Quantitative paleoecology of marine faunas in the lower Hamilton Group (Middle Devonian, central New York): Significance for probing models of long-term community stability

Cathryn R. Newton*
Willis B. Newman†
James C. Brower‡

Department of Earth Sciences, Syracuse University, Syracuse, New York 13244-1070, USA

ABSTRACT

Beautifully fossiliferous strata in the Hamilton Group (Middle Devonian, central New York) constitute a rich “ecological archive” sufficient to probe and test foundational concepts in paleontology. The evident community stability of Hamilton faunas over 4–6 m.y.—including two proposed mechanisms for coordinated stasis—has ignited controversy. Resolving community structure and both taxonomic and ecological temporal persistence within the Hamilton Group thus becomes critical to testing whether these Hamilton communities are stable and whether they are ecologically “locked.” Toward this end, we conducted multivariate analyses (cluster and correspondence analysis) of marine faunas in 81 large samples (~300 specimens each) in shallowing-upward sequences of the Cardiff and Pecksport Members (Marcellus Subgroup, Oatka Creek Formation) of the Hamilton Group.

Eight statistically and ecologically distinctive benthic communities characterize the vertical gradient, from depauperate, deeper-water dark shales below to species-rich shelf siltstones above. These communities correlate strongly with grain size, bioturbation intensity, bedding thickness, density of fossils, and faunal and ecological diversity. Species richness varies inversely with weight percent organic matter. We characterized taxonomic distributions using multivariate statistics; these statistical analyses were based on percentages of 50 taxa. In order of decreasing depth, the communities are: Cephalopod-Pterochaenia, Pterochaenia-Eumetabolotoechia, Eumetabolotoechia, Emanuella, Eumetabolotoechia-Ambocoelia, Arcuaminetes-Eumetabolotoechia, Arcuaminetes-Ambocoelia, and Mucrospirifer-Ambocoelia. The Cephalopod-Pterochaenia community represents a mixed benthic-pelagic fauna associated with the deepest and finest-grained facies. The Pterochaenia-Eumetabolotoechia, Eumetabolotoechia, and Emanuella communities have low to

*corresponding author: crnewton@syr.edu
†deceased

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moderate species richness and are dominated by epifaunal, active suspension feeders, especially the small epibysate bivalve *Pterochaenia fragilis*, and the pedunculate brachiopods *Eumetabolotoechia multicostata* and *Emanuella subumbona*. The *Pterochaenia-Eumetabolotoechia* community is an opportunistic fauna that developed when the substrate first became favorable for colonization by benthic organisms. To a lesser extent, this probably also holds true for the *Eumetabolotoechia* assemblage. Communities near the top of the shallowing-upward cycle—*Eumetabolotoechia-Ambacoelia, Arcuaminetes-Eumetabolotoechia, Arcuaminetes-Ambacoelia*, and *Macrospirifer-Ambacoelia*—have higher taxonomic and ecological heterogeneity, with a more diverse array of trophic and locomotory groups than their counterparts in the finer-grained, and inferred deeper, facies.

Cluster significance tests applied to all pairs of communities known from adequate numbers of samples demonstrated that the communities are statistically valid and distinctive. Multivariate means of all communities were significantly different; furthermore, most pairs of communities were drawn from populations that showed no overlap in terms of rectangular distributions. The community sequence and an ordination derived from the first two axes of the correspondence analysis provided relative depth curves. Our communities, with two exceptions, do not have clear counterparts among upper Hamilton Group faunas. The ecological locking model proposed to explain the stability of Hamilton faunas is not supported by our quantitative tests to date.

INTRODUCTION

Abundant and often exquisitely preserved marine faunas in the well-exposed Middle Devonian Hamilton Group of New York have long attracted international attention as a valuable “ecological archive” for testing new hypotheses in paleontology. Studied intensively by paleontologists and stratigraphers for more than 150 yr, these rich and temporally persistent Hamilton faunas have figured prominently in some of the largest evolutionary and paleoenvironmental debates, both past and present. The hypothesis of punctuated equilibria, the oft-debated speciationary and paleoenvironmental debates, both past and present. In more recent years, Hamilton Group faunas have yet again remained apparently stable for millions of years (Brett and Baird, 1995; Ivany et al., 2009; Brett, 2012). The marine communities in the Hamilton Group have been claimed to be one of the fossil record’s best-documented and most temporally persistent examples of coordinated stasis (Brett and Baird, 1995; Ivany et al., 2009; Nagel-Myers et al., 2009). Various scholars have analyzed taxonomic stasis during this 4–6 m.y. interval and explored the possibilities of ecological stasis, which include both stable community structure and even, in the view of some authors, stable rates of predation.

Explanatory proposals for coordinated ecological stasis in the Hamilton Group interval have engendered controversy. Scholarly discussion, intense and sometimes heated, has centered on possible mechanisms, principally “ecological locking” or “environmental tracking” (Morris et al., 1995; Ivany, 1996). The ecological locking (Morris et al., 1995) model views these marine communities as tightly structured and therefore, once established, resistant to large-scale taxonomic change. The environmental tracking model, in contrast, interprets stability as arising when faunas follow environments through time; during an interval of minimal environmental change, faunas will vary only minimally (Ivany, 1996; see also comments by Miller, 1997). Ivany (1996) and several others observed that brief intervals of accelerated environmental change serve to magnify this coordinated pattern. Synchronous regional environmental changes, expressed through sedimentology and geochemistry as well as paleontology, can produce concurrent faunal eliminations that include both regional disappearances and true extinction (lineage termination). In sum, the ecological locking hypothesis proposes that the observed patterns originate in ecological homeostatic mechanisms, whereas the environmental tracking model hypothesizes fidelity of organisms to their environments and posits

1Now *Eldredgeops rana*. 
coordinated extinctions (or regional disappearances) to create the boundaries of intervals of relative stasis.

Coordinated stasis is inherently a quantitative claim. Only through rigorous quantitative studies that sample rare taxa (not just abundant to common taxa) and that analyze the taxonomic and ecological structure of communities over time can coordinated stasis be properly tested (Bennington and Bambach, 1996; McKinney et al., 1996; Ivany et al., 2009). Moreover, demonstrating ecological stasis throughout the Hamilton interval requires such quantitative documentation from both lower and upper intervals. We present here the results of one such quantitative study of lower Hamilton communities, as one of several necessary steps in evaluating coordinated stasis models as they apply to this Middle Devonian interval.

The stratigraphic framework for the Hamilton Group was established by Carlton Brett and Gordon Baird, building in turn upon a series of earlier fundamental works by others; see discussions of this in the comprehensive stratigraphic volumes edited by Brett (1986) and Landing and Brett (1991). This classic Hamilton Group lithostratigraphy must be correlated with coarser sediments occurring eastward, closer to the deltaic source; these eastern strata were studied by Chuck Ver Straeten (Ver Straeten et al., 2011). These marine sediments of deltaic and other marine environments exhibit marked transgressive-regressive cycles (e.g., Brett and Baird, 1985; Brett et al., 1986). These cycles thicken eastward toward the delta and correspondingly thin westward. In western New York, these thinner cycles consist of shale, calcareous shale, and limestone, and they are approximately symmetrical (Miller, 1986; Savarese et al., 1986). Further east, in central and eastern New York, as the source area in the Acadian delta is approached, cycles increase in thickness, grain size, and clastic input (e.g., Baird et al., 2000; Ver Straeten et al., 2011); in addition, they become dominated by the regressive phase, with a corresponding reduction of the transgressive phase to a few thin beds that are commonly associated with a diastem and lag concentrate of phosphatic and other residual materials.

**SCOPE AND OBJECTIVES**

We present here the findings of our quantitative marine paleoecological research on faunas of portions of the lower Hamilton Group—specifically, the Cardiff and Pecksport Members of the Middle Devonian Marcellus Subgroup in central New York (Figs. 1 and 2). The lithologies of the Cardiff and Pecksport Members are well summarized and their faunas illustrated in Linsley (1994). These two members occur in the Oatka Creek Formation, which is best expressed in the Finger Lakes region further west; as this formation was established, it became necessary to examine the detailed correlations of these classic Hamilton Group localities in central New York with the more recently established lithostratigraphic units in western New York and in eastern New York, closer to the clastic source. How the member-level lithographic of the two new formations—one in the west, another in the east—correlates through central New York’s classic Hamilton Group remains to be resolved by the Brett and Ver Straeten lithostratigraphic teams. We are in a critical transition zone. Following Selleck (2010), we emphasize the member-level stratigraphy and its scientific replicability within the central region, with an understanding that the correlations to the east and west will continue to be studied by these other groups.

The stratigraphic interval we studied (upper Cardiff and Pecksport Members of the Oatka Creek Formation, Marcellus Subgroup) records the transition between basinal black shales and limestones with pelagic and mixed pelagic-benthic assemblages into highly oxygenated benthic communities of siltstones that formed in shallower areas of the depositional basin. Brower...
and Nye (1991), one of our Syracuse group’s earlier contributions, also discussed the pelagic and pelagic-benthic communities from the lower Hamilton Group.

We selected two typical outcrops that contain coarsening-upward sedimentary sequences and preserve all of the communities present in this part of the Marcellus Subgroup in central New York (Figs. 3 and 4). Gulf Road (Fig. 3), north of the village of Delphi Falls, is lined by a series of Cardiff Member exposures extending approximately from 42°54′15″N, 75°55′51″W to 42°54′3″N, 75°55′44″W, along a narrow road and creek. Swamp Road, shown in Figure 4, is a small roadside quarry at 42°56′6″N, 75°39′48″W; it has two adjacent portions that can be studied faunally and stratigraphically. The full data set included 50 taxa and 81 samples. We collected large samples of 300 specimens each to ensure that the presences and proportions of taxa could be adequately characterized. The taxa

Figure 3. Stratigraphic section for upper part of Cardiff Member (Oatka Creek Formation, Hamilton Group). The outcrop is located on the north side of Gulf Road, 2.2 km south of U.S. Route 20, just east of the hamlet of Pompey Center, Onondaga County, New York, USA. See Tables 1 and 2 for community codes.
are listed in Table 1. We reconstructed living habits using these and other references:

1. Brachiopods: Cooper (1937, 1957), Rudwick (1965, 1970), Grant (1972, 1981), Thayer (1981), Bizzarro (1995), and Williams et al. (1997–2007).
2. Bivalves: Morton (1967), Kauffman (1969), Stanley (1970, 1972, 2015), Runnegar (1974), Levinton and Bambach (1975), Bailey (1983), Seilacher (1984, 1985), and Nagel-Myers et al. (2013, 2018).
3. Cephalopods: Flower (1957), Furnish and Glenister (1964), Ward and Westermann (1985), Kroger et al. (2005), and Klug et al. (2010).
4. Gastropods: Rollins et al. (1971), Linsley (1977), Houbrick (1979), Hickman (1985), and Morris et al. (1991).
5. Hyolithids: Fisher (1962), Malinky et al. (1987), and Baumiller et al. (2010).
6. Trace fossils: Seilacher (1964), Frey (1975), Ekdal et al. (1984), Bromley (1991), and Brett et al. (2007).

The research we present here on marine communities in the lower Hamilton Group belongs to a much larger program of research at Syracuse University spanning more than 50 yr. With coauthor Jim Brower’s death while our manuscript was in review, it seems important to sum up this work. In this sustained and collaborative research effort, we (Cathryn R. Newton and James C.

