

BIOFACIES RECURRENCE IN THE MIDDLE DEVONIAN OF NEW YORK STATE: AN EXAMPLE WITH IMPLICATIONS FOR EVOLUTIONARY PALEOECOLOGY

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ABSTRACT

The diverse, well-preserved fauna of the Middle Devonian Hamilton Group of western New York has become an exemplar of long-term taxonomic and paleoecological stability and habitat tracking in response to sea-level change. Recent detailed, quantitative studies have challenged this view, suggesting instead a relatively low proportion of persistent lineages and recurrent biofacies sharing only the most abundant species; however, most studies have considered only limited geographic areas. As a result of shifting basin-forebulge positions and sedimentation patterns, analogous facies do not occur in every cycle of single geographic areas but show complex migration within the Appalachian Basin. Consequently, similarity of biofacies recurrence can only be fairly assessed by considering the most analogous facies wherever they occur across a major cross section of the basin. This paper evaluates patterns of biofacies recurrence based on samples from subsymmetrical cycles of dark-gray shale, calcareous mudstone, and argillaceous limestone. Low-sedimentation, depth-related biofacies, identified quantitatively using cluster analysis, recur symmetrically in single third-order regressive-transgressive cycles throughout the 5–6 myr duration of the Givetian Hamilton Group and Tully Formation at different geographic locations. Detrended correspondence analysis was used to recognize gradients of species and sample distribution both within and among depositional cycles; depth-related biofacies range from basinal, low-diversity leiorhynchid brachiopod-dominated associations to highly diverse coral-brachiopod (shallow subtidal) assemblages. This pattern is also comparable to the order of species-biofacies appearances in single, small-scale shallowing-upward cycles. In addition to similarities of species richness and guild structure, given biofacies show strong similarities of species composition. Low-diversity, high-dominance associations typical of deeper water biofacies show lower similarities (60%–75% species overlap), suggesting that they represent loosely structured aggregations of eurytopic taxa. Similarities are greatest in the diverse coral and brachiopod biofacies, for which most pairwise comparisons of samples throughout the Hamilton–Tully interval show >80% overlap in species composition and very strong similarity of richness and guild structures but not necessarily rank or relative abundance of taxa. Overall, these data suggest that gradients of species distribution in relation to environmental gradients, especially depth-related factors, were quite stable over several million years and that biofacies shifted in response to transgressive-regressive cycles. Such biofacies stability need not imply persistence of tightly integrated communities. Nonetheless, the long range of many species and maintenance of biotic gradients have important evolutionary implications—under relatively stable conditions, a majority of species track shifting habitats rather than adapt to changing local conditions.

INTRODUCTION

One of the principal problems in understanding the history of life is the interpretation of patterns of biotic recurrence. A number of important

questions remain unresolved: To what degree do stratigraphic patterns of faunal change mirror physical perturbations, particularly those related to sea-level change? What degree of similarity characterizes recurrent faunal associations or biofacies; that is, do they share similar diversities, general trophic structure, species composition, and relative or rank abundance? Can gradients of species composition arrayed along environmental gradations persist through time? These questions underlie some of the most contentious issues in evolutionary paleoecology. Specifically, numerous paleoecological studies have focused on the dichotomy of biofacies viewed as either persistent tightly structured communities (e.g., Clements, 1916) or ephemeral associations of species (the individualistic response view of Gleason, 1926). Renewed emphasis on these questions has arisen in part because of the observation of a high degree of similarity in some recurrent associations (e.g., Brett and Baird, 1995; Bennington and Bambach, 1996; Pandolfi, 1996). Such observations do not necessarily imply tight community integration, although they do suggest relative stasis in many lineages and persistence of similar environments. A number of studies of fossil associations and gradients, however, has challenged the idea of strongly recurrent marine biofacies (Buzas and Culver, 1994; Jackson, 1994a, 1994b; Patzkowsky and Holland, 1997, 1999; Buzas and Culver, 1994, 1998; Olszewski and Patzkowsky, 2001) for Cenozoic and Paleozoic biotas, even within one of the venues in which a strong degree of species-level and biofacies persistence has been previously claimed—the Middle Devonian of New York State (Bonuso et al., 2002a, 2002b).

The Middle Devonian Hamilton Group and Tully Formation of western and central New York (Figs. 1–3) comprise cyclic offshore marine mudrock, siltstone, and carbonate facies noted for diverse and well-preserved faunas of corals, brachiopods, mollusks, trilobites, echinoderms, and other marine benthic invertebrates (see papers in Brett, 1986; Landing and Brett, 1991; Brett and Baird, 1995, for reviews). The stratigraphic section is well documented, structurally simple, and contains numerous small- and large-scale facies alternations that record high-order sea-level oscillations (Johnson et al., 1985; Brett et al., 1990; Brett and Baird, 1996). Thus, this succession provides an exceptional opportunity to study patterns of biotic change at several scales (e.g., Eldredge and Gould, 1972; Eldredge, 1995). Brett and Baird (1995) used the record of the Hamilton fauna as an exemplar of a pattern of concurrent long-term species-level stasis and abrupt change, which they termed coordinated stasis (see Eldredge 1995, 1999; Brett et al., 1996). Preliminary comparison of the oldest and youngest samples of diverse, coral-rich biofacies of the Hamilton Group further suggested that species composition, relative abundance, and possibly rank abundance of species within biofacies or community types (Bennington and Bambach, 1996) might be maintained for prolonged intervals, up to several million years (Brett and Baird, 1995; Brett et al., 1996). Testing of this preliminary observation, however, requires detailed, quantitative studies of several biofacies or, perhaps more correctly, gradients of species occurrence through several recurring cycles of comparable facies through extended time spans.

Brett et al. (1990) and Brett and Baird (1995) reported a strong degree of compositional and ecological similarity in Silurian–Devonian faunas within stable ecological-evolutionary subunits in the Appalachian Basin,

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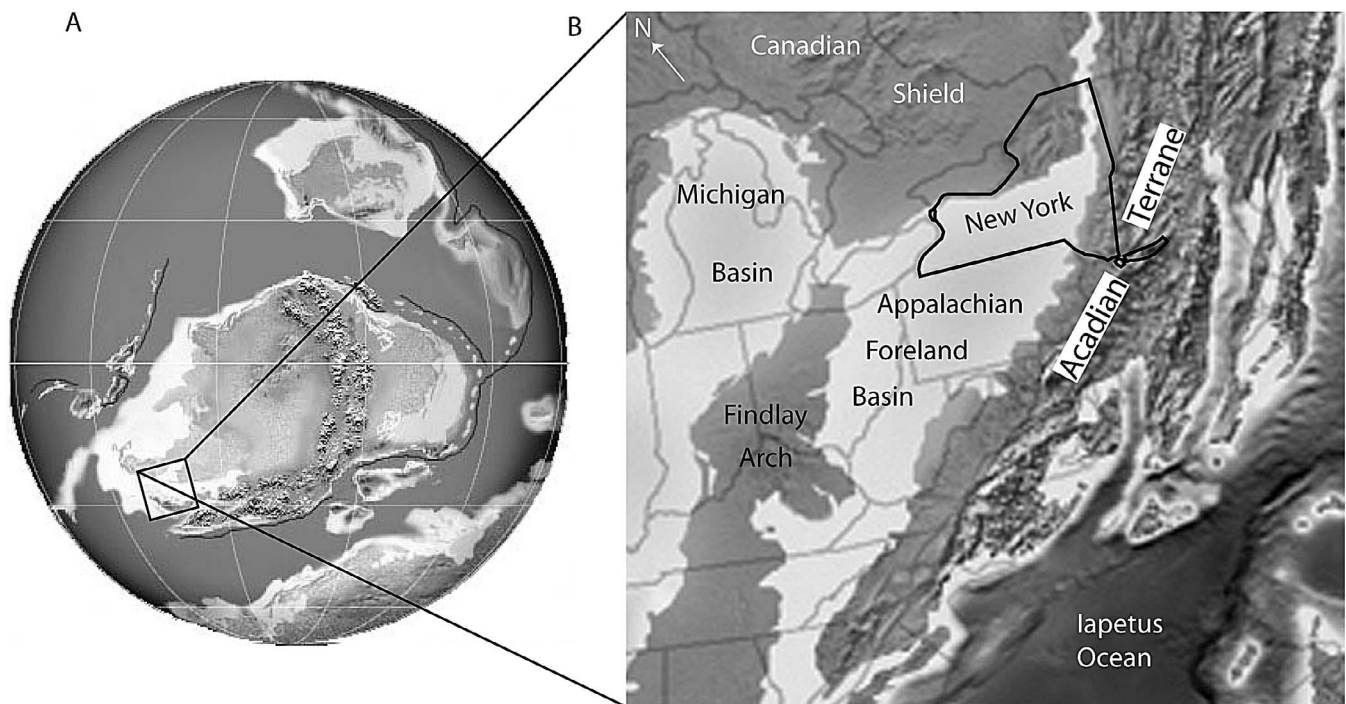


FIGURE 1—Paleogeographic setting for Laurentia during the Middle Devonian. Modified from Blakey (2005).

based largely on presence-absence data. Conversely, Bonuso et al. (2002a) quantitatively documented an apparent failure of a majority of species to persist and a consequent lack of similar biofacies throughout the Hamilton Group in central New York State. Obviously, their results do not accord with Brett and Baird's observations, which indicate that a majority of species and perhaps facies-specific associations of species, or biofacies, do persist through the Hamilton Group. Despite the fact that all samples were derived from a rather uniform gray, noncalcareous mudstone lithology, which Bonuso et al. (2002a, p. 1056) argue represents a single type of environment, the markedly different diversities and guild structures of various associations—as well as subtle, but significant differences in facies—strongly suggest that various samples were derived from different environments and do not form a completely fair comparison. Furthermore, Bonuso et al.'s samples were all derived from a single geographic region, in the vicinity of Syracuse, New York, and therefore may not be representative of the basin at large.

The degree of similarity or dissimilarity of recurrent biofacies can only be tested fairly by examining samples from along the outcrop belt as a whole and sampling the most closely similar facies, wherever they occur. Here we present an analysis of such data, which indicate that similar, though not identical, associations recur throughout the span of the middle-to-upper Hamilton Group and the overlying Tully Limestone but not at any single geographic area. Moreover, the consistent recurrence of rare, stenotopic species only in associations with one another and the recurrence of similar gradients of composition in shallowing- and deepening-upward phases of several cycles suggest that species associations persisted and tracked shifting environments.

The term tracking, as used in this paper, implies that populations of species were maintained throughout most of the Givetian interval (~5–6 myr) within the Appohimchi Subprovince, defined broadly to include the Appalachian foreland basin and surrounding platforms in eastern North America (Boucot, 1975), rather than being repeatedly restocked from species pools outside of the province (see further discussion in Brett et al., 2007). These populations shifted geographically through time, however, along with their preferred environments. As many species had broadly similar environmental preferences, associations of species also

may have tracked those environments, thus maintaining gradients of species composition through time.

The purposes of this paper are to evaluate patterns of recurrent biofacies in individual cycles of the Hamilton Group, to establish and compare gradients of species composition in relation to relative depth within subsymmetrical shallowing-deepening cycles (see Figure 6), and to compare properties of analogous biofacies through time in terms of diversity, species or genus composition, guild structure, and approximate relative abundance. In a sequence sense, these cycles include the regressive portion (late highstand to falling stage) of one sequence and the transgressive portion of the superjacent sequence; however, because we have worked in relatively basinal sections for which the sequence boundary approaches conformity, we find it convenient to refer to these intervals as shallowing-deepening cycles. The primary emphasis is on comparing samples of analogous biofacies of different age over a broad enough region to evaluate whether they recur with similar patterns of diversity, guild structure, species and genus composition, and relative abundance. Present data do not permit evaluation of similarity in relative (proportional) or rank abundance or evenness of distribution, although more detailed studies of specific biofacies (Sessa et al., 2002; Sessa, 2003; Bonelli, 2003; Bonelli et al., 2006; Brett et al., 2007) do provide data on these aspects, which we discuss here.

