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Statistical testing of community patterns: uppermost Hamilton Group, Middle Devonian (New York State: USA)

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Abstract

We present an extensive and rigorously controlled quantitative paleoecological study within an interval of inferred coordinated stasis. This Middle Devonian Hamilton Group study completes a 20-yr project by providing data within the unresolved upper Hamilton Group section. Together with other rigorously controlled studies, these data sets have the potential to address the larger question of coordinated stasis in the fossil record.

We collected data from the Windom Member, Moscow Formation (uppermost Hamilton Group), to test different statistical approaches to define paleocommunities. We evaluate various techniques, including non-parametric multidimensional scaling and agglomerative hierarchical clustering to decipher community patterns. Additionally, we advocate regular use of cluster significance testing along with ANOSIM (i.e. analysis of similarities) when examining ecological data. Together these techniques test the significance of sample groups more rigorously than conventional testing (e.g. discriminant analysis or analysis of variance (ANOVA)). Our results indicate that communities within this upper Hamilton Group interval exhibit variable taxonomic membership within a relatively stable ecological structure. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Hamilton Group; Middle Devonian; paleoecology; statistical methods

1. Introduction

The Middle Devonian Hamilton Group of New York State has captivated geologists and paleontologists for nearly 200 yr with its beautifully preserved and richly diverse fossils. Vanuxem (1840), one of the first to study this rock unit, introduced

the Hamilton Group to the scientific community through his work on regional stratigraphy. In the early 1900s, a number of studies on stratigraphy and associated facies were published (e.g. Cleland, 1903; Cooper, 1930, 1933). Cooper (1957) and Rickard (1975) later revised this work. By the 1970s, researchers began to take advantage of the Hamilton Group's excellent stratigraphic framework by embarking upon comparative facies analyses and paleoecological studies (Grasso, 1970, 1973; Thayer, 1974; Bowen et al., 1974; Brett, 1974; Selleck and Hall, 1977).

During this time, the speciation model of punc-

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tuated equilibria (Eldredge and Gould, 1972) was derived in part from observations of the Hamilton Group trilobite *Phacops rana*. Although this work as pivotal, the Hamilton Group was nonetheless considered scientifically underdeveloped with respect to paleoecology and paleoenvironmental studies especially in comparison to other classic fossiliferous sites (Brett, 1986). With this in mind, Brett and Baird, and others have established an outstanding stratigraphic and paleoenvironmental framework for the Hamilton Group (e.g. Baird and Brett, 1983; Brett and Baird, 1985, 1986; Brett, 1986; Landing and Brett, 1991).

Brower et al. (1978) also helped to expand Hamilton Group studies by contributing one of the first quantitative paleoecological analyses emphasizing faunal dynamics of a shallowing-upward cycle in the lower Hamilton. Brower's continuing research (Brower, 1987; Brower and Nye, 1991) and contributions of other workers (e.g. Savarese et al., 1986; McCollum, 1991; Lieberman et al., 1995; Newton et al., 2001) served to document faunal and ecological patterns within the lower and middle Hamilton Group, but quantitative data from the uppermost Hamilton intervals remain unresolved.

Hamilton Group paleoecological studies continued with the landmark proposal of coordinated stasis (Brett and Baird, 1992, 1995). This paleoecological and evolutionary model describes a pattern of co-occurring taxa that display a high degree of persistence and experience little morphological change for upwards of 3–7 Myr (Brett et al., 1996). These intervals of persistence are bracketed by contrasting intervals of simultaneous, abrupt, faunal turnover involving extinction of generally 70% or more of the original taxa (Brett et al., 1996).

Two mechanisms proposed to account for the faunal stability of coordinated stasis are the environmental tracking model and the ecological locking model. The environmental tracking model holds that taxa migrate with a preferred environment as it shifts in space and time (Brett and Baird, 1995; Bennington and Bambach, 1996). Morris (1995) believed that environmental tracking failed to account for the observed degree of coordinated stability and change across unrelated

taxa and proposed the ecological locking model. This model suggests that interspecific interactions introduce some degree of stability to the community; consequently, faunas can tolerate modest fluctuations in the environment.

In their original paper, Brett and Baird (1995) compiled data on the occurrence of species from the Silurian through mid-Devonian of New York, Pennsylvania, and Ontario. The Middle Devonian data set included counts of carryover and hold-over species and comparisons of common taxa within congruent facies. Brett and Baird (1995) concluded that 80% of species occur throughout the 5–6-Ma Middle Devonian, Hamilton–Tully interval and display minor or no net morphological change. Likewise, both common and rare taxa in coral-rich beds persist in similar rank abundances throughout the Hamilton Group (Brett and Baird, 1995).

The proposal of coordinated stasis engendered a wave of research on patterns of stability within the fossil record, before a quantitative test of stability patterns had fully been analyzed temporally within the Hamilton Group (e.g. DiMichele and Phillips, 1995; Morris, 1996; Tang and Bottjer, 1996; Patzkowsky and Holland, 1997; Ivany, 1997; Huynh et al., 1999; for a fuller overview, see Ivany and Schopf, 1996 and references herein). To date, within Hamilton Group studies, quantitative testing has been accomplished in the lower Hamilton (i.e. Newton et al. (2001)) and in the middle Hamilton (i.e. Savarese et al., 1986; Brower and Nye, 1991; McCollum, 1991) but uppermost Hamilton faunas have remained unresolved. Here, we present data from the uppermost Hamilton Group to complement these earlier works and to complete the picture of faunal stability and change within this important interval.

A crucial question, therefore, is whether community patterns, as revealed by quantitative paleoecological data, reflect stability throughout the temporal range of the Hamilton Group. To approach this question one needs consistent statistical methodologies in order to promote comparisons among studies. Quantitative analyses throughout the Hamilton, with standardization of methodologies, allow resolution of community

structural patterns throughout the Hamilton Group. Coordinated stasis raises interesting questions for both ecological and evolutionary theory. If coordinated stasis occurs, it implies that community patterns are stepwise and pulsed. If coordinated stasis is not occurring, then taxa might form transient, mosaic associations that might interact, but they are not synchronous in their ecological and evolutionary patterns (Goodall, 1954; Gauch, 1982; Etter, 1999). The potential significance of either outcome warrants aggressive large-scale statistical testing of communities throughout the Hamilton Group.

This paper is an integral part of a rigorous test of coordinated stasis throughout the Hamilton Group, because it provides the missing piece of quantitative paleocommunity data from the uppermost Hamilton interval (i.e. the Windom Member, Moscow Formation). We propose a consistent statistical methodology appropriate for testing stasis in well-preserved fossiliferous faunas such as the Hamilton Group. This approach not only allows us to decipher community patterns but also affords meaningful comparisons of quantitative paleocommunity data throughout this Hamilton interval, considered the paradigmatic example of coordinated stasis (Brett and Baird, 1995).

2. Methods for characterizing communities

2.1. Sampling strategy

Fossil collections were taken from an 11-m coarsening-upward cycle within the Windom Member of the Moscow Formation (Fig. 1). Forty-five samples were collected at 20-cm vertical spacing (Fig. 2). The sampling protocol involved uncovering bedding planes and identifying all common and rare taxa until 300 specimens were counted. Shell and trilobite fragments identifiable at the species level were included in these counts, whereas presence–absence of trace fossils, crinoid stems, bryozoans, and wood fragments was noted in the field but not included in multivariate analyses. Rarefaction curves for these data demonstrate that this 300 count captures an adequate

