

Devonian monospecific assemblages: new insights into the ecology of reduced-oxygen depositional settings

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Low-diversity fossil assemblages interpreted as representing dysaerobic communities are common in the Phanerozoic rock record, and those composed of a single species have particular utility for recognizing the lowest bottom-water oxygen levels. An unusually high-diversity of clades including three rhynchonelliform, two linguliform, and one bivalve species occur in monospecific assemblages within Middle and Upper Devonian black shales of New York State. These six taxa are interpreted to be adapted to extremely reduced bottom-water oxygen levels as inferred from detailed sedimentological data and their repeated monospecific occurrence; however these groups represent two distinct ecologies. Three of these taxa are restricted to sediments deposited under the lowest dysaerobic conditions, while the other three taxa, unlike other fossils characteristic of reduced-oxygen levels, also occur in and are even dominant in high-diversity assemblages. The rhynchonellid brachiopod *Eumetabolotoechia multicostrata* is the most abundant taxon within these units and has a remarkable ecological range as dominant from the lowest dysaerobic zone to near-normal marine oxygen levels. These Devonian groups, when present in monospecific assemblages, have utility for characterizing the lowest dysaerobic zone where trace fossil assemblages, most commonly used to describe these low-oxygen depositional settings, are absent or poorly developed. □ *Bivalves, black shales, brachiopods, dysaerobic, palaeoecology.*

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The dysaerobic biofacies was originally defined from observations in modern environments to describe the biozone between fully oxygenated normal marine conditions (aerobic) and the complete absence of bottom-water oxygen (anaerobic) (Rhoads & Morse 1971; Byers 1977). In modern marine environments as bottom-water oxygen levels decrease, there is a correlative decrease in benthic diversity, as well as the size and abundance of individuals until the shelly macrofaunal population is excluded (Parker 1964; Rhoads & Morse 1971; Pearson & Rosenberg 1978; Thompson *et al.* 1985; Tyson & Pearson 1991; Allison *et al.* 1995). As a result, low diversity fossil assemblages, when preserved in an appropriate sedimentological context and not a product of physical processes, are commonly interpreted as representing communities in reduced-oxygen bottom waters of the dysaerobic zone (e.g. Rhoads & Morse 1971; Savrda *et al.* 1984; Thompson *et al.* 1985; Sageman 1989; Wignall 1990; Allison *et al.* 1995).

Although numerous palaeoecological methods have been developed to characterize the dysaerobic zone (e.g. Rhoads & Morse 1971; Byers 1977; Savrda & Bottjer 1986; Wignall & Hallam 1991; Wignall 1994), for the most part they are all based on the same general principle that as oxygen levels decrease

so does benthic species richness. Thus, within a succession several macrobenthic species may be characteristic of low-oxygen conditions, but only one or a few typically occur under the lowest dysaerobic settings. Monospecific assemblages of shelly benthic taxa are interpreted to have inhabited extremely reduced-oxygen conditions, and when present within laminated sediments represent the exaerobic biozone (Savrda & Bottjer 1987). The exaerobic zone refers to the boundary between the dysaerobic zone and anaerobic zone at the edge of metazoan habitability. Although there is no modern analogue for this biozone, exaerobic taxa are interpreted to have harboured chemosymbionts (Savrda & Bottjer 1986; Savrda 1992; Wignall 1994).

Black and grey shales, interpreted to represent deposition under low-oxygen bottom-water conditions, are a common lithology throughout the Phanerozoic, and taxonomic groups common within these shales (Fig. 1) are typically restricted to low-oxygen settings (Kammer *et al.* 1986; Wignall 1990; Allison *et al.* 1995). The Devonian was a time of elevated diversity of taxa characteristic of this environment (Fig. 1). Middle and Upper Devonian strata of New York State preserve a succession of shales classically interpreted as dysaerobic (Brett *et al.* 1991; Brower & Nye 1991;

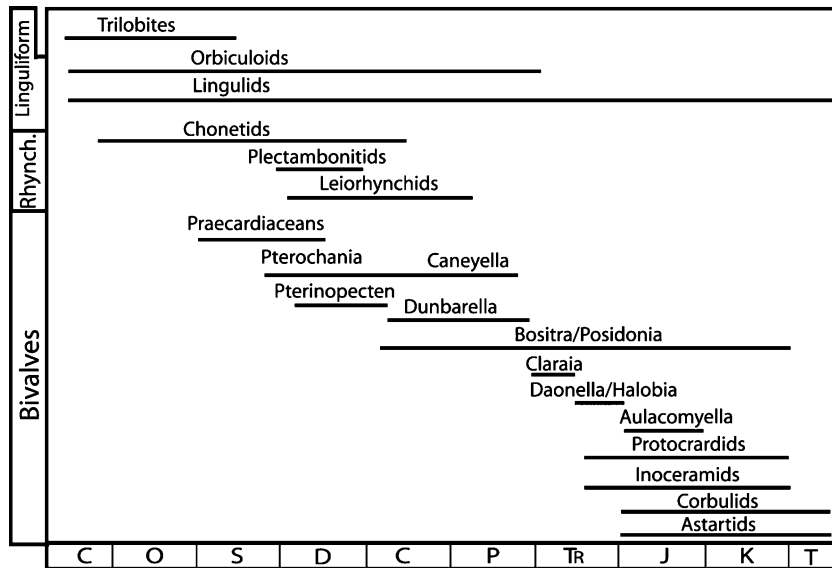


Fig. 1. Stratigraphic ranges of common dysaerobic groups through the Phanerozoic. Rhynch. = Rhynchonelliform (after Allison *et al.* 1995).

McCollum 1991; Murphy *et al.* 2000; Werne *et al.* 2002; Sageman *et al.* 2003). Fossil assemblages within these units are typically dominated by leiorhynchid brachiopod species; other taxa common in Devonian dysaerobic assemblages include ambocoeliids, chonetids, and orbiculoids, as well as nuculoid and *Pterochaenia* bivalves (e.g. Savarese *et al.* 1986; Thompson & Newton 1987; Brett *et al.* 1991; Brower & Nye 1991).

