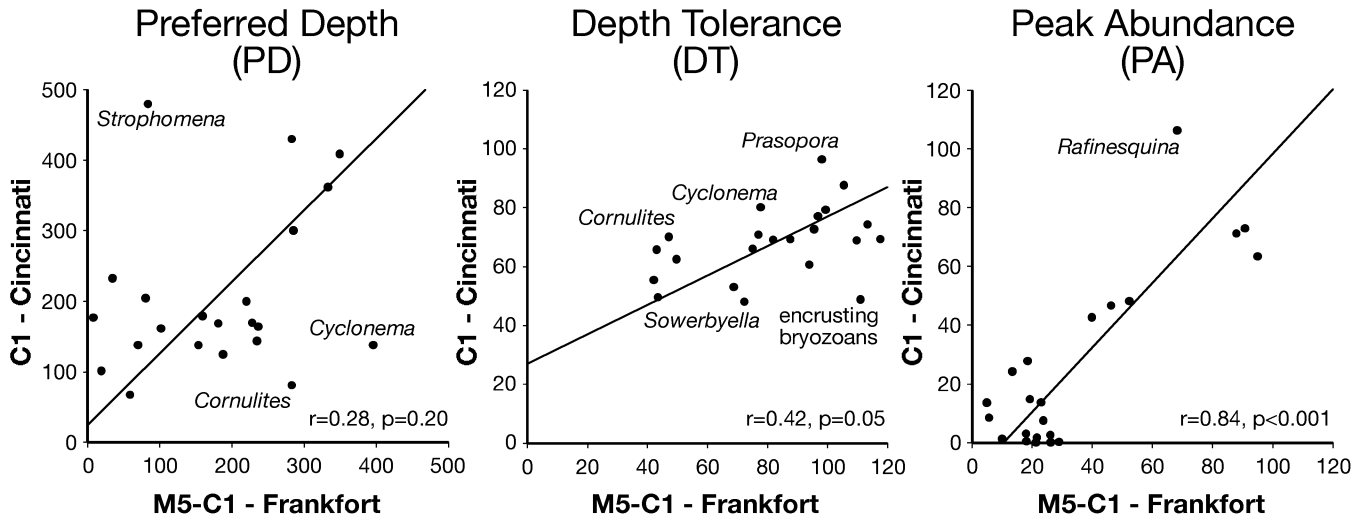
Depth Tolerance (DT)

Peak Abundance (PA)

FIGURE 10—Comparison of values of preferred depth, depth tolerance, and peak abundances for all taxa shared by this study and a previous study of the C1 Kope Formation of the Cincinnati, Ohio area (Holland et al., 2001). Reduced major axis regressions are shown and outlier points are labeled. PD axis units are DCA axis-1 scores, with higher values corresponding to shallower water depths. DT is expressed in terms of DCA axis-1 units, with larger values indicating more eurytopic taxa. PA axes are in units of probability expressed as a percentage, with larger values corresponding to higher probabilities of collection. Pearson's correlation coefficients (r) and their corresponding p-values (p) are indicated for each plot.

those of the sowerbyellids (Holland, 1997). In the pre-M5, *Sowerbyella* itself is found abundantly in the *Strophomena*, the *Sowerbyella*, and the *Paucicrura*-plectamboni- tacean biofacies of the deep subtidal and offshore (Patz- kowsky, 1995; Patzkowsky and Holland, 1999). In the C1 of central Kentucky, *Sowerbyella* is found only in offshore facies (Holland et al., 2001). In the C5 of the Cincinnati Arch in southeastern Indiana and southwestern Ohio, the closely related sowerbyellid *Eochonetes clarksvillensis* (formerly a subspecies of *Sowerbyella rugosa*) occurs only in deep-subtidal facies. These shifts between deep-subti- dal and offshore habitats are not a consequence of limited facies availability. Deep-subtidal facies occur in every se- quence from the M5 through the C5, but the C5 marks the first occurrence of abundant sowerbyellids in this facies since the M3 sequence (Patzkowsky and Holland, 1999). In cases such as this, changes in the habitat preference of a taxon can be recognized because the taxon occurs in an entirely different lithofacies. Given that taxa are known to be more sensitive indicators of sedimentary environments than are lithofacies (Miller, 1988; Brett, 1998; Holland et al., 2001), a finer method of tracking changes in the aut- ecology of taxa is needed.