GEOLOGIC SETTING OF STUDY AREA

Siliciclastic sediments of the Middle Devonian (Givetian Stage) Hamilton Group accumulated in the northern end of the foreland basin in New York, Ontario, Ohio, and Pennsylvania as part of the Catskill clastic wedge shed from the Acadian Orogen (Fig. 1). The basin axis extended approximately northeast to southwest and was occupied by dysoxic to anoxic deeper water during much of the Devonian (Fig. 1). It was bordered by shallow, muddy carbonate shelf environments to the northwest within the midcontinent platform and Canadian Shield and deltaic clastics to the southeast. The modern outcrop belt cuts obliquely across the facies strike in the central New York area providing natural cross sections (Fig. 2). During the Middle Devonian, eastern Laurentia was situated in the

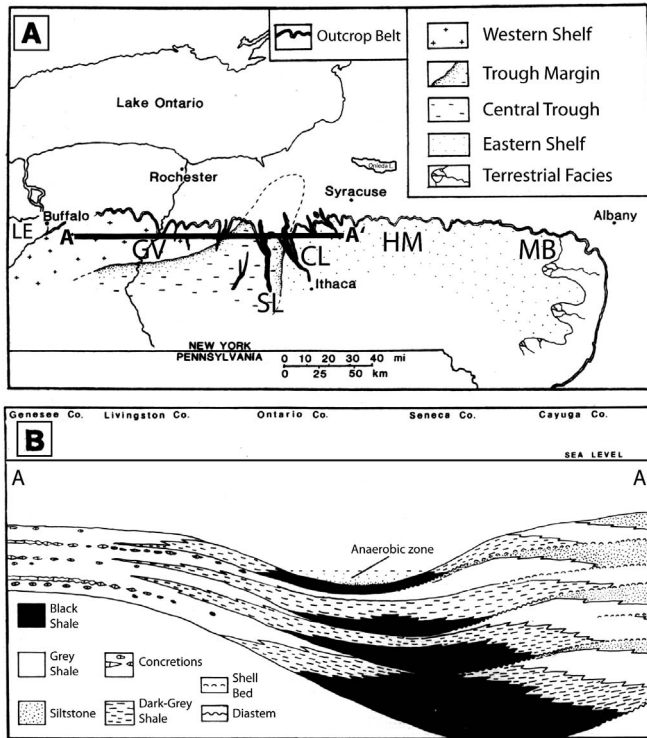


FIGURE 2—A) Outline map of New York State showing outcrop belt, position of main trough of Appalachian Basin, and deltaic areas during deposition of upper Ludlowville Formation. Locations of major study areas for particular intervals: LE = Lake Erie area south of Buffalo; GV = Genesee Valley area; SL = Seneca Lake area; CL = Cayuga Lake area, HM = Chenango Valley, Hamilton area; MB = Middleburgh area. A–A' shows position of cross section in B. B) Schematic cross section showing general westward migration of successive basin centers of the upper Ludlowville–lower Moscow sequences.

southern subtropics to warm temperate latitudes at 30°–35° S (Scotese, 1990; Witzke, 1990; Scotese and McKerrow, 1990; Fig. 1). Closure of the Iapetus Ocean resulted in docking of Avalonia with eastern Laurentia creating the Acadian Orogenic belt in a series of tectophases. Newly uplifting source areas were created during of the second tectophase of the Acadian Orogeny, reflecting oblique collision of the Avalonian terrane with eastern Laurentia (Ettensohn, 1985, 1987). Lithospheric flexure associated with Acadian tectonic loading also produced a retroarc foreland basin in eastern Laurentia extending from Alabama to the Maritime Provinces. A complementary forebulge formed the western rim of this basin, and the foredeep-forebulge couplet may have migrated cratonward through the course of Acadian tectonism (Ettensohn, 1985, 1987, 1998; Fig. 2). Conversely, times of relative tectonic quiescence or initial onset of new tectophases appear to have been characterized by retrograde, orogenward migration of the basin-forebulge couplet; this pattern is evident in the uppermost Hamilton Group and overlying Tully Formation (Heckel, 1973; Baird and Brett, 2003).

This latter observation is particularly important in this study because it implies that given localities experienced complex histories through time resulting both from allocyclic and probably eustatic changes in sea level and shifting basin-forebulge and depocenter geometries (Fig. 2). Thus, conditions appropriate to particular species or biofacies did not recur precisely in a given location through all successive cycles (Brett and Baird, 1996; Fig. 2B). Lower portions of the Hamilton Group in western-central New York are almost completely confined to deeper basinal anoxic to dysoxic shale facies. The degree of similarity of shallow oxic biofacies, typical of much of the upper Hamilton Group, cannot be tested for this area during this time interval. Moreover, because of the increasing progradation of siliciclastic sediments into the basin through time, calcareous, fossiliferous mudrock facies, typical of low-sedimentation areas,

were displaced successively further westward through time. Coral-rich calcareous beds in the Oatka Creek Formation, near the base of the Hamilton Group, occur only in eastern New York; those of the Skaneateles Formation occur in central New York; and those of the upper Hamilton Ludlowville and Moscow Formations occur in west-central to western New York (Figs. 2–3).

Strata of the latest Eifelian and Givetian stages (*Polygnathus ensensis* to *P. ansatus* conodont zones; Klapper, 1981) have been subdivided into a series of depositional sequences, approximately equivalent to four formations of the Hamilton Group (Oatka Creek, Skaneateles, Ludlowville, and Moscow Formations) and the Tully Formation (Fig. 4). These formations have been correlated widely within the northern Appalachian Basin (Brett and Baird, 1996; Bartholomew et al., 2006) and thus appear to reflect eustatic oscillations. Each depositional sequence commences with thin (0.3–10 m) but very widespread transgressive carbonates and calcareous shales and siltstones, such as the Stafford-Mottville, Stone Mill–Centerfield, and Tichenor–Portland Point members. These condensed fossiliferous intervals are overlain in western New York and Ontario by black-to-dark-gray shales and gray calcareous mudstones representing highstand-to-regressive systems tracts. In central New York and Pennsylvania the main, highstand-to-regressive portion of each formation consists of dark-gray shales, silty mudstones, siltstones, and sandstones. In areas sufficiently removed from heavy input of siliciclastics, however, such as western New York and southwestern Ontario, regressive portions of sequences are characterized by thin calcareous and fossiliferous facies that closely mirror those of the overlying transgressive systems tracts.

As noted, the Appohimchi Subprovince of the Eastern Americas Biogeographic Realm included the Appalachian Basin and surrounding mid-continent and Canadian Shield platforms. This biogeographic region, however, was partially isolated from the Michigan Basin Subprovince to the northwest and shared many genera but relatively few species.

DATA AND METHODS

Characterization of Individual Cycles

This study began with the recognition of consistent ordering of species in nearly symmetrical shallowing-deepening cycles of the Hamilton Group in western and central New York State (Fig. 4). To characterize gradients of biofacies change, we sampled two shallowing-deepening (or regressive-transgressive) cycles of comparable thickness (3–5 m) and lithology at two localities: (1) the Mottville Limestone (Skaneateles Formation) in the vicinity of the Tully Valley, South Onondaga Quadrangle, and (2) the Centerfield Limestone (Ludlowville Formation) in the Genesee Quadrangle, western New York (Figs. 3–4). These cycles commence with dark-gray-to-black shale and pass upward into calcareous shale and mudstone, with coral-rich argillaceous limestone beds at cycle centers. We documented patterns that we recognized visually by obtaining approximately equal-sized bulk samples of mudstone (~10 kg, or the contents of two gallon-sized plastic bags) at regular decimeter intervals throughout the cyclic intervals (Fig. 5); in most cases these samples yielded 250–300 identifiable specimens. Thicker limestones could be assessed only by examining weathered surfaces and making field censuses; when possible we tallied at least 200 specimens from these surfaces.

We identified all specimens of brachiopods, mollusks, and trilobites in the bulk samples to species level. A majority of Hamilton genera are monospecific, but others may have as many as 10 distinct species. Within the Hamilton Group, certain species of the same genus occur consistently in different biofacies; therefore identification only to genus level would blur some distinctive features of biotic distribution. In most cases, these species are readily distinguished (e.g., several species of the bivalve *Palaeoneilo*) and are sufficiently distinctive that they would not be synonymized by detailed study. Some species designations, however, may be overly lumped and actually comprise complexes of species. For example, recent detailed study of certain Middle Devonian taxa, long judged to represent persistent species (e.g., Cleland, 1903; Brett and Baird, 1995),

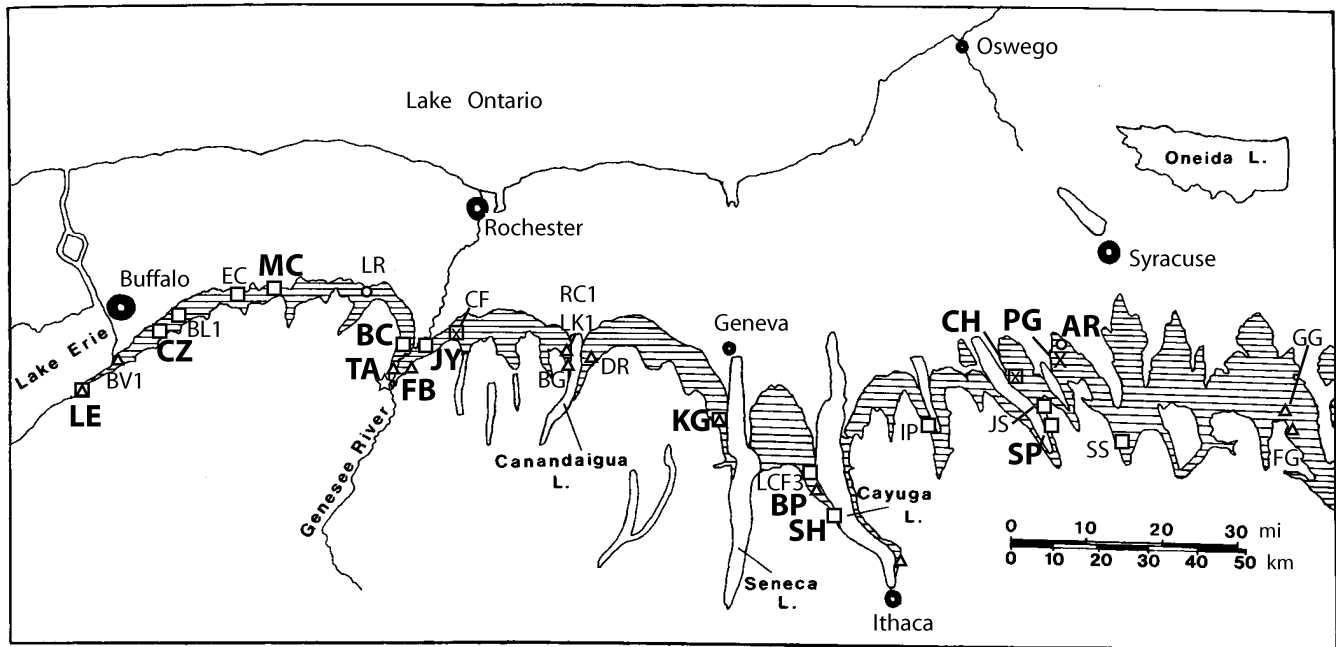


FIGURE 3—Map of western-central New York State showing locations of most samples used in this study coded to sections described in Supplementary Data.¹ Sections for Halihan Hill bed and Windom Shale–West Brook Shale sections (Hamilton–Chenango Valley, east of the area shown) are indicated on Figure 2. Numbers indicate locations of sampling sites. Certain major localities include several sampling sites; these are indicated in bold letters; symbols used to denote localities indicate the cycle sampled: circle = Oatka Creek Cycle (I), x = Skaneateles Cycle (II), square = Ludlowville Cycle (III), triangle = Moscow Cycle (IV), star = upper Tully Cycle (VI). The locations and their included samples are as follows, from west to east (abbreviations in parentheses give horizons sampled, coded to the Supplementary Data¹): LE = Lake Erie shore near the mouth of Eighteenmile Creek (BV1, MW3); CZ = Cazenovia Creek near Spring Brook (MW2–3, BL1); MC = Murder Creek, Darien (DC, MC1); BC = Browns Creek, York (LCF2, LL1); TA = Taunton Gully, Leicester (TA1, TA2, SP, BB); JY = Jaycox Run–Wheeler Gully, Genesee (UCF, HG, JAY1, DR); KG = Kashong Glen near Bellona (MW4, JAY2, LK2, RC2); BP = Barnum Creek shale pit (FG1, FB2); SH = Sheldrake Creek and point (UL, BL2); CH = Coon Hill Road ditch (BUT, PG1, LCF1); SP = Staghorn Point, Skaneateles Lake (LOT, UOT); PG = Peppermill Gulf (MV, MVD, PY, SR); AR = Abbey Road cut (CA).

indicate that minute but consistent differences may exist between populations of different age that could warrant further species splitting (see, e.g., Lieberman and Kloc, 1997, on asteropygine trilobites).

In counting specimens, we used the largest number of a particular valve (pedical or brachial) for most brachiopods, but for subequal valved taxa and bivalved mollusks, we halved the total count. For trilobites, we used the largest number of a single part. We converted counts of bulk samples and field estimates of abundance to approximate relative abundance categories, defined by the approximate number of specimens per hundred collected: rare, <5; uncommon, 6–10; common, 11–20; and abundant, >20. For purposes of weighting species in cluster and gradient analysis, we assigned relative abundance categories values of 4 for rare, 8 for uncommon, 12 for common, and 16 for abundant, following the conventions similar to those of Holland et al. (2001). This method of coding for relative abundance may inflate the importance of rare species and devalue the importance of abundant species. But, if anything, this biases results against the finding of similarity among samples, as rare species are less likely to be preserved or recognized in samples. We used these relative abundance categories because they permitted estimates of the importance of fragmentary and clonal organisms and also permitted incorporation of data from the literature.

Because of the difficulty of counting disarticulated crinoid material and fragmentary colonial corals and bryozoans, we noted the presence of such material as abundant, common, uncommon, and rare using the criteria given above but applied to fragments. We acknowledge that this method could overestimate the abundance of fragmentary material, but this was a minor component of most samples.