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Figure 4. Stratigraphic section for upper part of Pecksport Member (Oatka Creek, Hamilton Group). The outcrop is on the east side of Swamp Road, 4.3 km north of U.S. Route 20 in the village of Morrisville, Madison County, New York, USA. See Tables 1 and 2 for community codes.
| TABLE 1. LIST OF SPECIES AND THEIR CODES |
|------------------------------------------|
| **Brachiopods**                          |
| 1  Ambocoelia umbonata (Conrad) (AMB)    |
| 2  Arcuaminetes scitulus (Hall) (ARC)    |
| 3  Camarotoechia congregata (Conrad) (CAM)|
| 4  Cyrtina hamiltonensis (Hall) (CYR)    |
| 5  Emanuella subumbona (Hall) (EMA)      |
| 6  Eumetabolotoechia multicostata (Hall) (EUM)|
| 7  Lingula sp. (LIN)                     |
| 8  Mediospirifer audaculus (Conrad) (MED) |
| 9  Mucrospirifer mucronatus (Conrad) (MUC) |
| 10 Orbiculoidea doria (Hall) (ORB)       |
| 11 Protoleptostrophia periplana (Conrad) (PRT)|
| 12 Rhipidomella vanuxemi (Hall) (RHI)    |
| 13 Schuchertella arcostratiata (Hall) (SHU) |
| 14 Spinocyrtia granulosa (Conrad) (SPI)  |
| 15 Spinulicosta spinulicosta (Hall) (PRD) |
| 16 Tropidoleptus carinatus (Conrad) (TRO) |
| **Bivalves**                             |
| 17 Actinopteria boydi (Conrad) (ACT)     |
| 18 Buchiola retrostriata (von Buch) (BUC)|
| 19 Cornellites fasciculata (Goldfuss) (COR) |
| 20 Cypricardella bellistriata (Conrad) (CYP)|
| 21 Goniopora, mostly G. hamiltonensis (Hall) (GON) |
| 22 Gosseletia triquetra (Conrad) (GOS)   |
| 23 Grammysia sp., mostly G. bisulcata (Goldfuss) (GRA)|
| 24 Leiopteria sp. (LPT)                  |
| 25 Modiomorpha spp.; most represent M. concentrica (Conrad), M. mytiloides (Conrad), and M. alta (Conrad) (MOD) |
| 26 Nuculites oblongatus Conrad (NCO)     |
| 27 Nuculites triqueter Conrad (NCT)      |
| 28 Nuculoida sp. (NUC)                   |
| 29 Orthonota undulata Conrad (ORN)       |
| 30 Palaeoneilo constricta (Conrad) and Palaeoneilo emarginata (Conrad) (PAL) |
| 31 Paracyclas irata (Conrad) (PAR)       |
| 32 Pholadella radiata (Conrad) (PHO)     |
| 33 “Praecardium” robusta (Hall), termed Panenka by many workers (PAN) |
| 34 Pseudoaviculopecten princeps (Conrad) (PSV) |
| 35 Pterochaenia fragilis (Hall) (TER)    |
| 36 “Schizodus” appressus (Conrad) (SHZ)  |
| **Gastropods**                           |
| 37 Bembexia sulcomarginata (Conrad) (BEM) |
| 38 Gyronema irata (Hall) (GYR)           |
| 39 Palaeozygopleura hamiltoniae (Hall) (PZP) |
| 40 Praematuropis ovatus Rollins (PAE)    |
| 41 Ptomatis patulus (Hall) (PTO)         |
| 42 Sinuotopsis acutilira (Hall) (BEL)    |
| **Cephalopods**                          |
| 43 Goniatites, mostly Agoniatites vanuxemi (Hall) (AGO) |
| 44 Nephriticeras maximum (Conrad) (NPH)  |
| 45 Orthocones with large shells (ORT)    |
| 46 Orthocones with small shells (SOT)    |
| **Trilobites**                           |
| 47 Greenops boothi (Green) (GRE)         |
| 48 Eldredgeops rana (Green) (RAN)        |
| **Phyllocarid**                          |
| 49 Echinocaris punctata (Hall) (PHL)     |
| **Hyolithid**                            |
| 50 Hallotheca sp. (HYO)                  |
Brower) and our students obtained and analyzed large and closely spaced samples from the shallowing-upward sequences in central New York. Syracuse University faculty actively involved in this long-term program of Devonian paleontological research, and in working on this with graduate students, include James C. Brower, Cathryn R. Newton, Linda C. Ivany, Osborne B. Nye Jr., and now Christopher Junium. In conducting our quantitative paleoecological analyses over this span, we and our students have generally collected large samples, even from sparsely fossiliferous horizons such as those of the dark shales. In addition, several of our students in this larger program have conducted morphological and paleo-autecological studies of individual Hamilton Group taxa during these years. Some Syracuse graduate alumni supported in this group continue to publish on Hamilton Group faunas (e.g., Christopher McRoberts on trilobites and bivalves: McRoberts et al., 2013; Nagel-Myers et al., 2018).

This multidisciplinary research program at Syracuse University has consistently probed Devonian marine community structure and composition using systematically collected samples and analyzed with multivariate quantitative methods. During the 35 yr in which Brower and Newton worked together (1983–2018), we had the further goal of using these large data sets to test some fundamental principles of paleoecology, such as exploring the extent to which these paleocommunities were tightly structured. Our current study fits with both of these long-term aims and forms a key addition to the Hamilton Group record in allowing for tests of community structure and its temporal persistence.

The long lineage of Syracuse University studies on the paleoecology of Devonian siltstones and shales in upstate New York includes Brower and Chute (1964a, 1964b), Nye et al. (1975), Brower et al. (1978), Brower (1987), Thompson and Newton (1987), Brower and Kile (1988), Thompson and Newton (1988), Brower et al. (1988), Thompson (1989), Brower and Nye (1991), Bonuso (2001), Bonuso et al. (2002a, 2002b), Brett et al. (2009), Ivany et al. (2009), Ver Straeten et al. (2019), and diverse other studies cited therein. Nicole Bonuso and Joel Thompson were graduate students who worked with Newton. Another graduate student was Willis Newman, a fine field geologist who collected data for this paper, but who did not complete the doctorate and who died far too young.

This study critically extends, and in some ways completes, our earlier work by further analyzing community structures in the Marcellus Subgroup—that basal part of the Hamilton Group now famed for its hydrocarbon potential and production (Nyahay et al., 2007; Kargbo et al., 2010; Soeder, 2010). Our focus is not on the lowermost Marcellus Subgroup, which is the site of most hydrocarbon exploration, but on the intriguing interplay of communities higher, in the Cardiff and Pecksport Members—communities that find some, but not all, ecological counterparts further upward in the Hamilton Group. This strengthening of lower Hamilton Group quantitative paleoecology facilitates greater rigor in testing inferences about possible ecological stability and, in particular, ecological locking of marine communities over 4–6 m.y. of Hamilton Group deposition.

**Quantitative paleoecological methods**

Biological and sedimentological data were analyzed with multivariate statistics. Lucid ecological references for the methods applied herein include works by Clifford and Stephenson (1975), Orloci (1978), Whittaker (1978a, 1978b), Gauch (1982), Greig-Smith (1983), Legendre and Legendre (1983, 2012), Pielou (1984), Birks and Gordon (1985), Ludwig and Reynolds (1988), and Dray et al. (2012). Here, we deployed a variety of methods comparable to those used both in community ecology and in our earlier works on Hamilton Group paleoecology; this parallel approach best facilitates comparisons. The basic analytical strategy follows that of Brower (1987). Initially, clustering and ordination are used to identify and characterize the communities and gradients present in the data. These are tested subsequently to ascertain their statistical significance. In the final step, plotting the communities and gradients against geographic and stratigraphic position leads to the construction of a paleoecological scenario.

Previous paleoecological analyses of Middle Devonian macrofossils have been published by Miller (1986), Savarese et al. (1986), Brower (1987), Brower and Kile (1988), Brower et al. (1978, 1988), Brower and Nye (1991), McComb (1991), Newman et al. (1992), Bonuso et al. (2002a, 2002b), Nagel-Myers et al. (2009, 2013), and others. Earlier, pertinent papers on the somewhat comparable paleoecology of the Upper Devonian section of the Appalachians include works by Bowen et al. (1974), McGhee (1976), McGhee and Sutton (1981, 1983), Sutton et al. (1970), Sutton and McGhee (1985), and Thayer (1974). Examples of earlier quantitative studies that compared clustering and ordination and/or discussed the significance of communities and gradients in Ordovician rocks were published by Cisne and Rabe (1978), Cisne et al. (1982), Lockley (1983), and Springer and Bambach (1985).

We define communities herein as consistent, statistically recurrent groups of fossils. Both ordination and clustering methods are necessary for the recognition of faunal communities and gradients, because these methods are subject to different types of distortion. Ordination methods preserve the main patterns in the data, but the relationships between similar species and samples are often shown incorrectly. Clustering retains the distances between similar items, but at the cost of large-scale deformation. In both approaches, we used percentages of species in samples. Computational details of the exact algorithms are available in the textbooks listed above and Sneth and Sokal (1973). Clusters were calculated by the unweighted-pair-group method (UPGM) on a matrix of correlation coefficients. The ordination algorithm consists of correspondence analysis axis ordination or reciprocal averaging. The correspondence analysis was not detrended because its axes retain the dual space properties of the variable- and specimen-space eigenvectors specified by the Eckart-Young theorem (see any textbook on multivariate analysis). As outlined later, the first two axes of the correspondence analysis are highly anchored. Consequently, these were reduced to a single
axis by calculating orthogonal projections of the data points onto a polynomial as suggested by Ludwig and Reynolds (1988) and Phillips (1978). This is termed the “correspondence analysis axis ordination” in later parts of the paper. Clustering and ordination lead to similar and complementary conclusions.

The groups of samples recognized in the clusters and ordinations should be tested for statistical significance. We elected to employ significance tests for clusters rather than discriminant analysis because they are largely independent of the number of variables (taxa in this case), and they are less sensitive to statistical assumptions.

Inasmuch as cluster significance tests are probably not familiar, the statistical methods will be outlined briefly (for details, see Sneath, 1977, 1979). Visualize an axis connecting the centroids of two clusters of samples in the space defined by the species. The samples are projected onto this axis to form \( q \) (or \( Q \)) scores or distributions that illustrate the differences between the two clusters. These \( q \) scores are analogous to the scores of discriminant functions, except that they are more conservative, because the differences between the two clusters may not be maximized. Various tests can be applied to the \( q \) distributions. The conventional hypothesis for univariate or multivariate means ascertains whether or not the differences between them are statistically significant subject to a predetermined risk level. This is obviously trivial for groups that have been previously identified by cluster analysis; one almost invariably rejects the null hypotheses, even if the two groups overlap greatly. It is much more informative to query whether the samples were drawn from two populations that overlap more or less than some specified amount. The degree of overlap of the \( q \) distributions is measured by the \( W \) statistic of disjunction.

We regard communities as consistent faunal associations that may intergrade. The communities studied here changed in response to a paleoecological shallowing gradient caused by a marine regression. Consequently, a rectangular distribution of the \( q \) scores provides a reasonable null hypothesis (Sneath, 1977). In a rectangular distribution, the observed number of samples along equal intervals of the \( q \) scores follows a Poisson distribution, so the \( q \) distributions lack extended tails and behave like censored data. The null hypothesis specifies that the \( q \) scores of the two clusters are drawn from overlapping rectangular distributions. The alternative hypothesis is that the \( q \) distributions of the two clusters are disjunct. The critical test values were obtained from Sneath (1979, fig. 2).