Detection of finer differences may be possible by com- paring estimated values of PD, DT, and PA for taxa from different geographic areas or stratigraphic intervals. The values calculated in this study for central Kentucky can be compared to those previously calculated for the C1 Kope Formation of the Cincinnati, Ohio area (Holland et al., 2001). Although these two studies have minor temporal overlap limited to the lowermost C1, they are geographi- cally distinct. Because the Kope study and the present study are based on different data sets, axis-1 units from the two analyses are not equivalent. This nonequivalence arises not only from the inclusion of different taxa in the two studies, but also the unequal density and spacing of samples along the ecological gradients in the two studies.

Thus, only the deviations from a best-fit line of compari- sons of the three parameters can be considered, not the ab- solute differences in those parameters.

Values of preferred depth (PD) are weakly and non-sig- nificantly correlated between the two studies, suggesting that many taxa do not maintain a consistent water depth over evolutionary time (Fig. 10). Such a finding would be at odds with a large body of work indicating facies tracking of faunas (Boucot, 1981; Brett, 1995; Patzkowsky, 1995). On closer inspection, three outliers generate much of the poor correlation: *Strophomena*, *Cyclonema*, and the worm tube *Cornulites*. *Strophomena* displays a marked shift into shallower water during the C1, whereas *Cyclonema* and *Cornulites* shift to deeper water in the C1. When these three taxa are removed, the correlation improves to 0.68 (p < 0.001). Some of the weakness in this correlation may re- flect the smaller sample size in this study relative to the Kope study (Holland et al., 2001), since larger sample sizes should produce more robust estimates of PD, DT, and PA. If the comparison of PD is limited to the seven most abun- dant taxa (i.e., those with PA > 40% in both studies), the correlation improves to 0.87 (p < 0.005), indicating that preferred depth is strongly conserved for those taxa that dominate the fauna. In many cases, these dominant taxa are also the name-bearers for biofacies, including dalma- nellids, *Sowerbyella*, *Rafinesquina*, atrypids, and ramose bryozoans. This finding may suggest that much of the per- ception of stability in biofacies is driven by a focus on the most common taxa (McKinney et al., 1996).

Values of depth tolerance (DT) display a stronger and statistically significant correlation, suggesting that the widths of ecological niches of taxa are generally conserved (Fig. 10). Despite the overall correlation, it is clear that values of depth tolerance do differ to some extent between the two studies. Some taxa (e.g., *Prasopora*) became more eurytopic over time, whereas others (e.g., encrusting bryo- zoans) became more stenotopic. Some of this variation

may reflect differences in the sample size and counting methods of the two studies, but some may represent changes in the breadth of niches over geologic time.

Values of peak abundance (PA) show the strongest and most significant correlation of all, suggesting that abundance is a highly conserved property of taxa (Fig. 10). Substantial scatter exists at low values of peak abundance and this likely reflects the problem of estimating abundance of rare taxa given limited sample sizes. With one exception, the correlation of the two studies is remarkably strong at moderate to high values of peak abundance. The one exception is *Rafinesquina*, which becomes much more abundant in its preferred facies in the C1 relative to the M5–C1. Removal of *Rafinesquina* improves the correlation slightly, to 0.88 (p < 0.001).

Thus, these comparisons indicate that values of PD, DT, and PA are generally conserved within taxa shared by these two studies. Despite this overall autecological stability, some taxa significantly change their habitat preferences, degree of stenotopy, or peak abundance. The causes of such changes are unclear and more studies are needed to determine generalities in the types of taxa that make any given change in their ecology as well as generalities in the geologic circumstances under which these changes occur. Given that the study interval immediately follows the M4–M5 regional extinction (Patzkowsky and Holland, 1997; 1999) and that the entire Late Ordovician in the eastern United States witnessed changes in ocean temperature, nutrient levels, and water turbidity (Holland and Patzkowsky, 1996; 1997), it might be expected that the autecological preferences of at least some taxa would change.

Comparisons of PD, DT, and PA such as these are in their initial stages, but they show promise for addressing basic autecological questions such as whether ecological distribution is an intrinsic, static feature of a taxon or whether it is mutable over geologic time. This approach also can be used to recognize not only shifts in the preferred depth of taxa over time, which can be determined in extreme cases by changes in preferred lithofacies, but also changes in depth tolerance and peak abundance, which can be more difficult to diagnose otherwise. Future use of this approach could lead to a much more quantitative characterization of the relative stability of ecosystems than existing comparisons of the rank abundance of taxa in similar biofacies.