Here we report six brachiopod and bivalve species that occur repeatedly in monospecific assemblages within laminated to slightly bioturbated shale from the Middle Devonian of New York State. Typically, studies that describe dysaerobic taxa have not been conducted at a millimetre to centimetre, bed-by-bed scale (but see Savrda & Bottjer 1986; Savrda 1992; Gaines & Droser 2003; Algeo *et al.* 2004), therefore taxa from beds that potentially represent a range of subtly, but significantly different depositional environments may be grouped together. The scale of data collection in this study allows for the identification of ecologically significant associations that reveal a number of phylogenetically disparate groups that were adapted to the lowest dysaerobic zone. Unlike most groups characteristic of this setting, several of these taxa are not unique to the lowest dysaerobic zone and also occur in high-diversity assemblages.

Geological setting

The Middle–Upper Devonian (Eifelian–Frasnian) sequence of New York State is an eastward thickening package of dominantly clastic rocks that represents deposition of the Catskill Delta complex (Ettensohn

1985; Brett 1986). These units record variations in sea level due to fluctuations in tectonic activity as broad-scale siliciclastic deposition punctuated by carbonate-dominated sedimentation (Ettensohn 1985). Common Devonian aged black to grey shales representing a range of environments within an eperic sea-way are exposed across a broad geographical area at repeated stratigraphic intervals providing an ideal setting for palaeontological studies. These units are biostratigraphically well constrained and contain abundant monospecific to diverse fossil assemblages (Thayer 1974; Kirchgasser & House 1981; Brett 1986; McCollum 1991).

Methods

Samples were collected from mudstones at 14 localities (Fig. 2) from seven stratigraphic intervals (Fig. 3) across the palaeobasin from units previously interpreted as dysaerobic (Brett *et al.* 1991; Brower & Nye 1991; McCollum 1991; Murphy *et al.* 2000; Werne *et al.* 2002; Sageman *et al.* 2003). Units were selected to represent a potential range of relative oxygen levels from laminated units devoid of body fossils through fully bioturbated units with abundant body fossils of moderate benthic diversity. At each locality, samples were collected continuously through total exposure. All samples were then cut perpendicular to bedding and polished to reveal a continuous record of ichnofabric. Thin sections were used to examine lithologic features as well as individual burrows. Powdered samples were analysed through X-ray diffraction to determine mineral composition.

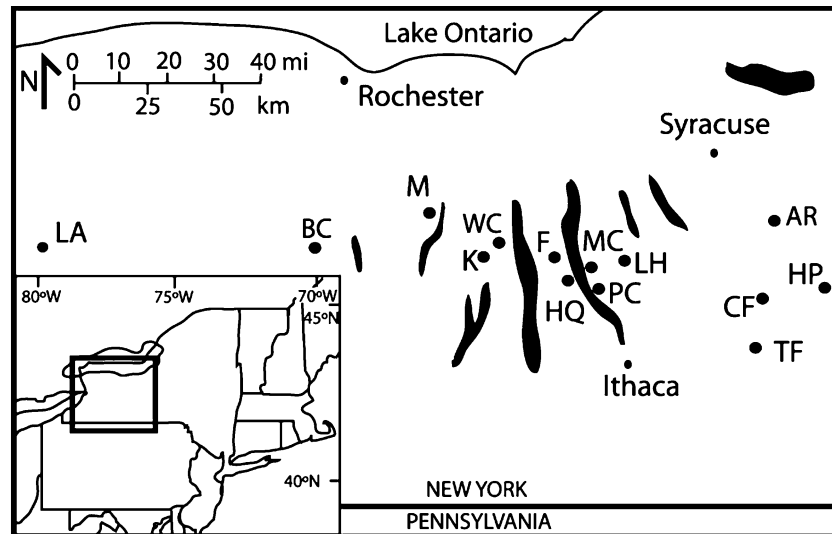


Fig. 2. Study area with labelled Middle and Upper Devonian aged localities. Exposed formations or members are given in parentheses. LA = Lake Ave. (Marcellus), M = Manteth Creek (Penn Yan), BC = Browns Creek (Levana), K = Kashong Glen (Ledyard), WC = Wilson Creek (Ledyard), F = Fayette (Levana), HQ = Hubbard Quarry (Genesee), PC = Paines Creek (Ledyard), MC = Mill Creek (Penn Yan), LH = Long Hill Road Cut (Windom), CF = Cheese Factory/Gulf Rd. (Marcellus), TF = Tinker Falls (Windom), AR = Abbey Rd. (Marcellus), HP = Highland Park (Windom).

Relative oxygen levels were determined from sedimentary features including the presence of laminations, the development of ichnofabric, relative amount of bioturbation, size of burrows, and ichnogenetic diversity, as well as general field based observations including colour and fissility. Ichnofabric indices (ii), as a method to quantify the amount of bioturbation (Droser & Bottjer 1986), were averaged through each centimetre. These characters were logged on a microstratigraphic scale and in combination were used to infer relative oxygen levels. These methods are consistent with other studies examining low-oxygen facies (Savrdra & Bottjer 1986; Wignall 1994; Gaines & Droser 2003; Martin 2004).

In correlation with ichnofabric data, bedding planes were exhumed. Over maximum exposure along each bedding plane surface, species richness, abundance and standard taphonomic data were collected. For most bedding planes, taxa were identified in the field because species richness and abundance are commonly low. Intervals with higher diversity and abundance were sampled and processed in the laboratory. Each fossiliferous bedding plane exposure was recorded digitally to capture distribution, orientation, and taphonomic condition of specimens.

Sedimentology

Over 6 m of section was examined at the millimetre scale in cross-section and in bedding plane view. These light grey to black shales range from claystones

to silty mudstones. All units have very similar mineralogical composition dominated by quartz (average 53.5%, SD 8.52), clay primarily in the forms of illite and chlorite (average 34.2%, SD 8.41), and calcite (average 9.1%, SD 12.31), as determined from analysis of thin sections and whole rock X-ray diffraction. Total organic carbon (TOC) in these units ranges from 0.06% to just over 4%. The ubiquitous presence of some amount of silt throughout these units provides subtle yet recognizable distinctions between laminae as well as the recognition of burrows from the surrounding sediments. Mudstone textures are primarily devoid of macro- or microscale grading as observed in hand-samples and thin sections. Sedimentary structures indicative of high energy are rare, but include scour marks, ripples, and minor graded laminations, and occur in association with increased silt content. Laminated intervals and discontinuous laminations are common within these intervals. Individual laminations range from the width of a single silt grain to several millimetres in thickness and are interpreted to represent fluid mud flow deposits within a broad, relatively shallow seaway.

