Ecologic stability of the dysaerobic biofacies during the Late Paleozoic

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Late Paleozoic faunas found in sediments of dysaerobic origin represent a unique community type that remained essentially unchanged from the Middle Devonian to the Early Permian. This dysaerobic community had the following unique characteristics: (1) dominance by vagile molluscs, with suspension-feeding brachiopods, bryozoans, corals and echinoderms usually subordinate; (2) a trophic structure dominated by deposit feeders and carnivorous or scavenging cephalopods; (3) small body size as the result of high juvenile mortality and possibly stunting; and (4) preservation of most individuals as pyritic steinkerns. All these characteristics are directly linked to the low oxygen levels of the dysaerobic environment. The relative stability of the deeper water, dysaerobic environment is consistent with Sanders' Stability-Time Hypothesis. The dysaerobic environment apparently offered a refuge for more archaic biotas that evolved in nearshore environments of the early Paleozoic. ☐ *Dysaerobic, ecologic stability, community evolution, biofacies, Devonian, Mississippian, Pennsylvanian, Late Paleozoic.*

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The late Paleozoic epicontinental seas of North America were from time to time density stratified. Times of extensive density stratification include the Middle (Byers 1977) and Late Devonian (Cluff 1980), the Early Mississippian (Cluff 1980), much of the Pennsylvanian (Heckel 1977), and the Early Permian (Babcock 1977). During these times, distinctive lithofacies and biofacies were associated with oxygen-deficient conditions within the deeper portions of the water column.

In studying dysaerobic faunas of Devonian through Pennsylvanian age, the present authors independently arrived at similar conclusions about the paleoecology of these faunas. We were much impressed by the stability of this community type throughout the Late Paleozoic. Recognition of this stability raised some major ecologic questions. Were the same major groups of organisms always dominant? Why did the trophic structure remain the same? And, why did the major components of these faunas show little change, other than generic replacement, over approximately 100 million years, while major evolutionary changes occurred within shallow water aerobic communities? The intention of this paper is to describe and discuss the fossil communities associated with the dysaerobic layer of the water column, and to address the questions raised above.

Ecology of oxygen-deficient basins

Anoxic conditions may occur in marine environments under the following conditions (Demaison & Moore 1980): (1) silled basins with a positive water balance may become anoxic, such as the Black Sea; (2) upwelling of nutrient-rich water can create high levels of biologic productivity at the surface, which can then deplete the oxygen supply in the water column, an example is the Peru coastal upwelling; and (3) oxygen-minimum layers in the open ocean can be produced by stagnation during periods of global warming and transgression, an example is the Cretaceous oceanic anoxic events (Arthur & Schlanger 1979).

Rhoads & Morse (1971) and Byers (1977) have all made important contributions to the understanding of the paleoecology of oxygen-deficient basins. Their work will be referred to as the Rhoads–Morse–Byers model. Both of these studies recognized three distinct biofacies based on the level of dissolved oxygen within the water column. These biofacies are as follows: (1) aerobic biofacies (> 1.0 ml/l dissolved oxygen), well-oxygenated surface water with a diverse shelly benthic fauna and bioturbation; (2) dysaerobic biofacies (0.1–1.0 ml/l dissolved oxygen), depth of water usually greater than 50 m, a low-diversity community with few or no calcified species and small body size with a dominance of infauna; and (3) anaerobic biofacies (< 0.1 ml/l dissolved oxygen), shelly benthic fauna and bioturbation lacking, sediment laminated.

More recent work, however, indicates that the biofacies of the Rhoads–Morse–Byers model should be redefined. In a study of the California Continental Borderland basins, Savrda *et al.* (1984) found on the basis of faunal criteria that there was no distinct boundary between the dysaerobic and aerobic facies. They indicated that the anaerobic biofacies could be separately recognized and that oxygen gradients above the anaerobic biofacies could be recognized on the basis of distinctive biotas in the lower and upper dysaerobic biofacies. However, there was no distinctive change between upper dysaerobic and lower aerobic faunas, instead, a distinct change in faunal diversity and composition was found at the shelf break within the aerobic biofacies. They concluded that while paleo-oxygen gradients can be recognized within the rock record, the dysaerobic and aerobic biofacies lack a distinct boundary and grade into one another. Thompson *et al.* (1985) proposed an alternative to the Rhoads–Morse–Byers model based on their study of the oxygen minimum zone off central California. Specifically, their model consists of: (1) a zone lacking macroinvertebrates, characterized by laminated sediments (< 0.1 ml/l dissolved oxygen); (2) a zone of small (1–2 mm) soft-bodied infauna with moderate bioturbation (0.1–0.3 ml/l dissolved oxygen); and (3) a zone of abundant calcareous macrofauna and bioturbation (> 0.3 ml/l dissolved oxygen). The calcareous macrofauna found between 0.3 and 0.5 ml/l dissolved oxygen was a low-diversity assemblage dominated by echinoderms.

Both of the above studies (Savrda *et al.* 1984 and Thompson *et al.* 1985) demonstrated that abundant calcareous faunas can be found in the dysaerobic biofacies as defined in the Rhoads–Morse–Byers model. The work presented in the present paper also indicates that a wide variety of calcareous organisms, in low-diversity communities, can be found in the dysaerobic biofacies, contrary to the Rhoads–Morse–Byers model. However, we feel that the Rhoads–Morse–Byers model is still useful if modified to include diverse calcareous faunas within the dysaerobic biofacies. Although our data on Paleozoic faunas provide no direct information on paleo-oxygen concentrations, the data do indicate that there is a distinctive community type of calcareous organisms that lived under conditions of lowered oxygen concentrations, probably within the dysaerobic biofacies as defined by the Rhoads–Morse–Byers model. We found that dysaerobic and aerobic communities were sometimes distinct from one another, perhaps because of a short diastem, but usually the dysaerobic and aerobic faunas were gradational. As will be shown, these community differences are real and are judged to have been controlled by relative differences in dissolved oxygen concentration, although we have no way of determining absolute oxygen values of the past water column. We must rely on studies of Recent oxygen-deficient basins to draw conclusions on absolute oxygen values.