CONCLUSIONS

1) Eight biofacies are described from the middle Upper Ordovician (M5–C1 sequences) of central Kentucky, each of which is associated with specific depositional environments. From deepest to shallowest, the dalmanellid biofacies and the *Sowerbyella* biofacies occur in the offshore, the *Rafinesquina*, the atrypid, and the ramose trepostome biofacies occur in deep-subtidal to shallow-subtidal facies, the *Constellaria-Cyclonema* and the *Rhynchotrema* biofacies occur in shallow-subtidal settings, and the *Solenopora-Hebertella* biofacies occurs in sand-shoal facies. Overlap in the constituent genera of these biofacies suggests that these biofacies are not discrete, sharply bounded units, but represent intervals along an ecological gradient.

2) As indicated by DCA axis-1 scores, upsection changes in faunal assemblages in the Lexington Limestone and Clays Ferry Formation reflect sequence stratigraphic architecture, particularly net shallowing and deepening trends within systems tracts.

3) The distribution of biofacies along an onshore-offshore gradient in the Upper Ordovician of Kentucky is similar to that reported in other case studies of Middle and Upper Ordovician strata. The general pattern consists of rhynchonellaceans (*Rostricellula*, *Rhynchotrema*, and *Orthorhynchula*) and plectorthines (*Doleroides* and *Hebertella*) in the shallow subtidal, strophomenids (*Strophomena* and *Rafinesquina*) in the deep subtidal, and dalmanellids (*Dalmanella* and *Paucicrura*) and plectambonitaceans (*Sowerbyella*, *Eoplectodonta*, and *Bilobia*) in the offshore. Similarly, values of preferred depth, depth tolerance, and peak abundance of taxa—particularly those that are abundant—are generally conserved through time, indicating that some aspects of this biotic gradient were relatively stable.

4) Despite such evidence of stability, four lines of evidence suggest that other aspects of ecosystem structure were not static. First, not all biofacies are present in all depositional sequences in the study, despite the availability of suitable facies. Second, within-biofacies changes in the relative abundance of taxa are indicated by sorting of samples along DCA axis 2. Third, taxonomic turnover at the species level occurs in many genera, even those that are most abundant. Fourth, some taxa show significant departures through time in their values of preferred depth, depth tolerance, or peak abundance. Collectively, these results argue that associations of taxa were not generated by a rigid system of biotic interactions, but by a set of shared environmental preferences along an onshore-offshore gradient. Ongoing changes in oceanographic conditions, such as water temperature, nutrient levels, and turbidity, may be a possible cause for the instability in ecosystem structure seen here.

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APPENDIX 1

Locality Descriptions

Frankfort North—Road cuts on both sides of US 127, beginning at intersection with Cove Spring Road, 0.2 miles north of intersection of US 127 and US 421 north of Frankfort, Kentucky, and continuing northward for 0.4 miles; 38° 13.386′ N, 84 51.338′ W.

Frankfort North Upper—Road cuts on both sides of US 127, at intersection with Kentucky State Route 1900 (Peaks Mill Road), north of Frankfort, Kentucky; 38° 13.684′ N, 84° 51.149′ W.

Frankfort 421—Road cuts on northeast side of US 421, 0.1 miles northwest of intersection with US 127 on northwest side of Frankfort, Kentucky; 38° 12.440′ N, 84° 53.075′ W.

Peaks Mill—Road cut on east side of US 127, beginning at intersection with Strohmeier Bypass, 0.4 miles south of US 127 bridge over Elkhorn Creek, and extending southward for 0.4 miles; 38° 18.505′ N, 84° 50.711′ W.

Swallowfield—Road cuts on both sides of US 127, beginning 1.3 miles north of intersection with KY 2919 near Swallowfield, Kentucky, and extending 0.9 miles to the north; 38° 20.581′N, 84° 51.014′ W.

Clays Ferry—Road cut on south side of KY 2328, 1.0 mile north of intersection with US 25 / US 421 at Clays Ferry, Kentucky; 37° 52.845′ N, 84° 20.447′ W.

APPENDIX 2

Biofacies Composition

TABLE 1—Percent abundance of genera in the dalmanellid biofacies, based on combined totals of all samples.

Taxon	% Abundance
dalmanellid	75.4
atrypid	5.4
modiomorphid	4.8
ramose trepostome	3.2
Rafinesquina	1.7
Sowerbyella	1.6

Less than 1%: bivalve, calymenid, encrusting trepostome, *Isotelus, Strophomena*, bifoliate trepostome, cryptostome, *Rhynchotrema, Prasopora, Conularia, Hebertella, Lingulella*, orthoconic nautiloid, *Pseudolingula, Cryptolithus*, odontopleurid, inarticulate, *Deceptrix, Cornulites, Decoroproetus*, ostracode, and *Eridorthis*

S (95% confidence limits): 5.0 (4.9–5.2).