The ichnological signal preserved in these units ranges from laminated sediments (ii 1) to fully bioturbated and homogenized strata (ii 5), across various scales but can be recognized at sub-centimetre resolution. Calcareous macrofaunal diversity varies from zero to 19 species on individual bedding planes. These characteristics are consistent with a range of oxygen levels throughout the dysaerobic zone.

Stage	Formation	Member	
Givetian	Frasnian	Penn Yan Shale ◆	
		Genesee	
	Hamilton Group	Moscow	Geneseo Sh. ◆
			Tully Ls.
		Windom Sh. ◆	
		Kashong Sh.	
		Ludlowville	Jacox Sh.
			Wanakah Shale
	Ledyard Shale ◆		
	Centerfield Ls.		
	Skaneateles	Levanna Shale ◆	
		Stafford	
	Eifelian	Marcellus	Oatka Creek Shale ◆
Union Springs			
	Onondaga		

Fig. 3. Stratigraphy of central and western New York State. Sampled intervals marked with diamonds.

Monospecific assemblages

Of over 600 bedding planes analysed for this study, more than 350 contain body fossils, and of those, 158 assemblages are comprised of a single species (Table 1). Six species occur repeatedly in monospecific assemblages within laminated (ii 1) to weakly bioturbated strata (ii 2–3) (Table 2). Burrows are typically thin and horizontal to sub-horizontal in orientation.

Monospecific assemblages consist of two linguliform brachiopods, *Orbiculoides lodensis* and *Lingula spatulata*, three rhynchonelliform brachiopods of the subfamily Leiorhynchinae (*Leiorhynchus quadracostata*, *Le. sinuata*, and *Eumetabolotoechia multicostata*) and one bivalve species, *Pterochaenia fragilis*. These species are present in distributions ranging from disparate, less than 10 individuals/m², to over 900 individuals/m², but are typically present in abundances of less than 60 individuals/m². At all localities, fossils demonstrate minimal fragmentation and abrasion with no size sorted or oriented populations. A range of sizes of individuals is preserved in monospecific assemblages and specimens are nearly all preserved as whole valves with rare articulated or butterflyed individuals. None of these groups demonstrate preferential distribution that correlates with lithology.

Orbiculoides lodensis is a linguliform brachiopod with small (< 2 cm), flat, circular valves (Fig. 4A). This species occurs at two localities, most commonly in monospecific assemblages, from dispersed to moderately abundant (> 52 individuals/m²) along bedding plane exposures. *O. lodensis* is typically associated with minimal bioturbation (ii 2), but is also preserved within laminated strata (ii 1). It occurs rarely with other species and then only with *E. multicostata* and *P. fragilis* in moderately bioturbated strata (ii 2–3).

The thin-shelled *Le. quadracostata* (Fig. 4B) is variable in size but reaches over 3 cm in length. The ribbed, inflated, sub-circular valves of this species are commonly flattened or compressed. *Le. quadracostata* is restricted to low diversity assemblages and most commonly occurs in monospecific associations in laminated through moderately bioturbated strata (ii 1–3). Within a 1-m section at Hubbard Quarry, there are 47 monospecific bedding plane assemblages of *Le. quadracostata* (Fig. 5). This species is present in moderate to high abundances on individual bedding planes (~12–300 individuals/m²), although only rarely more than 100 individuals/m². On individual bedding planes, *Le. quadracostata* is associated with only two other species, *Li. spatulata* and/or *Chonetes* sp., of which, the former is also common in monospecific assemblages.

Leiorhynchus sinuata (Fig. 4C), a smaller (0.5–1.7 cm in length) member of the genus *Leiorhynchus* is present at two localities. *Le. sinuata*, most common in monospecific assemblages, is associated with laminated to moderately bioturbated strata (ii 1–3), but most commonly within strata that have rare burrows or breaks in lamination that are interpreted to be biologically disrupted. The distribution of this species on an individual bedding plane ranges from, most commonly, dispersed to abundant (900 individuals/m²).

Table 1. Diversity, abundance, and ichnofabric index averaged to each centimetre associated with each occurrence of the six monospecific taxa in these units. Sample number indicates cm above base of sampled intervals. Locality abbreviations are MC = Mill Creek; W = Wilson Creek; LH = Long Hill Road; PC = Paines Creek; TF = Tinker Falls; M = Manteth; HQ = Hubbard Quarry; HP = Highland Park; K = Kashong Creek; F = Fayetteville.

Locality	Sample number	Diversity	Abundance	Abundance/m ²	Ichnofabric index	<i>Eumetabolotoechia multicostata</i>	<i>Leiorhynchus quadracostata</i>	<i>Leiorhynchus sinuata</i>	<i>Lingula spatulata</i>	<i>Orbiculoides lodensis</i>	<i>Pterochaenia fragilis</i>
MC	-1	1	1	3.5	2			1			
MC	1	1	1	2.7	1.5			1			
MC	2	1	5	8.5	2			5			
MC	3	1	1	2.0	2			1			
MC	5	1	1	3.7	1.5			1			
MC	6	1	6	22.3	2			6			
MC	8	1	2	9.3	1.5			2			
MC	9	1	4	12.3	2			4			
MC	10	2	11	33.9	2			10			
MC	11	1	4	8.4	1.5			4			
MC	12	2	7	13.0	2			6			
MC	13	1	5	7.5	2.5			5			
MC	19	1	12	52.3	2					12	
TF	4	4	26	400	2.5	7					
TF	5	10	53	779.4	3	21					
TF	6	9	328	3123.8	4	242					
TF	8	16	463	4026.1	4	322					1
TF	9	4	42	409.4	2	34					
TF	10	2	8	87.1	3	6					
TF	11	2	4	41.2	4	1					
TF	12	6	14	144.0	3.5	4					
TF	13	16	371	4041.4	3.5	111			1		
TF	14	12	252	2652.6	4	42					
TF	15	11	291	1995.9	4	205					
W	-1	1	1	8.8	2						1
W	1	1	5	30.6	2						5
W	2	2	4	12.5	2	1					3
W	3	2	5	13.6	2	3					2
W	4	2	26	86.5	2	2					23
W	5	2	5	14.3	3	1					4
W	6	3	5	16.5	2	1					3
W	7	1	4	10.1	2						3
W	18	1	1	16.7	1.5	1					
W	19	2	2	33.3	2	1					1
W	20	1	1	3.9	2						1
W	22	1	1	3.9	2						1
W	23	4	7	15.6	2.5	2					3
W	24	1	1	2.2	3						1
W	25	3	6	13.4	2	3					2
W	27	1	1	5.2	2						1
W	28	1	3	15.6	1.5						3
W	33	2	2	6.1	2	1					
W	34	1	2	6.06	2	2					
W	37	1	1	3.03	2	1					
W	40	1	1	3.03	2	1					
W	42	1	2	6.06	2	2					
W	44	1	1	2.67	2	1					
W	47	1	1	4.76	2	1					
W	54	1	1	22.2	2	1					
PC	10	1	2	7.58	2	2					
PC	13	1	1	3.79	2	1					
PC	14	2	3	11.4	2	2					
PC	15	1	4	15.2	2	4					
PC	20	3	12	26.5	2	10					
PC	21	1	7	26.5	1	7					
PC	32	1	3	11.4	2						3
PC	33	1	2	19.5	1	2					
PC	37	1	1	9.75	1	1					
PC	42	3	8	30.3	4	6					1
PC	43	1	5	30.3	4	5					
PC	44	2	4	18.9	4	3					
PC	45	2	7	15.2	4	6					
PC	46	1	1	26.5	2	1					
PC	47	1	2	3.79	2	2					
PC	48	1	1	7.58	2	1					
PC	49	1	1	3.79	1	1					
PC	51	1	1	3.79	4	1					
PC	52	1	1	3.79	1	1					
PC	55	1	2	7.58	3	2					
PC	56	1	3	11.4	1	3					
PC	58	1	5	18.9	1	5					
PC	59	2	7	26.5	2	6					
PC	60	1	8	30.3	1.8	8					
PC	61	1	26	98.5	4	26					
PC	62	4	16	60.6	2	12					1
PC	63	2	11	41.7	1	8					
PC	64	1	2	7.58	2.5	2					
PC	65	2	4	15.2	4	3					1
PC	66	3	5	18.9	4	3					1
PC	67	1	3	11.4	2	3					