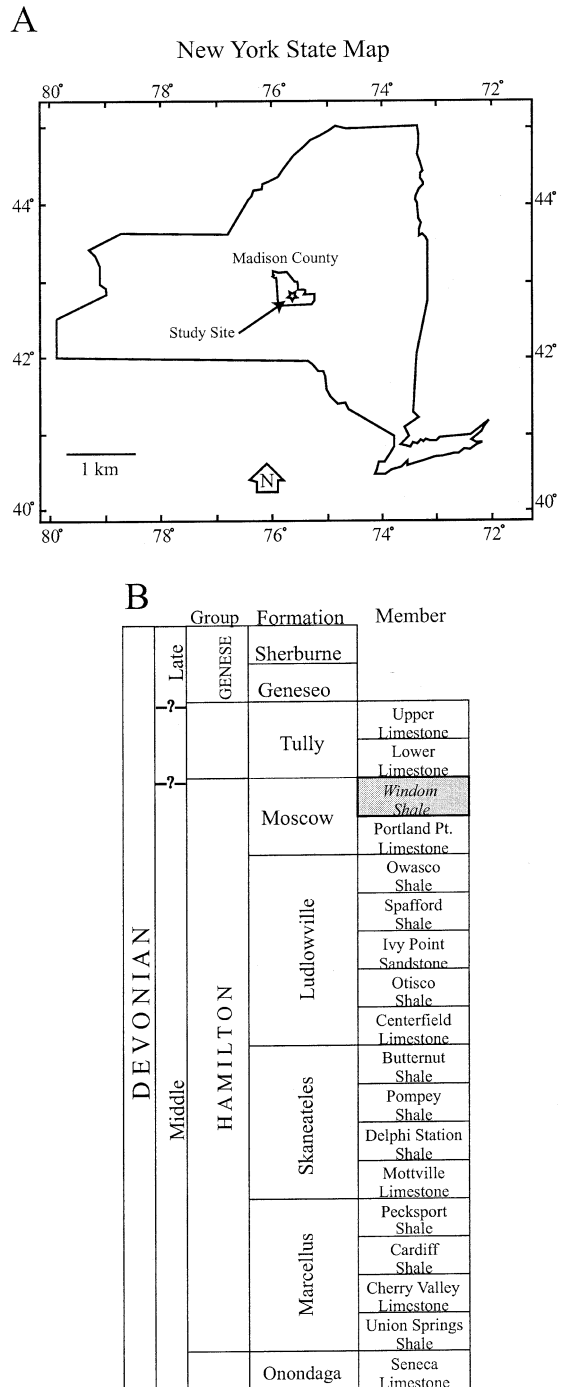
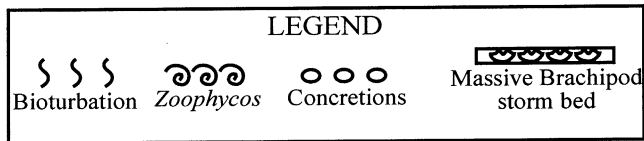
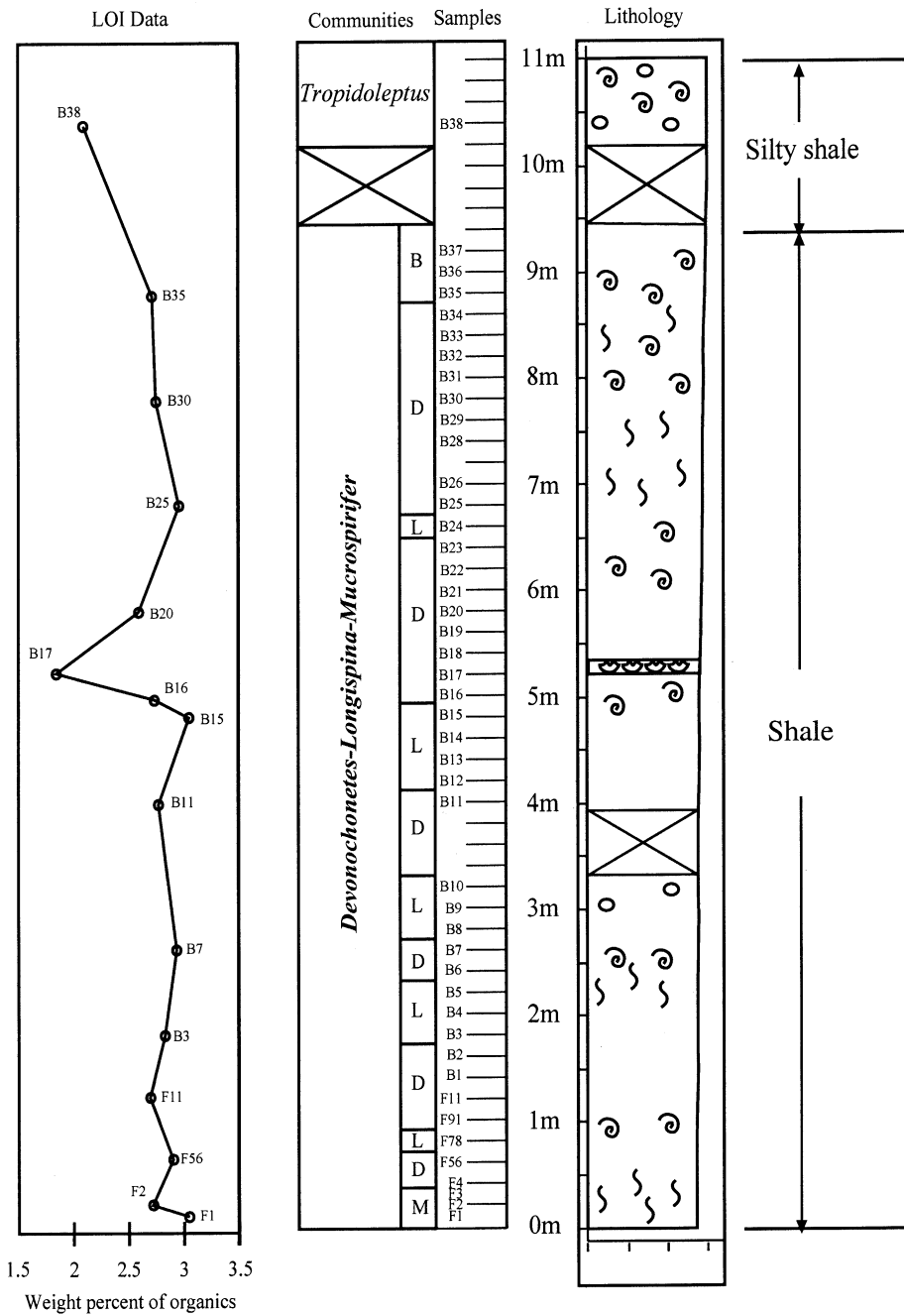


Fig. 1. (A) Index map. (B) Stratigraphic section of the Hamilton Group in Morrisville area, Madison County, New York.



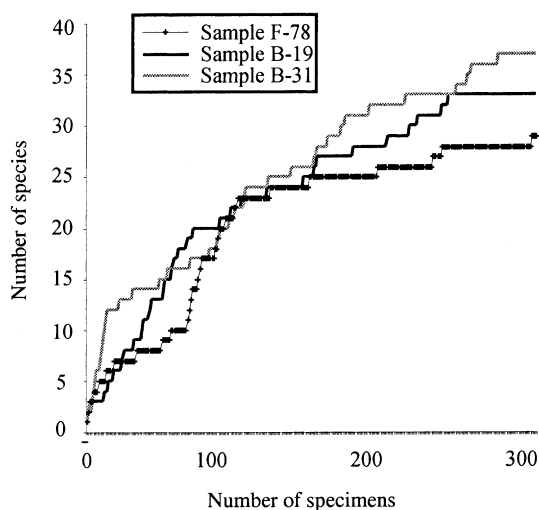


Fig. 3. Rarefaction curve for three samples. Curves are listed from stratigraphic bottom to top: F-78, B-19, and B-31.

number of species (Fig. 3). At vertical increments of 1 m, replicate samples were also collected from sites approximately 4 m laterally along the same bedding plane. Samples that lie in the same bedding planes were compared to establish the lateral reproducibility of faunal composition.

2.2. Statistical analysis

When attainable, relative abundance data are known to include more information in a study in comparison to presence–absence data (Sneath and Sokal, 1973; Gauch, 1982; Rahel, 1990). Quantitative abundance data are obtainable at this outcrop and therefore are used to describe faunal composition. Absolute counts were standardized to percentages prior to statistical analysis (see Appendix 1). Rare taxa generally exhibit high rates of turnover in both ecological and geological time (Boucot, 1990; Stanley, 1990; Eldredge, 1992; Gaston, 1994; Lawton et al., 1994; Sepkoski, 1994; Boucot, 1996; McKinney et al., 1996). According to binomial sampling probabilities, counting 300 specimens gives a

95% probability of finding a species that makes up 1% of the individuals (Davis, 1986). Consequently, any species comprising less than 1% of each sample were deleted due to the possibility of sporadic occurrence and unreliability. All taxa constituting over 1% of a sample were retained in order to contribute temporal and spatial variation in this analysis. The data set includes 67 taxa (Table 1).

Multivariate statistics, such as ordinations and clustering, establish a visual picture of samples and species groups within a data set. Both techniques should be employed together in paleoecology because clustering and ordinations are subject to different sources of distortion (Sneath and Sokal, 1973; Gauch, 1982; Brower and Nye, 1991; Shi, 1993; Ivany, 1999; Newton et al., 2001). Clustering preserves small-scale similarities at the expense of large-scale distortion; conversely, ordinations retain large-scale patterns at the cost of small-scale distortion. We selected the unweighted pair group method (UPGM) for agglomerative hierarchical clustering because it minimizes the amount of distortion in the dendrogram relative to the original similarity or difference matrix (Sneath and Sokal, 1973). Two coefficients were used: the Bray–Curtis dissimilarity distances for samples and Pearson's product-moment correlation coefficient for species.

Ordination methods include techniques such as polar ordination, principal component analysis, reciprocal averaging, and non-parametric multidimensional scaling (NMDS). The general patterns derived from these procedures are largely the same. Since NMDS uses the rank order for ordination and therefore removes the assumption of normality, this technique is most appropriate for paleoecological data. The NMDS analysis presented uses the Euclidean distances and rank orders a Bray–Curtis dissimilarity matrix.

After communities and clusters were recognized using clustering and ordinations, we then applied cluster significance testing (Sneath, 1977) and the

Fig. 2. Loss on ignition, community and lithology data in reference to stratigraphic position of samples. Letters within the *Devonochonetes*–*Longispina*–*Mucrospirifer* community represent assemblage variation in relation to stratigraphic position. M = *Mucrospirifer* cluster, B = Bivalve cluster, D = *Devonochonetes scitulus* cluster, and L = *Longispina* cluster.