FACIES ANALYSIS

In these Hamilton Group regressive intervals in central New York, lithofacies vary consistently in ways that are traceable laterally but exhibit a narrow range of lithologic variation. The cycles at our two study sites are typical: They begin in basal strata of dark-gray, noncalcareous shales (Figs. 3 and 4). These are overlain by progressively siltier, concretion-rich shales, and each regressive cycle culminates in noncalcareous silty shales or siltstones. Dark-gray shales at the base of these cycles preserve bioturbated fabrics at one site (Fig. 3) and are only sparsely bioturbated at the other (Fig. 4).

In addition to faunal data, we analyzed grain size (scaled meristemically from 1.0 for shale to 5.0 for siltstone) and weight percent of total organics (measured by loss on ignition). These lithologic variables were then analyzed relative to the percentages of common species in the assemblages. Statistics considered included correlation coefficients, multiple correlation coefficients, and regression weights for polynomials, where the correspondence analysis axis ordination of species composition was written as a function of the lithologic code and/or organic content. Inasmuch as the organics were measured continuously, whereas the grain size was coded meristemically, it is difficult to compare regression coefficients based on both parameters. Visual inspection and significance tests suggested that third-order polynomials provide reasonable fits to the data. These polynomials were calculated for the lithology, organic matter, and lithology and organic matter considered together. The conclusions were largely based on comparing the squared multiple correlation coefficients. Interactions between lithology and organic matter were not treated, because significance tests indicated that the interactions did not explain significant components of the variance for the dependent variable.

The squared multiple correlations for the correspondence axis ordination versus the lithology and organics were 0.758 and 0.802, respectively, whereas the same value for both lithology and organics was 0.855. (Detailed results of the correspondence axis ordination, including relation of lithologic data to communities, appear in the “Sequence of Communities” section.) Thus, the correspondence axis ordination seems to represent an approximately equal compound of organic matter and grain size if all eight communities are considered. This is evidenced by the fact that the variances associated with the two polynomial regressions for the organics and lithology do not differ significantly. The regression for both lithology and organic matter explains a significantly larger amount of the variance in the ordination than those of lithology or organic matter alone. The \( F \) ratio for the added component of variance is 6.91 with 3 and 65 degrees of freedom, which is significant at the 0.05 and 0.01 probability levels. The seven exclusively benthic communities yielded similar results, except that grain size was slightly more important than organic matter.

CLUSTER ANALYSIS

Figure 5 illustrates the dendrogram for 81 samples based on 50 species and the unweighted-pair-group method clustering of a matrix of correlation coefficients. Eight main clusters or communities can be recognized at correlations of 0.7 and higher. The dendrogram is tightly structured, and virtually all of the links within the clusters take place at levels of 0.85 and higher. Communities will be discussed in order of increasing grain size and decreasing organic content. As seen in Figures 3 and 4, the
Figure 5. Dendrogram for 81 samples. The data matrix consists of percentages of 50 species in each sample. The clusters are based on the unweighted-pair-group method of a matrix of correlation coefficients. The stratigraphic distributions of samples are shown on Figures 3 and 4.
lithologies vary, including relatively dark and fine-grained shales and siltstones with 3% total organic matter; gray silty shales with lower organic content; and siltstones in with approximately 2 wt% of total organic matter.

Samples 1–9 on the dendrogram constitute the Cephalopod-Pterochaenia community (Fig. 5). Diversity is low, with only three to eight species per sample. Cephalopods dominate the community; these include both large orthocones and Agoniatites vanuaxeni, which represent from 43% to 81% of the individuals, respectively (Table 2). Pterochaenia fragilis, also common (11%–30% of the community), is enigmatic in terms of living habits; it is clearly a byssate suspension feeder (e.g., Brower and Nye, 1991; see illustrations in Clarke, 1904), but the site of byssal attachment (i.e., benthic vs. epipelagic) is uncertain. We interpret it here as a nonendemic benthic opportunist, but we recognize that others might also reasonably infer it was an epiplanktonically attached taxon; this can likely be resolved with further studies. Eumetabolotoechia multicostata also occurs in many samples. This community characterizes the finest-grained rocks observed in this study—namely, thinly bedded dark-gray shales with small burrows and relatively high organic contents (averaging 3.0 wt%).

Samples 10, 12, and 13 belong to the Pterochaenia-Eumetabolotoechia community. Pterochaenia fragilis and the pedicle-attached brachiopod Eumetabolotoechia multicostata are about equally abundant, together accounting for 85% of the assemblage. Emanuella subumbona, Nuculoidea sp., and large orthocones occur consistently in minor proportions (Table 2).

The Eumetabolotoechia community contains samples 11–24 on the cluster diagram (Fig. 5). The pedunculate rhynchonellid Eumetabolotoechia multicostata invariably dominates; in one sample, it represents 81% of the individuals present. Other taxa encountered in all or most samples are (in decreasing order of abundance): Emanuella subumbona, Pterochaenia fragilis, Nuculoidea sp., and Arcuaminetes scitulus (Table 2). Samples 11–45 join the cluster at high correlation coefficients of 0.955–0.997. However, samples 31 and 24 group at somewhat lower correlation coefficients of 0.903–0.885; these two samples also contrast in having a rather high species richness and a somewhat lower proportion of Eumetabolotoechia.

Fourteen samples, listed from 35 to 55 on the dendrogram, represent the Eumetabolotoechia-Ambocoelia community. Eumetabolotoechia multicostata and, to a lesser extent, the pedicle-attached brachiopod Ambocoelia umbonata and the recliner Arcuaminetes scitulus form the core of this cluster. Eumetabolotoechia and Ambocoelia individuals occur in all samples, whereas Arcuaminetes is present in only 13 samples. Although generally present, Nuculoidea sp., Nuculites oblongatus, and large orthocones are less abundant; they typically constitute 1% to 5% of any one sample. Accessory species that occur in approximately half of the samples are Mucrospirifer mucronatus, Pterochaenia fragilis, Lingula sp., and Palaeozygopleura hamiltoniae (Table 2).

Samples 25 and 26 differ greatly from all others; more than 50% of the fauna is Emanuella subumbona, a small, pedicle-attached spiriferid brachiopod. We thus designate this the Emanuella community. Eumetabolotoechia multicostata and Arcuaminetes scitulus each typically account for 10%–15% of the fauna. A few shells of Mucrospirifer mucronatus and Nuculoidea sp. are associated (Table 2). Although the geographic distribution of this assemblage is uncertain, it seems locally to be restricted to a small stratigraphic interval within the Cardiff Member along Gulf Road.

The Arcuaminetes-Eumetabolotoechia community, represented by samples 27–44 on the clusters in Figure 5, is dominated by Arcuaminetes scitulus and Eumetabolotoechia multicostata, which together generally comprise slightly over 50% of each sample. In most samples, these are followed by Ambocoelia umbonata, Nuculoidea sp., Mucrospirifer mucronatus, Lingula sp., and Nuculites oblongatus (in decreasing order of abundance). A few specimens of large orthocones and Bembexia sulc marginal occur in most samples (Table 2).

The Arcuaminetes-Ambocoelia community characterizes the sequence of samples 28–73 on the dendrogram. Approximately half of the individuals consist of Arcuaminetes scitulus, in conjunction with highly variable numbers of Ambocoelia umbonata. Other common constituents in most samples include Mucrospirifer mucronatus, Nuculoidea sp., and Emanuella subumbona. Eumetabolotoechia multicostata is conspicuously absent from most samples (Table 2).

Four samples, numbers 69, 78, 79, and 81, are assigned to the Mucrospirifer-Ambocoelia community (Fig. 5). The pedicle-attached brachiopod Ambocoelia umbonata and the recliner Mucrospirifer mucronatus lead the roster of species, but significant numbers of Arcuaminetes scitulus also occur. Spinocystyria granulosa, Tropidoleptus carinatus, Nuculites oblongatus, Bembexia sulc marginal, and Modiomorpha spp. are frequently accessory taxa (Table 2).

The Mucrospirifer-Ambocoelia and Arcuaminetes-Ambocoelia communities occupy the coarsest sediments at both the Gulf Road and Swamp Road localities. These sediments are gray silty shales and siltstones that are relatively thick and poorly bedded. Average organic matter content is 2.17%–2.3%.

The previous discussion indicates that the communities are mainly defined by the most common or dominant species. This was expected for clustering of a matrix of correlation coefficients between the original percentages of taxa within samples.

Consequently, we further explored community composition by calculating constancy (proportion or percent of samples within a community in which a species, say species i, is present) and fidelity (proportion or percent of samples within a community, with species i divided by total number of samples over all communities containing that species). The basic pattern is clear (Table 2).

Species with high constancies generally have low fidelities for any one community, and vice versa. This reflects the ecological strategies of Hamilton Group taxa. Common forms are broadly adapted and inhabit a wide variety of communities and environments. Such organisms are ecological generalists. Conversely, forms with a high fidelity for a certain community are
| Community                        | Cephalopod-Pterocharia (CEPH-PTER) | Pterocharia-Eumetabolotoechia (PTER-EUM) | Eumetabolotoechia (EUM) | Eumetabolotoechia-Ambocoelia (EUM-AMB) | Emanuella (EMA) | Arcuaminetes - Eumetabolotoechia (ARC-EUM) | Arcuaminetes - Ambocoelia (ARC-AMB) | Mucrospirifer - Ambocoelia (MUC-AMB) |
|--------------------------------|-----------------------------------|------------------------------------------|----------------------|----------------------------------------|----------------|-------------------------------------------|-----------------------------------|-----------------------------------|
| General characteristics        |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Lithologic code                | 1.000                            | 1.000                                    | 2.000                | 2.140                                   | 3.000          | 2.670                                      | 3.410                             | 4.000                             |
| Weight percent of organic matter | 3.000                           | 2.840                                    | 2.790                | 2.380                                   | 2.530          | 2.270                                      | 2.300                             | 2.170                             |
| Number of species              | 5.220                            | 8.330                                    | 8.790                | 11.900                                  | 9.000          | 13.000                                     | 15.500                            | 15.800                            |
| Information function diversity for species | 0.542          | 0.535                                    | 0.507                | 0.724                                   | 0.533          | 0.831                                      | 0.710                             | 0.799                             |
| Equitability for species       | 0.814                            | 0.583                                    | 0.538                | 0.680                                   | 0.559          | 0.756                                      | 0.600                             | 0.671                             |
| Number of ecological categories | 3.560                            | 5.000                                    | 5.210                | 6.210                                   | 4.500          | 6.330                                      | 7.120                             | 7.500                             |
| Information function diversity for ecological categories | 0.361          | 0.438                                    | 0.337                | 0.490                                   | 0.274          | 0.551                                      | 0.453                             | 0.517                             |
| Equitability for ecological categories | 0.713          | 0.626                                    | 0.467                | 0.621                                   | 0.427          | 0.698                                      | 0.538                             | 0.593                             |
| Taxonomic and ecological structure |                                 |                                          |                      |                                        |                |                                           |                                    |                                   |
| Pedicle-attached suspension feeders | 8.670                        | 45.600                                   | 77.100               | 59.300                                  | 78.200         | 37.900                                     | 23.700                            | 38.700                            |
| Ambocoelia umbonata            | —                                | —                                        | 1.390                | 13.400**                                | —              | 9.280**                                    | 18.200**                          | 35.200**                          |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Camarotoechia congestata       | —                                | 0.24                                     | 0.434                | 0.094                                   | 0.075          | 0.057                                      | —                                 |                                   |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Cyrtina hamiltonensis          | —                                | 0.024                                    | 0.094                | 0.505**                                 | 0.847          | 0.750                                      | —                                 |                                   |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Emanuella subumbona            | 0.778                            | 4.210**                                  | 9.220**              | —                                       | 61.400*        | 4.890*                                     | 3.170*                            | 0.678                             |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Eumetabolotoechia              | 7.890*                           | 40.600**                                 | 65.900**             | 44.700**                                | 14.700*        | 22.400**                                   | 0.928                             | —                                 |
| multicostata                   |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Mediospirifer audaculus         | —                                | 0.753**                                  | 0.474                | 0.498                                   | 1.510**        | 0.712                                      | 0.019                             | —                                 |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Orthoculidea doria             | —                                | —                                        | 0.024                | 0.094                                   | 0.505**        | 0.075                                      | 0.057                             | —                                 |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Rhipodomella vanuxemi          | —                                | —                                        | —                    | 0.095                                   | —              | —                                         | —                                 | —                                 |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Spinocyrtia granulosa          | —                                | 0.024                                    | 0.095                | 0.530                                   | 1.260**        | 1.500**                                    | 1.940*                            | 2.770*                            |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Reclining suspension feeders   | 1.110                            | 2.910                                    | 7.410                | 21.300                                  | 18.600         | 40.800                                     | 60.900                            | 47.000                            |
| Arcuaminetes scitulus          | —                                | 1.520*                                   | 4.780**              | 17.200**                                | 12.200**       | 31.8**                                     | 49.100**                          | 18.6**                            |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Mucrospirifer mucronatus       | —                                | 0.852                                    | 0.310                | 3.440*                                   | 6.430**        | 6.150**                                    | 6.980**                           | 23.700**                          |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Protoleptostrophia periplana   | —                                | —                                        | —                    | 0.319                                   | —              | 0.847                                      | 1.350*                            | —                                 |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Schuchertella arctostriata     | —                                | —                                        | 0.400                | —                                       | 0.844          | 0.750                                      | —                                 |                                   |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Spinulicosta spinulicosta      | 1.110                            | 0.543                                    | 2.330*               | —                                       | 1.140          | 1.940*                                     | 2.770*                            | —                                 |
| (Hall)                         |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |
| Tropidoleptus carinatus        | —                                | —                                        | —                    | —                                       | —              | —                                         | —                                 | —                                 |
| (Conrad)                       |                                   |                                          |                      |                                        |                |                                           |                                    |                                   |