Table 1. Continued.

Locality	Sample number	Diversity	Abundance	Abundance/m ²	Ichnofabric index	<i>Eumetabolotoechia multicosata</i>	<i>Leiorhynchus quadracostata</i>	<i>Leiorhynchus sinuata</i>	<i>Lingula spatulata</i>	<i>Orbiculoides lodensis</i>	<i>Pterochaenia fragilis</i>
PC	68	2	2	7.58	2	1					1
PC	69	1	1	3.79	2	1					
PC	70	1	1	2.84	1	1					
PC	72	1	1	11.4	1				1		
MC	7	1	1	5.0	2		1				
MC	15	1	1	2.8	2					1	
MC	20	1	1	4.4	2					1	
MC	23	1	1	3.4	1.5					1	
LH	1	11	117	736.8	4	117					
LH	2	1	10	81.6	4	10					
LH	4	9	58	448.6	3	58					
LH	12	7	90	551.4	3	89					1
LH	13	1	27	145.9	3	27					
LH	14	2	6	57.1	3	6					
LH	16	2	3	32.7	3	3					
LH	17	8	37	252.1	3	36					1
LH	19	2	3	32.7	4	3					
LH	20	1	1	8.2	4	1					
LH	21	1	1	8.2	3	1					
LH	22	2	1	16.3	3	1					
LH	23	5	139	822.2	3	138					1
LH	32	1	1	8.2	3	1					
LH	42	1	5	222.2	3	5					
LH	48	1	5	222.2	2						5
LH	50	3	4	177.8	2.5	1			1		2
LH	54	1	2	88.9	2	2					
LH	60	3	1	133.3	2	1					
LH	73	8	11	1911.1	3	11					
LH	75	1	1	44.4	3	1					
LH	79	1	1	44.4	3	1					
LH	80	17	29	3733.3	3	28					1
LH	81	1	1	44.4	3						1
LH	87	5	12	711.1	5	12					
LH	90	6	61	3511.1	5	61					
M	1	1	1	2.3	1.9			1			
M	2	1	2	4.6	1			2			
M	5	1	1	3.1	2.6			1			
M	7	1	2	5.2	3			2			
M	8	1	4	18.5	2			4			
M	9	1	1	10.5	2.9			4			
M	10	1	12	12.1	2			2			
M	11	1	61	30.3	1.1			5			
M	17	1	7	64.8	2.9			7			
M	23	2	2	12.5	2.7			1			
M	24	1	18	56.3	2			18			
M	25	2	90	900	1.5			89			
M	12	1	1	70.5	2.9			10			
M	13	1	2	11.0	2			2			
M	14	1	1	21.1	3			7			
M	15	1	1	4.5	2			1			
M	26	2	12	102.6	3			10			
M	27	1	4	133.3	3			4			
M	29	1	56	700	2			56			
M	30	1	8	100	1.5			8			
K	2	1	2	11.4	1.5	2					
K	4	2	3	17.1	2	2					
K	5	1	1	4.4	2	1					
K	6	2	3	13.3	1	2					
K	7	1	7	31.1	1.5	7					
K	8	2	9	180	1.5	7					
K	9	1	1	20	2	1					
K	12	2	29	190.8	1.5	28					1
K	13	1	1	6.6	2	1					
K	14	1	3	14.2	1.5	3					
K	15	1	3	14.2	1	3					
K	16	1	5	50	2	5					
K	17	1	2	33.3	2	2					
K	18	1	11	183.3	2	11					
K	19	2	5	83.3	2	4					
K	20	1	3	50	2	3					
K	21	1	7	116.7	3	7					
K	22	1	2	33.3	3	2					
K	23	1	2	33.3	3	2					
K	24	1	1	16.7	1						1
K	25	1	2	33.3	1	2					
K	26	1	1	16.7	1	1					
F	5	1	5	58.8	2	5					
F	8	1	18	211.8	1	18					
F	11	2	3	35.3	3	1					2
F	13	1	1	11.8	2	1					
F	15	2	20	235.3	2	19					
F	17	2	10	117.6	1	8					2
F	18	1	1	11.8	1	1					

Table 1. Continued.