H = 1.5.

E = 0.85.

TABLE 2—Percent abundance of genera in the *Sowerbyella* biofacies, based on combined totals of all samples.

Taxon	% Abundance
Sowerbyella	54.6
atrypid	14.5
dalmanellid	7.7
Cryptolithus	3.3
bifoliate trepostome	2.1
calymenid	1.5

Less than 1%: bivalve, *Isotelus, Ambonychia, Eridorthis, Geniculograptus, Liospira*, lophospirid, odontopleurid, *Petrocrania, Rafinesquina, Trematis*, encrusting trepostome, and *Cyclonema*

S (95% confidence limits): 7.1 (6.9–7.3).

H = 1.5.

E = 0.65.

TABLE 3—Percent abundance of genera in the *Rafinesquina* biofacies, based on combined totals of all samples.

Taxon	% Abundance
Rafinesquina	50.2
ramose trepostome	9.3
Hebertella	7.8
atrypid	7.6
Platystrophia	3.7
dalmanellid	3.2
Constellaria	3.2
encrusting trepostome	1.7
bifoliate trepostome	1.2
lophospirid	1.2
Isotelus	1.2

Less than 1%: *Orthorhynchula, Lingulella*, bivalve, orthoconic nautiloid, *Strophomena, Escharopora, Prasopora*, modiomorphid, *Cyclonema, Cornulites*, calymenid, *Petrocrania, Sowerbyella, Ambonychia*, hyolithid, *Decoroproetus, Cryptolithus*, and *Anomalocrinus*

S (95% confidence limits): 8.4 (8.1–8.7).

H = 2.0.

E = 0.91.

TABLE 4—Percent abundance of genera in the atrypid biofacies, based on combined totals of all samples.

Taxon	% Abundance
atrypid	70.7
ramose trepostome	10.0
Hebertella	3.5
Isotelus	2.3
dalmanellid	1.7
Sinuites	1.6
Rhynchotrema	1.5
lophospirid	1.5
Rafinesquina	1.2
Constellaria	1.0

Less than 1%: cryptostome, *Cornulites, Decoroproetus, Liospira*, bifoliate trepostome, *Cyclonema, Ambonychia*, calymenid, *Prasopora*, bivalve, gastropod, *Platystrophia*, encrusting trepostome, orthoconic nautiloid, ostracode, *Petrocrania*, and modiomorphid

S (95% confidence limits): 8.0 (7.8–8.2).

H = 1.3.

E = 0.47.

TABLE 5—Percent abundance of genera in the ramose trepostome biofacies, based on combined totals of all samples.

Taxon	% Abundance
ramose trepostome	58.5
Rafinesquina	11.0
dalmanellid	9.2
biofoliate trepostome	4.0
atrypid	3.9
bivalve	3.0
Prasopora	2.8
Hebertella	1.3
encrusting trepostome	1.2

Less than 1%: *Strophomena, Isotelus, Platystrophia*, lophospirid, *Orthorhynchula*, cryptostome, *Ambonychia, Liospira, Sinuites, Cornulites*, calymenid, *Anomalocrinus, Rhynchotrema, Escharopora, Cyclonema*, and starfish

S (95% confidence limits): 7.6 (7.5–7.8).

H = 1.7.

E = 0.70.

TABLE 6—Percent abundance of genera in the *Constellaria-Cyclonema* biofacies, based on combined totals of all samples.

Taxon	% Abundance
ramose trepostome	42.0
Constellaria	27.4
Cyclonema	14.2
atrypid	10.4
Rafinesquina	4.4

Less than 1%: encrusting trepostome, calymenid, and *Hebertella*

S (95% confidence limits): 6.0 (5.9–6.1).

H = 1.5.

E = 0.71.

TABLE 7—Percent abundance of genera in the *Solenopora-Hebertella* biofacies, based on combined totals of all samples.

Taxon	% Abundance
ramose trepostome	38.5
Solenopora	28.6
Hebertella	17.7
Rhynchotrema	7.8
Rafinesquina	3.1
atrypid	1.6
Strophomena	1.0

Less than 1%: *Orthorhynchula, Platystrophia,* and encrusting trepostome

S (95% confidence limits): 5.8 (5.6–5.9).

H = 1.5.

E = 0.81.

TABLE 8—Percent abundance of genera in the *Rhynchotrema* biofacies, based on combined totals of all samples.