We examined patterns of vertical faunal replacement for consistency in the ordering of appearance and disappearance and relative abundance of taxa within single well-constrained cycles. This patterning is demonstrated in Figure 5, where we ordered species occurrences (denoted by dots of varying diameter to reflect approximate relative abundance) in

terms of first appearance and abundance in samples. This ordering shows when several species occurred for the first time together in the same sample. Biofacies were identified quantitatively on the basis of Q- and R-mode cluster analysis of samples and species, respectively, using the Bray–Curtis similarity coefficient. This procedure was performed for the Centerfield cycle in western New York (Figs. 6–7), using the data set of Savarese et al. (1986) and, again, for all samples from the Hamilton Group of western and central New York (Fig. 8). Detrended correspondence analysis (DCA) was used to quantify gradients of faunal distribution within individual cycles (see Holland et al., 2001; Scarponi and Kowalewski, 2004, for discussion of application in fossil data). Q-mode DCA axis 1 scores were then plotted against the stratigraphic succession to document cyclicity quantitatively (Fig. 7).

Testing for Patterns of Biofacies Consistency in the Givetian Interval

To better examine patterns of biofacies recurrence in the full lower-to-middle Givetian interval (~5–6 myr), we analyzed relative abundance data from samples representative of comparable facies throughout the Middle Devonian Hamilton Group and the overlying Tully Formation (Fig. 4). Figure 4 shows a matrix of sampled biofacies plotted against the stratigraphy of the Hamilton Group parsed according to conodont zonation and scaled to the relative time duration estimated for each zone on the basis of cyclostratigraphy by House (1995). In contrast to previous studies in which all samples were obtained from a restricted geographic area (e.g., Savarese et al., 1986; Brower, 1987; Brower and Nye, 1991; Bonuso et al., 2002a), we derived samples for this study from analogous lithofacies and taphofacies, wherever they occurred in the New York outcrop of the basin for particular ages. That is, samples were controlled for similarity of facies, rather than geographic location (Figs. 3, 5).

¹ www.sepm.org/archive/index.html

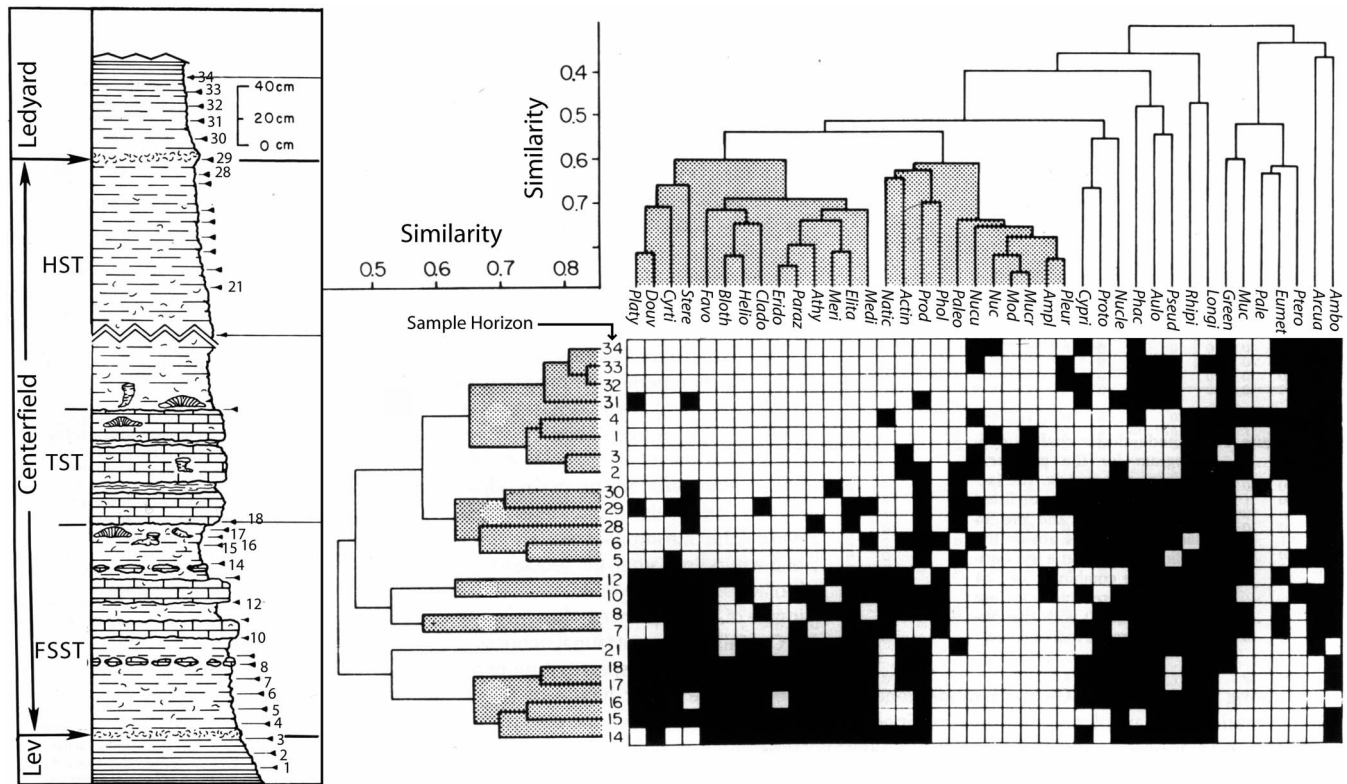


FIGURE 6—Two-way cluster analysis of 40 taxa and 23 samples from a symmetrical cycle in the Centerfield Member; section from the Genesee Valley composite section at Browns Creek, near York and Trihammer Falls, Genesee, Livingston County, New York; certain sample numbers are not represented because sample sizes were small (Platy = *Platyceras*; Douv = *Protodouvillina*; Cytri = *Cyrtina*; Stere = *Stereolasma*; Favo = *Favosites*; Bloth = *Blothrophyllum*; Helio = *Heliophyllum*; Clado = *Cladopora*; Erido = *Eridophyllum*; Paraz = *Parazyga*; Athy = *Athyris*; Meri = *Meristella*; Elita = *Elita*; Medi = *Mediospirifer*; Nati = *Naticonema*; Actin = *Actinopteria*; Prod = *Productella*; Paleo = *Paleoneilo*; Nucul = *Nuculites*; Nuc = *Nuculoidea*; Mod = *Modiomorpha*; Mucr = *Mucroclipeus*; Ampl = *Amplexiphyllum*; Pleur = *Pleurodictyum*; Cypri = *Cypricardina*; Proto = *Protoleptostrophia*; Nucl = *Nucleospira*; Phac = *Phacopids*; Aulo = *Aulocystis*; Pseud = *Pseudoatrypa*; Rhipi = *Rhipidomella*; Longi = *Longispina*; Green = *Greenops*; Muc = *Mucrospirifer*; Pale = *Paleozygopleura*; Eumet = *Eumetabolotoechia*; Ptero = *Pterochaenia*; Arcua = *Arcuaminites*; Ambo = *Ambocoelia*). Sequence stratigraphic abbreviations as in Figure 5 (from Savarese et al., 1986).

approximate relative abundance values for samples of each biofacies in calculating relative proportions of life habit and trophic groups.

Patterns of similarity among samples assigned to biofacies on the basis of cluster analysis are compared in Table 1. For each sample, we determined an estimate of species richness by simply counting species present. In addition, we made pairwise comparisons between all samples and computed percentages of species shared in common (Table 1). In making these comparisons, we employed both raw numbers of species and culled data sets. Only very rare singletons—that is, species that were identified based on one or two specimens at single localities—were deleted in these calculations. Finally, we tabulated relative eurytopy of species (occurrence within the eight biofacies recognized in this study) and the ubiquity of distribution of species (number of samples of occurrence among all 58 samples) in Table 2.

RESULTS

Biofacies and Gradients in Single Cycles

Vertical Gradients of Species Replacement.—As noted, symmetrical cycles such as the Mottville in central New York and the Centerfield Member in western New York show strong evidence for shallowing-deepening patterns. Evidence for shallowing-upward as well as increased oxygenation toward the cycle centers includes: (1) increased silt and carbonate content upward (correlative parts of these cycles in eastern areas show a distinctly coarsening upward pattern; see Brett and Baird, 1985), (2) upward change from black, laminated shale with rare threadlike burrows to *Zoophycos*-bioturbated mudstones, (3) increased abundance of

storm-disturbed beds (Savarese et al., 1986), and (4) upward increased abundance and diversity of microendolithic borings of photoautotrophs (Vogel et al., 1987). Thus, faunal changes within these cycles are reasonably related to changing water depth (Fig. 5).

Figure 5 shows the pattern of occurrence and relative abundance of typical species arranged in order of first appearance in bulk samples, upward through the section and the consequent pattern of gradual faunal replacement, and through the basal regressive-transgressive cycles of the Skaneateles and Ludlowville major third order. The order of addition of species is similar, though not identical, in both cases and forms a roughly V-shaped, subsymmetrical pattern, especially in the well-preserved Centerfield cycle. Note that certain species that occur lowest in the cycle, such as *Eumetabolotoechia multicostum*, largely or completely disappear in the shallow center of the cycle but reappear in higher samples. Other species, such as *Ambocoelia umbonata* and *Arcuaminites scitulus*, which appear relatively low in the cycle, persist through much or all of the shallowing, albeit in greatly reduced numbers, and become common again during the deepening (transgressive phase). Species that occur near the cycle center are apparently shallow-water stenotopes. Note also the tendency of additive species diversity and thus a trend toward increasing species richness in shallower water facies toward the centers of the cycles.

Cluster Analysis.—Figure 6 shows a Q- versus R-mode plot of species in samples based on data from relatively small but uniform-sized (<10 kg) samples from the Centerfield Limestone basal cycle in western New York (Savarese et al., 1986). This analysis was used to recognize the major biofacies of a well-defined cycle developed in relatively abbreviated, low-sedimentation facies. Note that the biofacies recognized in this

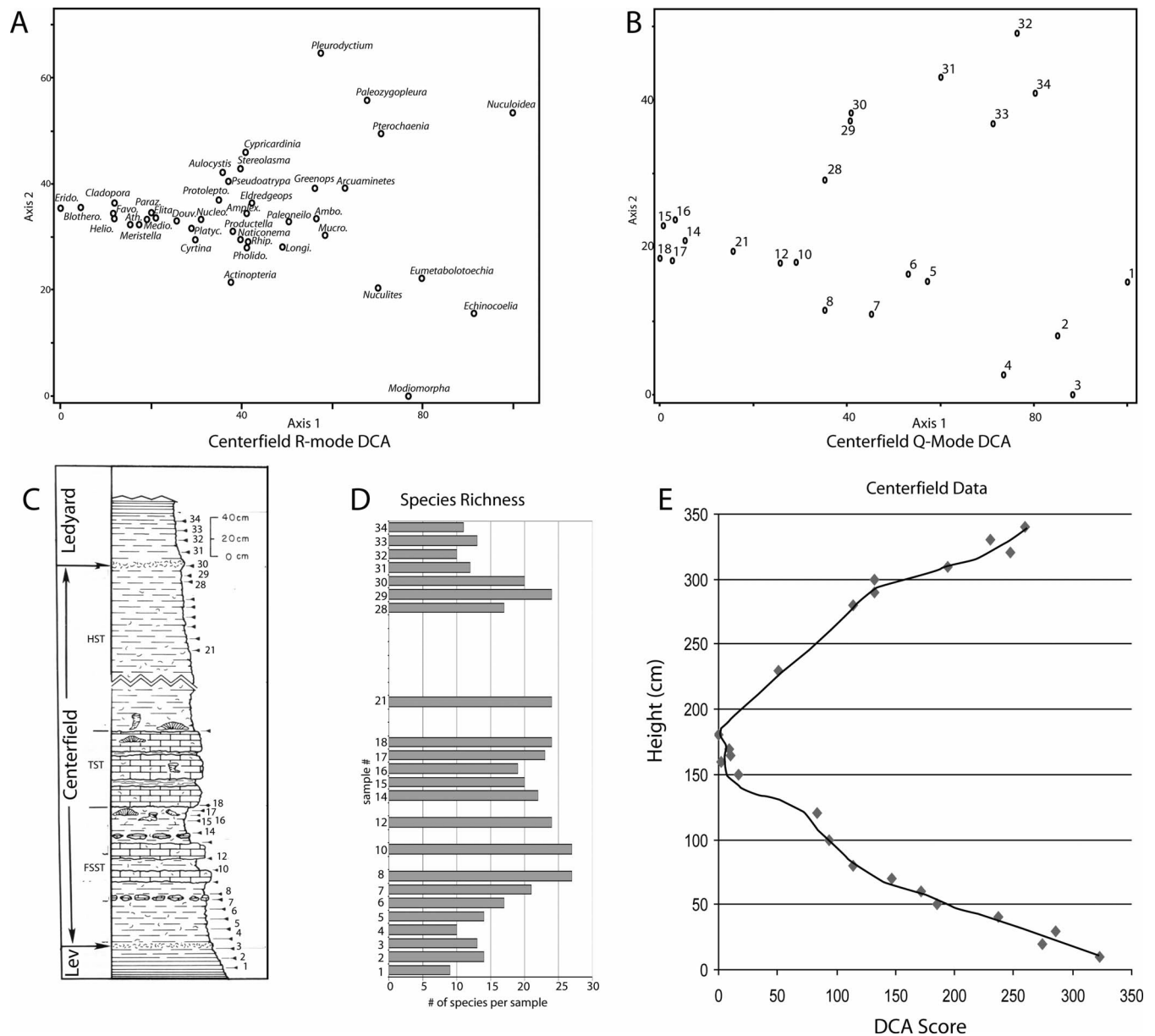


FIGURE 7—Faunal replacement and cyclicity in the Centerfield Member, Ludlowville Formation. A) R-mode DCA axis 1 vs. axis 2 plot for 40 genera (*Ambo.* = *Ambocoelia*, *Amplex.* = *Amplexiphyllum*, *Blothro.* = *Blothrophyllyum*, *Douv.* = *Protodouwillina*, *Erido.* = *Eridophyllum*, *Favo.* = *Favosites*, *Helio.* = *Heliophyllum*, *Medio.* = *Mediospirifer*, *Mucro.* = *Mucrospirifer*, *Nucleo.* = *Nucleospira*, *Platyc.* = *Platyceras*, *Protolepto.* = *Protoleptostrophia*). B) Q-mode DCA axis 1 vs. axis 2 plot for 28 samples. C) Stratigraphic section. D) Species richness vs. sample position. E) DCA axis 1 scores vs. sample position showing nearly symmetrical cycle. Data from Savarese et al. (1986).

analysis also are arrayed symmetrically in the cycle and thus show the same pattern as revealed by the order of appearance of taxa.