(Continued)
TABLE 2. AVERAGE TAXONOMIC AND ECOLOGICAL STRUCTURE OF COMMUNITIES (Continued)

| Community | Cephalopod - Pterochaenia (CEPH-PTER) | Pterochaenia - Eumetabolotoechia (PTER-EUM) | Eumetabolotoechia - Eumetabolotoechia (EUM) | Eumetabolotoechia - Ambocoelia (EUM-AMB) | Emanuella (EMA) | Arcuaminetes - Eumetabolotoechia (ARC-EUM) | Arcuaminetes - Ambocoelia (ARC-AMB) | Mucrospirifer - Ambocoelia (MUC-AMB) |
|-----------|--------------------------------------|--------------------------------------------|--------------------------------------------|------------------------------------------|----------------|------------------------------------------|---------------------------------|----------------------------------|
| Epibyssate or shallow endobyssate suspension feeders | 23.200 | 45.700 | 7.590 | 3.250 | 0.167 | 1.520 | 1.210 | 2.710 |
| Actinopteria boydi (Conrad) | — | — | — | — | — | — | 0.098 | 0.663* |
| Buchiola retrostriata (von Buch) | 0.222 | 0.866* | 0.213 | — | — | 0.239 | 0.057 | — |
| Cornillites fasciculata (Goldfuss) | — | — | — | — | — | — | — | — |
| Gosseletia triquetra (Conrad) | — | — | — | — | — | 0.038 | 0.374 | 0.407 |
| Leiopteria sp. | — | — | — | 0.097 | — | — | 0.177 | 0.288 |
| "Pracecardium" (?Panenka) cf. P. robusta (Hall) | — | — | 0.024 | 0.263 | 0.167* | 0.073 | 0.117 | — |
| Pseudoaviculopecten princeps (Conrad) | — | — | — | — | — | — | 0.059 | — |
| Pterochaenia fragilis (Hall) | 23.000** | 44.800** | 7.360** | 2.890* | — | 1.170 | 0.333 | 0.847 |
| Endobyssate suspension feeders | — | — | 0.095 | 0.330 | 0.167 | 0.369 | 0.623 | 1.700 |
| Goniophora sp., cf. G. hamiltonensis (Hall) | — | — | — | — | — | 0.037 | 0.057 | 0.251* |
| Grammysia sp., cf. G. bisulcata (Goldfuss) | — | — | 0.068 | — | 0.148 | — | 0.020 | 0.336* |
| Modiomorpha spp. cf. M. concentrica (Conrad), M. mytiloides (Conrad), and M. alta (Conrad) | — | — | 0.095 | 0.238 | 0.167* | 0.092 | 0.527 | 0.945** |
| Pholadella radiata (Conrad) | — | — | — | 0.024 | — | 0.093 | 0.020 | 0.169 |
| Burrowing suspension feeders | — | — | 0.424 | 3.14 | — | 4.430 | 3.390 | 1.750 |
| Cypricardella bellisiatria (Conrad) | — | — | — | — | — | — | 0.020 | — |
| Lingula sp. | — | — | 0.095 | 1.830* | — | 3.100* | 1.210 | — |
| Orthonota undulata Conrad | — | — | — | 0.048 | — | 0.075 | — | — |
| Paracyclus trirata (Conrad) | — | — | 0.305 | 0.379 | — | 0.92 | 1.340* | 1.410** |
| Schizodus appressus (Conrad) | — | — | 0.024 | 0.88 | — | 0.334 | 0.824 | 0.339 |

(Continued)
### TABLE 2. AVERAGE TAXONOMIC AND ECOLOGICAL STRUCTURE OF COMMUNITIES (Continued)

| Community                                           | Cephalopod - Pterochaenia (CEPH-PTER) | Pterochaenia - Eumetabolotoechia (PTER-EUM) | Eumetabolotoechia (EUM) | Eumetabolotoechia - Ambocoelia (EUM-AMB) | Emanuella (EMA) | Arcuaminetes - Eumetabolotoechia (ARC-EUM) | Arcuaminetes - Ambocoelia (ARC-AMB) | Mucrospirifer (MUC-AMB) |
|-----------------------------------------------------|--------------------------------------|--------------------------------------------|--------------------------|------------------------------------------|-----------------|-------------------------------------------|---------------------------------|----------------------|
| Burrowing deposit feeders                           | 1.110                                | 3.670                                      | 5.940                    | 10.100                                    | 2.550           | 11.600                                     | 6.550                           | 5.600                |
| Nuculites oblongatus Conrad                         | —                                    | —                                          | 0.234                    | 3.32**                                    | 0.171*          | 2.660**                                    | 1.160*                           | 2.060**              |
| N. triqueter Conrad                                 | —                                    | 0.214                                      | 0.831                    | —                                         | 1.150           | 0.861                                      | 2.110*                           | —                    |
| Nuculoidea sp.                                      | 1.110                                | 3.670**                                    | 5.230**                  | 4.990**                                   | 2.370**         | 7.370**                                    | 3.680**                          | 0.997*               |
| Palaeoneilo constricta (Conrad) and P. emarginata  (Conrad) | —                                    | —                                          | 0.262                    | 0.650                                     | —               | 0.390                                      | 0.845                           | 0.424                |
| Surface grazers                                     | —                                    | —                                          | —                        | 1.21                                      | —               | 1.72                                       | 2.45                             | 2.19                 |
| Bembexia sulcomarginata (Conrad)                    | —                                    | —                                          | —                        | 0.405                                     | —               | 0.922*                                     | 0.959**                          | 1.510**              |
| Gyronema lirata (Hall)                              | —                                    | —                                          | —                        | —                                        | —               | 0.039                                      | —                                | —                    |
| Palaeozygopleura hamiltoniae (Hall)                 | —                                    | —                                          | —                        | 0.738*                                    | —               | 0.709                                      | 1.290*                           | 0.590*               |
| Praematurops ovatus Rollins                         | —                                    | —                                          | —                        | —                                        | —               | 0.018                                      | 0.137                            | —                    |
| Planis patulus (Hall)                               | —                                    | —                                          | —                        | —                                        | —               | 0.056                                      | —                                | 0.089                |
| Sinuotopsis acutilra (Hall)                         | —                                    | —                                          | —                        | —                                        | —               | 0.02                                       | —                                | —                    |
| "Collectors"                                        | 0.333                                | —                                          | —                        | —                                        | 0.037           | 0.059                                      | 0.063                            | —                    |
| Echinocaris punctata (Hall)                         | —                                    | —                                          | —                        | —                                        | 0.037           | —                                          | —                                | —                    |
| Greenops boothi (Green)                             | —                                    | —                                          | —                        | —                                        | 0.037           | —                                          | —                                | —                    |
| Hallotheca sp.                                      | 0.333                                | —                                          | —                        | 0.069                                     | —               | 0.016                                      | —                                | —                    |
| Eldredgeops rana (Green)                            | —                                    | —                                          | —                        | —                                        | 0.039           | 0.083                                      | —                                | —                    |
| Swimming predators and scavengers                   | 65.600                               | 2.160                                      | 1.460                    | 1.320                                     | 0.340           | 1.750                                      | 1.040                            | 0.332                |
| Goniatites, mostly Agoniatites vanuermi (Hall)      | 19.100**                             | 0.325                                      | 0.222                    | 0.071                                     | —               | 0.358                                      | —                                | 0.081                |
| Orthocones, large forms                             | 46.500**                             | 1.8300**                                   | 1.240*                   | 1.250**                                   | 0.342*          | 1.370*                                     | 0.788*                           | 0.081                |
| Orthocones, small forms                             | —                                    | —                                          | —                        | —                                        | —               | 0.018                                      | 0.216                            | 0.169                |
| Nephriticeras maximum (Conrad)                      | —                                    | —                                          | —                        | —                                        | —               | —                                          | 0.039                            | —                    |

*Note: Data for taxa and ecological categories are listed as percentages. Species present in at least half and three quarters of the samples in a community are denoted by * and **, respectively. Lithology is coded from 1 for shales to 5 for siltstones.*
environmentally restricted, specialized, and usually rare. Also, such taxa are usually restricted to one or a small number of samples within that community. Figure 6 illustrates the distribution of species in samples, showing that only a few taxa are found in a large number of samples, and vice versa.

Clusters were also generated for the 50 species (Fig. 7). As is usual for paleoecological data, this dendrogram is much more loosely structured than that for the samples. For example, only 6% and 14% of the links are above correlation coefficients of 0.70 and 0.60, respectively. Despite low levels of similarities, the clusters do identify coherent groups of taxa with common distribution patterns, as shown below in telegraphic form. The species are listed as given on the dendrogram.

Cluster 1: *Eumetabolotoechia* to *Orbiculoidea* on the dendrogram of Figure 7. Common and rare taxa found in fine sediments; these taxa are most abundant in the *Eumetabolotoechia*, *Eumetabolotoechia-Ambocoelia*, *Emanuella*, and *Arcuaminetes-Ambocoelia* communities.

Cluster 2: *Pterochaenia* to *Hallotheca*. Common and rare species found in the finest sediments, mostly from the *Cephalopod-Ambocoelia*, *Eumetabolotoechia-Ambocoelia*, *Emanuella*, and *Arcuaminetes-Ambocoelia* communities.