Modern oxygen-deficient basins have a low-diversity assemblage of macroinvertebrates in the dysaerobic biofacies of the Rhoads–Morse–Byers model. These faunas include polychaetes, gastropods, nuculoid bivalves, chitons, asteroids, ophiuroids, echinoids, holothurians and crustaceans (Hartman & Barnard 1958; Savrda *et al.* 1984; Thompson *et al.* 1985). These faunas characteristically have small body size and are dominated by deposit feeders. Deposit feeders are the dominant trophic group because of the increased abundance of organic detritus due to low rates of oxidation. In order to feed in this environment, deposit feeders must have a high tolerance for low-oxygen, sulfide-rich sediments (Theede *et al.* 1969). Suspension feeders are rare or absent because of a restricted food supply associated with poor circulation in oxygen-deficient basins. In addition, suspension feeders are not known to tolerate low-oxygen conditions (Theede *et al.* 1969).

Dysaerobic faunas

Dysaerobic faunas of Early Paleozoic, Devonian, Mississippian and Pennsylvanian age are briefly discussed below. Detailed treatment of these faunas may be found in Brett *et al.* (in press), Dick & Brett (in press), Kammer (1985), and Boardman *et al.* (1984).

Early Paleozoic representatives. – Although this paper is primarily concerned with Late Paleozoic dysaerobic faunas, we will briefly summarize the composition of pre-Middle Devonian biotas as a prelude to more detailed discussion of later communities. Several previous studies of Ordovician and Silurian community gradients across shelf to basin transects (Ziegler 1965; Ziegler *et al.* 1968; Calef & Hancock 1974; Titus & Cameron 1976; Cisne & Rabe 1978; Hurst 1979) indicate that the Early Paleozoic dysaerobic facies are characterized by pelagic forms such as graptolites and nautiloids, and poorly developed, low-diversity benthic communities composed of small inarticulate brachiopods and a few species of molluscs, ostracodes and trilobites. Species richness in Ordovician dysaerobic benthic communities is particularly low (e.g. 8 macrofossil species in Trentonian *Triarthrus* community of Titus & Cameron 1976) and only slightly increased by the Late Silurian (18–20 macrofossil species in Ludlovian *Visbyella* community of Calef & Hancock 1974).

Detailed studies of Late Silurian communities (Watkins & Berry 1977; Watkins 1978) demonstrate that dysaerobic environments had begun to develop characteristic community attributes that persisted through to the end of the Paleozoic. Dark gray mudstones transitional between black, laminated graptolitic shales of the Welsh basin and silty mudstones of the shelf contain a benthic assemblage of small lingulid, orthid and chonetid brachiopods, dalmanitid trilobites, nuculoids and small archaeogastropods as well as minute praecardiacean bivalves (e.g. *Cardiola*) and craniid inarticulates, which may have been epiplanktic (Watkins & Berry 1977). Compared with later Paleozoic communities, these Silurian assemblages exhibit lower diversity and greater dominance by trilobites and considerably lower proportions of carnivores. Notably absent from these early dysaerobic communities are ambocoeliid brachiopods, bactritoids and ammonoids, all of which apparently evolved in offshore dysaerobic areas during the Early Devonian. However, the abundance of deposit-feeding nuculoids, archaeogastropods and diminutive brachiopods, is comparable to that seen in later dysaerobic communities.

Devonian. – The Devonian faunas occur in at least seven different pyrite-bearing beds of the Ludlowville and Moscow formations of the Middle Devonian Hamilton Group of western New York near the axis of the northern Appalachian Basin (Brett *et al.* in press). Similar, though non-pyritized, assemblages have been documented from the Lower Devonian Needmore Shale (Newton 1979) of the central Appalachians and the Marcellus Formation of New York (Brower *et al.* 1978).

The presence of phacopid trilobites with well-developed eyes indicates that these faunas lived within the photic zone, although, quite possibly in the dysphotic region. Rare or absent micrite envelopes, generally attributed to endolithic algae, suggest the dysphotic zone (Bathurst 1976). The absence of proximal tempestites, bearing hummocky cross stratification, indicates deposition below storm wave base. However, the occurrence of horizons of exceptionally well-preserved fossils indicates very rapid deposition of muds, probably following storm resuspension of sediment in more proximal, upslope areas. The pyritic faunas are enclosed within bioturbated gray mudstones that are transitional between well-laminated, anaerobic black shales and calcareous and silty, bioturbated gray mudstones with an aerobic fauna.

The dysaerobic faunas have a distinctive composition and are intermediate in species richness (about 35–40 species) between the pelagic assemblages of black, fissile shales (15–20) and the more species-rich aerobic faunas (60–100). Truly pelagic forms include styliolinids and perhaps the bivalves(?) *Buchiola* and *Pterochaenia*, which occur in great abundance on some bedding planes. The ammonoid *Tornoceras*, the nautiloid *Michelinoceras* and the bactritoid *Bactrites* are locally abundant. Their complete size range and exceptional preservation suggest that these organisms lived in close proximity to the seafloor, where they were buried. Presumably they were nektobenthic scavengers and carnivores which preyed on epifaunal organisms.