DCA Results.—Ordination of the relative abundance data using DCA revealed a very strong gradient along axis 1 (DCA axis 1; Fig. 7). Figure 7 shows both R- and Q-mode DCA axis 1 versus axis 2 plots for the well-defined Centerfield cycle in western New York based on the data set of Savarese et al. (1986). The R-mode DCA axis 1 versus axis 2 plot shows distribution of species along a similar, putatively depth-related gradient. Species typical of the high-diversity Diverse Coral Bed Biofacies, recognized in cluster analysis, yield low DCA axis 1 scores (Fig. 7A, far left), followed by members of the Diverse Brachiopod and *Ambocoelia*-Chonetid Biofacies and finally those of the low-diversity *Eumetabolotoechia* Biofacies (high DCA axis 1 scores, far right).

The order of sample numbers upward through the inferred shallowing portion of the cycle (samples 1–18) is expressed in the Q-mode plot (Fig.

7B) with lowest (deepest and most dysoxic facies) at the far right (high DCA axis 1 scores) and shallow, coral-rich samples near the cycle center to the left (low DCA axis 1 scores). Likewise, samples from the deepening-upward (transgressive) part of the cycle (samples 28–34) show the reverse progression of increasing DCA axis 1 scores, although they are separated from samples of the analogous portion of the regressive transition along axis 2, which is a reflection primarily of different proportions of *Ambocoelia* versus chonetid brachiopods in lower versus upper samples.

Plotting DCA axis 1 scores of samples against the stratigraphic section yields a strong and relatively symmetrical pattern, mirroring the lithological cycle and further delineating a pattern of symmetrical replacement (Fig. 7E). These results are similar to those observed in other studies of faunal data in which DCA axis 1 scores have been interpreted as a reflection of relative bathymetry (Holland et al., 2001; Holland and Patzkowsky, 2004; Scarponi and Kowalewski, 2004).

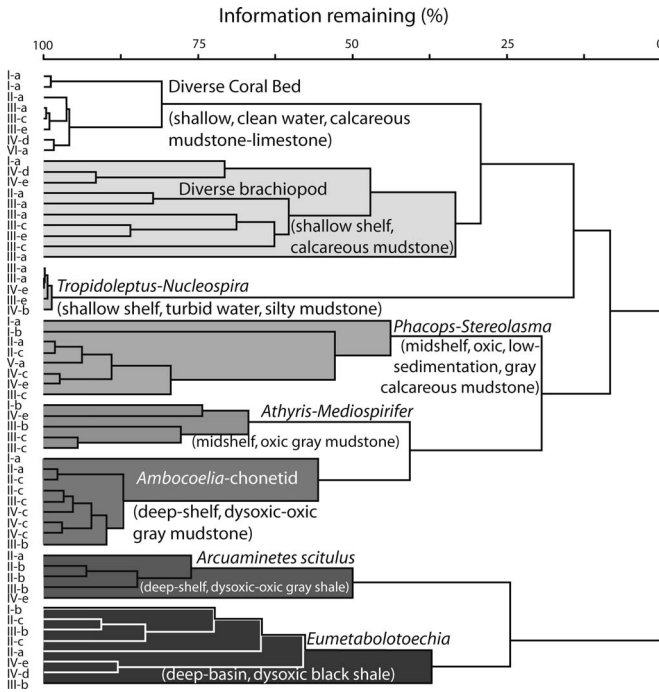


FIGURE 8—Q-mode cluster analysis of representative samples of biofacies from throughout the Hamilton Group. Biofacies (see Fig. 5 for letter designations) cluster together in all cases. In each major cluster (defined at >0.4 similarity level), however, samples from the lowest cycle are less tightly clustered than others. This is most pronounced for the low-diversity biofacies (e.g., *Eumetabolotoechia*) and least for the high-diversity Diverse Coral Bed Biofacies.

Biofacies Recurrence and Gradients in the Entire Hamilton–Tully Interval

Cluster Analysis.—On the basis of Q-mode cluster analysis, the 58 large samples distributed throughout the Hamilton–Tully interval (Fig. 8), were assigned to biofacies categories named for dominant taxa: (1) *Eumetabolotoechia multicostum*, (2) *Arcuaminites scitulus*, (3) *Ambocoelia umbonata* and small chonetids, (4) *Athyris* spp.–*Mediospirifer audaculus*, (5) *Stereolasma rectum*–*Eldredgeops rana*, (6) *Tropidoleptus carinatus*–*Nucleospira concinna*, (7) Diverse Brachiopod Biofacies (at least three species of larger strophomenid or atrypid brachiopods), and (8) Diverse Coral Bed Biofacies (abundant large rugose and tabulate corals). This suite of biofacies spans the full range of depth-related associations present in a typical cycle in western to west-central New York, as previously recognized qualitatively based on order of appearance and cluster analysis of particular taxa in single Hamilton cycles (Figs. 6–7); they are also consistent with, but are somewhat more precisely defined than, the biofacies recognized in single cycle studies. In all cases, qualitatively recognized biofacies were grouped together by Q-mode cluster analysis of relative abundance data for all species, despite marked differences in age (Fig. 8). The oldest samples (Halihan Hill cycle) of low-diversity biofacies clustered at a considerably lower level of similarity than the other samples (Fig. 8), but they are still within the same basic biofacies groupings. This difference reflects genuine differences in taxonomic composition of these oldest Hamilton samples, notably the presence of the brachiopods *Hallinetes lineatus* and *Coelospira camilla*, which are absent in all higher samples. Samples of the Diverse Coral Bed Biofacies, however, still clustered with other samples at a high similarity, as previously noted (Brett and Baird, 1995).

DCA Results.—Ordination of the relative abundance data for all 58 samples using DCA in each case again revealed a very strong gradient along DCA axis 1 (Figs. 9–10). The results of DCA for the larger set of biofacies samples encompassing the entire Hamilton–Tully interval yielded results strikingly similar to those of a single cycle. R-mode analysis

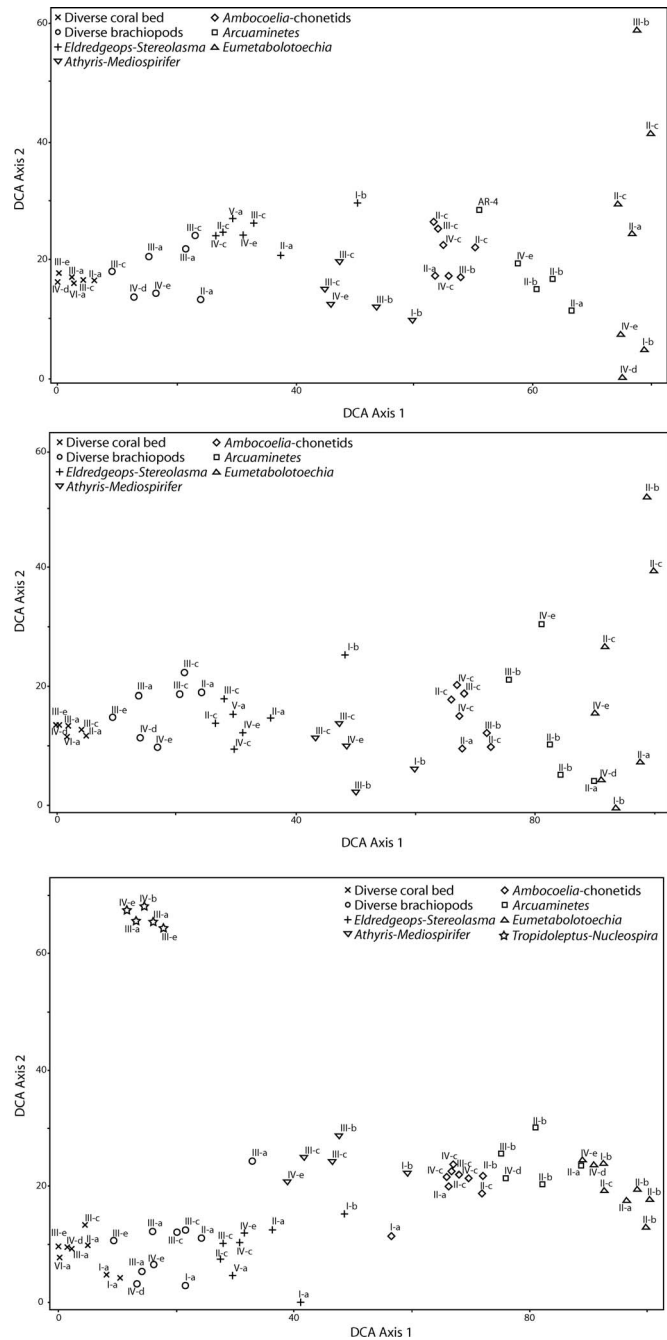


FIGURE 9—Q-mode DCA plots for upper Hamilton–Tully samples. A) All 58 samples (from lowest Hamilton fauna, Oatka Creek Formation to highest cycle, West Brook bed, Tully Formation). Note that *Tropidoleptus-Nucleospira* (TN) Biofacies forms outlier along DCA axis 2. B) All data excluding the *Tropidoleptus-Nucleospira*-rich set. Samples of the lowest cycle (Halihan Hill–LeRoy bed), while plotting with related biofacies along DCA axis 1, form outliers along DCA axis 2. C) Data from corals, brachiopods, trilobites, and bivalves only, with less-abundant groups eliminated; data exclude *Tropidoleptus-Nucleospira*.

again plots taxa similarly to those seen in the Centerfield cycle with diverse coral and brachiopod taxa clumping tightly to the left (low axis 1 scores) and *Eumetabolotoechia* and associated species to the right (Fig. 10).

Q-mode axis 1 versus axis 2 plots again show a very robust pattern of biofacies, which resembles that seen for the single cycle and is only slightly varied when using three different permutations of the data (Fig. 9). Again, samples grouped into biofacies on the basis of cluster analysis

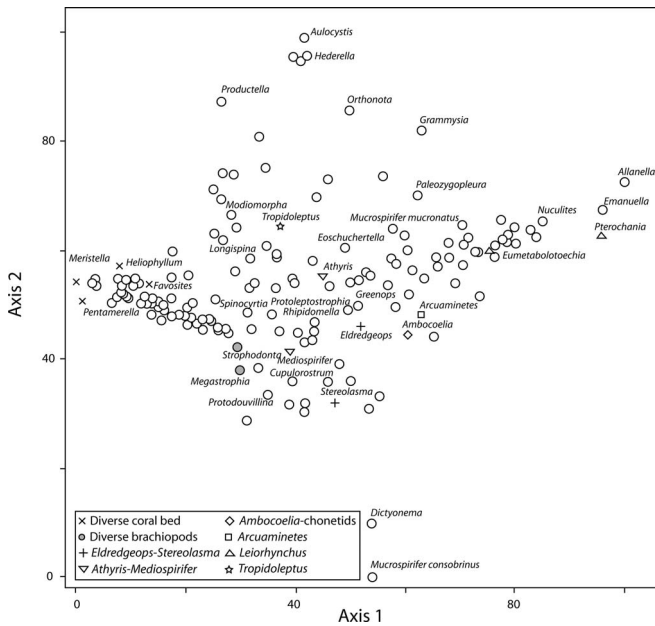


FIGURE 10—R-mode DCA plot of 158 species identified in the 58 samples, with abundant species labeled. Lateral positioning of species along DCA axis 1 approximately coincides with order of first appearance in an individual cycle (see Fig. 5). Key taxa of different biofacies are represented by symbols corresponding to the specific biofacies where they are most common; all other taxa are represented by open circles. Taxa plotting toward the right are from deeper-water facies; taxa plotting on the left from shallow-water facies.