Taxon	% Abundance
Rhynchotrema	70.3
ramose trepostome	10.7
Hebertella	7.6
atrypid	5.7
Rafinesquina	3.8
Prasopora	1.6

Less than 1%: bifoliate trepostome, fenestrate bryozoans, and *Isotelus*

S (95% confidence limits): 4.5 (4.4–4.6).

H = 1.1.

E = 0.64.

APPENDIX 3

Comparison of Lexington Limestone biofacies to biofacies reported from Upper Ordovician rocks.

Lexington limestone biofacies	Other reported biofacies
Dalmanellid biofacies	M5–C2 (Chatfieldian–Maysvillian), southwest Virginia: *Onniella* sp. 1/*Rafinesquina alternata* assemblage, with *Prasopora* and *Craniops* (Springer and Bambach, 1985)
	M5–C1, central Tennessee: *Dalmanella* biofacies, with *Rafinesquina, Prasopora, Anazyga, Rhynchotrema*, and *Zygospira* (Patzkowsky and Holland, 1999)
	Whiterockian–Turinian, eastern United States: *Paucicrura*-plectambonitacean biofacies, with *Christiana, Oxoplecia*, and *Bilobia* (Patzkowsky, 1995)
	Welsh Borderland: *Sowerbyella-Dalmanella* community, with *Kjaerina, Oxoplecia, Balacrinus*, and *Lophospira* (McKerrow, 1978; Lockley, 1983)
Sowerbyella biofacies	M5–C2 (Chatfieldian–Maysvillian), southwest Virginia: *Sowerbyella rugosa*/*Zygospira lebanonensis* assemblage (Springer and Bambach, 1985)
	M5–M6, New York: *Sowerbyella, Paucicrura*, and *Flexicalymene* (Cisne and Rabe, 1978)
	Whiterockian–Turinian, eastern United States: *Sowerbyella* biofacies, with *Multicostella, Glyptorthis, Mimella*, and *Oepikina* (Patzkowsky, 1995)
	Welsh Borderland: *Sowerbyella-Dalmanella* community, with *Kjaerina, Oxoplecia, Balacrinus*, and *Lophospira* (McKerrow, 1978; Lockley, 1983)
Rafinesquina biofacies	M5–C2 (Chatfieldian–Maysvillian), southwest Virginia: *Onniella* sp. 3/*Rafinesquina fracta* assemblage, with numerous bivalves (Springer and Bambach, 1985)
	Whiterockian–Turinian, eastern United States: *Strophomena* biofacies, with *Hesperorthis, Pionomena, Sowerbyella, Multicostella, Pionodema*, and *Doleroides* (Patzkowsky, 1995)
	Welsh Borderland: diverse brachiopod community, with strophomenids, *Leptaena, Onniella, Platystrophia, Brogniartella, Calyptaulax, Platylichas*, bellerophontids, orthoceratids, and *Tentaculites* (McKerrow, 1978; Lockley, 1983)
Atrypid biofacies	M5–C1, central Tennessee: *Anazyga* biofacies, with *Lophospira* and *Hebertella* (Patzkowsky and Holland, 1999)
Ramose trepostome biofacies	M5–C2 (Chatfieldian–Maysvillian), southwest Virginia: large ramose bryozoan assemblage, with *Rafinesquina alternata*, isotelid trilobites, *Rafinesquina fracta*, and *Onniella* sp. 3 (Springer and Bambach, 1985)
Constellaria-Cyclonema biofacies	No equivalent biofacies reported
Rhynchotrema biofacies	C1–C3, central Tennessee: *Platystrophia* biofacies, with *Hebertella, Rafinesquina, Zygospira, Strophomena, Lophospira*, and *Rhynchotrema* (Patzkowsky and Holland, 1999)
	Whiterockian–Turinian, eastern United States: *Rostricellula-Doleroides* biofacies, with *Strophomena* (Patzkowsky, 1995)
Solenopora-Hebertella biofacies	M5–C2 (Chatfieldian–Maysvillian), southwest Virginia: small ramose bryozoans/*Hebertella sinuata*/*Zygospira modesta* assemblage, with *Rafinesquina fracta, Onniella* sp. 3, and numerous bivalves (Springer and Bambach, 1985)
	C1–C3, central Tennessee: *Platystrophia* biofacies, with *Hebertella, Rafinesquina, Zygospira, Strophomena, Lophospira*, and *Rhynchotrema* (Patzkowsky and Holland, 1999)
	Whiterockian–Turinian, eastern United States: *Rostricellula-Doleroides* biofacies, with *Strophomena* (Patzkowsky, 1995)