Nuculoid bivalves such as *Nuculoidea* and *Paleoneilo* are abundant at certain stratigraphic intervals. Like modern protobranch bivalves, they were probably shallow-burrowing deposit feeders. Epifaunal elements are dominated by thin-shelled, diminutive brachiopods, including lingulids, chonetids, ambocoeliids, *Productella* and juvenile(?) *Tropidoleptus*. The thin, concavo-convex shells of the common articulate brachiopods may have been adapted for the substrate instability associated with nuculoid bioturbation. Gastropods are abundant at some levels and include *Palaeozygopleura*, pleurotomariids such as *Glyptotomaria*, *Bembexia* and *Mourlonia*, and the bellerophontid *Retispira.* Archaeogastropods are commonly believed to have been grazers or deposit feeders, depending on the food sources available. Other epifaunal organisms included the scavenging or deposit-feeding trilobites, *Greenops* and *Phacops,* and ostracodes. Suspension-feeding demosponges, auloporid corals, crinoids and blastoids occur rarely within certain pyrite beds.

Upper Devonian dysaerobic faunas are less well documented than those of the Middle Devonian Hamilton Group. However, community studies in the late Givetian to Frasnian Genesee, Sonyea and West Falls Groups (Bowen *et al.* 1974; Thayer 1974; McGhee & Sutton 1981) indicate the persistence of most families or genera typical of Hamilton dysaerobic facies into the Upper Devonian. Auloporid corals, ambocoeliid and chonetid brachiopods, nuculoid bivalves, pleurotomariid and bellerophontid gastropods, orthoconic nautiloids, bactritoids and tornoceratid goniatites are all well represented in the 'Naples faunas' (see Clarke 1898) of the prodelta Portage magnafacies. The Portage magnafacies is transitional between black shales and fossiliferous siltstones and sandstones of the delta platform. A notable change from the Hamilton is the virtual elimination of phacopid trilobites from the dysaerobic (and other) biofacies. The extinction of this group appears to have taken place approximately coincidentally with the Givetian–Frasnian boundary.

In contrast, relatively little major change in dysaerobic faunas is noted at the Frasnian–Famennian boundary in the Appalachian Basin. For example, a pyritic fauna recently discovered from the early Famennian Gowanda Shale in western New York (Babcock 1982) is very similar to those from the underlying Frasnian beds.

Mississippian. – Two dysaerobic faunas are known to occur in the Lower Mississippian Borden Formation of Kentucky and Indiana (Mason & Kammer 1984). Both faunas occur in a basinal setting underlain by Late Devonian–Early Mississippian anaerobic black shales of either the New Albany or Sunbury shales. The faunas are overlain by sediments of the Borden delta containing aerobic faunas. The older fauna, of early Osagean age, is termed the Cave Run Lake fauna and is found in the basal part of the Nancy Member in eastern Kentucky. The younger fauna, of late Osagean age, is termed the Coral Ridge fauna and is found in the basal part of the New Providence Shale Member in north-central Kentucky and southern Indiana (Kammer *et al.* 1983; Kammer 1985).

The Cave Run Lake fauna consists almost entirely of diminutive molluscs. The ammonoid *Kazakhstania* is numerically dominant. This ammonoid apparently displays adult suture patterns on juvenile-size individuals. Common archaeogastropods include the bellerophontids *Sinuitina* and *Euphemites* and the pleurotomariid *Glabrocingulum.* Rarer faunal elements include the nuculoid bivalve *Nuculopsis* and an unidentified strophomenacean brachiopod. This fauna is still being actively collected and studied.

The Coral Ridge fauna consists of gastropods, bivalves, cephalopods, corals and rare faunal elements including brachiopods, trilobites, blastoids, crinoids and rostroconchs (Kammer 1985). A total of 29 taxa of macroinvertebrates have been recognized in this fauna. The fauna is dominated by molluscs, which comprise 90 percent of all specimens collected. The pleurotomariid *Glabrocingulum* alone comprises 76 percent of the fauna and is judged to have been an opportunistic species. Opportunistic species are not resource limited, but rather are limited by some aspect of the physical environment (Levinton 1970). Conditions may have been favorable for *Glabrocingulum* when there was a slight increase in the oxygen content of the water. The overwhelming majority of mollusc specimens are juvenile-size, which suggests high juvenile mortality, although the ammonoid specimens provide some evidence of stunting from oxygen deficiency (see Discussion). Adult-size specimens were found for the gastropods *Glabrocingulum, Sinuitina,* and *Loxonema* and the nuculoid *Ctenodonta.* No adult-size specimens were found for the nuculoids *Phestia* and *Nuculopsis,* the rostroconch *Hippocardia,* the nautiloid *Michelinoceras* and the ammonoids *Ammonellipsites, Beyrichoceras* and *Merocanites.* Non-molluscan faunal elements did not appear to be stunted.

The dominant trophic mode was deposit feeding. The deposit feeders included the archaeogastropods *Glabrocingulum, Sinuitina* and *Trepospira,* the caenogastropod *Loxonema,* the nuculoids *Phestia, Nuculopsis* and *Ctenodonta,* the rostroconch *Hippocardia* and the proetid trilobites *Brachymetopus* and *Phillibole.* Modern archaeogastropods in shallow water browse on benthic algae, whereas those living in the aphotic zone are deposit feeders (Rex 1973). The depth of water at the base of the New Providence Shale was between 90 and 170 m, based on stratigraphic analysis of associated turbidites (Kepferle 1977). These depths would have been well below the photic zone in the turbid water of the deltaic environment. Thus the archaeogastropods of the Coral Ridge fauna lived in an aphotic environment and, therefore, must have been deposit feeders.

Cephalopods are common in the Coral Ridge fauna compared to other Borden delta communities (Ausich *et al.* 1979). They include two nautiloids and four ammonoids. All are considered to have been nektobenthic because of their restricted areal distribution and their small size, indicating stunted growth as the result of oxygen deficiency. The cephalopods apparently preyed or scavenged upon the benthic fauna of the dysaerobic environment.