Cluster 3: *Arcuaminetes* to *Eldredgeops*. Widely tolerant, common to rare forms, generally from the *Eumetabolotoechia* to *Macrospirifer-Ambocoelia* communities; all or most species occur in the *Arcuaminetes-Ambocoelia* and *Macrospirifer-Ambocoelia* communities.

Cluster 4: *Cornellites* and *Ptomatis*. Rare species in the *Macrospirifer-Ambocoelia* community.

Cluster 5: *Rhipidomella* and *Modiomorpha*. Rare species in a variety of assemblages, ranging from the *Eumetabolotoechia* to the *Macrospirifer-Ambocoelia* communities.

Cluster 6: *Leiopteria* to *Greenops*. Rare species, mostly centered in the *Arcuaminetes-Ambocoelia* and adjacent communities.

Cluster 7: *Lingula* to *Echinocaris*. Broadly adapted, common to rare organisms ranging from the *Eumetabolotoechia* to the *Macrospirifer-Ambocoelia* communities, with all or most being recorded in the four communities from the coarsest sediments.

Cluster 8: *Praceardium* and *Orthonotus*. Rare taxa in the *Eumetabolotoechia-Ambocoelia* and *Arcuaminetes-Eumetabolotoechia* communities.

Cluster 9: *Pholadella* to *Gyroema*. Rare forms, mostly in the *Arcuaminetes-Ambocoelia* community.

Cluster 10: *Schuchertella* to *Grammysia*. Wide-ranging, rare species found in communities varying from *Pterochaenia-Eumetabolotoechia* to *Macrospirifer-Ambocoelia* communities; all of these taxa are known from the *Arcuaminetes-Eumetabolotoechia* and *Arcuaminetes-Ambocoelia* communities.

CORRESPONDENCE ANALYSIS

The first three axes of the correspondence analysis for 81 samples and 50 species account for 30.4%, 17.9%, and 10.2% of the information in the data set, respectively. The third axis mainly polarizes the unique *Emanuella subumbona* community from the rest, and this axis will not be discussed further. Correspondence axes I and II display the overall relations between the eight communities (Fig. 8A). The communities are arranged in a horseshoe-shaped figure in a systematic sequence: (1) the *Cephalopod-Pterochaenia* community; (2) the *Pterochaenia-Eumetabolotoechia* community; (3) the *Eumetabolotoechia* community; (4) the *Emanuella* community and (5) the *Eumetabolotoechia-Ambocoelia* community; (6) the *Arcuaminetes-Eumetabolotoechia* community; (7) the *Arcuaminetes-Ambocoelia* community; and (8) the *Macrospirifer-Ambocoelia* community. The *Emanuella* community is most closely linked to that of *Eumetabolotoechia*. Interestingly, these relations resemble those that could be inferred from the dendrogram of Figure 7, except that the position of the *Emanuella* community is greatly distorted by the clusters. From left to right on the graph of the correspondence analysis (Fig. 8A), the communities reflect a trend of increasing sedimentary grain size, generally decreasing amounts of organic matter, and increasing sedimentary bed thickness. This sequence presumably reflects an overall tendency of decreasing depth, increasing agitation, and higher amounts of oxygenation. Furthermore, the sequence also replicates the most frequent vertical changes between and within communities, as annotated below.

Other information can also be gleaned from the correspondence analysis plot. The wide gap between the *Cephalopod-Pterochaenia* and the *Pterochaenia-Eumetabolotoechia* communities is notable. This gap indicates considerable cleavage between the two groups and suggests much variance between the two clusters. However, the *Cephalopod-Pterochaenia* and *Pterochaenia-Eumetabolotoechia* communities sometimes occur in adjacent samples. Perhaps a critical or threshold change in one or more environmental parameters dictated the assemblage that is found. Likewise, the *Pterochaenia-Eumetabolotoechia* community is discontinuously separated from the more diverse communities.
and shallower-water communities that are closely packed on the right side of the graph. Although they tend to occupy different regions in the correspondence axis plot, overlap can be seen between the *Eumetabolotoechia* and the *Eumetabolotoechia-Ambocoelia* communities, the *Eumetabolotoechia-Ambocoelia* and the *Arcuaminetes-Eumetabolotoechia* communities, the *Arcuaminetes-Eumetabolotoechia* and the *Arcuaminetes-Ambocoelia* communities, and the *Arcuaminetes-Ambocoelia* and the *Mucrospirifer-Ambocoelia* communities.

To study the patterns for the more shallow-water communities, we performed another correspondence analysis, in which the nine samples of the *Cephalopod-Pterochaenia* community were deleted in order to decrease the total dispersion of the data set. Axes I and II extracted 27.7% and 14.8% of the variance of the 72 samples and 50 species, respectively. The graph of the first two axes for the samples groups the communities from *Pterochaenia-Eumetabolotoechia* to *Mucrospirifer-Ambocoelia*, but the intergradations between the *Eumetabolotoechia*, *Eumetabolotoechia-Ambocoelia*, *Arcuaminetes-Eumetabolotoechia*, *Arcuaminetes-Ambocoelia*, and *Mucrospirifer-Ambocoelia* communities are illustrated more clearly (Fig. 8B). Although the second axis isolates the *Emanuella* community from the others, this assemblage remains closest to that of the *Eumetabolotoechia* community. The third correspondence axis, which is associated with 9.07% of the variance, separates the *Pterochaenia-Eumetabolotoechia* community from the rest of the data; it thus does not provide any new information.

Figure 9 contains the first correspondence axes for the 50 species in all 81 samples. The horseshoe-shaped pattern for the taxa duplicates that of the samples and communities. The organ-
isms that are restricted to the finest-grained and darkest shales lie on the left side of the graph. Proceeding from left to right along the horseshoe, taxa represent associations found in progressively coarser rocks and shallower lithofacies.

**CLUSTER SIGNIFICANCE TESTS**

Cluster significance tests were applied to the communities known from adequate numbers of samples, namely, Cephalopod-Pterochaenia, Eumetabolotoechia, Eumetabolotoechia-Ambocoelia, Arcuaminetes-Eumetabolotoechia, and Arcuaminetes-Ambocoelia. The Pterochaenia-Eumetabolotoechia, Emanuella, and Mucrospirifer-Ambocoelia communities were deleted because of the small numbers of samples (which varied from two to four, in the communities deleted). Allowing for the missing communities, all pairs of communities that occurred adjacent stratigraphically were tested; the results are given in Table 3.

Student’s $t$ values demonstrate that mean species compositions of all pairs of communities differ significantly at the 0.01 probability level. The multivariate means of the different communities were clearly derived from different populations. However, this hypothesis tells little about the amount of overlap between the parent populations. This information is provided by
the W statistics of disjunction, which were tested using the data of Sneath (1979). The W figures denote that most pairs of communities were drawn from populations with rectangular distributions that do not overlap, again subject to a risk of 0.01. However, the Eumetabolotoechia-Ambocoelia community overlaps with the Eumetabolotoechia and Arcuaminetes-Eumetabolotoechia communities in terms of rectangular distributions. The Eumetabolotoechia and Arcuaminetes-Eumetabolotoechia communities are completely disjunct. The statistics suggest that one assemblage, the Eumetabolotoechia-Ambocoelia community, may not have occupied a completely separate region in the ecological gradient seen in the Cardiff Member.

SEQUENCE OF COMMUNITIES

Figures 3 and 4 show the stratigraphic sections with the communities superimposed. The stratigraphic order of the communities is summarized in Figure 10 for the two sections and their composite. Each arrow denotes a vertical change from older to younger rocks. In general, the composite sequence of communities, listed from base to top, is Cephalopod-Pterochaenia, Pterochaenia-Eumetabolotoechia, Eumetabolotoechia, Emanuella or Eumetabolotoechia-Ambocoelia, Arcuaminetes-Eumetabolotoechia, Arcuaminetes-Ambocoelia, and Microribofe-Ambocoelia; this sequence agrees with that given by

| TABLE 3. RESULTS OF CLUSTER SIGNIFICANCE TESTS |
|-----------------------------------------------|
| Pairs of communities                          |
| W statistic of disjunction (** denotes values significant at 0.01 probability level) | Total sample size | Observed percent of overlap in q scores | Student's t values comparing multivariate means (** denotes values significant at 0.01 probability level) |
| Cephalopod-Pterochaenia versus Eumetabolotoechia | 3.340** | 23 | 0 | 16.000** |
| Eumetabolotoechia versus Eumetabolotoechia-Ambocoelia | 1.83 | 28 | 7.14 | 9.680** |
| Eumetabolotoechia-Ambocoelia versus Arcuaminetes-Eumetabolotoechia | 1.62 | 32 | 0 | 9.1500** |
| Eumetabolotoechia versus Arcuaminetes-Eumetabolotoechia | 3.220** | 32 | 0 | 18.200** |
| Arcuaminetes-Eumetabolotoechia versus Arcuaminetes-Ambocoelia | 2.980** | 35 | 0 | 17.600** |
the correspondence analysis. Several lines of evidence suggest that this sequence reflects decreasing depth. The basic sequence, ranging from the Cephalopod-Pterochaenia to Mucrospirifer-Ambocoelia communities, correlates strongly with increasing sedimentary grain size, increasing bed thickness, and progressively more intense bioturbation; it also relates to decreasing amounts of organics, increased species richness, and ecological diversity. Thus, the main trend is one of decreasing depth, with changes in associated parameters, such as increasing agitation, and we acknowledge that additional ecological factors may also have been operative.

The two collections with the Emanuella community are only known at the Gulf Road section; these samples follow a large stratigraphic interval dominated by the Eumetabolotoechia community and are in turn overlain by the Arcuaminetes-Eumetabolotoechia community. Both Eumetabolotoechia and Emanuella subumbona are pedicle-attached brachiopods, although they exhibit few other common features. For example, the former is a rhynchonellid, whereas the latter is a spirifer, and Emanuella subumbona is much smaller than Eumetabolotoechia multicostata. The paleoecological changes involved here are not entirely certain and are discussed later.

Both stratigraphic sections analyzed here have thick intervals characterized by frequent changes in community composition. Examples are: Pterochaenia-Eumetabolotoechia and Eumetabolotoechia communities in the lower part of Gulf Road; Eumetabolotoechia, Eumetabolotoechia-Ambocoelia, Arcuaminetes-Eumetabolotoechia, and Arcuaminetes-Ambocoelia in the upper-middle part of Gulf Road; Arcuaminetes-Eumetabolotoechia and Arcuaminetes-Ambocoelia communities in the upper portion of Gulf Road; Eumetabolotoechia-Ambocoelia and Arcuaminetes-Eumetabolotoechia communities in the middle of Swamp Road; and Arcuaminetes-Ambocoelia and Mucrospirifer-Ambocoelia communities in the upper part of Swamp Road (Figs. 3, 4, and 10). Obviously, the two sections experienced times in which benthic communities (and possibly environmental conditions) fluctuated considerably.

Different ranges of communities and environments occur in the two stratigraphic sequences. The oldest and youngest communities at the Swamp Road section consist of Eumetabolotoechia and Mucrospirifer-Ambocoelia, but those at Gulf Road vary from Cephalopod-Pterochaenia to Arcuaminetes-Eumetabolotoechia and Arcuaminetes-Ambocoelia. Thus, the Swamp Road area began and ended in shallower habitats than did the Gulf Road section.