Locality	Sample number	Diversity	Abundance	Abundance/m ²	Ichnofabric index	<i>Eumetabolotoechia multicosata</i>	<i>Leiorhynchus quadracostata</i>	<i>Leiorhynchus sinuata</i>	<i>Lingula spatulata</i>	<i>Orbiculoides lodensis</i>	<i>Pterochaenia fragilis</i>
F	20	1	14	164.7	2	14					
F	22	1	5	58.8	2	5					
F	24	2	6	70.6	4	5					
F	25	1	4	47.1	4	4					1
F	30	2	2	23.5	1	1					
F	31	1	1	11.8	1	1					
F	32	3	10	117.6	3	1					8
F	37	1	1	11.8	1	1					
F	43	1	1	11.8	1	1					
F	44	1	1	11.8	1						1
HQ	3	1	3	34.3	1.8				3		
HQ	4	2	5	57.1	2				2		
HQ	7	1	1	11.4	1		1				
HQ	8	1	1	11.4	2		1				
HQ	16	3	8	91.4	2		2				
HQ	18	1	5	57.1	1				2		
HQ	18	1	5	57.1	1				5		
HQ	20	1	1	11.4	1				1		
HQ	21	2	7	80.0	1				3		
HQ	22	2	6	68.6	2				5		
HQ	30	1	1	11.4	1				1		
HQ	31	1	2	22.9	1		2				
HQ	35	1	2	22.9	1		2				
HQ	36	1	1	11.4	1		1				
HQ	37	1	3	34.3	1.5		3				
HQ	38	2	2	22.9	2		1				
HQ	39	2	5	57.1	1.5		1			4	
HQ	46	2	40	457.1	2		10		30		
HQ	49	2	2	22.9	1.5		1		1		
HQ	50	2	5	57.1	2		4		1		
HQ	52	2	3	34.3	1.5		2		1		
HQ	53	1	1	11.4	2		1				
HQ	54	2	3	34.3	2		2		1		
HQ	56	1	4	45.7	2		4				
HQ	57	1	2	22.9	1.5		2				
HQ	60	1	5	57.1	2		5				
HQ	63	1	1	11.4	1.5		1				
HQ	64	1	1	11.4	2		1				
HQ	65	1	1	11.4	1.5		1				
HQ	66	1	9	102.9	1.5		9				
HQ	67	1	2	22.9	2		2				
HQ	68	1	1	11.4	2.5		1				
HQ	69	1	1	11.4	3		1				
HQ	70	1	1	11.4	1		1				
HQ	71	2	17	194.3	2		13		4		
HQ	72	1	2	22.9	1		2				
HQ	73	1	1	11.4	2		1				
HQ	74	1	27	308.6	2		27				
HQ	75	1	6	68.6	2	6					
HQ	76	1	1	11.4	3	1					
HQ	77	1	19	217.1	2	19					
HQ	78	1	5	57.1	2	5					
HQ	79	1	1	11.4	2	1					
HQ	80	1	1	11.4	2	1					
HQ	81	1	1	11.4	1.5	1					
HQ	82	1	5	57.1	2	5					
HQ	83	1	1	11.4	2	1					
HQ	84	1	1	11.4	1.5	1					
HQ	85	1	1	11.4	2	1					
HQ	86	1	1	11.4	2	1					
HQ	87	2	10	114.3	2	6	4				
HQ	88	1	1	11.4	2.5	1					
HQ	89	1	3	34.3	2	3					
HQ	90	1	20	228.6	1.5	20					
HQ	91	1	4	45.7	1	4					
HQ	92	1	15	171.4	1.5	15					
HQ	93	1	1	11.4	1	1					
HQ	94	1	5	57.1	1	5					
HQ	95	1	2	22.9	1	2					
HQ	99	2	5	57.1	3	4	1				
HQ	100	1	1	11.4	3	1					
HQ	101	1	1	11.4	3	1					
HP	8	6	99	1800	4	78					
HP	10	10	31	563.6	4	11					
HP	14	18	154	2800	3	37			1		
HP	15	6	22	400	4	12					
HP	17	9	70	1272.7	4	39					
HP	18	7	88	1600	3	52					
HP	23	6	81	1472.7	4.5	63					
HP	24	4	67	1218.2	4	30					
HP	26	2	5	90.9	5	3					
HP	28	8	170	3090.9	4	127					
HP	29	9	149	2709.1	4	65					
HP	32	9	67	1218.2	5	37					

Table 2. Range of ichnofabric values, species richness, and life habit of each monospecific species with lithologic units in which each species occurs.

Monospecific taxa	ii1*	ii2	ii3	ii4	ii5	S†	Life habit	Lithologic unit
<i>Orbiculoides lodensis</i>	X	X	-	-	-	1-3	Epifaunal, SF	Penn Yan
<i>Leiorhynchus quadracostata</i>	X	X	X	-	-	1-3	Epifaunal, SF	Geneseo
<i>Leiorhynchus sinuata</i>	X	X	X	-	-	1-2	Epifaunal, SF	Penn Yan
<i>Lingula spatulata</i>	X	X	X	X	-	1-16	Infaunal, SF	Geneseo, Windom, Ledyard
<i>Pterochaenia fragilis</i>	X	X	X	X	-	1-18	Epifaunal/semi-infaunal, SF	Hamilton Group
<i>Eumetabolotoechia multicostata</i>	X	X	X	X	X	1-18	Epifaunal, SF	Hamilton Group

*Ichnofabric (ii) 1 indicates laminated sediments.

†Species richness along individual bedding planes.

SF = suspension feeder.