Epifaunal suspension feeders include the rugose corals *Amplexus, Trochophyllum* and *Cyathaxonia,* the brachiopods *Rhynchopora* and *Punctospirifer,* the blastoid *Orbitremites,* and the crinoids *Synbathocrinus, Barycrinus* and *Taxocrinus.* Collectively, suspension feeders make up almost half of the species richness, but they comprise only about 10 percent of the total number of individuals. Their presence suggests occasional fluctuations of the dysaerobic–aerobic boundary.

Upper Mississippian dysaerobic faunas are not well documented. Richard Alexander of Rider College (pers. comm., July, 1984) reports that molluscan faunas, similar to those reported in this paper, can be found in the Chesterian Chainman Formation of the Confusion Range in west-central Utah. The faunas occur in black, phosphatic limestone.

Pennsylvanian. – Dysaerobic faunas from Midcontinent Middle and Upper Pennsylvanian cyclothems have been identified in dark gray to black, clay-rich, phosphatic, non-fissile shales in 28 cyclothems in Oklahoma, Texas, Kansas, Nebraska, Iowa, and Missouri (Boardman *et al.* 1984). These shales occur within many of the 'core' shales of the simplified typical cyclothems as defined by Heckel & Baesemann (1975). Distribution of these dysaerobic faunas is generally limited to the Terrigenous Detrital Facies Belt of Heckel (1980), which encompasses southern Kansas and Oklahoma; although a small number of dysaerobic faunas have been found in the Open Marine and Phylloid Algal Mound Facies belts of the northern Midcontinent. Dysaerobic faunas may have been present in these northern facies belts but have not been preserved due to excessively low rates of clastic sedimentation associated with aragonite dissolution (Boardman *et al.* 1984).

Lithofacies of the 'core' shales, together with their corresponding biofacies, illustrate deposition along a paleo-oxygen gradient ranging from anaerobic to aerobic. The anaerobic lithofacies is characterized by black, fissile, finely laminated, non-bioturbated, phosphatic shale. Faunal elements within this lithofacies are entirely pelagic and consist of conodonts, sharks, radiolarians, and occasional ammonoids. The black shale faunal association is therefore a composite of planktic and nektic communities without benthic taxa. The anaerobic black shales represent the most offshore portion of the cyclothems and correspond to maximum transgression coinciding with interglacial stages in Gondwanaland (Heckel 1977). Depths of 100–200 m have been postulated for these deposits based upon faunal and lithologic criteria (Evans 1967; Heckel 1977).

The position of the dysaerobic lithofacies depends upon whether it is in a transgressive or regressive phase. In a transgressive sequence the dysaerobic facies underlies anaerobic black shale, whereas in a regressive sequence it overlies the black shale. The lithic contact between these two facies is typically sharp. The dysaerobic lithofacies is characterized by dark-gray to black, clay-rich, pyritic, bioturbated shale. At the junction of the anaerobic and dysaerobic environments lies a profusion of radiolarian-bearing phosphate nodules that are highly variable in size and form. The dysaerobic biofacies contains pelagic taxa similar to that recovered from the anaerobic shale, but also there is a benthic and nektobenthic fauna. This biofacies, which contains a diminutive molluscan-dominated assemblage defined as the *Sinuitina* Community (Boardman *et al.* 1984), has moderate species richness (10–56 species) and poor species equitability. The diminutive molluscs are typically preserved as pyritic or limonitic internal molds. Non-molluscan taxa comprise a relatively small percentage of the total fauna. Two of these faunas have been extensively investigated; the Lake Neosho Shale (Boardman *et al.* 1984) and the Eudora Shale (Malinky & Mapes 1982). A comprehensive study of the remainder of these faunas is currently underway and remains to be completed. In both the Lake Neosho and Eudora shales the dominant benthic faunal element was the bellerophontid gastropod *Sinuitina.* Bellerophontids have historically been interpreted as algal grazers, however, with outer shelf depths of 100–200 m interpreted for the *Sinuitina* Community, a deposit-feeding mode of life is suggested. Other less numerous gastropods occurring within the dysaerobic biofacies include the bellerophontids *Euphemites* and *Retispira*; pleurotomariids *Glabrocingulum, Mourlonia,* and *Trepospira*; the euomphalid *Cylicoscapha*; and the pseudozygopleurids *Pseudozygopleura* and *Helminthozyga.* These gastropods are also interpreted as deposit feeders. The dominant bivalves are the pholadomyoidid *Wilkingia* and the nuculoids *Quadratonucula, Anthraconeilo, Phestia, Nuculopsis,* and *Clinopistha.* These bivalves are interpreted as having been shallow-burrowing deposit feeders similar to modern protobranch bivalves. Ammonoids and bactritoids are often exceedingly abundant and constitute over 90 percent of the cephalopods. Nautiloids are generally rare in the dysaerobic biofacies. Overall, the generic composition of the cephalopods within the cyclothems is variable and changes relatively rapidly through time as a result of rapid evolution and periodic extinctions (Boardman *et al.* 1984). The cephalopods are interpreted to have been opportunistic nektobenthic scavengers or predators, based on their closest living analog, *Nautilus* (Saunders 1984). The preponderance of evidence suggests that the cephalopods present in the dysaerobic biofacies are not allochthonous accumulations (drifted shells), but are an integral part of the benthic community (Boardman *et al.* 1984). The remainder of the molluscs within the dysaerobic facies include rare scaphopods, hyolithids, and rostroconchs.