The relations between the samples are shown by the first two axes of the correspondence analysis, as has been discussed above (Fig. 8A). Inasmuch as the overall pattern involves both axes, the data were combined into a single sequence, which will be termed the correspondence ordination. First, a fourth-order polynomial was fitted to the first two axes of the correspondence analysis, yielding a squared correlation coefficient of 0.890 (Fig. 11). Next, orthogonal projections of the 81 samples onto the polynomial were determined. Finally, the polynomial was “unfolded” and scaled so that the points on the left and right of the curve equaled 0 and 95, respectively. This technique is commonly employed by ecologists to reduce curvilinear ordinations of various types (e.g., Ludwig and Reynolds, 1988; Phillips, 1978), although typically with lower-order polynomials.

The correspondence ordination is interpreted as a general-ized measure of relative depth and position along an ecological gradient, as has been suggested in other studies, including Cisne and Rabe (1978), Brower and Kile (1988), and Brower et al. (1988). Several facts indicate that this ordination does provide
such information. Scores for the samples on the ordination are highly correlated with sedimentary grain size and community composition, and they vary inversely with the organic matter content. For example, the Spearman’s rank correlations between the correspondence ordination versus sedimentary grain size, organic matter content, and community composition are 0.828, –0.732, and 0.964, respectively. In addition, there are associations between the correspondence axis ordination and increasing amounts of sedimentary bed thickness, bioturbation, density of fossils, and taxonomic and ecological diversity, although the exact correlations have not been calculated. High ordination scores in this analysis were linked with comparatively shallow water, high agitation, coarse substrates, and high oxygen contents, and vice versa. The correlation between the correspondence axis ordination and depth is both generalized and blurred; the independent effects of depth, such as agitation and substrate texture, cannot be completely disentangled, although some suggestions are presented below.

The scores for the samples on the correspondence axis ordination are plotted against stratigraphic position in Figure 12. For the purposes of interpretation, we will assume that depths and scores exhibit a linear relationship. The first-order pattern in both stratigraphic sections is regression or relative fall of sea level. The rapid increase in the scores at the base of the Gulf Road section, especially involving the Cephalopod-Pterochaenia, Pterochaenia-Eumetabolotoechia, and perhaps the Eumetabolotoechia communities, suggests rapid shoaling and augmented oxygenation. Later rates of falling sea level at Gulf Road are
more gradual and exhibit several smaller-scale transgressions and regressions superimposed on the overall trend.

The base of the Swamp Road outcrop began in deeper water than that seen in the youngest beds at Gulf Road. Consequently, the range of depths spanned by the two sections overlaps considerably. The Swamp Road area is characterized by a decrease in relative sea level that appears almost linear. The superimposed fluctuations of scores for the correspondence axis orientation are minor, and they may or may not be statistically significant. The Mucrospirifer-Ambocoelia community caps the Swamp Road section, which ended in shallower habitats than did the older section at Gulf Road.

ECOLOGICAL STRUCTURE

Ecological groups within the eight Cardiff Member communities will be discussed in order of decreasing depth. The living habits of the shelled organisms are divided into ecological categories that represent a combination of feeding habits and mode of locomotion or attachment. The nine categories are:

1. pedicle-attached suspension feeders;
2. reclining suspension feeders in which the shell may lie at, or slightly above, the substrate;
3. epibyssate or very shallow endobyssate suspension feeders;
4. endobyssate suspension feeders;
5. burrowing suspension feeders that are probably mostly sedentary (rather than active) burrowers;
6. burrowing deposit feeders;
7. grazers that crawl along the surface;
8. a highly variable suite of “collectors,” which includes mainly bottom plowers, crawlers, or walkers, some of which may have been capable of swimming or burrowing; the organisms denoted as “collectors” may have been deposit feeders, scavengers, or predators on small animals and plants; and
9. swimming predators and scavengers.

Reconstruction of living habits for most species is straightforward, and it was based mainly on references listed previously. Several forms do require additional explanation. The shape of the small and thin-shelled bivalve Pterochaenia fragilis definitely denotes the presence of a byssus (Stanley, 1972), but the site of byssal attachment is uncertain. This bivalve spans a wide variety of facies, from laminated black shales and limestones to siltstones. The species may be extremely abundant in dark-gray shales, where some specimens are preserved in inferred living position; such occurrences are interpreted as representing organisms attached to the seafloor. Pterochaenia fragilis is a common accessory in various level-bottom Hamilton Group communities, a distribution consistent with a benthic habit. A few shells were obtained from laminated black shales, where they are associated with pelagic faunas. These could represent epipelagic organisms, as suggested by Thayer (1974) for Upper Devonian material (see also discussion in Boyer and Droser [2009] on such organisms).

Although much less common, the distribution and some morphological features of Buchiola retrostriata parallel those of Pterochaenia fragilis, and their living habits are considered to be the same. “Praecardium” robusta, a rare element in many Cardiff Member communities, is a large (up to 60 mm long) bivalve that was probably epifaunal and may have been epibyssate. Although “Praecardium” often occurs in deeper-water, fine-grained facies, its large size is not typical of most epipelagic taxa. The asymmetric valves suggest this bivalve did not have the swimming capacity characteristic of some modern pectinaceans in comparable habitats (cf. Stanley, 1972). We therefore conclude that most individuals of Praecardium likely dwelled epifaunally, but some specimens may have been epipelagic.

Shell shapes and apertural orientations of the gastropods and bellerophontids in the Cardiff Member demonstrate that these animals dwelled epifaunally on the sedimentary substrate or on plants (e.g., Linsley, 1977). Their food supplies are uncertain. Recent shallow-water counterparts graze on benthic algae, whereas those dwelling in aphotic regions are deposit feeders (Rex, 1973). Insomuch as stratigraphic position and lithology indicate that these sediments were deposited at moderate depths, the Cardiff Member gastropods are tentatively considered to have been herbivores. The bellerophontids—extinct molluscs thought by some to have been gastropods and by others possibly to have been monoplacophorans (this latter grouping is, however, itself considered polyphyletic)—are here classified as herbivores as well. Following Bouchet et al. (2005, 2017), we consider bellerophontids as incertae sedis within Class Gastropoda for now.

Cephalopod-Pterochaenia Community

This community occurs only in the organic-rich, deep-water shales of the Gulf Road section (Fig. 3). Both species richness and ecological diversity are low, with means of 5.22 species and 3.56 ecological categories, respectively (Table 2). Surprisingly, equitabilities are comparatively high, with a more even distribution of species frequencies and ecological categories than in any other Cardiff Member community. The assemblage is dominated by pelagic cephalopods. Among the most common bivalves, Pterochaenia fragilis is tentatively interpreted as either epipelagic or more likely epibyssate. Eumetabolotoechia multicostata, a pedunculate rhynchonellid that also occurs in samples from the upper stratigraphic range of this community,2 commonly forms dense accumulations in dark-gray shales stratigraphically higher in the sections, and it is likely that individuals of this species were moored to the substrate. The presence of pedicle borings on valves further demonstrates that some individuals were attached to other individuals of multicostata (see also discussions of the ecology of this brachiopod genus in Thompson and Newton [1987] and Boyer and Droser [2009]). Epipelagic specimens of Eumetabolotoechia multicostata are not known. We thus infer

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2Formerly known as Leiorhynchus; this taxonomy was revised by Paul Sartenaer.
that *Eumetabolochoecia multicostata* and *Pterochaenia fragilis* were epibenthic rather than epipelagic. If our interpretation is correct, the Cephalopod-*Pterochaenia* community reflects a mixed pelagic-benthic fauna.

**Pterochaenia-Eumetabolotoechia Community**

Although many taxa in this community occur in the lower Cephalopod-*Pterochaenia* assemblage discussed above, the frequency of cephalopods is much lower (~2.16%, or an order of magnitude lower than that of the underlying Cephalopod-*Pterochaenia* community; Table 2). Many benthic species in this community also occur in the deeper-water Cephalopod-*Pterochaenia* community; the most common of these are pedunculate brachiopods (*Eumetabolotoechia multicostata* and a few specimens of *Emanuella subumbona*) and epibysseate bivalves, most notably *Pterochaenia fragilis*. These two ecological categories taken together account for over 90% of the individuals in this community. Minor frequencies of intraunal deposit-feeding bivalves (*Nuculoidea* sp.) and reclining brachiopods represent the lowest stratigraphic occurrences of these groups in our study. Most of the sediments associated with this community show some traces of bioturbation (usually small, well-defined, horizontal burrows) of 1.5–2.0 mm diameter, implying that the bottom waters were at least dysoxiaerobic (and probably aerobic). Such burrows do not occur in the Cephalopod-*Pterochaenia* community. The introduction of new species and ecological categories in the *Pterochaenia-Eumetabolotoechia* fauna augments species richness and ecological diversity considerably, with means of 8.33 species and 5.0 ecological types per sample. This greater diversity suggests a shift in environmental conditions relative to those of the mixed pelagic-benthic Cephalopod-*Pterochaenia* community. Because of the dominance of pedicle-attached and epibysseate suspension feeders, the equitability of the *Pterochaenia-Eumetabolotoechia* community is less than that of most of the other assemblages.

The *Pterochaenia-Eumetabolotoechia* community likely reflects a pioneer fauna developed as the substrate initially became favorable for benthic settlement. The grain size of sediments associated with this community (Table 2) is lower than that of the underlying Cephalopod-*Pterochaenia* community, but the mean organic content declines slightly, from 3.0% to 2.8%. The contrast between the Cephalopod-*Pterochaenia* and *Pterochaenia-Eumetabolotoechia* communities appears constant, but the mean organic content declines slightly, from 3.0% to 2.8%. The contrast between the Cephalopod-*Pterochaenia* and *Pterochaenia-Eumetabolotoechia* communities is consistent with a threshold or trigger effect, in which small environmental changes may have catalyzed large ecological and taxonomic shifts in faunal composition. One such environmental change between these two communities may have been an increase in oxygenation.

**Eumetabolotoechia Community**

The pedunculate brachiopod *Eumetabolotoechia multico- stata* attains peak abundance in this community, where it constitutes nearly two thirds of the individuals (Table 2). Some beds of dark-gray shale are densely covered with this assemblage, whereas other bedding surfaces are almost barren, a pattern we interpret as reflecting opportunistic settlement behavior. Pedicle-attached brachiopods, especially *Eumetabolotoechia multico- stata* and small numbers of *Emanuella subumbona*, form 77% of the fauna. Other accessory taxa, at levels of 6% to 7% each, include epibysseate bivalves (mainly *Pterochaenia fragilis*), reclining brachiopods such as *Arcuaminetes scitulus* (formerly *Devonochonetes scitulus*) and *Spinulicosta spinulicosta*, and deposit-feeding nuculoids. *Nuculoidea* sp., the most common burrowing deposit feeder, was a shallow-burrowing, asiphonate bivalve. Other ecological categories are either sparsely represented or unrepresented. Species richness and ecological diversity continue to be comparatively low, with means of 8.79 species and 5.21 ecological categories, respectively. The dominance of a few pedicle-attached suspension feeders results in an equitability that is the lowest of all eight communities in the data set.

The *Eumetabolotoechia* community is usually underlain by, and often succeeded by, the *Pterochoenia-Eumetabolotoechia* community. In fact, most taxa in the *Eumetabolotoechia* community were already present in the *Pterochaenia-Eumetabolotoechia* fauna; the community transition mostly involves changes in the frequencies of these fossils (e.g., Figs. 5 and 8). The *Eumetabolotoechia* community occurs in distinctly coarser rocks with thicker beds, more bioturbation, and slightly lower organic content (Figs. 3, 4, and 10). These interrelated changes suggest a pattern of decreasing depth, with an associated increase in agitation and a shift toward firmer substrates.