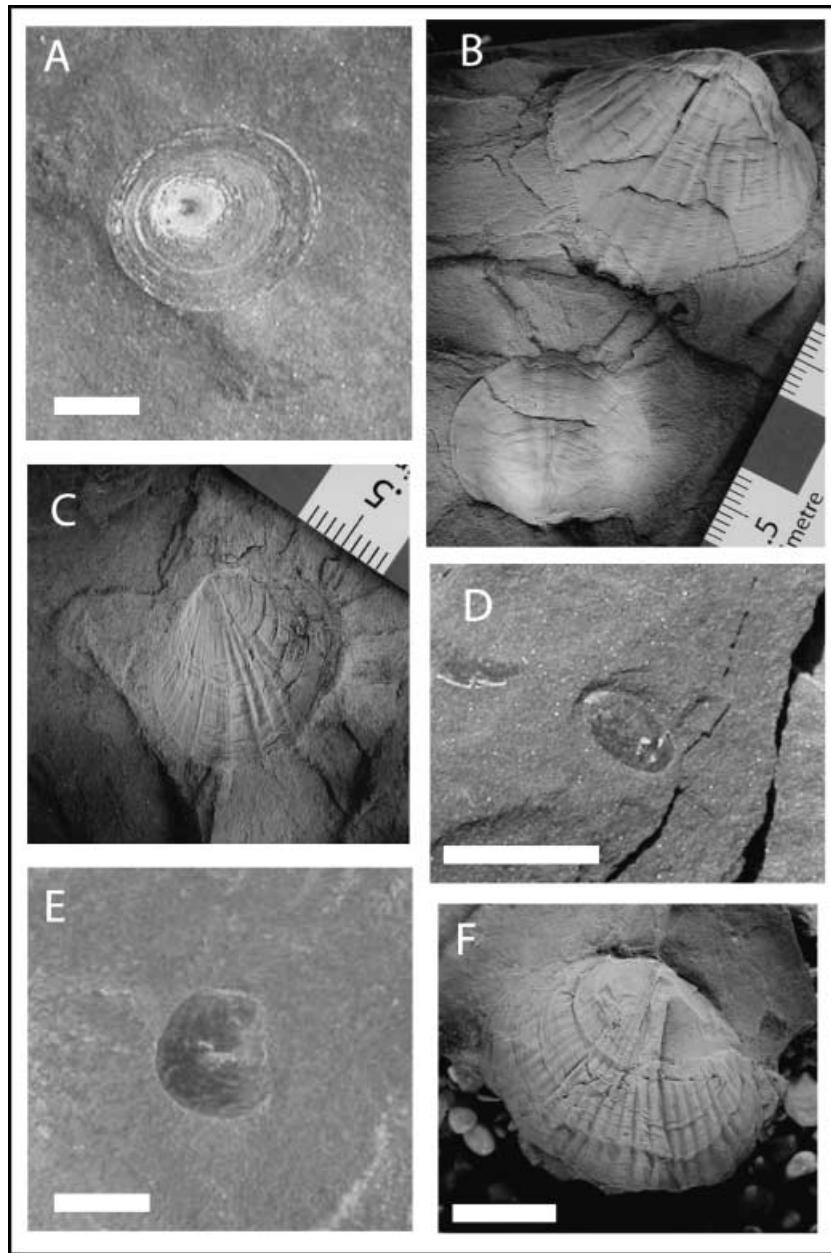


Fig. 4. Taxa present in monospecific assemblages □A. *Orbiculoides lodensis*, scale 0.5 cm. □B. *Leiorhynchus quadracostata*. □C. *Leiorhynchus sinuata*. □D. *Lingula spatulata*, scale 0.5 cm. □E. *Pterochaenia fragilis*, scale 0.5 cm. □F. *Eumetabolotoechia multicostata*, scale 0.5 cm.

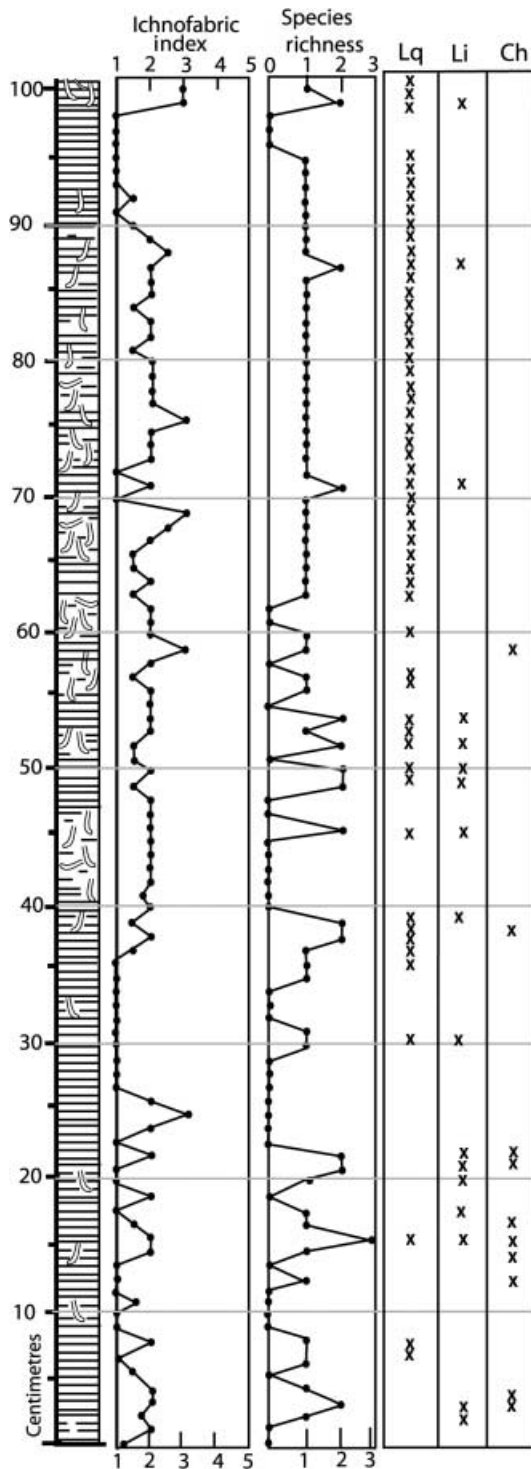


Fig. 5. Body fossil distribution and associated ichnofabric through a 100-cm interval of the Genesee Member exposed at Hubbard Quarry, New York. This interval is interpreted to represent consistently depleted bottom-water oxygen levels based on minimal bioturbation (ii 1–3) and consistently low diversity along bedding planes. Columns from left to right are a schematic representation of ichnofabric, quantification of relative amount of bioturbation as ichnofabric index averaged through each cm, species richness along individual bedding planes, and distribution of individual taxa through the section. Lq = *Leiorhynchus quadracostata*, Li = *Lingula spatulata*, Ch = *Chonetes* sp.

This species is restricted to bedding plane assemblages with species richness of one or two and uncommonly co-occurs with several Rhynchonelliform species that are otherwise rare at these localities.

Lingula spatulata (Fig. 4D) is a flat valved species that is consistently very small, typically 0.2–0.5 cm in length, and occurs at three localities. *Li. spatulata* is most commonly present in laminated and slightly bioturbated strata (ii 1–2) in monospecific assemblages or associated with *Le. quadracostata*. The distribution of individuals ranges from dispersed to moderately abundant (> 57 individuals/m²). *Li. spatulata* is uncommon in assemblages of species diversity > 2, and rarely occurs in high diversity assemblages (species richness 16). Within more diverse assemblages, this species is associated with an increased amount of bioturbation (ii 2–4).