(denoted by different symbols on Fig. 9) are also grouped closely on the DCA plot and form an array that closely parallels the one seen in single shallowing-deepening cycles; putative deep-water biofacies (Figs. 8–9) plot to the far right while shallow high-diversity assemblages plot to the left. As noted, data were used from all 58 samples, including those of the *Tropidoleptus-Nucleospira* biofacies in one run. These latter samples are known to occur in thicker and more sparsely fossiliferous mudstones and have long been interpreted (Brett et al., 1990) as representing a high sedimentation-turbidity analog of the Diverse Brachiopod Biofacies (see Fig. 14). Therefore, it is interesting to note that these samples form an outlier on DCA axis 2, separated well above the main gradient but with similar axis 1 scores to the Diverse Brachiopod Biofacies. Subsequent runs of DCA with the *Tropidoleptus-Nucleospira* samples removed show a similar pattern of biofacies arrayed along axis 1 but with considerable scatter of low-diversity (high axis 1 scoring) samples along axis 2. Removing all taxa except brachiopods, bivalves, corals, and trilobites and eliminating both the *Tropidoleptus-Nucleospira* and the lowest (Halihan Hill–LeRoy bed) samples still produced a very similar pattern. In all cases, the basic depth-related gradient is well illustrated in the ordination.

Ecological Properties of Biofacies

Richness.—Species richness varies from 10 species in the least-diverse sample of the *Eumetabolotoechia* biofacies to 108 species in the most species-rich Diverse Coral Bed Biofacies. For a given biofacies, species richness values for pooled samples were found to be similar from lowest to highest samples with only slight variation (Table 1). Note that these diversities are based on samples, which include all moderately rare to common taxa of megafossils. Average richness ranges from 12–19 species (mean = 16) for the *Eumetabolotoechia* biofacies, to 30–35 species (mean = 33) for the *Ambocoelia*-Chonetid Biofacies, and to 90–105 species (mean = 98) for the Diverse Coral Bed Biofacies (Table 1).

Taxonomic Composition.—The composition of biofacies is also similar through time. Pairwise comparisons of all samples of the same general biofacies identified by Q-mode cluster analysis (Fig. 8; Table 1) show a

generally high degree of similarity in species composition. In pairwise comparisons of faunal composition, there does not appear to be a trend of decreasing similarity for samples separated by increasing age; note that some of the most stratigraphically separated sample pairs are more similar to each other than to intervening samples.

For high-diversity Diverse Coral Bed Biofacies, the similarities are greatest; 79%–90% species (average = 85.8% for 30 pairwise comparisons) were shared between particular samples when rare singletons are culled (Table 1). Indeed, 71 of the total recognized pool of 125 species, or 56.8% (culling rare singletons yielded a slightly higher 63.6%), were found to be present in all samples, from the Mottville Limestone, near the base of the Hamilton Group, and the last known coral bed in the West Brook bed of the Tully Formation.

Figure 11A shows a representation of the top 10 most abundant taxa from four separate horizons of the Diverse Coral Bed Biofacies, including the lowest and highest beds of this biofacies (Halihan Hill and West Brook beds). All of the top 10 taxa in these beds have a common abundance, and four of the taxa appear in all horizons (Fig. 11A). The two horizons from the middle portion of the Hamilton Group, the Mottville and Centerfield beds, are identical in their top 10 taxa (Fig. 11A), with the Halihan Hill Bed differing from these by only one taxon, demonstrating an overall strong signal of compositional consistency for this biofacies.

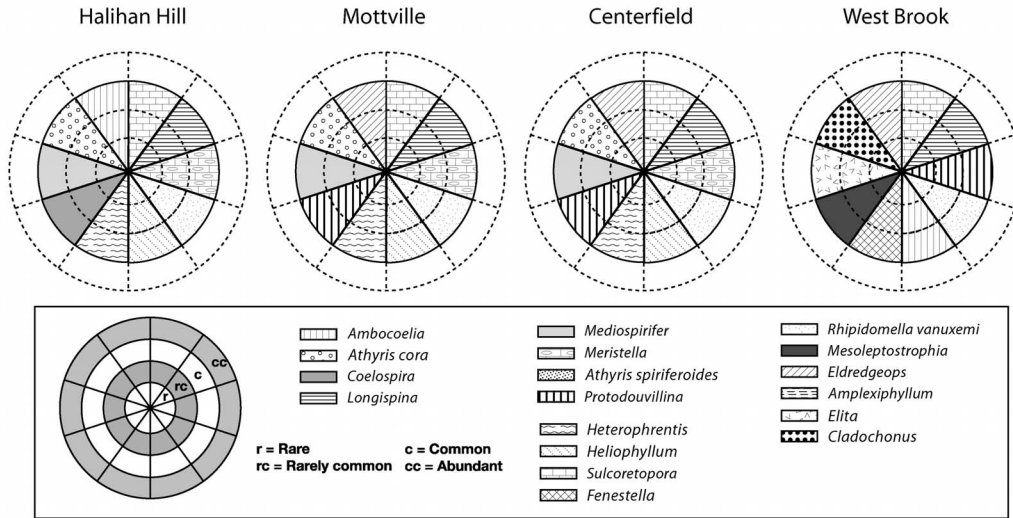
For an intermediate diversity association, the *Ambocoelia*-Chonetid Biofacies, the similarities were slightly lower, 68.6%–97% (average = 82.9% for 42 pairwise comparisons; Table 1). This reflects a larger number of rare taxa that occur in only a few samples; only 17 of the pool of 62 species, or 27.4%, occur in all seven samples. This proportion is considerably improved if rare taxa, found in only one or two samples, are culled. The top 10 taxa for four separate horizons representing this biofacies are very similar with taxonomic composition of the three samples from the Ludlowville and Moscow Formations, differing only in the relative abundance of a few taxa (Fig. 11B). The lowest sample from the lower Skaneateles Formation differs from the others by only two taxa (Fig. 11B).

In the case of the low-diversity *Eumetabolotoechia* Biofacies, even lower similarities were observed (Table 1). While two samples from adjacent cycles in the Windom Member show strong similarities (83% and 93% of species overlap in respective faunas), most pairwise comparisons show neither very high nor consistent patterns of similarity among successive samples. The overall average percent similarity for all samples (60.7%) reflects not only the variable appearance of a few rare taxa but also the overall low richness of the *Eumetabolotoechia*-dominated biofacies. Difference in presence-absence of a few species has a strong proportional impact. In the list of the top 10 taxa from four separate beds representing this biofacies, six taxa occur in all samples (Fig. 11C). There is certainly a strong indication that these low-diversity associations are very loosely structured, are physically controlled, and may be reassembled into a variety of species combinations while everywhere being dominated by a few taxa. Of the latter, *Eumetabolotoechia multicostum* itself and *Pterochaenia fragilis* appear relatively stenotopic to these dysoxic settings, but most other species are generalists that can be present in most other biofacies. We suggest that their occurrence in the *Eumetabolotoechia* Biofacies may partly represent chance larval dispersal and partly be a function of the level of oxygenation. *E. multicostum* is abundant in all of the four samples in which the top 10 taxa were calculated, with most of the other taxa in the top 10 list being uncommon (Fig. 11C). In the Gage Gully samples, five of the top 10 taxa are rare, indicating the overall low diversity of this biofacies. Nearly monospecific assemblages of *E. multicostum* are present in black, laminated facies, and these may represent the extreme end member of dysoxic facies. Such samples were not included in this study, although at least two samples may have bordered on this condition.

We conclude that there is generally a greater consistency of composition from sample to sample for the higher-diversity biofacies than for low-diversity associations. This greater uniformity of composition in di-

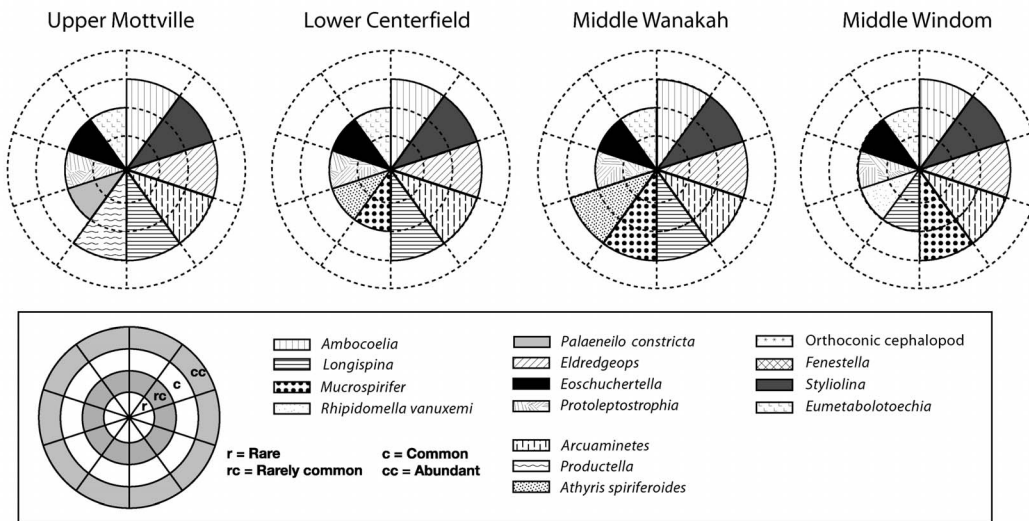
A

Diverse Coral Bed Biofacies



B

Ambocoelia-Chonetid Biofacies



C

Eumetabolotoechia Biofacies

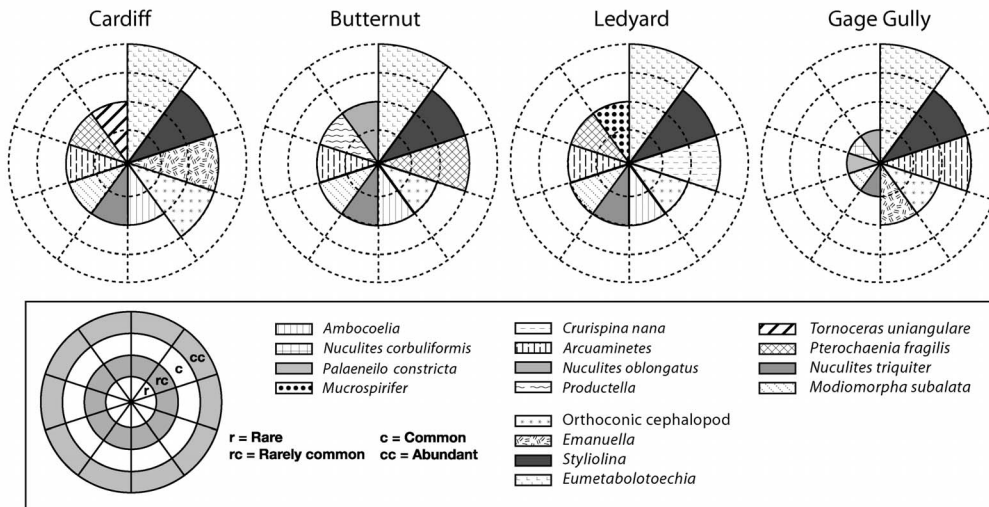


FIGURE 11—Polar diagrams displaying the top 10 taxa in each of 3 biofacies (combined samples from 4 horizons from each biofacies). A) Diverse Coral Bed Biofacies. B) *Ambocoelia*-Chonetid Biofacies. C) *Eumetabolotoechia* Biofacies. Distance of shading outward from the center of the diagram represents relative abundance of each taxon in that sample; see Supplementary Data!