Table 1
List of taxa and taxon codes used for the data sets

Code	Species	Code	Species
2	<i>Actinopteria boydi</i>	48	<i>Tellinopsis submarginata</i>
4	<i>Carydium bellistriata</i>	49	<i>Ambocoelia umbonata</i>
5	<i>Carydium varicosum</i>	50	<i>Athyris cora</i>
6	<i>Cimitaria recurva</i>	52	<i>Athyris spiriferoides</i>
7	<i>Cornellites fasciculata</i>	53	<i>Craniops hamiltoniae</i>
8	<i>Cypricardella bellastrata</i>	56	<i>Cyrtina hamiltonensis</i>
9	<i>Cypricardella tenuistriatus</i>	57	<i>Devonochonetes coronatus</i>
10	<i>Eoschizodus chemungensis</i>	58	<i>Devonochonetes scitulus</i>
11	<i>Goniophora hamiltonensis</i>	59	<i>Elita fimbriata</i>
13	<i>Gramatodon hamiltoniae</i>	60	<i>Lingula punctata</i>
14	<i>Grammysia bisulcata</i>	61	<i>Longispina mucronata</i>
15	<i>Grammysioidea alveata</i>	62	<i>Mediospirifer audaculus</i>
17	<i>Grammysioidea arcuata</i>	64	<i>Mucrospirifer consobrinus</i>
16	<i>Grammysioidea constricta</i>	65	<i>Mucrospirifer mucronatus</i>
18	<i>Grammysioidea globosa</i>	66	<i>Petrocrania hamiltoniae</i>
22	<i>Leiopteria rafinesqui</i>	67	<i>Prototeleostrophia perplana</i>
23	<i>Leiopteria sayi</i>	69	<i>Rhipidomella penelope</i>
25	<i>Modiella pygmaea</i>	71	<i>Spinocyrtia granulosa</i>
28	<i>Modiomorpha amygdaloides</i>	72	<i>Spinulicosta spinulicosta</i>
26	<i>Modiomorpha concentrica</i>	73	<i>Strophodonta demissa</i>
27	<i>Modiomorpha mytiloides</i>	74	<i>Tropidoleptus carinatus</i>
33	<i>Nuculites oblongatus</i>	75	<i>Dipleura dekayi</i>
29	<i>Nuculites triqueter</i>	77	<i>Greenops boothi</i>
30	<i>Nuculoidea corbuliformis</i>	79	<i>Phacops rana</i>
31	<i>Nuculoidea lirata</i>	80	<i>Glyptotomaria capillaria</i>
36	<i>Orthonota undulata</i>	82	<i>Palaeozygopleura hamiltoniae</i>
37	<i>Palaeoneilo constricta</i>	84	<i>Retispira leda</i>
38	<i>Palaeoneilo emarginata</i>	85	<i>Ruedemannia trilix</i>
39	<i>Palaeoneilo filosa</i>	88	' <i>Orthoceras</i> ' sp.
40	<i>Paracyclas proavia</i>	90	<i>Straight orthocone</i>
41	<i>Parallelodon</i> sp.	91	<i>Tornoceras uniangulare</i>
42	<i>Pholadella radiata</i>	95	<i>Hyalolithes</i> sp.
45	<i>Pterinopecten undosus</i>		
46	<i>Pterinopecten vertumnus</i>		
47	<i>Pterochaenia fragilis</i>		

ANOSIM (analysis of similarities) technique (Clarke, 1993) to quantitatively test for stability through time among samples. Cluster significance testing, though seldom applied in paleoecology, proves to be a more informative test than discriminant analysis (Sneath, 1977, 1979). Unlike discriminant analysis, which determines whether cluster means differ statistically, cluster significance testing resolves whether samples from two clusters are drawn from parent populations that overlap more or less than a specified percentage. This test can be done for Gaussian or rectangular distributions. The specified overlap percentage for

Gaussian distributions is usually 10%, 5%, or 1%. For rectangular distributions, the specified percentage is 0% overlap. The more reasonable question for paleoecology is whether the samples were drawn from two parent populations that have overlapping or non-overlapping rectangular distributions (Sneath, 1977, 1979). However, for this analysis, calculations using either Gaussian or rectangular distributions result in similar significance testing results.

Cluster significance testing is accomplished by calculating q -scores as the orthogonal projection of samples onto an axis that connects the cen-

troids of the two clusters in question. The W statistic of disjunction is calculated from these q -scores and the significance is determined from fig. 2 of Sneath (1979). q -scores resemble discriminant function scores but differ in two major respects. First, they may not maximize the separation between the two clusters, whereas discriminant function scores do. Secondly, q -scores are not sensitive to the number of variables involved, whereas discriminant function scores are. Since this data set contains 45 samples and 67 species, cluster significance testing must be used rather than discriminant analysis.

With suitable replicate samples, the ANOSIM technique (Clarke, 1993) tests for spatial and temporal differences in community structure by combining permutation tests with the general 'Monte Carlo' randomization approach (Hope, 1968; Clarke, 1993). This non-parametric, permutation procedure is based on the rank ordering of the Bray–Curtis similarities (Clarke and Warwick, 1994). The null hypothesis (H_0) states there are no differences in community composition between sample intervals. To test the null hypothesis, this procedure follows three main steps (refer to Clarke, 1993 and Clarke and Warwick, 1994 for more details). The first step computes a test statistic (Global R) that contrasts the variation between pre-defined clusters with variation within clusters (Clarke, 1993). Next, the samples are randomly reshuffled and the R statistic recomputed for a chosen number of permutations. This calculation establishes a predicted distribution of R in the case that H_0 is correct (Clarke, 1993). In the third step, the observed value of R and the predicted permutation distribution are compared; If H_0 is true, the observed R value will fall within the range of the computed permuted distribution. For more information about any of the above techniques, see Sneath and Sokal (1973), Sneath, (1977, 1979), Pielou (1977), Gauch (1982), Greig-Smith (1983), Legendre and Legendre (1983), Pielou (1984), Clarke (1993) and Clarke and Warwick (1994).

Ordination and clustering techniques were produced using a combination of *PC-ORD 3* and *SYSTAT 9* statistical packages. A program written by Dr. J.C. Brower of Syracuse University

calculated the statistics for the cluster significance testing. *PRIMER 4.0* produced the ANOSIM calculations.

2.3. Facies analysis

An excellent stratigraphic framework for the Hamilton Group exists in the literature (e.g. Cooper, 1930, 1933; Grasso, 1978; Brett, 1986; Landing and Brett, 1991; Mayer, 1994; Brett and Baird, 1996). Data collected for field samples in this study include grain size, sediment color, weight percent of total organics (measured by loss on ignition; Dean (1974)) bedding type and thickness, type of burrows (if any), and any other noteworthy features.

2.4. Ecological analysis

Two measures of species diversity, species richness and species evenness, aid in describing the ecological characteristics of community data. A commonly applied measure of species diversity is the Shannon–Wiener index:

$$H' = -\sum(p_i)(\log_2 p_i)$$

where H' = index of species diversity and p_i = proportion of total sample belonging to the i th species. Although the Shannon–Wiener index incorporates species evenness in its calculation, this measure is useful on its own. Equitability (E) is a measure that indicates how evenly taxa are distributed within an assemblage. The equitability index is derived from the Shannon–Wiener index and is calculated as:

$$E = H' / H'_{\max}$$

where H'_{\max} is equal to the value of H' if all species are evenly distributed, and is calculated using $\log_e S / \log_e 2$ where S = number of species. A value of one indicates that all taxa are equally abundant in the sample.

We group taxa into eight ecological categories based on trophic strategy and attachment-locomotion type in order to characterize the ecological

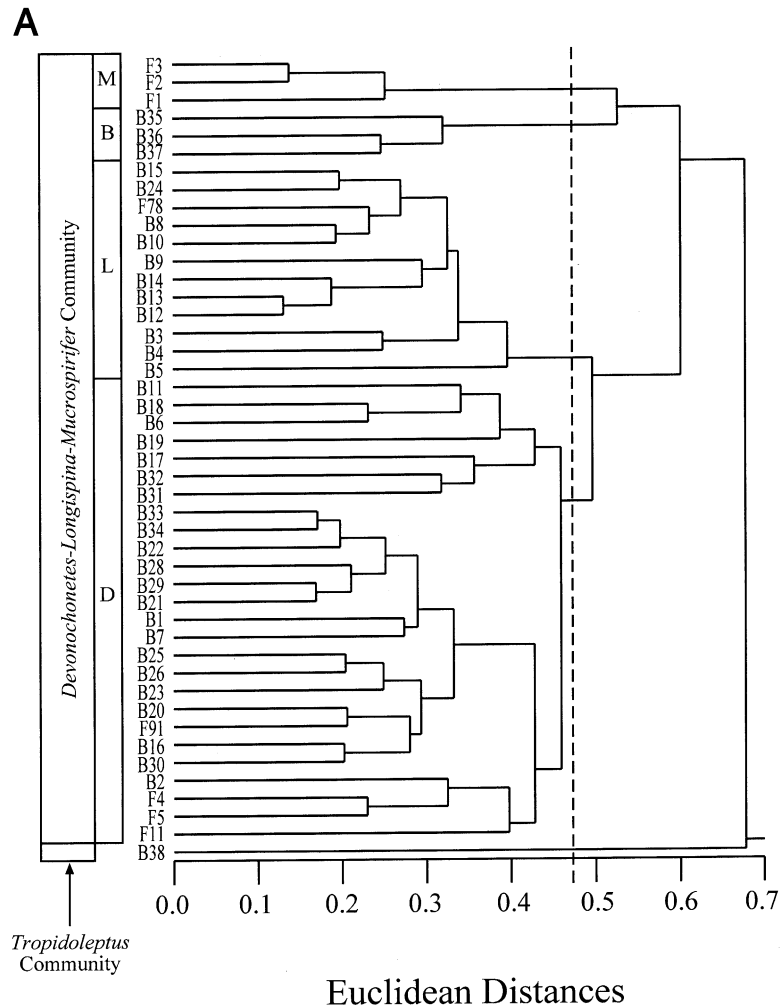


Fig. 4. (A) Dendrogram for samples from the Windom Member, upper Moscow Formation. Original data are percentages of 67 species and 45 samples. Letters on the left of the dendrogram represent assemblages within the *Devonochonetes-Longispina-Mucrospirifer* community. M = *Mucrospirifer* cluster, B = Bivalve cluster, D = *Devonochonetes scitulus* cluster, and L = *Longispina* cluster. Communities are also labeled. Location of samples is shown in Fig. 2. (B) Dendrogram for taxa from the Windom Member, upper Moscow Formation. Original data are percentages of 67 species and 45 samples. Species groupings are named after the most common species in that particular group. Species codes are found in Table 1.

structure of the various communities and clusters. Ecological categories follow Newton et al. (2001) in order to make consistent comparisons with previously published data. These include deep endobysate suspension feeders, epibysate or shallow endobysate suspension feeders, epifaunal benthic crawlers, infaunal deposit feeders, infaunal fully buried suspension feeders, nektonic carnivores, pedunculate suspension feeders, and reclining suspension feeders.