Pterochaenia fragilis (Fig. 4E), a small pteroid bivalve less than 1 cm in length, occurs at seven localities. This species is most common in low diversity assemblages (species richness < 4) but is repeatedly present in bedding plane assemblages of higher diversities, up to a species richness of 18. When present in monospecific assemblages, *P. fragilis* occurs within laminated (ii 1) to moderately bioturbated strata (ii 3), but most commonly in association with minimal bioturbation (ii 2). Monospecific assemblages of this bivalve species are most commonly dispersed, but do occur as densely packed assemblages (> 200 individuals/m²). In assemblages with species richness > 4, *P. fragilis* is always rare on bedding planes and the associated bioturbation is increased (ii 2–4). It commonly co-occurs with *E. multicostrata*, a species also common in monospecific assemblages.

Eumetabolotoechia multicostrata (Fig. 4F) is a sub-circular, thin-shelled and inflated rhynchonellid, present at seven localities and is the most common species within these units. This species is variable in size ranging from less than 0.5 cm to nearly 3 cm in length and is typically preserved compressed. *E. multicostrata* is common in both monospecific and higher diversity assemblages, up to a species richness of 18 along an individual bedding plane. In monospecific assemblages, *E. multicostrata* is associated with a range of bioturbation, but most commonly laminated to slightly bioturbated (ii 1–2). This species most commonly occurs in association with increased amount of bioturbation (ii 2–5) in higher diversity assemblages. At the Paines Creek locality (Fig. 6), *E. multicostrata* is present in assemblages with species richness ranging from one to four on individual bedding planes and ichnofabric ranging from laminated to almost fully bioturbated (ii 1–4). Through a 75-cm interval, this particular species occurs in monospecific assemblages within laminated sediments as well as

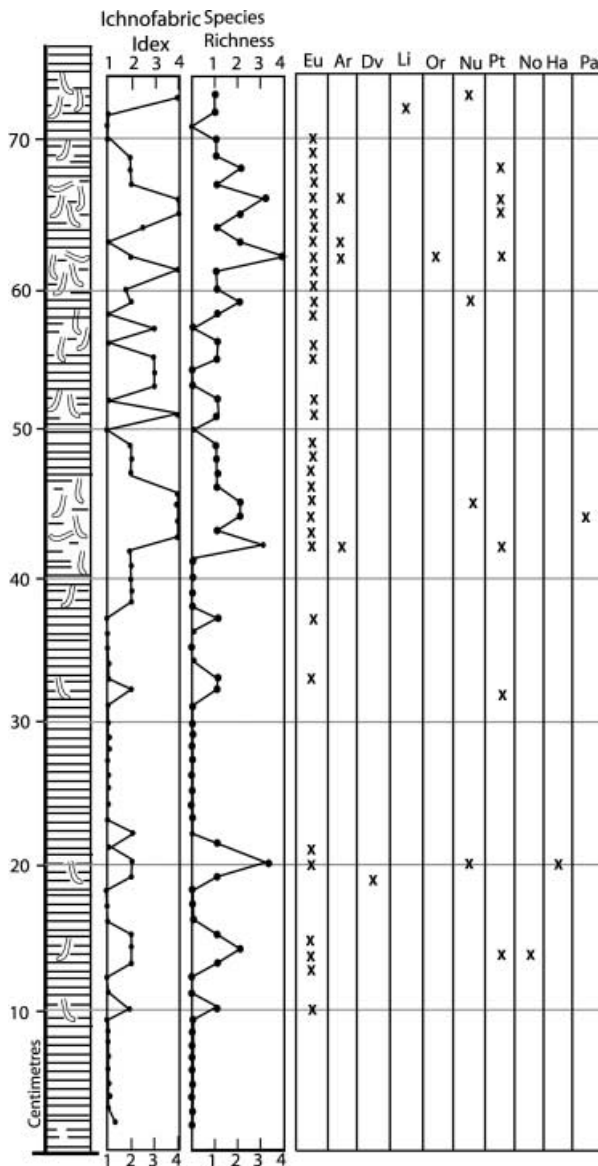


Fig. 6. Body fossil distribution and associated ichnofabric through a 75-cm interval of the Ledyard Shale at Paines Creek, New York. This section is interpreted to reflect small-scale fluctuations in oxygen ranging from anoxic (ii 1 devoid of body fossils) through near normal marine bottom-water oxygen levels (ii 4). Columns from left to right are a schematic representation of ichnofabric, quantification of relative amount of bioturbation as ichnofabric index averaged through each centimetre, species richness along individual bedding planes, and distribution of individual taxa through the section. Eu = *Eumetabolotoechia multicostata*, Ar = *Arcuaminetes scitulus*, Dv = *Devonchonetes coronatus*, Li = *Lingula spatulata*, Or = *Orbiculoides newberryi*, Nu = *Nuculoidea* sp., Pt = *Pterochaenia fragilis*, No = *Nuculites oblongatus*, Ha = *Hollandclark jennyae*, Pa = *Palaeozygoplura* sp.

associated with nearly fully bioturbated intervals (ii 4). *E. multicostata* is numerically dominant along bedding planes with species diversities ranging from two to 18 and associated with minimal bioturbation (ii 2) through nearly fully bioturbated strata (ii 4).

Palaeoecology of Devonian low-oxygen taxa

Species present in monospecific assemblages in these Devonian units can be divided into two distinct ecological groups. Half of the species that occur in monospecific assemblages, *Le. quadracostata*, *Le. sinuata*, and *O. lodensis*, are restricted to assemblages with low species richness (< 3) and minimal bioturbation (ii 1–3) interpreted to represent the lowest dysaerobic settings. These species are ecologically restricted to, and therefore are interpreted to be specialized for, extremely low bottom-water oxygen conditions. The other three taxa occurring in monospecific assemblages also occur in much higher diversity assemblages in association with bioturbated strata that suggest near fully oxygenated conditions at the time of deposition. This is important because despite the fact that *Li. spatulata*, *P. fragilis*, and *E. multicostata* are very successful in the lowest oxygen settings as indicated by repeated occurrences in monospecific assemblages associated with laminated or weakly bioturbated (ii 2) strata, they are not restricted to these environments. These taxa are interpreted to have a broad ecological range and in monospecific assemblages within laminated sediments are interpreted to be exploiting the underutilized dysaerobic habitat (Pearson & Rosenberg 1978).