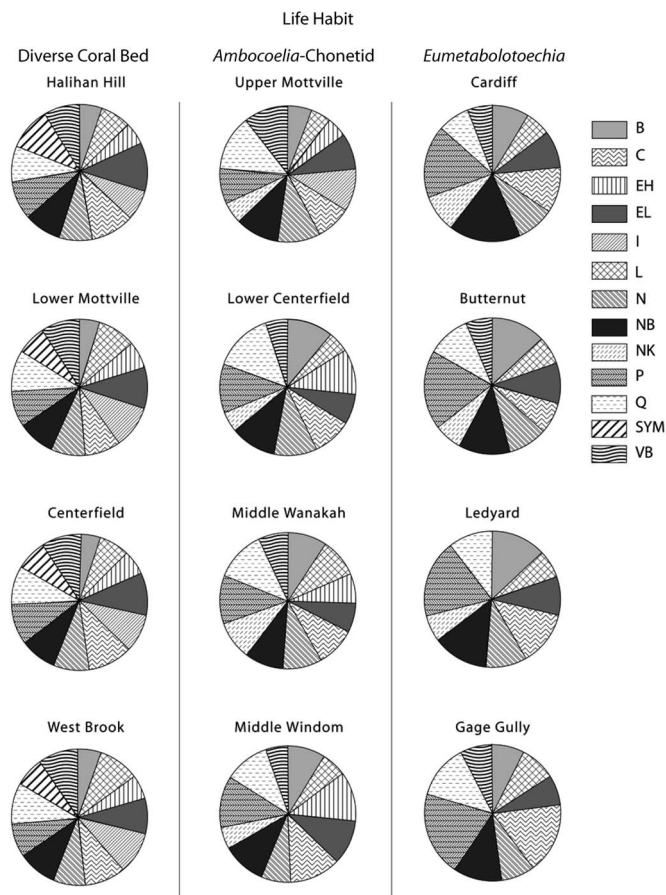


FIGURE 12—Pie diagrams showing relative proportions of life habit groups for various samples. Diverse Coral Bed Biofacies; *Ambocoelia*-Chonetid Biofacies; *Eumetabolotoechia* Biofacies. Note general similarity of proportions for Diverse Coral Bed Biofacies and substantially less similarity for lower-diversity biofacies. B = epibyssate; C = cemented-encrusting; EH = erect epifaunal, high-to-intermediate level (>5 cm above substrate); EL = erect epifaunal, low level (<5 cm above substrate); I = infaunal burrower; L = liberosessile (free lying); N = endobyssate; NB = nektobenthic; P = pedically attached; Q = quasi infaunal; SYM = symbiotic (commensal-parasitic); VB = vagrant epibenthos; see Supplementary Data¹.

verse biofacies is also reflected in the high-level similarity of samples in cluster analysis and in DCA plots (compare Figs. 6, 7, and 10). In the case of high-diversity biofacies, it is evident that the similarity does not simply reflect persistence of long-ranging eurytopic or abundant species (as suggested, e.g., by McKinney, 1996). Indeed, certain rare stenotopes were found to occur in nearly all samples of high-diversity biofacies.

Rank and Absolute Abundance Comparisons of Hamilton Biofacies.—To date, only a few studies have considered absolute or rank abundance in a single biofacies. Present evidence, however, indicates that even within the most similar recurrent assemblages there is substantial variation in this parameter in contrast to results reported from a preliminary analysis of the lowest and highest coral beds of the Hamilton Group (Brett and Baird, 1995).

A detailed case study of the diverse coral and brachiopod biofacies from the Middle Devonian in New York and Pennsylvania documents substantial variation in relative and rank abundance within this biofacies. Bonelli et al. (2006) used a rigorous nested sampling scheme and quantitative analyses to compare compositional and structural variability within and among samples from coral beds in the Hamilton Group and overlying Tully Formation. The coral beds had broadly similar species lists, including rare stenotopic taxa. None of the four latest Hamilton coral beds, however, shared the same species composition or abundance struc-

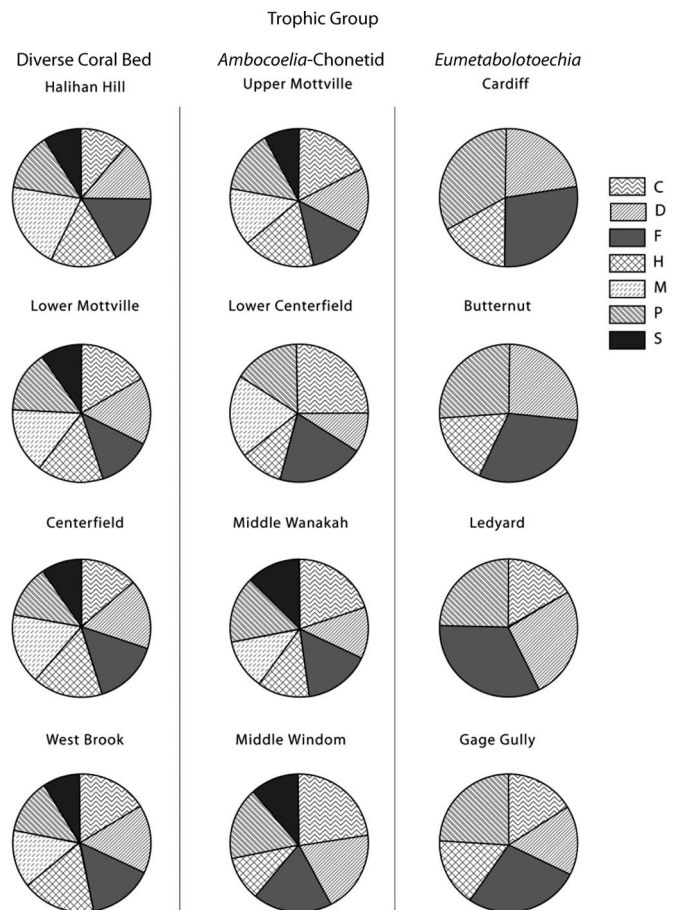


FIGURE 13—Pie diagrams showing relative proportions of trophic groups for various samples. Diverse Coral Bed Biofacies; *Ambocoelia*-Chonetid Biofacies; *Eumetabolotoechia* Biofacies. Note general similarity of proportions for Diverse Coral Bed Biofacies and substantially less similarity for lower-diversity biofacies. C = carnivore-scavenger; D = deposit feeder; F = filter feeder; H = herbivore-grazer; M = microcarnivore (cnidarians); P = predator; S = passive suspension feeder; see Supplementary Data¹.

tures; indeed, there was significantly more variation among coral-rich horizons than within any one horizon.

Bonelli et al. (2006) showed that the abundances of the most common species within successive coral-rich beds varied significantly. As a consequence, lists of dominant species were markedly different among Hamilton and Tully coral-rich horizons. This does not indicate that the differences seen between levels simply reflect chance reassemblies. An alternative explanation is that organisms responded to changes in environmental conditions (e.g., temperature, water chemistry) which shifted the balance in favor of particular species, even though these parameters are not obvious from the sediments.

Guild Structure.—Figures 12 and 13 present pie charts representing the approximate relative abundances of life habit (Fig. 12) and trophic groups (Fig. 13), based on approximate relative abundances of species assigned to various categories, within three distinct biofacies: Diverse Coral Bed, *Ambocoelia*-Chonetid, and *Eumetabolotoechia* assemblages (Figs. 12–13). Again, samples of high-diversity associations from throughout the Hamilton–Tully interval consistently show a large range of guild types in approximately similar proportions. The same is true to a lesser extent for intermediate diversity assemblages. Low-diversity *Eumetabolotoechia* Biofacies, however, show much more heterogeneity in the partitioning of a smaller number of guilds, dominated by epifaunal suspension feeders and shallow burrowing deposit feeders (Figs. 12–13). The lesser degree of similarity in guild structure may in fact indicate that rather distinct types of assemblages have been lumped together (qualitatively and quan-

TABLE 1—Matrices of comparisons among all samples of three biofacies listing the proportion of species in common (as both fraction and percentage) in relation to total species number (less rare singleton species). Number and percentage of species present in different numbers of samples also listed; see Supplementary Data; see Supplementary Data¹.

Comparison of Diverse Coral Bed Biofacies (rare singletons culled)							
	Mottville S = 90	Centerfield S = 104	Wanakah DB S = 104	Jaycox S = 105	Windom Fall Brook S = 94	Tully West Br. S = 91	
Mottville Mbr.	XXXXX	86/104: 86.7 %	84/104: 80.8%	86/105: 81.1%	84/94: 89.4%	80/91: 87.7%	
Centerfield Mbr.	86/90: 95.5%	XXXXX	94/104: 81.1%	94/105: 89.5%	80/94: 85.1%	86/91: 94.5%	
Wanakah Darien Bed	84/90: 93.3%	94/104: 90.4%	XXXXX	97/105: 92.4%	89/94: 94.7%	83/91: 91.2%	
Jaycox Mbr.	86/90: 95.5%	94/104: 90.4%	97/104: 93.3%	XXXXX	89/94: 94.7%	85/91: 93.4%	
Windom Fall Brook Bed	84/90: 93.3%	83/104: 78.8%	89/104: 85.6%	89/105: 84.8%	XXXXX	84/91: 92.3%	
Tully: West Brook Bed	80/90: 88.8%	86/104: 82.7%	83/104: 79.8%	85/105: 86.9%	80/94: 85.1%	XXXXX	
Total N= 125 species		Total Culled = 12 species		Culled N= 113 species			
Species in Each Category	Number in Each	% of Total		% of Culled			
# in six of six	71	56.80%		63.60%			
# in five of six	15	12.00%		13.60%			
# in four of six	15	12.00%		13.60%			
# in three of six	4	3.20%		3.64%			
# in two of six	8	6.40%		6.36%			
# in one of six	12	9.60%					
Comparison of <i>Ambocoelia</i>-chonetid biofacies (rare singletons culled)							
	Pecksport Sh. S = 35	Mottville D S = 34	Centerfield A S = 33	Ledyard Shale S = 35	Wanakah SB S = 30	Windom-1 S = 30	Windom-2 S = 35
Pecksport Shale	XXXXXX	32/34: 97.0%	27/33: 81.8%	30/35: 85.7%	25/30: 83.3%	24/30: 80.0%	28/35: 80.0%
Mottville D	32/35: 94.3%	XXXXX	26/33: 78.8%	27/35: 77.5%	27/30: 90.0%	24/30: 80.0%	28/35: 80.0%
Centerfield A	27/35: 77.1%	26/34: 76.5%	XXXXXX	28/35: 80.0%	25/30: 83.3%	24/30: 80.0%	25/35: 71.4%
Ledyard Shale	30/35: 85.7%	27/34: 79.4%	28/33: 84.8%	XXXXXX	28/30: 93.3%	26/30: 86.6%	29/35: 82.8%
Wanakah Shale Spring Brk	25/35: 71.4%	27/34: 79.4%	21/33: 76.7%	28/35: 80.0%	XXXXX	24/30: 80.0%	28/35: 80.0%
Windom Sh Ambo Bed-1	24/35: 68.6%	24/34: 70.6%	24/33: 68.6%	26/35: 74.3%	24/30: 80.5%	XXXXX	27/35: 77.1%
Windom Sh Ambo Bed-2	28/35: 80.0%	28/34: 82.4%	25/33: 78.1%	29/35: 82.8%	28/30: 93.3%	27/30: 90.0%	XXXXX
Total N= 62 species		Total culled = 26 species		Culled N= 36 species			
Species in Each Category	Number in Each	% of Total		% of Culled			
# in seven of seven	17	27.42%		47.22%			
# in six of seven	6	9.67%		16.67%			
# in five of seven	6	9.67%		16.67%			
# in four of seven	1	1.61%		2.78%			
# in three of seven	6	9.67%		16.67%			
# in two of seven	11	17.74%					
# in one of seven	15	24.19%					
Comparison of <i>Eumetabolotoechia</i> biofacies (rare singletons culled)							
	Cardiff Shale S = 16	Delphi Sta. Sh. S = 12	Butternut Shale S = 19	Levanna Shale S = 16	Ledyard Shale S = 17	Windom Fisher Gully S = 18	Windom Gage Gully S = 16
Cardiff Shale	XXXXXX	8/12: 66.7%	12/19: 63.1%	9/16: 56.3%	9/17: 52.9%	12/18: 66.7%	11/16: 68.75%
Delphi Station Shale	8/16: 50.0%	XXXXXX	9/19: 47.0%	8/16: 50.0%	10/17: 58.0%	8/18: 44.0%	8/16: 50.0%
Butternut Shale	12/16: 75.0%	9/12: 75.0%	XXXXX	11/16: 68.7%	14/17: 82.3%	14/18: 77.8%	12/16: 75.0%
Levanna Shale	9/16: 56.0%	8/12: 66.7%	11/19: 52.9%	XXXXX	12/17: 70.7%	9/18: 50.0%	8/16: 50.0%
Ledyard Shale	9/16: 56.0%		14/19: 73.7%	12/16: 75.0%	XXXXX	12/18: 66.7%	10/16: 62.0%
Windom Sh Fisher Gully	12/16: 75.0%	8/12: 66.7%	14/19: 73.7%	9/16: 56.0%	12/17: 70.5%	XXXXX	15/16: 93.0%
Windom Sh Gage Gully	11/16: 56.0%	8/12: 66.7%	12/19: 63.0%	8/16: 50.0%	10/17: 58.8%	15/18: 83.0%	
Total N= 42 species		Total culled = 12 species		Culled N= 30 species			XXXXX
Species in Each Category	Number in Each	% of Total		% of Culled			
# in seven of seven	5	11.9%		16.7%			
# in six of seven	4	9.5%		13.3%			
# in five of seven	3	7.1%		10%			
# in four of seven	5	11.9%		16.7%			
# in three of seven	6	14.3%		20%			
# in two of seven	7	16.7%		23.3%			
# in one of seven	12	28.6%		40%			