Non-molluscan dysaerobic taxa are dominated by the opportunistic eurytopic brachiopods *Crurithyris, Orbiculoidea,* and a variety of chonetids. Contemporaneous aerobic shelf faunas, as well as environments interpreted to represent brackish conditions, also contain these taxa, often in considerable abundance (Boardman *et al.* 1984). These brachiopods were probably adapted for a muddy substrate and were tolerant of low oxygen as well as low-salinity conditions. Brachiopods that were largely restricted to the deeper, low-oxygen regimes include the rhynchonellid *Leiorhynchoidea,* the spiriferid *Spiriferella,* and the small-size productids *Heteralosia* and *Fimbriaria.* Corals are generally rare and include the button coral *Gymnophyllum,* the tabulates *Michelinia* and *Palaeacis,* as well as various solitary rugose corals similar to *Lophophyllidium.* Arthropods are represented by *Ditomopyge* trilobites. Suspension-feeding organisms are quite rare but include the crinoid *Exocrinus,* the blastoid *Angioblastus,* and hyalosponges.

The diminutive molluscs have been shown by Boardman *et al.* (1984) and Malinky & Mapes (1980) to represent mass mortality of juveniles along with possible stunting of mature individuals. Evidence for stunting of mature individuals is equivocal, and therefore requires additional investigation. Contemporaneous aerobic shelf faunas also have a high infant mortality that is probably the result of an *r*-mode selection strategy. These faunas typically show a sigmoidal-shaped survivorship curve with a high infant mortality followed by low juvenile-early mature mortality and a high gerontic mortality. The dysaerobic faunas differ markedly from the aerobic shelf faunas in that while there is a high infant mortality, juveniles and early mature mortality is also high with little or no survival of adults of comparable size with the shelf faunas. Ammonoids are the only exception to the absence of normal-size gerontic individuals within the dysaerobic facies. In the ammonoids, there is an exceptionally high infant mortality (diameters 1–3 mm) followed by a high early-late juvenile mortality (diameters 10–12 mm) then a low early mature mortality (diameters 12–35 mm) and a normal gerontic mortality (diameters 35–150 mm). Contemporaneous ammonoids within the aerobic *Trepospira* Community show a high infant mortality (diameters 1–3 mm) followed by low juvenile-early mature mortality and then a high gerontic mortality.

The dysaerobic biofacies and lithofacies is often gradational with the aerobic biofacies and lithofacies which contains the *Trepospira* Community (Boardman *et al.* 1984). The trophic structure of the *Trepospira* Community is similar to the dysaerobic *Sinuitina* Community, but the former community has a higher species richness together with greater species equitability. Additionally, the *Trepospira* Community typically exhibits the aerobic-shelf sigmoidal survivorship curve, and, there are no indications of mass mortality or stunting of individuals.

Discussion and conclusions

The composition, trophic structure, specimen size, taphonomy and stratigraphic position of these Upper Paleozoic faunas are indicative of dysaerobic conditions during deposition. These

Table 1. Summary of taxonomic data for the molluscan-component of Devonian through Pennsylvanian dysaerobic faunas.

Taxonomic group	Devonian Hamilton Group	Mississippian Coral Ridge Fauna	Pennsylvanian (Table 2, Boardman *et al.* 1984)
GASTROPODA			
Archaeogastropoda			
Bellerophontacea			
Sinuitidae	–	*Sinuitina*	*Sinuitina*
Bellerophontidae	*Retispira*	–	*Retispira*
	Bucanopsis	–	*Euphemites*
Euomphalacea	–	–	*Cylicioscapha*
Pleurotomariacea			
Raphistomatidae	–	*Trepospira*	*Trepospira*
Eotomariidae	*Bembexia*	*Glabrocingulum*	*Glabrocingulum*
	–	–	*Ananias*
	Mourlonia	–	*Mourlonia*
Caenogastropoda			
Loxonematacea			–
Loxonematidae	–	*Loxonema*	–
Pseudozygopleuridae	–	–	*Pseudozygopleura*
	–	–	*Helminthozyga*
Palaeozygopleuridae	*Palaeozygopleura*	–	–
CEPHALOPODA			
Nautiloidea	*Michelinoceras*	*Michelinoceras*	8 genera
Bactritoidea	*Bactrites*	–	*Bactrites* plus 5 genera
Ammonoidea	*Tornoceras*	*Ammonellipsites*	
		Beyrichoceras	45 genera
		Merocanites	
BIVALVIA			
Nuculoida			
Ctenodontidae	–	*Ctenodonta*	*Clinopistha*
Nuculidae	*Nuculoidea*	*Nuculopsis*	*Nuculopsis*
Malletiidae	*Palaeoneilo*	–	*Anthraconeilo*
	–	–	*Quadratonucula*
Nuculanidae	*Phestia*	*Phestia*	*Phestia*
Pterioida	–	–	*Dunbarella*
Heterodonta	–	–	*Astartella*
Pholadomyoida	*Grammysia*	–	*Wilkingia*
ROSTROCONCHIA	*Conocardium?*	*Hippocardia*	–
MONOPLACOPHORA	*Cyrtolites*	–	–
SCAPHOPODA	–	–	*Plagioglypta*
HYOLITHINA	*Hyolithes*	–	*Hyolithes*

faunas have a number of features in common that can be used to characterize the dysaerobic biofacies during Late Paleozoic time.

First, the faunas are dominated by molluscs both with regard to species richness and abundance of individuals. Articulate brachiopods, corals and other stenohaline taxa may comprise a significant proportion of the faunas, but they are never dominant. This dominance by molluscs is in sharp contrast with typical open-shelf, aerobic environments that were dominated by brachiopods, bryozoans, corals and echinoderms during the Late Paleozoic. The taxonomic composition of the molluscan component remained relatively stable from the Devonian through Pennsylvanian (Table 1). For example, the pleurotomariids *Bembexia* (Devonian), *Glabrocingulum* (Carboniferous) and *Ananias* (Carboniferous) are very closely related genera and are all in the Tribe Eotomariides of the Family Eotomariidae (Knight *et al.* 1960). Within the nuculoids, *Ctenodonta* (Mississippian) and *Clinopistha* (Pennsylvanian) are in the Family Ctenodontidae; *Nuculoidea* (Devonian) and *Nuculopsis* (Mississippian) are in the Family Nuculidae; and *Palaeoneilo* (Devonian), *Anthraconeilo* (Pennsylvanian) and *Quadratonucula* (Pennsylvanian) are in the Family Malletiidae (Cox *et al.* 1969). The taxonomic com-

Table 2. Summary of taxonomic data for the non-molluscan-component of Devonian through Pennsylvanian dysaerobic faunas.