Eumetabolotoechia multicostata is abundant in assemblages throughout the dysaerobic zone associated with all levels of bioturbation and a broad range of species richness (1–18). What is particularly unusual about *E. multicostata* is that it occurs in strata representing a wide range of relative bottom-water oxygen levels, but that it is commonly the dominant taxon in these communities. This species is interpreted to be adapted to and successful under an exceptionally broad range of relative oxygen levels.

Although all of taxa discussed above occur in laminated sediments those common in high-diversity assemblages associated with variable amounts of bioturbation are clearly not exaerobic species. *Leiorhynchus quadracostata*, along with associated fauna, has been interpreted from one locality as gregarious, opportunistic, suspension feeders inhabiting a narrow environmental setting associated with the intersection of the chemocline and the seafloor (Thompson & Newton 1987). *Le. quadracostata* and *Le. sinuata* are not restricted to monospecific assemblages and are found with little to moderate amounts of bioturbation, which make an exclusively chemosymbiotic lifestyle unlikely for these taxa. These findings are consistent with earlier interpretations (Thompson & Newton 1987). *O. lodensis* is associated

with minimal bioturbation (ii 1–2) and is present exclusively in monospecific assemblages with one exception as a single individual on a bedding plane on which it is co-occurring with *E. multicosata* and *P. fragilis*. The bioturbation could be a biological overprint originating at some time after the death of these organisms and therefore, a chemosymbiotic lifestyle for this taxon cannot be ruled out from these data alone.

The six taxa present in monospecific assemblages are all interpreted to be suspension feeders. This is in contrast to studies of modern environments that find that as oxygen levels decrease, there is a general trend towards the deposit feeding life habit, replacing suspension feeding as the dominant life habit (Wu 2002). Similarly, deposit-feeding bivalves are the dominant group in dysaerobic settings in the Late Palaeozoic (Kammer *et al.* 1986). However, data from this study suggest that under the most depleted bottom-water oxygen conditions suspension feeding was dominant. This is likely due largely to the abundance of brachiopods in these units as obligate suspension feeders yet a taxonomic bias cannot entirely account for this trend as the suspension-feeding bivalve *P. fragilis* also occurs in monospecific assemblages.

Low-oxygen taxa are commonly small as an increased surface area to volume ratio is a strategy for increased oxygen intake (Levin 2003). Flat valved morphology (i.e. paper pecten) is a further adaptation to the soft substrate conditions in these environments (Wignall 1990, 1994; Levin 2003). *Leiorhynchus quadracostata* and *E. multicosata* in particular are unusually large and inflated for this setting. The negative effects of an inflated shape in soft substrates may be counteracted by the thin shells on these specimens, allowing them to be more easily suspended in soft sediment (Alexander 2001). These rhynchonellids are interpreted to have a coiled spirolophore, which maximizes the area of filtering filaments for increase oxygenation of mantle material and has been proposed as the best lophophore design for Palaeozoic rhynchonelliform brachiopods in low-oxygen settings (Alexander 2001).

Discussion

The diversity of taxa present in the lowest dysaerobic zone within laminated sediments from these Devonian shales is particularly remarkable as extremely low amounts of oxygen (0.1 ml/L) are recorded in modern marine settings that support a fauna that completely destroys any primary sedimentary signal (Levin *et al.* 2003). Although it is difficult to quantify ancient bottom-water oxygen levels, it is likely that these

Devonian groups were adapted to extremely low-oxygen conditions based on their repeated occurrence within laminated strata across broad spatial and temporal timescales ranging from dispersed and abundant on individual bedding planes. In modern marine environments, the abundant occurrence of taxa such as *Capitella capitata*, and *Macoma baltica*, that are not considered especially tolerant of severely depleted oxygen conditions, in dysaerobic settings is interpreted to reflect the exploitation of transient depositional conditions through rapid colonization (Pearson & Rosenberg 1978; Modig & Olafsson 1998; Diaz & Rosenberg 1995; Rosenberg *et al.* 2001; Guerra-Garcia *et al.* 2003; Laine *et al.* 2007). An opportunistic ecology may be considered as an alternative to the interpretation of being fully adapted to reduced oxygen conditions for *Li. spatulata* and *P. fragilis*; however, the traditional ecological model of opportunistic taxa exploiting fluctuating environmental conditions through rapid colonization results in large abundances (Pearson & Rosenberg 1978, but see Norkko *et al.* 2006), which is not consistently observed in these taxa. The consistent abundance and dominance by *E. multicosata* through a broad range of relative oxygen levels are inconsistent with the interpretation of an opportunistic species. *E. multicosata* instead is interpreted to be successful throughout the dysaerobic zone, and even under near-normal marine oxygen levels.

In the Devonian, low-oxygen depositional settings were likely more common than today, as supported by the widespread distribution of black shales (Klemme & Ulmishek 1991; Arthur & Sageman 1994; Negri *et al.* 2006). The abundance of low-oxygen settings may have promoted the proliferation of dysaerobic taxa with variable ecological affinities not observed in modern oceans. Furthermore, the environments in which low-oxygen fauna are studied in modern oceans represent either near permanent low-oxygen conditions (oxygen-minimum zones) (Levin 2003) or fluctuations over short, even seasonal timescales in shallow coastal environments such as estuaries, fjords, and bays (Diaz & Rosenberg 1995). Epeiric seas are interpreted to be relatively shallow over a very broad geographical range with limited connectivity to the open ocean unlike any depositional setting present today, therefore modern depositional environments are not likely directly analogous to epeiric seas of the past (Tyson & Pearson 1991). As a result, different oceanographic settings may result in ecological and taxonomic distributions inconsistent with those inhabiting modern dysaerobic settings. Specifically, this may account for the presence of taxa with exceptionally broad ecological ranges that are successful under lowest dysaerobic conditions. Although eurytopic groups

are common in low-oxygen settings, the breadth of environmental dominance by *E. multicosata* from oxygen levels at the edge of metazoan habitability to fully oxygenated settings is not common in modern settings, and demonstrates a remarkable ecological range for this species.

Trace fossils are traditionally used to describe the most reduced-oxygen settings as the soft-bodied infaunal community is typically the last to be excluded as oxygen levels approach zero (Thompson *et al.* 1985; Savrda 1992). In addition to being palaeoecologically significant, these six taxa in monospecific assemblages are important as they can be used to identify trace levels of bottom-water oxygen, differentiating between anaerobic and dysaerobic depositional conditions beyond the resolution of trace fossil models and other sedimentological methods.

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