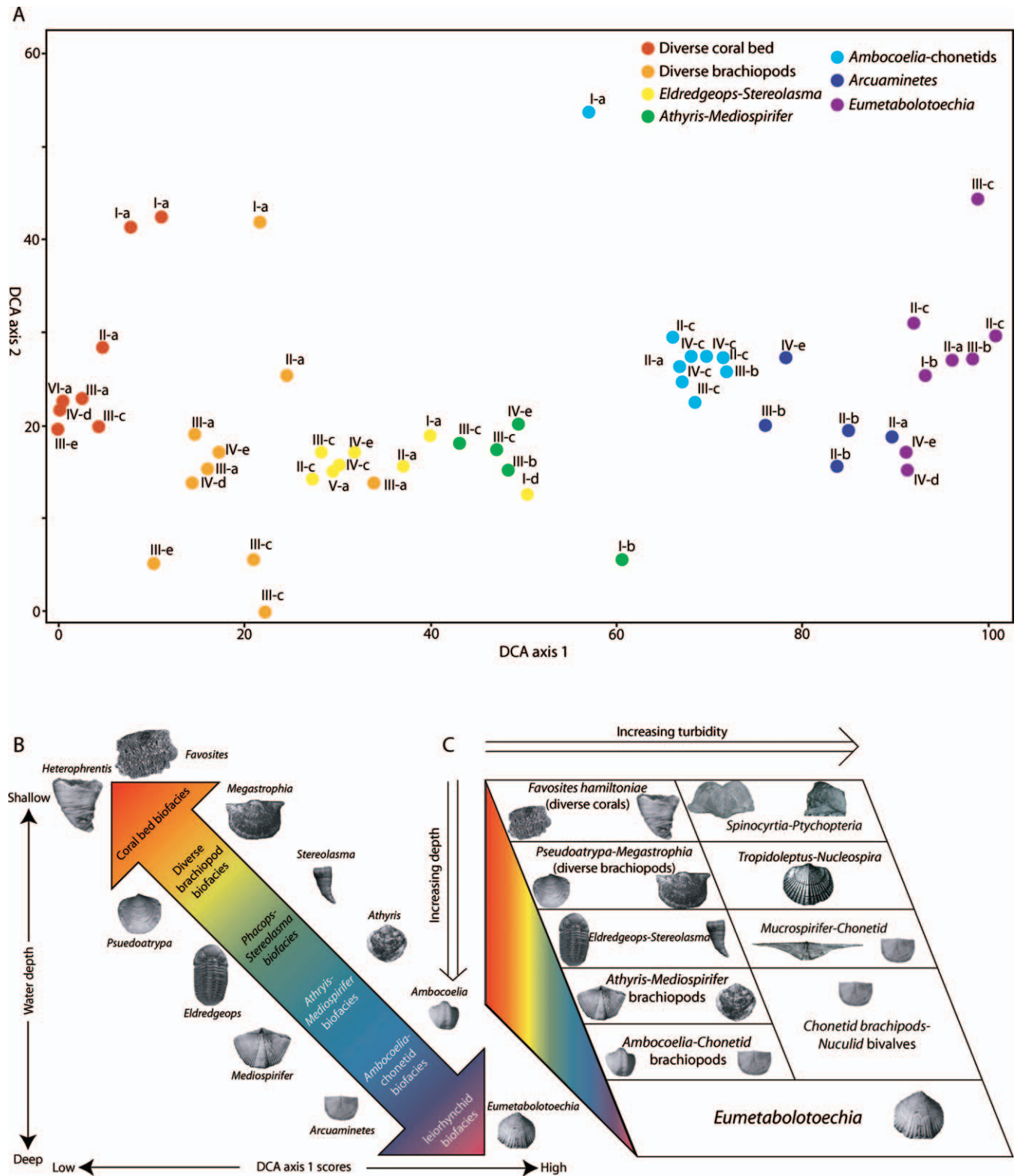


FIGURE 14—Faunal gradients in the Middle Devonian. **A**) Q-mode DCA axis 1 vs. axis 2 scores of samples from seven major biofacies, excluding *Tropidoleptus-Nucleospira*-rich set, showing close grouping of points from cycles of differing age (indicated by numbering). For key to color coding see Figure 5. Note tight grouping of Diverse Coral Bed and Diverse Brachiopod Biofacies, left side of plot (inferred shallow water, diverse brachiopod and coral-rich biofacies), indicating overall close similarities among these diverse samples throughout the ~5 myr time span. **B**) Schematic showing arrangement of peak abundances of common species along DCA axis 1, inferred to represent relative depth in areas of low sedimentation or turbidity, typical of transgressive systems tracts based on gradient analysis as in **A**. **C**) Schematic diagram illustrating position of major biofacies relative to gradients of relative depth and sedimentation rate. Note that axis shown in **B** is equivalent to the left side of this diagram; also note the position of *Tropidoleptus-Nucleospira* Biofacies. *Spinocyrtia-Ptychopteria* Biofacies was not included in present study. Modified from Vogel et al. (1987).

TABLE 2—Eurytopy and ubiquity of Middle Devonian Hamilton species. Eurytopy = number of biofacies (based on Q-mode cluster analysis of 57 samples) in which a species is represented by at least one occurrence; ubiquity = % of samples (out of 57) in which species is present.

Eurytopy index	# of species	% of species	Ubiquity index	# of species	% of species
8	4	2.4	76–100	6	3.6
7	3	1.8	51–75	12	7.3
6	9	5.5	26–50	30	18.2
5	12	7.3	16–25	33	20.0
4	11	6.7	11–15	29	17.6
3	23	13.9	6–10	38	23.0
2	52	31.5	2–5	17	10.3
1	51	30.9	<2		
Total	165	100%	Total	165	100%

titatively) because of the high dominance of the leiorhynchid brachiopod *Eumetabolotoechia*. Moreover, it may suggest that these low-diversity assemblages are poorly structured and capable of reassociating in many different combinations of eurytopic dysoxic adapted species.

Eurytopy and Ubiquity of Taxa.—Table 2 shows the eurytopy relative to the eight biofacies recognized in this study and ubiquity (% of the 58 samples in which a taxon occurs) for common species. Only a single species, *Arcuaminites scitulus* (formerly *Devonochonetes scitulus*; see Bizzarro, 1995), was found in all samples; 19 of 165 species (11.5%) were found in at least half the samples, and 49 (<30%) were found in more than a quarter of the samples. Of the 165 species identified in this study only 4 (2.4%; the brachiopods *Arcuaminites scitulus* and *Protopleptostrophia perplana*, and the trilobites *Eldredgeops rana* and *Greenops* cf. *G. boothi*) were found in all eight biofacies, 3 (1.8%) in seven, 9 (3.5%) in six, and 12 (7.3%) in five; 51 (31%) were found in just a single facies. Not surprisingly, low-diversity biofacies typical of deeper, dysoxic facies contain a very high proportion of eurytopic species, whereas more than half of the species in high-diversity shallow water coral rich assemblages are restricted to that facies.

DISCUSSION

Persistence of Biotic Gradients

Vertical Gradients.—An important comparison involves gradients of biofacies at different stratigraphic levels in the Hamilton–Tully interval. Although more rigorous tests require more detailed sampling of several cycles, two major lines of evidence suggest that the general order of species occurrence along gradients is similar for shallowing–deepening cycles in calcareous mudstone facies throughout the interval (Figs. 5, 14).

A first line of evidence for persistence of nearly similar gradients is provided by the order of appearance of species in cycles separated by considerable periods of time. For example, the nearly symmetrical appearance of taxa in the Centerfield cycle (Fig. 5, top) indicates that approximately the same gradient existed in the transgressive as in the regressive portion of a fourth-order cycle (~10⁵ yr). Moreover, a similar pattern of species replacement is apparent in the Mottville as in the Centerfield Member (Fig. 5, bottom); these are successive third-order transgressive cycles (separated by ~10⁶ yr). The order of addition of species is similar, though not identical in both cases.

A second test for similarity of gradients was provided by the detrended correspondence analysis of all 58 samples from various biofacies (Fig. 14, above). The samples are arrayed along DCA axis 1 in a series that parallels that seen in the order of first appearance for successive vertical samples in single cycles (Figs. 5, 7, 14, above). The close proximity of samples of particular biofacies from multiple cycles in the overall DCA axis 1 versus axis 2 plot (Fig. 14, above) thus indicates that a similar biofacies existed during deposition of each of these cycles in the Hamilton Group and into the upper Tully Limestone. A general gradient of

species distribution, as shown in Figure 14, apparently persisted through the ~5 myr span represented by these sediments. The case for faunal tracking, however, as opposed to repeated reassembly, remains to be more fully tested.

Lateral Gradients.—A critical test of the notion of tracking involves Walther's law—vertical gradients of replacement through time should mirror lateral gradients of species distribution at a given time. Unfortunately, it is difficult to apply Waltherian tracking tests to the Hamilton, not because of a lack of independent isochronous markers, which are numerous (Brett et al., 1986), but because the outcrop belt in much of western New York parallels depositional strike (Brett and Baird, 1985, 1986). As a result it is difficult to delineate lateral gradients at single points in time. Conversely, the facies strike-parallel nature of the outcrop provides direct evidence for similarity of given biofacies along distances of up to 150 km, as indicated by careful sampling of the same fossil beds in the upper Hamilton Group at multiple localities throughout western New York (see Gray, 1991, for Centerfield; Miller, 1991, for lower Wanakah Shale; Parsons et al., 1988, for the Windom Member; and Bonelli, 2003, for the upper Windom and Tully Formation). The repeated observation of faunal similarity along considerable distances underscores the conclusion that biofacies formed rather faunally consistent belts that are elongated for tens to hundreds of kilometers parallel to depositional strike. The approximately strike-parallel nature of the outcrop belt in western New York (Fig. 2; see Brett, 1986), however, permits delineation of only subtle and minor gradients for much of this area.

The best opportunities for examining lateral changes along marker beds are in the central Finger Lakes region of New York where the north-south orientation of lake valleys permits partial down-ramp transects oblique to depositional strike. The high-diversity coral and brachiopod associations, which appear as thin coral-rich beds near the shallow centers of cycles of the Hamilton Group in western-central New York, can be seen here to pass laterally into Diverse Brachiopod Biofacies, and detailed correlation shows that deeper water biofacies of small brachiopods and mollusks (*Ambocoelia*-Chonetid Biofacies) coexisted down ramp (Brett et al. 1986). For example, a single distinctive marker bed within the Centerfield Limestone, sampled along an inferred depth gradient in west-central New York (Lafferty et al., 1994), yielded a general pattern of lateral change, from *Ambocoelia*-dominated samples to diverse brachiopod-rich samples to coral-rich biostromal beds, that roughly parallels the vertical gradient within the lower Centerfield in western New York. By this interpretation, vertical change in water depth seen in <0.5 m of an abbreviated stratigraphic section is approximately equivalent to that seen laterally over 130 km, obliquely along a gently dipping ramp.

Another excellent example of a lateral gradient that has, as yet, only been qualitatively analyzed, is a faunal gradient seen in the lower Otisco Member (Staghorn Point submember of Smith, 1935) in the vicinity of Skaneateles Lake. Here an extraordinarily steepened ramp exists along the margin of a prograded siltstone platform as a result of submarine slumping or erosion (Fig. 15). In this case, a spectrum of biofacies types can be traced along a condensed, phosphatic nodule-bearing bed through several gully exposures from high-diversity coral and brachiopod assemblages near the platform top through typical *Eldredgeops*-*Stereolasma* rich biofacies to *Athyris* and low-diversity *Eumetabolotoechia*-rich biofacies (compare Figs. 5, 14, 15). This example provides evidence not only for the lateral gradient but also for the approximate magnitude of water depth change, which appears to have been on the order of only 10–20 m for the full spectrum of biofacies. Further studies of this sort are needed to provide a more rigorous test of the notion of tracking.

Biofacies Persistence across Environmental Perturbations

An important question that has arisen in studies of biofacies comparisons is whether similar biofacies may persist through major environmental perturbations (e.g., Miller, 1997). The main result of this study is that a variety of biofacies recur with considerable similarity in richness,

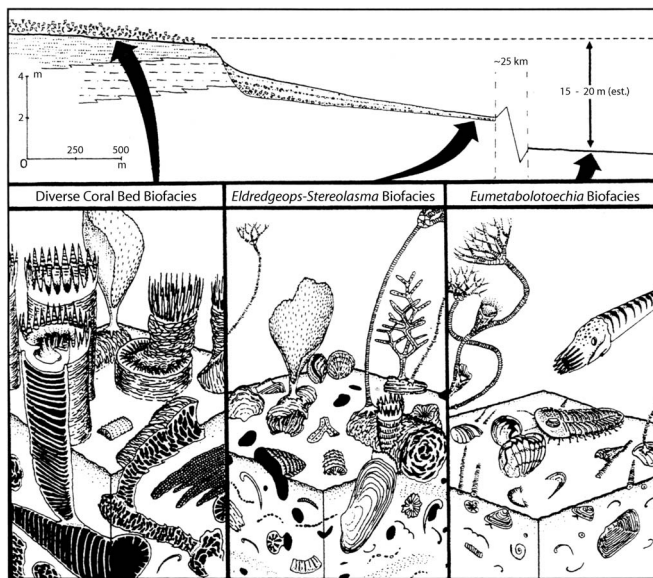


FIGURE 15—Schematic showing reconstruction of biofacies along a submarine depth gradient. Based on fossil assemblages observed along a preserved submarine escarpment, shore of Skaneateles Lake. Actual depth difference is estimated to be about 10–15 m based on preserved paleoslope.

guild structure, and composition throughout the 5–6 myr Hamilton–Tully interval. In the case of the Hamilton Group biotas, it could be argued that persistence of biofacies reflects a general absence of severe environmental perturbations and tracking of environments by persistent gradients of species. The larger, third-order cycles of the Hamilton Group, however, are bracketed by widespread, sequence-bounding unconformities. Moreover, the highstands separating intervals of several third- and fourth-order cycles are represented by very widespread dysoxic-to-anoxic conditions. For example, both the Halihan Hill bed (lowest appearance of many typical diverse Hamilton biotas) and the Mottville Member (second occurrence of most of these taxa) are separated by black, pyritic Chittenango (Oatka Creek) Shale. Geochemical proxies, especially degree of pyritization and Vn/Cr ratios, indicate very widespread euxinic conditions during this interval (Murphy et al., 2000; Werne et al., 2002), yet a majority of species and biofacies reappear after this interval.