3. Lithostratigraphy

The Windom Member lithofacies constitutes thinly bedded, light-olive gray, non-calcareous shale gradually grading up into a medium-dark gray, highly indurated, silty shale (Fig. 2). This 11-m section has an extensive storm bed deposit at the 5.25-m mark. This storm bed laterally extends across the entire outcrop and consists mainly of *Spinocyrtia granulosa*. Due to the un-

B

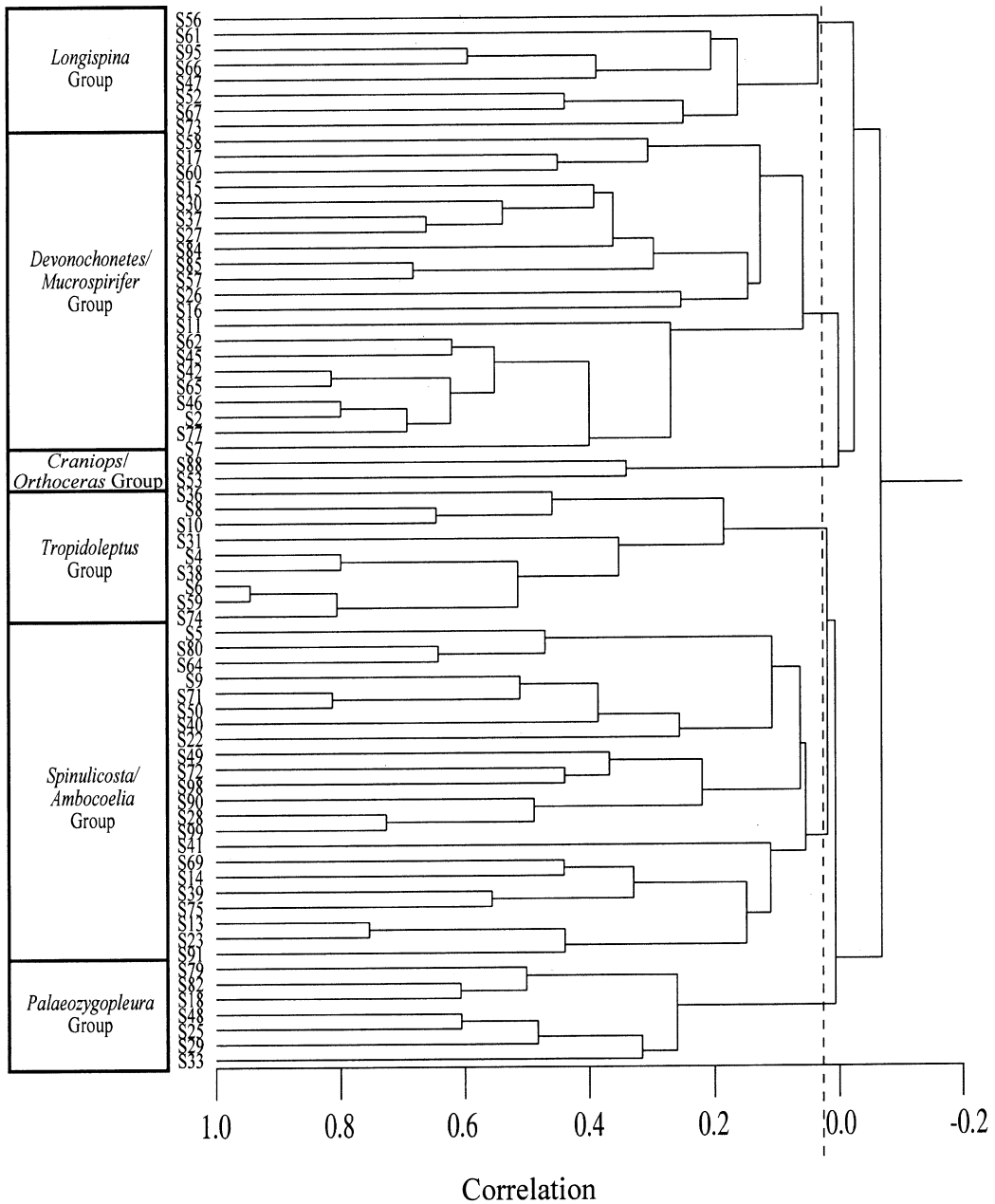


Fig. 4 (Continued).

usual nature of this bed, (i.e. transported, size sorted), it is not included in further analyses. *Zoophycos* trace fossils range throughout the succession, becoming more abundant upsection.

Organic content slightly decreases upsection from 3.1 wt% of organics to the 2.1 wt% of organics. Average weight percent of organics for the entire outcrop is approximately 2.7. An anomalous decrease in organics to 1.9 wt% of organics

in sample B-17 (Fig. 2) occurs at the base of the storm bed. This anomalous drop in organics was most likely caused by winnowing during deposition. In summary, both grain size and weight percent of total organics indicate that the site generally has a dark and fine-grained lithofacies that subtly changes into a slightly coarser lithofacies with a lower organic content (Fig. 2).

4. Description of community patterns

4.1. Cluster analysis

4.1.1. Sample clusters

Fig. 4A illustrates the dendrogram for the 45 samples based on 67 species. Five distinct groups cluster out at a distance of 0.475: a *Mucrospirifer* cluster, Bivalve cluster, *Longispina* cluster, *Devonochonetes scitulus* cluster and a *Tropidoleptus* sample (Fig. 4A). Names are assigned after the most common taxon in its group. All samples with these groups are labeled in Fig. 4A and their stratigraphic positions are shown in Fig. 2. Beginning at the bottom, the stratigraphic sequence of clusters originates with the *Mucrospirifer* cluster. Next, the *D. scitulus* cluster and *Longispina* cluster alternate with one another throughout the middle of the section with the *Longispina* cluster being concentrated toward the bottom and the *D. scitulus* cluster toward the top (Fig. 2). The Bivalve cluster is then overlain by the *Tropidoleptus* sample (Fig. 2). According to the dendrogram, sample B-38 (i.e. the *Tropidoleptus* sample) clusters at a similarity of 0.679 suggesting that this sample is an outlier from the other clusters (Fig. 4A).

4.1.2. Species clusters

Clusters were also generated for 67 species (Fig. 4B). The following groups of species can be recognized, beginning at the top of the dendrogram (Fig. 4B); species codes are in parentheses after each species group name (see Table 1 for identifications).

- *Longispina* group: (S56 through S73) consists mostly of rare species with the exception of *Longispina mucronata* (ranging from 2% in the Bi-

valve cluster to 30% in the *Longispina* cluster). Other taxa occur in relatively low percentages (i.e. <1%) throughout the section.

- *Devonochonetes scitulus*/*Mucrospirifer* group: (S58 through S53) contains many common species, such as *D. scitulus* (ranging from 13% to 56% in all clusters except the *Tropidoleptus* sample), *Mucrospirifer mucronatus* (9% to 50%), *Palaoneilo constricta* (3% to 6%), *Devonochonetes coronatus* (3% to 4%), and *Greenops boothi* (1% to 8%). All species are present within the *Mucrospirifer*, *Longispina*, Bivalve and *D. scitulus* sample clusters except where noted.

- *Tropidoleptus* group: (S36 through S74) contains common and rare species. The most common taxon in the group, *Tropidoleptus carinatus*, ranges from 2% to 31% and is present in all clusters. *Carydium bellistriata*, *Cypricardella tenuistriatus*, and *Palaoneilo emarginata* are the dominant bivalves found in this group.

- *Spinulicosta*/*Ambocoelia* group: (S5 through S91) consists mainly of rare species. *Spinulicosta spinulicosta* and *Ambocoelia umbonata* are the only common species with relatively high percentages. Notably, both taxa display low frequencies (i.e. ~2%) in all clusters especially the *Mucrospirifer* sample cluster (<0.3%). *Rhipidomella penelope* is another notable taxon that comprises approximately 3% of the *Tropidoleptus* sample.

- *Palaeozygopleura* group: (S79 through S33) contains rare species that range throughout the outcrop, including *Palaeozygopleura hamiltoniae*. All are present in the *Mucrospirifer*, *Longispina*, Bivalve, and *Devonochonetes scitulus* sample clusters. Only small frequencies of *Nuculites oblongatus* and *Tellinopsis submarginata* (i.e. 1%) are also encountered in the *Tropidoleptus* cluster.

4.2. NMDS

NMDS reveals a community pattern similar to that in the cluster analysis (Figs. 5 and 4A). All the clusters swarm together and are distinct from the *Tropidoleptus* sample. Within that cluster swarm, NMDS emphasizes the relationships between clusters by partitioning each cluster and visually displaying them together. In Fig. 5, the samples within the *Devonochonetes scitulus* cluster

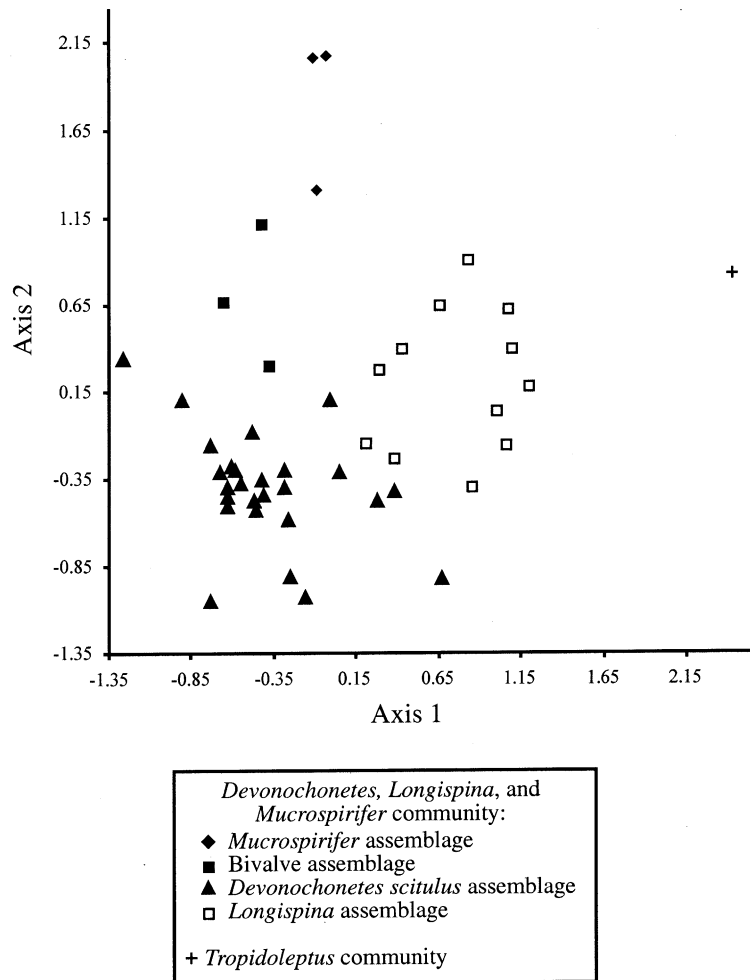


Fig. 5. NMDS analysis for benthic assemblages. Original data are percentages of 67 species and 45 samples. Final stress for the two-dimensional solution is 13.86%.