Taxonomic group	Devonian Hamilton Group	Mississippian Coral Ridge Fauna	Pennsylvanian (Table 2, Boardman *et al.* 1984)
BRACHIOPODA			
Inarticulata	*Orbiculoidea*	–	*Orbiculoidea*
	Lingula	–	–
Articulata			
Chonetidae	*Devonochonetes*	–	–
	Longispina	–	–
Strophalosiidae	–	–	*Heteralosia*
Productellidae	*Productella*	–	–
Overtoniidae	–	–	*Fimbriaria*
Camarotoechiidae	*Leiorhyncus*	–	*Leiorhynchoidea*
Rhynchoporidae	–	*Rhynchopora*	–
Ambocoeliidae	*Ambocoelia*	–	*Crurithyris*
	Echinocoelia	–	–
Brachythyrididae	–	–	*Spiriferella*
Spiriferinidae	–	*Punctospirifer*	–
ANTHOZOA			
Tabulata			
Auloporidae	*Aulocystis*	–	–
Micheliniidae	*Pleurodictyum*	–	*Michelinia*
Favositidae	–	*Emmonsia?*	–
Palaeacidae	–	–	*Palaeacis*
Rugosa			
Amplexiidae	–	*Amplexus*	–
Cyathaxoniidae	–	*Cyathaxonia*	–
Laccophyllidae	–	*Trochopyllum*	–
family uncertain	–	–	*Gymnophyllum*
Stereolasmatidae	*Stereolasma*	–	–
Lophophyllidae	–	–	*Lophophyllidium*
ECHINODERMATA			
Crinoidea			
Synbathocrinidae	–	*Synbathocrinus*	–
Anamesocrinidae	*Anamesocrinus*	–	–
Cyathocrinitidae	–	*Barycrinus*	–
Exocrinidae	–	–	*Exocrinus*
Decadocrinidae	*Decadocrinus*	–	–
Taxocrinidae	*Eutaxocrinus*	*Taxocrinus*	–
Blastoidea			
Phaenoschismatidae	*Hyperoblastus*	–	–
Codasteridae	–	–	*Angioblastus*
Orbitremitidae	–	*Orbitremites*	–
TRILOBITA			
Proetacea			
Proetidae	–	*Phillibole*	–
Phillipsiidae	–	–	*Ditomopyge*
Brachymetopidae	–	*Brachymetopus*	–
Phacopacea			
Phacopidae	*Phacops*	–	–
Dalmanitidae	*Greenops*	–	–

position of the ammonoids changed continuously during this time because of their rapid evolution. The taxonomic composition of the non-molluscan component shows no clear pattern of stability during the same time, with the possible exception of the Ambocoeliidae and *Orbiculoidea* (Table 2).

Second, the faunas have a similar trophic structure. The benthic component of the faunas is dominated by deposit-feeding nuculoid bivalves and archaeogastropods. Because the Carboniferous faunas of this study are judged to have lived below the photic zone (Boardman *et al.* 1984; Kammer 1985), the trophic role of the archaeogastropods probably was deposit feeding rather than grazing. Many modern browsing gastropods also eat organic detritus (Rex 1973; Walker & Bambach 1974). The pelagic component of the faunas consisted of ammonoid and nautiloid cephalopods. The cephalopods are judged to have been nektobenthic and probably preyed and scavenged on the benthic fauna.

Third, the majority of individuals are smaller than normal adult size for their respective species. Compared to contemporaneous aerobic faunas with a wide range of specimen sizes, the dysaerobic faunas are striking in their dominance by small-size individuals. For many species this may be from high juvenile mortality. Fluctuations of the anaerobic–dysaerobic boundary in the water column may have been responsible for mass mortality of entire populations containing large percentages of juveniles. Another possibility is that once individuals reached a certain body mass, their oxygen requirements became too great and they died. Although most specimens are undoubtedly juveniles, some individuals may have been stunted. Hallam (1965) cites several studies in which the growth of marine invertebrates was shown to be inhibited by oxygen deficiency. In order to demonstrate stunting, adult features must be found on juvenile-size specimens. Many invertebrates do not display uniquely adult features on their hard parts. Ammonoid suture patterns, however, show distinct ontogenetic stages. The juvenile-size ammonoids from the Mississippian Borden Formation exhibit close packing of the sutures near the living chamber, which is a characteristic late ontogenetic pattern (Mason & Kammer 1984). Thus for several of the Mississippian ammonoids, at least, there does appear to have been stunting associated with oxygen-deficient conditions. Boardman *et al.* (1984), however, report that the suture patterns on juvenile-size Pennsylvanian dysaerobic ammonoids are those of juveniles. Evidence for stunting remains inconclusive and needs additional study.