The Tully Formation is not only separated from the Hamilton by a major, regional unconformity; there is also evidence of a substantial change in environment and the influx of an exotic, possibly warm-water biota. Typical offshore Hamilton taxa and biofacies (*Eumetabolotoechia*, *Ambocoelia-Chonetid*, and *Athyris-Mediospirifer* Biofacies) are absent in dysoxic, deeper facies in the lower beds of the Tully Formation, both in western carbonate and eastern siliciclastic settings (Heckel, 1973; Sessa et al., 2002; Baird and Brett, 2003; Sessa, 2003). In place of these biofacies, a new suite of taxa, including *Leiorhynchus mesacostale*, *Rhyssochonetes aurora*, *Emmanuella subumbona*, and *Tullypothyridina venustula*, appears abruptly in the lowermost Tully strata; Baird and Brett (2003) referred to this faunal turnover as the lower Tully bioevent. These species appear to have immigrated into eastern Laurentia from Old World realm biotas in present-day western Canada. Moreover, recent oxygen isotopic studies indicate a climatic warming, commencing in the middle *P. ansatus* conodont zone, coinciding with the lower Tully bioevent (Joachimski et al., 2004).

Despite the major physical and biotic changes evident in the lower Tully interval, shallow-water biotas evidently survived and recur in appropriate facies of the upper member of the Tully Formation (Cooper and Williams, 1935; Heckel, 1973; Baird and Brett 2003). Bonelli (2003) made detailed quantitative comparison of samples from the uppermost (South Lansing) coral bed of the Hamilton Group with samples from the very latest known occurrence of this biofacies in the West Brook bed of

the overlying Tully Formation. The West Brook sample still showed a species carryover of 85%, despite the major lower Tully faunal perturbation (Sessa et al. 2002; Baird and Brett 2003). In fact, only one species found in this sample was not present somewhere in the Hamilton Group (Bonelli, 2003; Bonelli et al., 2006). This evidence indicates that a majority of species in the diverse shallow-water portion of the Hamilton gradient does persist, and biofacies may recur even in the face of major environmental change.

Implications for Tracking

Not only does pervasive recurrence of species indicate similar environments, the high-fidelity occurrence of stenotopic species in specific biofacies also provides evidence of habitat tracking. The rather high ubiquity and eurytopy of taxa in many low-diversity associations (*Eumetabolotoechia* and *Arcuaminetes* Biofacies) typical of dysoxic mudstone facies in the Hamilton Group (Figs. 14–15) indicates that such associations could have frequently reassembled from various combinations of eurytopic species and that biofacies characterized by a particular combination of taxa might not coexist at all times, as suggested by Bonuso et al. (2002b). The relative abundance distributions of various species appear to have been approximately maintained along depth gradients and shifted in response to shifting sea level and other environmental change, although the exact order of appearance of these species in gradients was found to be slightly variable from one cycle to the next (Figs. 5, 14), in accord with the findings of Olszewski and Patzkowsky (2001).

Evidence for tracking is observed for deeper-water *Eumetabolotoechia*, *Arcuaminetes*, and *Ambocoelia-chonetid* assemblages that are known to have existed in basin center localities contemporaneously with higher-diversity biofacies (e.g., Lafferty et al., 1994; Brett et al., 1996).

In the high-diversity biofacies, a stronger case can be made for tracking. As noted, a large number of species found in these biofacies have low eurytopy and ubiquity indices. Approximately one-third of the species are never found in other contemporaneous biofacies. Given their large number of species, Diverse Coral Bed Biofacies might be expected to yield a high degree of variability through time if they were reassembling from multiple species pools. But this is clearly not the case. The coral-rich biofacies show very high compositional similarities, and a majority of stenotopic species, both common and rare, recur in all or nearly all of the samples of the Diverse Coral Bed biofacies from lowest to highest (Brett et al., 1990; Table 1).

Diverse coral-brachiopod-rich beds occur in the shallowest, relatively thin, and abbreviated, portions of each of 15 successive cycles in New York and Pennsylvania (Figs. 4, 14) that constitute only a small fraction (<2% by thickness) of the Hamilton Group facies exposed in western New York and a fraction of a percent in eastern New York, providing one indication of the truly facies-restricted nature of the occurrences. Large rugose and tabulate corals (e.g., *Heterophrentis*, *Cystiphyllodes*, *Heliophyllum*, and *Favosites*) and many associated brachiopods, trilobites, and echinoderms are found in all samples of the biofacies, but they are absent from all intervening facies (see Baird and Brett, 1983; Bonelli, 2003; Bonelli et al., 2006). Detailed morphological studies of these stenotopes, including corals (Sorauf and Oliver, 1976) and proëtid trilobites (Lieberman, 1994) indicate morphological stasis through the interval, despite their rare or stenotopic nature.

The sedimentary record of much of the Appalachian foreland basin is accessible for the duration of the Middle Devonian, yet these taxa have never been observed in other facies associations. The foreland basin was evidently too deep, turbid, or dysoxic to sustain these stenotopic forms most of the time; rather, it was usually occupied by assemblages typical of outer shelf to basinal environments (*Eumetabolotoechia*, *Arcuaminetes*, and *Ambocoelia-Chonetid* Biofacies). There are relatively few regions in which these faunas could have persisted. Large areas of the North American continental interior were exposed or covered by peritidal environments and could not have been occupied by the stenotopic corals and

other taxa. Most of the shallow-water stenotopic taxa, particularly the corals, are endemic to the Appohimchi Subprovince of eastern North America (Oliver, 1977; Oliver and Pedder, 1979; Boucot, 1982). Thus, other areas, such as the vast region from Michigan northwestward to the Canadian Arctic, are ruled out because coral and brachiopod faunas that are well known from these areas contain different species representing a separate biogeographic subprovince. Presumably, corals and other shallow, clear-water taxa survived during long intervals (hundreds of thousands of years) in their preferred environments, which had shifted northward of the present outcrop belt in New York State into shallow water regions on the Canadian Shield. Unfortunately, this area is now largely devoid of Devonian outcrop owing to later erosion; however, rare inliers, such as the Sainte Hélène breccia, do prove the existence of Hamilton strata and faunas in this area (Boucot et al., 1987). That area could be thought of as a refugium or reservoir for the restocking of the stenotopic species into the basin (Holterhoff, 1996), but this is not fully correct. When shallow, relatively low-turbidity environments returned to any particular area within the foreland basin, these species returned with them. At such times, however, given the extent of shallowing within the foreland basin and evidence for its widespread, eustatic origin (Brett and Baird, 1996), the upramp area was almost certainly too shallow (even exposed land in some cases) to permit survival of the corals and associated organisms. Hence, the erstwhile refugium in shallow upramp areas was destroyed, and the biofacies are absent from that area. At such times, the refugium for this suite of species was in the foreland basin itself. Likewise, during subsequent deepening, the requisite habitat of these organisms was destroyed throughout the entire foreland basin, and these stenotopic species were able to survive by retreating again to upramp areas. This is not the same as maintenance of a persistent pool of species in the Canadian Shield from which the Appalachian Basin was repeatedly restocked. Moreover, inasmuch as many of the species always recur in association with one another when they are in the basin, it is unlikely that the biofacies was ever really disassembled; rather, it tracked the shifting narrow belt of tolerable environment.

Implications for Coordinated Stasis

In the last 10 years, following the publication of the initial example of coordinated stasis in the Silurian–Devonian of the Appalachian Basin (Brett and Baird, 1995), a number of studies have been conducted that show a variety of patterns in marine environments. The results range from strong recurrence of species composition and relative abundance (Bambach and Bennington, 1996; Bennington and Bambach, 1996; Holterhoff, 1996; Pandolfi, 1996; Pandolfi and Jackson, 1997; Bennington, 2003; Scarponi and Kowalewski, 2004), to general similarity of genus-level composition, guild structure, and species compositional differences (Westrop, 1996; Patzkowsky and Holland, 1997, 1999; Holland and Patzkowsky, 2004), to nearly continuous change in species-genus composition and ecological structure (Stanton and Dodd, 1997).

Certain of these conflicting claims of stability or the lack thereof may well represent genuine differences in the behavior of different ecological systems (e.g., Stanton and Dodd, 1997) or different times in the evolution of the biosphere (see, e.g., discussion of possibly greater evolutionary lability in the Cambrian vs. mid-Paleozoic benthic invertebrates in Westrop, 1996). Other claims, however, may arise from comparing different levels of ecological or taxonomic hierarchy (see the review in Brett et al., 2007). In particular, Rahel (1990) demonstrated that certain recurring biofacies or community types may be stable in some ecological properties, such as diversity, guild structure, or taxonomic composition, but not in others, such as rank order or relative abundance (see also Visaggi, 2004). Hence, the ecological level at which stability is being tested must be specified carefully. For example, in terms of species composition, general diversity and guild structure, the recurrent Pennsylvanian assemblages studied by Bennington and Bambach (1996) appear highly stable or recurrent, even though rank and relative abundance among samples of

different ages are significantly more different than local samples or those at a single horizon (see also Bonelli, 2003; Bonelli et al. 2006). Thus, while individual communities do not persist, community types or biofacies may well either persist or reassemble with considerable fidelity when viewed from the perspectives of diversity, guild structure, and even species or genus composition.

One further very important consideration is that the degree of similarity observed in comparisons of biofacies samples through time may be a function of where those samples were obtained relative to gradients and, therefore, how truly analogous the original environments were. Recurrence of biofacies can only be observed if a particular combination of environmental factors is resampled because species respond to more than one type of gradient (e.g., depth-related variables as well as sedimentation-related variables). Even if this set of conditions were maintained continuously, it may not reappear cyclically in the same area, as is the case in the Hamilton Group. This is a critical factor that has artificially given rise to perceptions of low persistence and a lack of stability of biofacies in some cases (e.g., Bonuso et al., 2002a).

Results of the present study indicate that in the Hamilton Group a high degree of biofacies recurrence does exist, but it only becomes apparent if a broad cross section of the depositional basin is examined. These data suggest that biofacies can recur with high levels of similarity in species richness, general guild structure, and taxonomic composition, although the rank and absolute abundance vary from cycle to cycle (Brett and Baird, 1995; Bonelli et al., 2006).

Biofacies similarities through time appear to be greater in high-diversity associations composed of stenotopic species than in low-diversity associations of generalized eurytopic taxa. This may suggest that the latter were more loosely structured than the high-diversity assemblages. This effect could partially reflect biases, however. The Diverse Coral Bed Biofacies typically occurs in condensed, carbonate-rich facies, and the high degree of time-averaging within samples could have produced a more homogenous fossil assemblage. Moreover, the large number of distinctive forms, especially diverse large rugose and tabulate corals, may make identification of analogous samples easier. In the case of low-diversity associations there is some possibility that the most nearly comparable facies were not sampled; the apparent differences among samples, which do not seem to have a systematic trend, could simply be a case of not comparing the most nearly analogous parts of species gradients. This can only be tested with much more comprehensive sampling and intensive comparison of many more samples.

This study provides a partial, though not complete, test of the process of habitat tracking and addresses issues of compositional and ecological persistence through a geologically prolonged interval of relative stability. The results do not, of course, indicate that the patterns observed are widespread or even typical, but comparisons with other recent studies (e.g., Bennington and Bambach, 1996; Holterhoff, 1996) indicate some general similarities of pattern. Comparative studies indicate that the Hamilton Group may well lie toward the stable end member of a spectrum of biotic stability. This study, however, does provide insights as to the possible degree of stability that can exist under favorable conditions.

These observations should not be taken to imply a strong degree of community integration. Indeed, a variety of evidence points to individualistic tracking of habitats by various species. These results do, however, suggest that for most species habitat tolerances and preferences remain constant, and, consequently, gradients of species distribution may persist for millions of years under appropriate conditions. The general lack of species-level change further suggests that tracking of shifting environments, rather than evolutionary change, may be a common response of species to gradually shifting environments. This is a critical aspect of evolution, or the lack thereof, that has been partly eclipsed by recent intense debate over community unity.

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