are plotted together near the samples within the *Longispina* cluster. Together, these two clusters are more closely related to the Bivalve cluster and the Bivalve cluster is linked to the *Mucrospirifer* cluster. All other clusters differ from the *Tropidoleptus* sample. These relationships between sampling units correspond well to the dendrogram in Fig. 4A. An underlying ecological gradient is not evident within this NMDS plot or within other ordinations (i.e. polar ordination, principal component analysis, and reciprocal averaging). This may be due to distortion because 45 dimensions (i.e. 45 samples) are represented in two dimensions (i.e. Axis 1 and Axis 2).

5. Taxonomic and ecological patterns through time

Fig. 6 demonstrates that *Devonochonetes scitulus* generally dominates this outcrop and is notably present in all samples except B-38 (i.e. the *Tropidoleptus* sample).

In addition, there is visible variation of dominant taxa within each cluster. At the bottom of the section, *Mucrospirifer mucronatus* dominates the first cluster. As we move upsection, the *Longispina* and *Devonochonetes scitulus* clusters have a similar taxonomic composition but vary in category percentages. Next, although the Bivalve cluster is dominated by *D. scitulus*, bivalves mark-

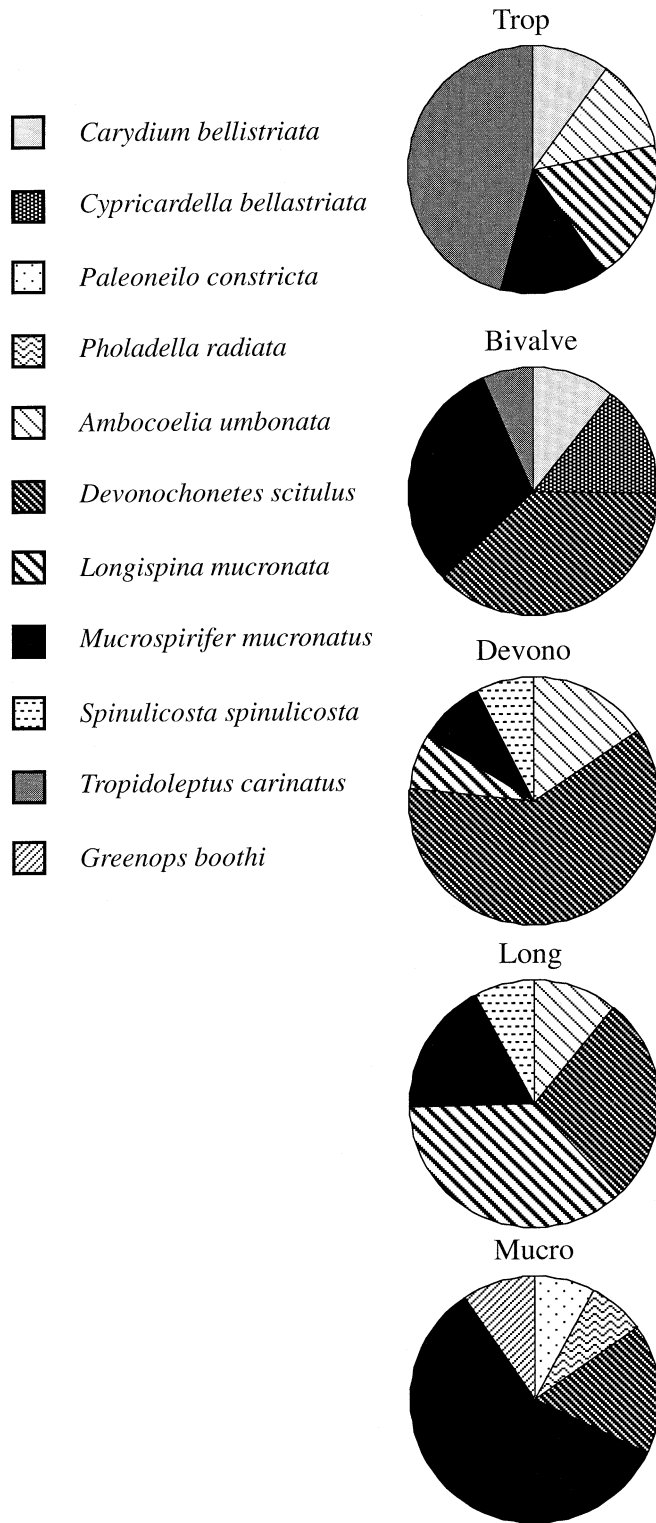


Fig. 6. Taxonomic composition through time within the Soule Road outcrop.

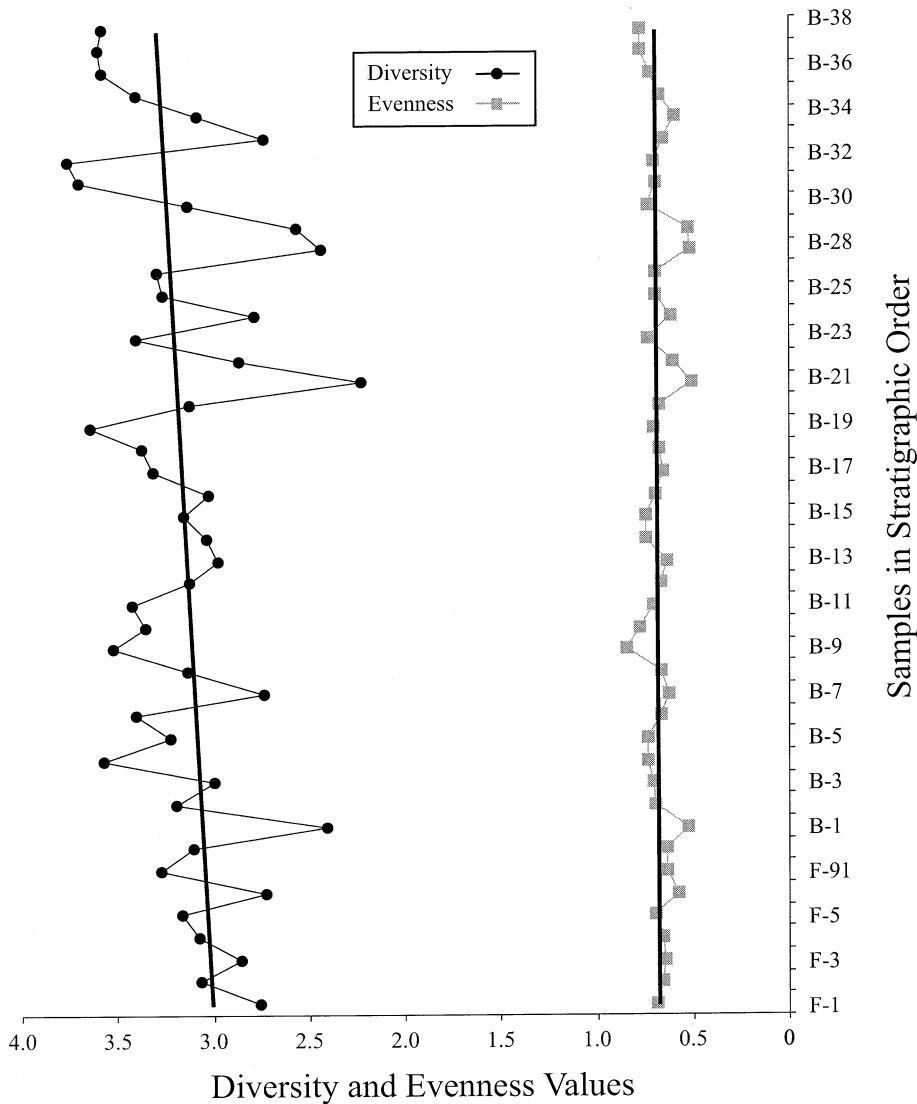


Fig. 7. Shannon–Wiener diversity index and equitability index plotted through time.

edly increase in percentages within this cluster. The *Tropidoleptus* sample is clearly different in reference to taxonomic composition; *D. scitulus* disappears and *Tropidoleptus carinatus* dominates the sample.

5.1. Taxonomic patterns

5.1.1. The *Mucrospirifer* cluster

Beginning from stratigraphic bottom, the *Mucrospirifer* cluster, containing samples F1 through

F3 (Fig. 4A), contains a high percentage of *Mucrospirifer mucronatus* (approximately 50%) and a low percentage of *Devonoconetes scitulus* (approximately 14%). *Greenops boothi*, another common species, constitutes 8% of the three samples.