Fourth, the specimens are taphonomically similar. Specimens are commonly preserved as pyritic steinkerns. Detailed taphonomic and petrographic studies of these and similar pyritized fossils (Hudson 1982; Dick 1982; Dick & Brett, in press) indicate that much of the pyrite is of early diagenetic origin, and thus provides an indication of sediment geochemistry at the time of formation. Pyrite aggregates do not generally form in black, organic-rich muds of the anaerobic or lower dysaerobic zones. Here, pyrite may be very abundant as disseminated framboids, but it does not form localized aggregations due to an absence of concentration gradients in the uniformly reducing sediments. Pyritized macrofossils are thus characteristic of anoxic, non-sulfidic sediments, poor in organic matter, typical of the upper dysaerobic zone (Berner 1981). A recent study by Reaves (1984) demonstrated that several factors are critical for the formation of syngenetic pyrite aggregates, including: (1) moderately well-oxygenated overlying water, (2) low background sedimentation rates, coupled with (3) episodic burial of organic matter, (4) low concentrations of metabolizable organic matter in the bulk sediment, (5) an active benthic fauna and (6) warm, rather constant environments. All of these factors apparently apply to the Paleozoic pyritic fossil assemblages considered herein. Apparently, the enclosed shell cavities provided reducing microenvironments favorable to the formation of pyrite. In the absence of oxygen, sulfate-reducing bacteria produced hydrogen sulfide which reacts with ferrous iron to form monosulfides and/or pyrite (Berner 1981). Muds in the dysaerobic zone probably were oxygenated only within the top few centimeters, and were anoxic below this level. Originally aragonitic shells were occasionally replaced by pyrite but more commonly were dissolved, perhaps because of a lowered pH associated with the oxidation of monosulfides to form sulfuric acid within the upper sediment (Reaves 1984). Clarke & Lutz (1980) documented the formation of pyrite in shells of still living bivalves just a few centimeters below the sediment–water interface.

Fifth, the faunas all occupy similar stratigraphic positions. The stratigraphic position of the faunas can be used as an independent check of their dysaerobic origin. In every case, the dysaerobic gray shales are either bracketed between anaerobic black shales lacking a benthic fauna, and gray shales with an aerobic fauna, or the dysaerobic gray shales grade laterally, in opposite directions, to anaerobic black shales basinward and aerobic gray shales shoreward (Fig. 1). In the Middle Devonian Hamilton Group of western New York, the Ludlowville and Moscow formations contain several dark shales, with pyritic faunas, that grade laterally (eastward) into black shales in the vicinity of the 'Finger Lakes Trough'. To the west, the dark shales grade laterally into well-oxygenated shallow-water sediments (Brett *et al.*, in press). The dysaerobic faunas of the basal portion of the Lower Mississip-

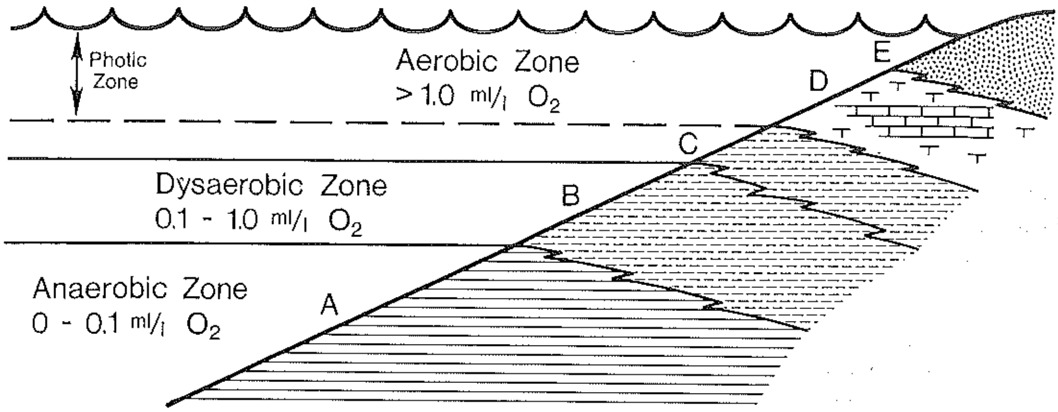

Fig. 1. Generalized diagram showing biofacies and lithofacies in an oxygen-deficient basin. Biofacies boundaries based on Rhoads–Morse–Byers model; as discussed in text, recent work in modern anoxic basins may necessitate revision of these boundaries. □ A. Pelagic fauna preserved in laminated black shale. □ B. Dysaerobic, molluscan-dominated fauna in dark to medium gray shale. □ C. Stenotopic, suspension-feeding community (brachiopods, corals, crinoids, etc.) in gray shale. □ D. Same as C, but in photic zone with carbonate lithologies. □ E. Eurytopic molluscan community in nearshore sediments. The position of the photic zone is not fixed relative to biofacies.

pian Borden Formation in Kentucky are sandwiched between the black shales of the New Albany Shale below and the aerobic faunas of the Borden above (Kammer 1985). The dysaerobic faunas of the midcontinent Pennsylvanian are found within the 'core' shales of cyclothems situated both below and above the black fissile shales that were deposited in the deepest portion of the cyclothem (Boardman *et al.* 1984). Thus, it is always possible to recognize the original stratified water column by the distribution of sedimentary facies.

Late Paleozoic dysaerobic faunas exhibited ecologic stability during a corresponding period of change in shallow-water benthic faunas. These dysaerobic faunas showed continual dominance by archaeogastropods, nuculoid bivalves and ammonoids (Table 1). Dominance within these three groups varied between faunas, probably because of subtle environmental differences that have gone unrecognized. Trophic structure was stable with deposit feeders and carnivores as the primary ecologic groups. In sharp contrast, shallow-water benthic communities saw major taxonomic changes. For example, among Middle Devonian brachiopods the Spiriferida contained approximately 90 genera while the Strophomenida contained approximately 45 genera. By the Late Pennsylvanian the situation was reversed with the Strophomenida (mostly Productidina) containing approximately 95 genera and the Spiriferida contained approximately 30 genera (Williams 1965, Fig. 149). The Crinoidea offer another example with the Camerata dominant in Devonian and early Mississippian communities, whereas the cladid inadunates were dominant in late Mississippian and Pennsylvanian communities (Lane 1971, Fig. 2, 1984; Ubaghs 1978). Moreover, the Late Devonian Frasnian–Famennian mass extinction had no appreciable effect on the dysaerobic community, as previously noted. This mass extinction event affected shallow-water organisms with the resultant extinction of shallow-water corals, tentaculitids, eight families of trilobites, several families of brachiopods and ammonoids, and virtually all of the stromatoporoids (McLaren 1983).