**Eumetabolotoechia-Ambocoelia Community**

This assemblage represents a higher species richness community closely related to the *Eumetabolotoechia* community (Table 2), as is documented by the multivariate analyses discussed above (Figs. 5 and 8) and by recurring stratigraphic juxtapositions of these two assemblages. The *Eumetabolotoechia-Ambocoelia* community invariably succeeds the *Eumetabolotoechia* community stratigraphically (Figs. 3, 4, and 10). Pedunculate brachiopods, typically *Eumetabolotoechia multico- stata* and *Ambocoelia umbonata*, account for nearly 60% of the fauna. This represents a significant decline from the 77% in the *Eumetabolotoechia* community. Reclining suspension feeders—*Arcuaminetes scitulus* and a few individuals of *Mucrospirifer mucronatus*—constitute 21% of the fauna, which is also significantly higher than in the *Eumetabolotoechia* community. Burrowers, both deposit and suspension feeding, are also present. Deposit-feeding burrowers are represented by forms that lived at various depths. *Nuculoidea* sp. was a shallow burrower, whereas *Nuculites oblongatus*, which becomes common in this community for the first time, has a shell shape signaling the presence of siphons and a deeper burrow. Epibysseate bivalves decline to about 3%, a downshift caused by decreasing *Pterochaenia fragilis*.

High species richness values and ecological diversities appear for the first time in this community, averaging 11.9 and
6.21 species and ecological categories, respectively. Likewise, the equitabilities increase, as the *Eumetabolotoechia-Ambocoelia* community consists of a greater number of taxa and ecological categories than do the communities occurring stratigraphically lower in the sections. Sediments associated with this community resemble those of the *Eumetabolotoechia* suite, except that organisms are sparser, with an average of 2.4 wt%, as compared with 2.7 wt%. We infer that the *Eumetabolotoechia-Ambocoelia* assemblage reflects a more agitated, and possibly slightly more oxygenated, habitat than the underlying *Eumetabolotoechia* and other communities.

**Emanuella Community**

Multivariate analyses demonstrate that this peculiar community relates most closely to the *Eumetabolotoechia* fauna. These communities are associated, and they share similar ecological roles, species, diversity, and equitability (Figs. 3, 4, and 10; Table 2). Pedicle-attached suspension feeders dominate, but *Emanuella subbona* is much more abundant than *Eumetabolotoechia multicosata*. Compared to the *Eumetabolotoechia* community, reclining brachiopods—mostly *Arcuaminetes scitulus* and *Mucrospirifer mucronatus*—are more frequent, but burrowing deposit feeders and epibyssate bivalves are rarer. The *Emanuella* community is associated with silty shales, in contrast to the *Eumetabolotoechia* community, which occurs in shales. Organic content is slightly less abundant than in the rocks of the *Eumetabolotoechia* community. These lithologic differences suggest that the *Emanuella* community occupied a slightly shallower and more agitated habitat than the *Eumetabolotoechia* community.

**Arcuaminetes-Eumetabolotoechia Community**

The statistical data and stratigraphic distribution indicate that this community most closely resembles the *Eumetabolotoechia-Ambocoelia* fauna (Figs. 3, 4, 5, 8, and 10). Samples of the *Arcuaminetes-Eumetabolotoechia* community are usually underlain by the *Eumetabolotoechia*, *Eumetabolotoechia-Ambocoelia*, or *Arcuaminetes-Ambocoelia* assemblages, although in one part of the Gulf Road section, the *Arcuaminetes-Eumetabolotoechia* fauna follows that of *Emanuella*. Reclining brachiopods, especially the ubiquitous *Arcuaminetes scitulus*, along with some *Mucrospirifer mucronatus*, make up 43% of the assemblage (Table 2). Pedunculate brachiopods—*Arcuaminetes multicosata*, *Ambocoelia umbonata*, and *Emanuella subbona* (in decreasing order)—constitute 37% of the individuals. About 10% of the fauna consists of the deposit-feeding bivalves *Nuculoida* sp. and *Nuculites oblongatus*. Burrowing suspension feeders, notably lingulids, are consistent accessories in most samples in this community.

Taxonomic and ecological diversity exceed those of the *Eumetabolotoechia-Ambocoelia* assemblage. The *Arcuaminetes-Eumetabolotoechia* fauna occurs in gray shale and silty shales that are generally coarser than those of the associated *Eumetabolotoechia* and *Eumetabolotoechia-Ambocoelia* assemblages. Organic contents are lower than in the sediments of the *Eumetabolotoechia* community, but they are comparable to those of the *Eumetabolotoechia-Ambocoelia* community. The inferred environmental changes include decreasing depth and increasing agitation.

The abundance of the small reclining brachiopod *Arcuaminetes scitulus* deserves special note. Small recliners such as *Arcuaminetes scitulus* are often considered characteristic of soft soupy substrates in quiet water. In fact, suspension-feeding brachiopods require some water movement to provide fresh food and oxygen and to remove wastes. The chonetid shell must have lain close to the substrate and the boundary layer between the substrate and seawater. Current velocity decreases exponentially as the seafloor is approached. Consequently, a certain minimal amount of agitation is required to enable these small reclining animals to survive. This is wholly consistent with the distribution of these small reclining taxa in the Cardiff Member communities. *Arcuaminetes scitulus* is either completely absent or rare in the deepest and quietest water benthic communities (*Pterochaeinia-Eumetabolotoechia* and *Eumetabolotoechia*). The species appears only after a critical amount of agitation is reached.

**Arcuaminetes-Ambocoelia Community**

This fauna is closely linked to, and is interbedded with, the *Arcuaminetes-Eumetabolotoechia* and *Mucrospirifer-Ambocoelia* communities (Figs. 3–5, 8, and 10). Reclining suspension feeders, mostly *Arcuaminetes scitulus*, along with some shells of *Mucrospirifer mucronatus* and *Spinulicosta spinulicosta*, lead the roster of ecological categories and represent 58% of the individuals (Table 2). Next are pedunculate brachiopods, largely *Ambocoelia umbonata* with rare *Emanuella subbona*, which comprise 21% of the assemblage. Burrowing deposit feeders are diverse, but they are slightly less abundant than in the *Arcuaminetes-Eumetabolotoechia* community. The small cohort of burrowing suspension feeders includes forms that occur also in the deeper-water communities. Species richness values and ecological diversities of the *Arcuaminetes-Ambocoelia* community slightly exceed those of *Arcuaminetes-Eumetabolotoechia*, but the relatively high abundance of a few reclining suspension feeders leads to lower equitabilities in this assemblage. Lithologies associated with the *Arcuaminetes-Ambocoelia* community are shaly siltsstones and silty shales that are coarser, thicker bedded, and more highly bioturbated than those of the *Arcuaminetes-Eumetabolotoechia* fauna. Organic contents of the three relatively shallow-water communities in the Cardiff Member are quite similar. Thus, the *Arcuaminetes-Ambocoelia* assemblage almost certainly occupied shallower, higher-energy habitats than the *Arcuaminetes-Eumetabolotoechia* community.

**Mucrospirifer-Ambocoelia Community**

This group of organisms occurs in the coarsest sediments in the study—silty shales to siltstones—and represents the most
shallow-water fauna present (Figs. 3 and 4). However, the lithologies and sedimentary structures indicate gentle to moderate (rather than high) amounts of wave and current agitation below normal wave base.

Reclining brachiopods (45%) and pedunculate brachiopods (37%) form the trophic nucleus of this community (Table 2). The most common taxa in this assemblage, e.g., Ambocoelia umbo-nata, Mucrospirifer macroratus, and Arcuaminetes scitulus (in decreasing order of abundance), are also known from the closely associated Arcuaminetes-Eumetabolotoechia and Arcuaminetes-Ambocoelia communities (Figs. 5, 8, and 10). The large spiriferid Spinocyrtia granulosa is a common accessory in this fauna; this is the lowermost stratigraphic occurrence of significant numbers of Spinocyrtia granulosa. Burrowing deposit feeders continue to decline, a trend probably related with the higher agitation and lower amounts of organic matter. Large epibysate bivalves, such as Actinopteria boydi, Cornellites fasciculata, Gosseletia triquetra, and Leiopteria sp., and endobysate clams such as Goniophora hamiltonensis, Grammysia bisulcata, and Modiomorphia spp., show increased abundance. Maximum diversities—both taxonomic and ecologic—are attained in some samples of the Arcuaminetes-Ambocoelia and Mucrospirifer-Ambocoelia faunas. However, taxonomic and ecological evenness are higher in the Mucrospirifer-Ambocoelia community.

Cluster Analysis of Trophic Structures

Taxonomic and ecological structures of the communities are highly correlated, as is strongly indicated in the cluster analysis of the 81 samples for the nine ecological categories (Fig. 13). This dendrogram derivs from the unweighted-pair-group method on a matrix of correlation coefficients. The communities can be divided into four major types with respect to the ecological data:

1. Samples 1–9 belong to the Cephalopod-Pterochaenia community, characterized by a very low species richness and mixed pelagic-benthic assemblage.
2. The Pterochaenia-Eumetabolotoechia community includes samples 10, 12, and 13. This is a low-species-richness pioneer fauna that mostly includes pedicle-attached brachiopods and small epibysate bivalves. These organisms seem to appear as soon as the seafloor becomes generally suitable for occupation by bottom dwellers.
3. The samples ranging from numbers 11 to 55 on the dendrogram are mostly from the Ambocoelia and the Emanuella communities. All of these samples are dominated by pedicle-attached brachiopods. Species richness values and equitably range from low to moderate. Within this large group, the samples within the Eumetabolotoechia community tend to separate from those of the Eumetabolotoechia-Ambocoelia and Emanuella communities, which are more diverse, both ecologically and taxonomically.
4. A large cluster extends from samples 27 to 29 on the dendrogram. These samples are grouped in the Arcuaminetes-Eumetabolotoechia, Arcuaminetes-Ambocoelia, and Mucrospirifer-Ambocoelia communities. Pedicle-attached and reclining suspension feeders form the trophic core for all of these assemblages. Maximum taxonomic and ecological diversities are observed in these faunas.

A matrix of correlation coefficients among the nine ecological roles was calculated for 72 samples from the seven benthic communities (Table 4). The magnitudes for the correlations that differ significantly from a population value of nil, i.e., no correlation at all, equal 0.232 and 0.302 at the 0.05 and 0.01 probability levels. Most (53%) of the observed correlations are not statistically significant. The correlation with the highest magnitude is –0.906 for the pedicle-attached versus reclining suspension feeders. Thus, these two categories are inversely related, as would be expected from the composition of the communities. Many Cardiff Member recliners—particularly common groups such as chonetids—had relatively low profiles with respect to the sediment. Therefore, these animals could not become well established until critical amounts of gentle agitation were attained, in order to supply them with food and oxygen and to remove waste materials from near the substrate. Most pedicle-attached brachiopods filtered water higher above the substrate, where more water movement would have been available in the quieter habitats. In addition, the fine sediments of the deeper communities could easily have fouled the shells of small recliners such as Arcuaminetes scitulus. The correlation coefficient with the next highest magnitude, a value of 0.469 between reclining filter feeders and surface grazers, reflects mainly the rarity of both groups in the finest sediments of the Cardiff Member. Here, one category only explains 22% of the variance of the other (i.e., correlation coefficient squared). Therefore, except for the pedicle-attached and reclining brachiopods, the various ecological categories seem to be basically independent of each other, as would be predicted from diversity theory.