5.1.2. The *Devonoconetes scitulus* and *Longispina* cluster

The next two clusters, when superimposed on the stratigraphic section, alternate with one another throughout the next interval (Fig. 2). With-

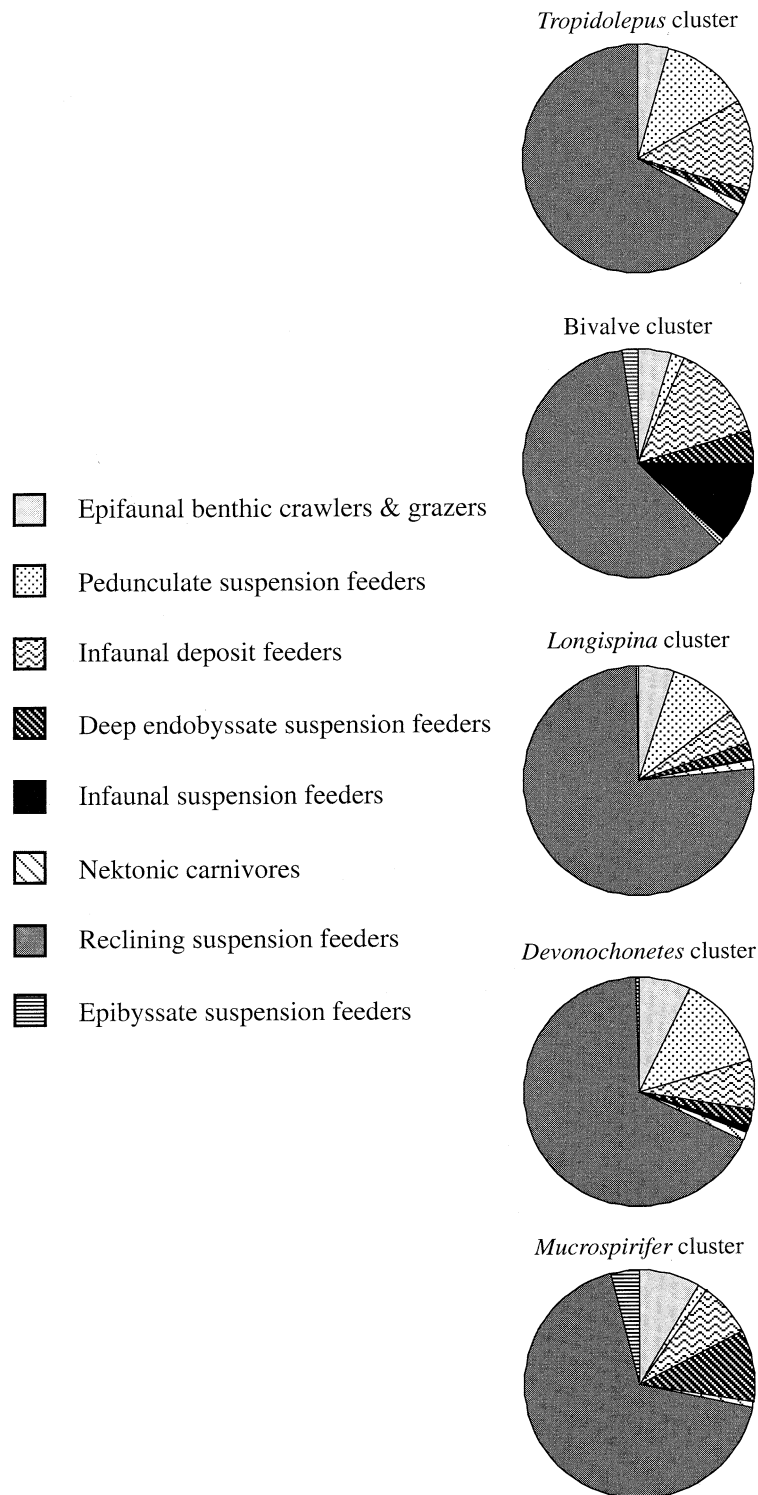


Fig. 8. Ecological structure of the clusters.

Table 2
Results of cluster significance testing for the Soule Road outcrop

Pairs of clusters	<i>W</i> statistic of disjunction	Approximate critical <i>W</i> statistic value (at $p=0.05$)	Total sample size	Observed percentage of <i>q</i> -score overlap	Non-central Student's <i>t</i> values	Min. and Max. critical Student's <i>t</i> values with corresponding percentage of population overlap (<i>t</i> value at 0.95)
<i>Devonochonetes</i> vs. <i>Longispina</i> cluster	1.7	2.1	38	7.9	10.3	Min: $t=9.9$, 25% overlap; Max: $t=10.9$, 20% overlap
<i>Devonochonetes</i> , <i>Longispina</i> cluster vs. <i>Mucrospirifer</i> cluster	1.5	2.2	41	0	9.8	Min: $t=9.7$, 25% overlap; Max: $t=10.2$, 20% overlap
<i>Devonochonetes</i> , <i>Longispina</i> , <i>Mucrospirifer</i> cluster vs. Bivalve cluster	1.6	2.1	44	9.1	10.2	Min: $t=9.7$, 70% overlap; Max: $t=12.5$, 60% overlap
<i>Devonochonetes</i> – <i>Longispina</i> – <i>Mucrospirifer</i> community vs. <i>Tropidoleptus</i> community	3.9	2.1	45	0	26.3	Min: $t=21.7$, 0% overlap; Max: $t>21.7$, 0% overlap
Replicate sample comparisons	0.4	2.9	11	27.3	1.4	Min: $t<1.8$, 100% overlap; Max: $t=1.8$, 100% overlap

The critical values for the *W* statistic are for non-overlapping rectangular distributions of the parent populations. The *W* statistic is taken from Sneath (1979, fig. 2). See Sneath (1977) for discussion of the non-central Student's *t* values.

in the *Devonochonetes scitulus* cluster, *D. scitulus* averages 58%, *Ambocoelia umbonata* 13%, *Mucrospirifer mucronatus* 7%, and *Longispina mucronata* 6% (Fig. 6). The *Longispina* cluster averages approximately 33% *L. mucronata*, 24% *D. scitulus*, 15% *M. mucronatus*, and 10% *A. umbonata* (Fig. 6).

5.1.3. The Bivalve cluster

Samples B-35 through B-37 constitute the Bivalve cluster (Fig. 4A). Although almost equally high in average percentages of *Devonochonetes scitulus* and *Mucrospirifer mucronatus* (i.e. 32% and 26%), this cluster shows the highest percentages of bivalves. For example, *Cypricardella bel-*

Table 3
ANOSIM results for the Windom Member data

Global test:					
Sample statistic (Global <i>R</i>)	0.377				
Number of permutations:	5000				
Number of permuted statistics greater than or equal to Global <i>R</i> :	0				
Significance level of sample statistic:	0.0%				
Pairwise tests:					
Groups used ^a	Statistic value	Possible permutations	Permutations used	Significant statistics	Significance level
1, 2	1.000	10	10	1	10.0%
1, 3	0.851	445	445	1	0.2%
1, 4	0.870	3654	3654	1	0.0%
2, 3	0.738	455	455	1	0.2%
2, 4	0.315	3654	3654	185	5.1%
3, 4	0.160	2.707D+09	5000	119	2.4%

^a 1 – *Mucrospirifer* cluster; 2 – Bivalve cluster; 3 – *Longispina* cluster; 4 – *Devonochonetes scitulus* cluster.

Table 4
Species correlations for the following species

	<i>D. scitulus</i>	<i>L. mucronata</i>	<i>M. mucronatus</i>	<i>T. carinatus</i>
<i>D. scitulus</i>	1.00			
<i>L. mucronatus</i>	−0.43	1.00		
<i>M. mucronata</i>	−0.52	0.00	1.00	
<i>T. carinatus</i>	−0.20	0.25	−0.22	1.00

lastrata and *Carydium bellistriatum* constitute 12% and 9% of this cluster.

5.1.4. The *Tropidoleptus* sample

Sample B-38 clusters at a distance of 0.679 (Fig. 4A). *Tropidoleptus carinatus* comprises 36% of this sample (Fig. 6). Among the common chonetids, *Devonochonetes scitulus* is conspicuously absent from this sample, but *Longispina mucronata* contributes 14%. *Mucrospirifer mucronatus* and *Ambocoelia umbonata* display a frequency of 11%, and 9% in this sample. Sample B-38 differs particularly from the other clusters with respect to the less common taxa. For example, *Carydium varicosum* and *Elita fimbriata* represent 8% of this sample, whereas within the other clusters, *C. varicosum* and *E. fimbriata* constitute on average 1–2%.

5.2. Ecological patterns

The Shannon–Wiener diversity index fluctuates greatly from sample to sample (Fig. 7). Specific equability calculations for each sample indicate that samples are relatively consistent at an average of 0.67 (Fig. 7).

Fig. 8 indicates that the dominant ecological structure of all clusters is relatively similar, with faunas dominated by reclining suspension feeders (i.e. *Devonochonetes scitulus*, *Mucrospirifer mucronatus*, *Longispina mucronata*, *Tropidoleptus carinatus*, and *Spinulicosta spinulicosta*). Ecological structures of remaining cluster proportions are more variable. Beginning with the stratigraphic bottom, the *Mucrospirifer* cluster has a substantial amount of deep endobysate suspension feeders, as well as infaunal deposit feeders and epifaunal benthic crawlers (Fig. 8). The *Longispina* and

D. scitulus clusters differ from the *Mucrospirifer* cluster by their increase in pedunculate suspension feeders; essentially these two clusters have identical ecological structure aside from slight differences in ecological category percentages. Upsection, the Bivalve cluster begins to increase in infaunal deposit and suspension feeders and decrease in pedunculate suspension feeders.

The *Tropidoleptus* sample consists mostly of reclining suspension feeders (Fig. 8). However, the dominant recliner is *Tropidoleptus carinatus* rather than *Devonochonetes scitulus*, which is prevalent throughout the rest of the section (Fig. 6). In fact, *D. scitulus* is absent entirely from sample B-38. Pedunculate suspension feeders (e.g. *Ambocoelia umbonata* and *Rhipidomella penelope*) and infaunal deposit feeders (e.g. *Carydium bellistriatum* and *Paleoneilo emarginata*) constitute 13–12% of the community. Other ecological categories display minor frequencies within this cluster, or are absent altogether (Fig. 8).