Correlations between the taxonomic and ecological diversities and between the taxonomic and ecological equitability are all high; these range from 0.808 to 0.858 (Fig. 14). Thus, these pairs of parameters consistently track one another, as can be inferred from the annotations on the communities. Equitabilities in our samples are largely independent of the diversities, and vice versa. Contrary to popular belief, communities with low species richness may have taxa that are evenly distributed; they are not necessarily dominated by a single species. To some extent, the converse is also true for the Cardiff Member data. For example, the Arcuaminetes-Ambocoelia community is rich in taxa, yet Arcuaminetes scitulus makes up almost half of the individuals.

SUMMARY OF VERTICAL ECOLOGIC AND TAXONOMIC CHANGES

Progressive changes in communities of the lower Hamilton Group can be summarized by tracing various paleoecological parameters from the base to the top of the stratigraphic successions. These parameters include species richness and equitability,
Figure 13. Dendrogram for 81 samples. The data matrix consists of percentages of the nine ecological categories in each sample. The clusters were extracted by the unweighted-pair-group method on a matrix of correlation coefficients. Stratigraphic locations of samples are given in Figures 3 and 4.
Species Richness and Equitability

As expected from the previous discussion of the communities, both taxonomic richness and ecological diversity increase with progressively younger beds in both stratigraphic sections (Fig. 15). The stratigraphically highest samples at Swamp Road (including portions of the Mucrospirifer-Ambocoelia and Arcuminetes-Ambocoelia communities) exhibit slightly lower species richness values, representing a slight reversal of the overall trend of increasing species richness in the sections. For both sections, species richness and ecological diversity are highly correlated. The overall environmental changes of decreased depth
Figure 15. Plots of taxonomic and ecological diversity for the two sections. (A) Species richness per sample; (B) number of ecological categories per sample. Both figures show increases upward at Swamp Road. The samples are designated by the community types discussed in the text. Stratigraphic locations of samples are given in Figures 3 and 4. The species codes are listed in Table 1.
and increased sedimentary grain size, agitation, and oxygenation favor greater diversities.

Equitabilities are more independent of stratigraphic position. The most evenly distributed communities are those of Cephalopod-Pterochaenia, with low species richness and ecological diversity, and Arcuaminetes-Eumetabolotoechia, with higher species richness and higher ecological diversity. The Eumetabolotoechia fauna, highly dominated by the pedicle-attached brachiopod E. multicostata, yields the lowest equitabilities. Low equitabilities also characterize the Pterochaenia-Eumetabolotoechia and Emanuella communities. This reflects the fact that these deep-water communities are basically pioneer epifaunal assemblages that developed when conditions first became favorable for the establishment of benthic organisms. As depth decreased in both stratigraphic sections, the increased agitation and oxygenation favored more numerous taxa and ecological categories that exploited more resources.

**Taxonomic Composition**

Vertical distributions of some of the dominant taxa appear in Figure 16. Several generalizations can be made. Virtually all common Hamilton Group species are protoan organisms with broad environmental tolerances, and they span many types of communities. Some organisms are concentrated in one or several assemblages—for example, orthocones, Emanuella subumbona, and Pterochaenia fragilis—but others range more widely, such as Eumetabolotoechia multicostata, Arcuaminetes scitulus, Mucrospirifer mucronatus, and Ambocoelia umbonata. In some instances, species composition and abundance can fluctuate widely between adjacent samples within a stratigraphic section, especially at transitions between different communities; however, in most cases, less dramatic variation occurs during transitions. On average, changes between communities explain more of the variation in the data than changes within assemblages.

Among abundant species, Ambocoelia umbonata, Arcuaminetes scitulus, Eumetabolotoechia multicostata, Mucrospirifer mucronatus, and Pterochaenia fragilis seem controlled more by factors related to grain size than by organic content, even though both parameters contribute significantly. Conversely, Nuculoides sp. and large orthocones are more closely correlated with organic content. This was expected for Nuculoides because of its deposit-feeding habits. Likewise, the orthocone frequency declines drastically from the Cephalopod-Pterochaenia community to the Pterochaenia-Eumetabolotoechia community. The distribution of Emanuella must be influenced by parameters other than grain size and organic content, based upon the regressions for these variables, which are not significant.

**Ecological Roles**

Ecological categories exhibit the following major systematic vertical changes in the two stratigraphic sections (Figs. 17 and 18):

1. Swimming predators abound in the Cephalopod-Pterochaenia community at the base of the Gulf Road section, but frequencies of nektonic predators decline sharply in all other communities.
2. Following establishment of benthic faunas, the dominant ecological categories vary among three groups of epifaunal suspension feeders. In the deepest waters, small epibysate bivalves, notably Pterochaenia, predominate. Pedicle-attached brachiopods, especially Eumetabolotoechia multicostata, become most abundant in the Eumetabolotoechia and associated faunal suites. Communities in shallower water exhibit an inverse relation between reclining and pedicle-attached brachiopods, in which recliners are most frequent in the shallowest sediments in the two sections. Higher agitation is apparently required to provide adequate water circulation close to the seafloor for small recliners such as Arcuaminetes scitulus.
3. Benthic assemblages of deeper waters are predominantly epifaunal. Burrowing deposit feeders commonly appeared at shallow depths below the substrate in the Eumetabolotoechia community, and greater burrowing depths were penetrated when the Eumetabolotoechia-Ambocoelia and Arcuaminetes-Eumetabolotoechia communities occupied the area. Burrowing deposit feeders began to decline in shallower waters as sediments progressively had decreasing amounts of organic matter and coarser sediment grain sizes.
4. Endobyssate and burrowing suspension feeders are not abundant. Both groups were most frequently collected in the faunas of the shallower lithofacies, ranging from Eumetabolotoechia-Ambocoelia to Arcuaminetes-Ambocoelia for the burrowers and to Mucrospirifer-Ambocoelia for the endobyssates. Peak abundances of burrowing and endobyssate suspension feeders coincided with the decline of burrowing deposit feeders.
5. Surface-dwelling gastropods, believed to have grazed on plants, occurred most commonly in comparatively shallow regions with diverse associated taxa.
6. Surface collectors, such as trilobites and hyolithids, were erratically distributed as minor accessories of varied communities. Admittedly, this ecological category is highly variable, and a range of feeding habits is included—for example, deposit feeding, scavenging, and predation. This trophic role accounts for no more than 1.0% of the individuals in any community.

**TESTING PROPOSALS OF COMMUNITY STABILITY AND COORDINATED STASIS**

Hamilton Group faunas are frequently cited as paradigmatic of the pattern of long-term community stability termed coordinated stasis (Brett and Baird, 1995; Brett et al., 1996; Schopf, 1996), with several workers referring to these assemblages as the
“type” example of coordinated stasis. However, this intriguing proposal—that some marine evolutionary ecological units (EEUs of Boucot [1983] and Sheehan [1996]) exhibit long-term stability on a scale of millions of years—has been discussed more far widely than it has actually been tested, even now. Presence-absence data and taxonomic ranges of common taxa do not suffice to demonstrate coordinated stasis (McKinney et al., 1996; Schopf and Ivany, 1997). Instead, quantitative analysis of large samples distributed over a significant temporal interval must be undertaken (see also Bennington and Bambach, 1996). In particular, the stability of rare taxa (and their variability) has not previously been explored adequately in general (Boucot, 1996; McKinney et al., 1996; Ivany, 1999), let alone within the faunas of the lower Hamilton Group.

This study provides both documentation and analysis of paleoecological structure and taxonomic composition for the lower Hamilton Group—an interval necessary for rigorous tests of whether the communities themselves, rather than just the taxa, range through this entire stratigraphic unit and the time it encompasses. It provides a first detailed look at community stability in this lower interval, integrating taxa that are moderately rare (>1% of the fauna). Taken together with the few other quantitative Hamilton Group studies (e.g., Savarese et al., 1986; Brower et al., 1988; Brower and Nye, 1991; McCollum, 1991; Bonuso,
2001; Bonuso et al., 2002a, 2002b), we can make some initial inferences about the structure and temporal persistence of Hamilton Group marine communities.

Our data reveal a few—but not all—lower Hamilton Group communities with counterparts in upper Hamilton Group faunas. This means that stability is indicated for some associations but not others. For instance, the *Arcuaminetes-Ambocoelia* community and the *Eumetabolotoechia* community apparently occur higher in the Hamilton Group, as described by other workers (cf. Savarese et al., 1986; McCollum, 1991). However, the other six communities we recognized herein do not clearly recur with the same array of taxa in other studies. Abundant and common taxa within these other associations are known from higher in the Hamilton Group, and hence range through (Brett and Baird, 1995), but the internal structure of later associations, as described in Savarese et al. (1986) and McCollum (1991), is incongruent with that of our communities.

In coordinated stasis, and particularly in the ecological locking model, these communities should recur temporally and

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Zambito et al. (2012) lumped different “chonetids” and “leiorhynchids” together and excluded rare taxa, so some further work will be necessary to demonstrate which of their EEU1s parallel those we describe quantitatively and ecologically here.
should prove statistically similar throughout the temporal interval. As Ivany has pointed out, frequencies of taxa may vary, but the associations ought to recur. This pattern would be predicted in both the environmental tracking and ecological locking models—and it would especially be an integral prediction of ecological locking. Our information from the lower Hamilton Group suggests that this is not supported by currently available data. In that regard, the Hamilton faunas may resemble those documented by Patzkowsky and Holland (1999, p. 301) from the Middle to Upper Ordovician of the Nashville Dome. Their results indicate that Ordovician communities “were not tightly integrated in their structure, but rather were fluid with species and genera moving in and out of communities in response to local changes in environmental conditions.” Further rigorous quantitative studies of upper Hamilton Group faunas should reveal whether, as in the Ordovician study, loosely integrated communities characterize the duration of Hamilton Group deposition.

Our study also yielded several quantitative results for the lower Hamilton Group that, in themselves, pose further questions for the hypothesis of ecological locking. First, these Marlcellus Subgroup communities exhibit low levels of integration and correlation among the constituent species, in contrast to the

Figure 17. Plots of ecological categories for the two sections. The samples are designated by the community types discussed in the text. Stratigraphic locations of samples are given in Figures 3 and 4. The species codes are listed in Table 1. (Continued on facing page).
predictions of ecological locking. Second, rapid swings in the abundance of taxa occur in adjacent beds, with no apparent corresponding shifts in lithology or other environmental indicators. Ecologic categories of lower Hamilton Group taxa in our study show low correlations (53% of observed correlations are not statistically significant). In sum, the lower Hamilton Group faunas analyzed here reflect only loosely structured associations, even though the individual communities are statistically discrete—results that seem not to suggest that the faunas are tightly integrated as has been predicted by some (but not all) coordinated stasis proponents.

These conclusions resemble those reached by Tang and Bottjer (1996), who inferred that Jurassic paleocommunities in western North America also fail to show evidence in support of the ecological locking model. However, Tang and Bottjer’s conclusions came solely from presence-absence data or data on dominant taxa; Schopf and Ivany (1997) therefore correctly pointed out that Tang and Bottjer had not conducted all the tests necessary to probe the question. Our study, with a far richer abundance database, now reveals that with appropriate tests of Hamilton Group faunas, 4–6 m.y. persistence of ecologically locked and tightly structured communities is still not indicated.
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Figure 18. Relative depth of Hamilton Group communities as indicated by ordination results.
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