6. Testing stability

6.1. Cluster significance testing

Two main communities are recognized in this study according to the clustering significance testing results, namely the *Devonochonetes*–*Longispina*–*Mucrospirifer* community and *Tropidoleptus* community. These communities are named for their most common taxa.

Cluster significance testing was applied to the samples in the clusters and then to the communities (Table 2). First, the *Devonochonetes scitulus* cluster and the *Longispina* cluster comparison revealed that the parent populations of the two

clusters have rectangular distributions that overlap. Next, the combination of the *D. scitulus* cluster and the *Longispina* cluster was compared with the *Mucrospirifer* cluster; according to the *W* statistic, these underlying populations overlap. Next, *D. scitulus*, *Longispina*, and *Mucrospirifer* clusters were tested against the Bivalve cluster. This comparison also indicates that the rectangular distributions of the parent populations overlap. Therefore, we place these four clusters into the *Devonochonetes–Longispina–Mucrospirifer* community. The *Devonochonetes–Longispina–Mucrospirifer* community was then compared to sample B-38. The *W* statistic of disjunction demonstrated that the two clusters were drawn from populations with rectangular distributions that do not overlap at the 0.05 probability level (Table 2). Consequently, these results confirmed the statistical separation of the *Devonochonetes–Longispina–Mucrospirifer* community from the *Tropidoleptus* community.

Cluster significance testing also confirms the lateral reproducibility of taxonomic composition. Replicate samples were taken every meter, approximately 4 m down bedding plane, and compared with samples along the same stratigraphic interval. The *W* statistic of disjunction illustrates that the replicate samples are drawn from the same distribution because their rectangular distributions overlap significantly (Table 2).

6.2. ANOSIM

In order to test community stability within a relatively consistent environment, sample B-38 was removed from the ANOSIM analysis data set. The deletion is justified, since sample B-38 occurs within a different lithofacies and belongs to a different community (see Figs. 2, 4A and 5, and Table 2). The new matrix includes data from the *Mucrospirifer*, Bivalve, *Longispina*, and *Devonochonetes scitulus* clusters, which make up the *Devonochonetes–Longispina–Mucrospirifer* community. This test resulted in an observed test statistic (Global *R*) of 0.377 with a significance level of 0.0%. This suggests there was a 0 in 5000 chance that Global *R* comes from the stochastic distribution (Table 3). According to

this procedure, the various clusters were not drawn from the same population; hence, there is significant change in taxonomic composition within this upper Hamilton Group community (Table 3).

7. Discussion

7.1. Taxonomic and guild-level patterns

According to the cluster significance testing, this particular site generally consists of one large community, the *Devonochonetes–Longispina–Mucrospirifer* community. When examined rigorously, this long-ranging community exhibits taxonomic variation within a relatively consistent ecological structure. Our ANOSIM results suggest the taxonomic variation seen between clusters differs from the taxonomic variation within clusters (Table 3). An example of this taxonomic variation begins with the most abundant species *Devonochonetes scitulus*. *D. scitulus* occurs widely within the *Devonochonetes–Longispina–Mucrospirifer* community, but fluctuates in percentage from sample to sample. When there is a high percentage of *Longispina mucronata*, there is a low percentage of *D. scitulus*. Likewise, when there is a percentage increase in *Mucrospirifer mucronatus* there is a decrease in *D. scitulus*. *D. scitulus* is negatively correlated with *L. mucronata* and *M. mucronatus*. However, *M. mucronatus* and *L. mucronata* are independent of each other as seen in their low correlation of 0.0 (Table 4). These patterns suggest that *D. scitulus* replaces *L. mucronata* and *M. mucronatus* perhaps as a consequence of larval recruitment.

This negative correlation between dominant taxa is consistent with the cluster groups in Fig. 6. Through time taxonomic composition changes from *Mucrospirifer mucronatus* to the alternating relationship of *Longispina mucronatus* and *Devonochonetes scitulus* followed by an increase in bivalves. According to Fig. 6, there are notable variations within the less common taxa as well. For example, *Ambocoelia umbonata* is abundant throughout the *Longispina* cluster, the *D. scitulus*

clusters but is absent from the *Mucrospirifer* and Bivalve clusters.

The dominant reclining suspension feeders are relatively consistent throughout this interval (Fig. 8). Although the ecological category persists through time, species composition within the reclining suspension feeders varies. For example, within the category of recliners, *Devonoconetes scitulus* is the most common in the *Devonoconetes* cluster, *Mucrospirifer mucronatus* is dominant within the *Mucrospirifer* cluster, and *Longispina mucronata* is common within the *Longispina* cluster. Aside from the reclining suspension feeding category, other ecological categories also seem to change through time. The *Mucrospirifer* cluster and *Longispina* cluster lack infaunal suspension feeders; however, infaunal suspension feeders comprise 12% of the Bivalve cluster (Fig. 8). Comparing the five clusters one can see that the *Longispina* and *D. scitulus* clusters are the only clusters nearly identical in percentages of ecological categories (Fig. 8).

7.2. Results in context to coordinated stasis

Although this study does not compare temporal community patterns throughout the Hamilton Group, it does characterize community patterns within one Windom Member site; therefore, some initial conclusions concerning patterns of coordinated stasis can be drawn.

According to coordinated stasis, taxonomic membership and ecological structure persist through time and are relatively stable within a similar Hamilton Group environment (Brett and Baird, 1995). Within this relatively stable environment, ecological structure continues to persist while taxonomic membership is significantly variable through time. These results are therefore not consistent with the present definition of coordinated stasis.

8. Conclusion

Resolution of stability patterns demands consistent statistical approaches. One of our main goals

in this study is to find the appropriate statistical methodologies for testing coordinated stasis. Different statistical methodologies are compared using an uppermost Hamilton Group data set. Our results confirm that the combination of NMDS and agglomerative hierarchical clustering (using the UPGM) reflects community structure most accurately. Furthermore, although not traditionally used, we advocate the use of cluster significance testing when examining ecological data. This technique examines a highly pertinent statistical question, that is, whether or not two clusters of samples were drawn from overlapping or disjunct parent populations, based on rectangular or Gaussian distributions. This technique for that reason is more rigorous than conventional significance tests such as the Student's *t*-test, canonical variates, discriminant analysis, and analysis of variance (ANOVA), which only compare the taxonomic means of two or more samples.

We also suggest the regular use of the ANOSIM technique. This non-parametric permutation procedure applied to the rank-ordered similarity matrix provides a more valid testing framework compared to ANOVA or MANOVA because it removes the assumption of normality (Clarke and Warwick, 1994). This technique also enables researchers to evaluate the taxonomic variation within clusters compared to between clusters in a simple and easily interpreted way.

Our second goal is to determine community patterns within this Windom Member interval (Moscow Formation, uppermost Hamilton Group) in context to coordinated stasis. According to our results, the general community pattern consists of two statistically distinct communities. The *Devonoconetes*–*Longispina*–*Mucrospirifer* community comprises four assemblages each differing in taxonomic composition and named after the most common taxon (i.e. *Mucrospirifer* cluster, *Longispina* and *Devonoconetes scitulus* clusters and the Bivalve cluster). Although consisting of one sample, the *Tropidoleptus* community constitutes different taxa than the *Devonoconetes*–*Longispina*–*Mucrospirifer* community and is determined to be statistically different. For these reasons, the *Tropidoleptus* community is deleted and the *Devonoconetes*–

Longispina–Mucrospirifer community is tested for stability.

Our results clearly indicate that between cluster variation and within cluster variation of the *Devonochonetes–Longispina–Mucrospirifer* community is drawn from different parent distributions. Hence, this implies that the community changes throughout time. Graphic representations of taxonomic and ecological structure show that taxonomic membership varies within a relatively stable ecological structure. Since coordinated stasis requires both taxonomic and ecological consistency within a similar environment; our results do not meet the criteria of coordinated stasis.

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Appendix 1

Data matrix in proportions

61	62	64	65	66	67	69	71	72	73	74	75	77	79	80	82	84	85	88	90	91	95
6.3123	0.9934	0.0000	40.5316	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	6.9767	0.0000	0.0000	0.3322	0.6645	0.0000	0.9967	0.0000	0.0000	0.0000
0.6623	0.9934	0.0000	44.7020	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	5.9603	0.0000	0.3311	0.0000	0.3311	0.0000	1.3245	0.0000	0.0000	0.3311
2.0202	2.3569	0.0000	47.8114	0.0000	0.0000	0.0000	0.3367	0.0000	1.0101	0.0000	0.0000	8.4175	0.0000	0.3367	0.0000	0.3367	0.0000	0.3367	0.0000	0.0000	0.0000
22.5490	0.0000	0.3268	0.3268	0.6536	8.8235	0.6536	0.0000	3.9216	7.5163	0.6536	0.0000	1.6340	0.3268	0.0000	0.3268	0.0000	0.0000	0.0000	0.0000	0.0000	0.3268
17.6871	0.0000	0.0000	0.3401	0.0000	0.0000	0.3401	0.3401	5.4422	7.1429	0.0000	0.0000	2.0408	0.0000	0.0000	0.0000	0.3401	0.0000	1.3605	0.6803	0.0000	0.0000
33.5463	0.0000	0.0000	0.0000	0.0000	0.0000	0.6390	0.0000	7.0288	6.6390	0.0000	0.3195	0.6390	0.0000	1.2780	1.2780	0.0000	0.0000	0.3195	0.3195	0.0000	0.3195
9.5831	0.0000	0.0000	1.6287	0.0000	0.6515	0.6515	0.0000	6.8404	6.3257	1.6287	0.6515	3.2573	0.0000	1.3029	4.5603	1.6287	0.0000	1.3029	1.6287	0.0000	0.0000
9.5832	0.0000	0.0000	0.6557	0.0000	0.3279	1.3115	0.0000	0.0000	0.9836	0.0000	0.3279	5.2459	0.9836	0.0000	1.9672	1.6393	0.9836	0.6557	0.9836	0.0000	0.0000
1.4620	0.0000	0.0000	5.5556	0.0000	0.2924	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.5848	1.4620	0.0000	0.5848	0.5848	0.0000	0.2924	0.0000	0.0000	0.0000
11.4379	0.3268	0.0000	9.4771	0.0000	4.5752	0.0000	0.0000	3.9216	0.0000	0.0000	0.0000	0.6536	0.0000	0.0000	0.3268	0.9804	1.6340	0.0000	0.0000	0.0000	0.0000
33.3333	0.3030	0.0000	18.7879	0.0000	1.8182	0.0000	0.0000	4.2424	0.0000	0.0000	0.6061	0.6061	0.0000	0.0000	0.3030	0.0000	0.6061	0.9091	0.0000	0.0000	0.3030
27.7070	1.2739	0.0000	14.3312	1.5924	2.2293	0.0000	0.3185	1.9108	1.5924	0.0000	0.0000	1.2739	0.0000	1.2739	0.6369	1.2739	0.0000	0.6369	0.0000	0.0000	0.9554
20.3883	0.0000	0.0000	10.6796	0.0000	2.9126	0.9709	2.9126	10.6796	0.0000	7.7670	0.0000	0.0000	0.9709	0.0000	0.0000	0.0000	0.9709	0.0000	0.0000	2.9126	0.0000
0.0000	0.0000	0.0000	5.3156	0.0000	1.6611	3.3223	0.0000	7.3090	0.3322	0.0000	0.9967	1.6611	1.9334	1.3289	1.3289	0.0000	0.0000	0.6645	1.3289	0.0000	0.0000
6.1350	0.6135	0.0000	3.9877	0.0000	1.2270	1.5337	0.0000	2.7607	0.6135	0.0000	1.2270	2.4540	0.0000	0.3067	0.0000	0.9202	0.0000	0.3067	0.0000	0.0000	0.3067
35.8601	0.8746	0.2915	8.7464	0.0000	2.0408	0.2915	0.5831	5.8309	0.5831	0.2915	1.1662	2.0408	0.0000	0.5831	0.0000	0.5831	0.0000	0.8746	0.0000	0.0000	0.2915
15.9864	0.0000	0.0000	0.6803	14.9660	0.0000	1.7007	0.0000	6.1224	2.3810	3.7415	0.0000	1.7007	0.0000	8.5034	0.3401	0.3401	0.0000	0.6803	0.0000	0.0000	0.0000
31.7726	0.0000	0.0000	5.0167	0.0000	0.6689	1.0033	0.0000	6.0201	2.0067	1.6722	0.6689	1.6722	0.0000	0.6689	3.0100	0.6689	0.0000	0.6689	1.0033	0.3344	0.0000
8.6817	0.0000	0.0000	7.3955	0.0000	4.1801	0.0000	0.0000	8.6817	1.9293	1.2862	0.0000	0.9646	1.6077	0.0000	1.9293	0.3215	0.0000	0.0000	0.0000	0.3215	0.0000
29.3930	0.0000	0.0000	26.1981	0.0000	0.6390	0.0000	0.0000	5.7508	1.2780	1.9169	0.0000	2.5559	0.0000	0.6390	0.9585	0.3195	0.0000	0.6390	0.0000	0.0000	0.3195
28.7540	0.0000	0.0000	24.2812	0.0000	0.0000	0.0000	0.0000	5.7508	1.5974	1.9169	0.0000	0.6390	0.3195	1.9169	0.6390	0.3195	0.0000	1.2780	0.0000	0.0000	0.3195
23.9344	0.0000	0.0000	21.9672	0.0000	0.3279	0.0000	0.0000	6.5574	1.3115	0.9836	0.0000	0.3279	0.0000	2.2951	0.9836	0.3279	0.0000	0.3279	0.0000	0.0000	0.0000
21.6561	0.0000	0.0000	7.6433	0.0000	0.9554	0.0000	0.0000	8.2803	0.3185	1.9108	0.9554	0.6369	0.0000	2.2293	0.3185	1.2739	0.0000	0.9554	0.0000	0.3185	0.0000
1.6181	0.0000	0.0000	7.4434	0.0000	0.9709	0.0000	0.0000	5.8252	1.6181	3.8835	0.0000	1.9417	1.2945	0.6472	0.3236	0.3236	0.0000	0.6472	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	4.0752	0.0000	0.9404	2.1944	8.4639	2.1944	1.8809	2.2571	0.0000	0.3135	0.6270	1.2539	1.2539	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
0.3460	0.0000	0.0000	5.8824	0.0000	0.3460	0.0000	0.6920	5.1903	0.3460	1.0381	0.0381	0.3460	1.7301	0.3460	7.2664	0.3460	0.0000	0.6920	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	9.2409	0.0000	0.9901	0.6601	0.6601	0.9901	1.9802	4.6205	0.0000	0.3300	3.9604	0.6601	14.8515	0.3300	0.0000	0.0000	0.6601	0.6601	0.3300
2.8269	0.0000	0.0000	1.7668	0.0000	1.4134	0.0000	0.0000	7.4205	6.3604	2.4735	0.0000	4.5936	0.3534	0.7067	5.6537	0.0000	0.0000	0.0000	1.7668	0.0000	0.7067
0.6557	0.0000	0.0000	0.6557	0.0000	0.6557	0.0000	0.0000	7.5410	4.5902	1.9672	0.0000	0.9836	2.9508	0.0000	4.5902	0.3279	0.0000	0.0000	0.6557	0.3279	0.0000
1.3115	0.0000	0.0000	8.1967	0.0000	0.6557	0.0000	0.0000	4.5902	2.9508	2.9508	0.0000	1.3115	0.3279	0.6557	8.8525	0.0000	0.0000	0.6557	1.3115	0.0000	0.0000
5.7239	0.0000	0.0000	6.7340	0.0000	0.6734	0.0000	0.0000	4.3771	7.4074	0.0000	0.0000	2.6936	1.6835	0.3367	8.0808	0.3367	0.0000	0.3367	0.0000	0.0000	0.0000
28.1553	0.0000	0.0000	5.8252	0.0000	0.0000	0.0000	0.0000	3.2362	0.9709	0.6472	0.0000	1.6181	0.3236	0.3236	1.9417	0.0000	0.0000	1.6181	0.3236	0.3236	0.0000
9.2150	0.0000	0.0000	3.7543	0.0000	0.0000	0.0000	0.0000	4.0956	0.6826	2.0478	0.0000	3.0717	0.6826	0.0000	6.4846	0.6826	0.0000	0.6826	2.3891	0.3413	0.0000
16.9492	0.0000	0.3390	4.7458	0.0000	0.0000	0.0000	0.0000	3.0508	2.0339	3.0508	0.0000	1.6949	0.0000	1.6949	4.4068	0.0000	0.0000	0.0000	0.3390	0.3390	0.0000
0.0000	0.0000	0.0000	7.8689	0.0000	0.0000	0.0000	0.6711	8.1967	0.3279	1.9672	0.0000	1.6393	0.0000	0.0000	0.6557	0.3279	0.0000	0.6557	0.3279	0.0000	0.0000
0.0000	0.0000	0.0000	3.3557	0.0000	0.0000	0.0000	0.0000	6.6913	0.3356	3.6913	0.3356	0.9678	1.0067	0.6711	0.0000	0.3356	0.0000	0.6711	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	14.1447	0.0000	0.0000	0.0000	4.2763	6.2500	2.3026	2.9605	0.0000	0.9868	0.6579	0.6579	0.3289	0.0000	0.0000	0.6579	0.3289	0.3289	0.0000
0.0000	0.0000	0.6431	9.3248	0.0000	0.6369	0.0000	20.9003	3.5370	1.9293	1.9293	0.0000	0.6431	2.2508	0.0000	0.9646	0.3215	0.0000	0.3215	1.6077	0.3215	0.0000
0.6369	0.0000	0.0000	6.0510	0.0000	0.6369	0.0000	12.1019	7.0064	3.8217	3.5032	0.3185	0.6369	0.6369	0.0000	1.2739	0.0000	0.0000	0.0000	0.6369	0.0000	0.0000
0.0000	0.0000	0.0000	8.0906	0.0000	0.0000	0.0000	0.0000	5.016	2.654	1.2945	0.6472	0.3236	0.6472	1.2945	1.2945	0.0000	0.0000	0.3236	0.3236	0.0000	0.0000
0.0000	0.3367	0.0000	8.4175	0.0000	0.0000	0.0000	0.3367	6.0606	4.0404	1.0101	0.3367	1.0101	0.3367	0.0000	1.0101	0.0000	0.0000	0.3367	1.0101	0.0000	0.6734
0.3413	0.0000	0.0000	33.1058	0.0000	0.0000	0.0000	0.6826	3.4130	0.0000	3.7543	0.6826	1.0239	1.3652	0.6826	1.7065	0.0000	0.0000	0.3413	0.0000	0.0000	0.6826
0.0000	0.0000	0.0000	18.6047	0.0000	0.0000	0.0000	0.0000	6.645	0.0000	6.3123	0.0000	1.3289	1.3289	0.0000	0.3322	0.0000	0.0000	0.0000	1.3289	0.3322	0.0000
6.9519	0.0000	0.0000	11.2299	0.0000	0.0000	0.0000	0.0000	1.6043	0.0000	3.2086	0.0000	2.1390	0.0000	2.1390	1.0695	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
12.1951	0.6098	0.0000	9.1463	0.0000	1.8293	2.4390	0.6098	3.0488	0.0000	30.4878	0.0000	2.4390	1.2195	0.6098	0.0000	0.0000	0.0000	1.2195	0.6098	0.0000	0.0000

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