The relatively low species richness of the dysaerobic biofacies agrees with Sanders' (1969) Stability-Time Hypothesis. This hypothesis predicts a decrease in species richness as physiological stress increases. Contemporaneous aerobic communities had more than twice the number of preserved species that dysaerobic communities had (Boardman *et al.* 1984; Kammer 1985; Brett *et al.*, in press). High physiological stress prevents complex species interactions and, thus, keeps species richness at a minimum. In the case of dysaerobic settings, the low and possibly fluctuating levels of oxygen represent a severe physiological stress that was responsible for low species richness. The ecologic stability of the dysaerobic biofacies probably was a function of the severe physical conditions associated with this biofacies. Bretsky & Lorenz (1970:527) found that ecologic stability, in the form of persisting taxa, was typical of environments of high physiological stress. This is so, presumably because of the highly generalized, eurytopic nature of the organisms as well as the general lack of biotic interactions. Also, the relatively deep water in which dysaerobic faunas lived may have provided insulation from environmental changes that greatly affected contemporaneous shallow-water faunas. Thus, although the dysaerobic environment was physiologically stressful, environmental conditions were stable and the faunas remained evolutionarily conservative. Although we have not studied post-Pennsylvanian dysaerobic faunas, the basic community type apparently remained unchanged into the Permian (Babcock 1977) and the Jurassic (Morris 1980).

Late Paleozoic dysaerobic faunas contain many relatively archaic taxa, such as hyolithids, bellerophontids, monoplacophorans and some of the last of the trilobites, which were largely absent from Late Paleozoic shallow-shelf biotas. Thus, these dysaerobic communities included some of the last representatives of the 'Cambrian' fauna as defined by Sepkoski (1981). Classes belonging to the 'Paleozoic' and 'Modern' faunas also occur within these communities. However, these designations are potentially misleading, because they are presently defined at too broad a level (on the basis of factor analysis of class level distribution data). For example, Sepkoski (1981) includes both bivalves and gastropods in the 'Modern' fauna, but the bellerophontids, pleurotomariids and nuculoids are geologically archaic members of these classes, more related in their temporal distribution to the 'Paleozoic' or even the 'Cambrian' faunas. These evolutionarily long-lived, conservative taxa, which were abundant in the Late Paleozoic, offshore, dysaerobic biotas, first appeared in shallow nearshore settings of the Early Paleozoic. These observations seem to support the hypothesis that deeper-water environments acted as a refuge for more archaic biotas. They are also consistent with the model of nearshore evolution–offshore migration of marine communities proposed by Sepkoski & Sheehan (1983) and Jablonski *et al.* (1983).

A closely related point is the taxonomic similarity between Paleozoic nearshore faunas and those of the offshore dysaerobic zone. Many of the same families, although typically different genera or species, are abundant in both of these disparate marine environments, but are very rare or absent in the intervening, shallow, fully aerobic shelf environments. For example, lingulid, orbiculoid and chonetid brachiopods, nuculoid bivalves, bellerophontid and pleurotomariid gastropods dominate many nearshore communities (Bretsky 1970; Bowen *et al.* 1974; Thayer 1974). As noted herein, these taxa are also common constituents of deeper water, dysaerobic faunas in the Late Paleozoic. Even more striking are certain disjunct distributions within genera or species. For example, in the Devonian the brachiopod *Tropidoleptus carinatus* first appeared in nearshore siltstone and mudstones of the Lower Devonian and remained abundant in these facies throughout much of the period; however, in Middle Devonian time a small morphotype of this species was also very abundant in dark gray, pyritic shales of the dysaerobic zone. This species is rarely found in intermediate facies. Evidently, the generalized, physiologically-tolerant, nearshore organisms were, in many cases, well adapted for life in poorly oxygenated slope and basinal environments as well. The rarity or absence of these organisms from high diversity, shallow-shelf communities may reflect an inability to compete with more specialized organisms.

Surveys of Paleozoic communities (Sepkoski & Sheehan 1983; Jablonski *et al.* 1983) indicate that most of these organisms appeared first in the nearshore environments of Early Paleozoic age and later expanded offshore. In some cases, both nearshore and deeper-water representatives persisted throughout the Paleozoic or beyond (e.g. lingulids, protobranch bivalves) giving rise to disjunct distributions. Conversely, other taxa declined and went extinct in the nearshore zone, but persisted as 'living fossil' groups in the deeper, and sometimes dysaerobic, environments (e.g. monoplacophorans, hyolithids, bellerophontids).

As previously noted, dysaerobic benthic communities of the Early Paleozoic appear to have been poorly developed and of low diversity, as compared with later representatives; they may have possessed vacant niches prior to mid-Paleozoic time. Hence, these environments could have served as collecting grounds for low-oxygen-tolerant organisms from shallow shelf regions. Such organisms may well have initially arisen in unstable nearshore environments such as bays or lagoons, where they evolved physiological mechanisms for coping with sporadically lowered oxygen levels during periods of stagnation. Hence, they were prepared to live in the dysaerobic biofacies.

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Taxonomy and informal newsletters

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Many groups of palaeontological specialists now publish informal newsletters which are widely circulated, much enjoyed, and serve as a valuable forum to present work in progress, problems in the course of resolution, or just plain gossip. Nobody doubts the value of such channels of communication. There are, however, problems when these newsletters become vehicles for taxonomy. Unlike most geological and palaeontological information taxonomy is governed by 'laws' which fix priority, designation of type species, and the like. The recently revised *International Code of Zoological Nomenclature* (1985) lists (Article 8) criteria which can be taken as defining a 'publication' for taxonomic purposes. After 1985, there is no reason to exclude newsletters from official 'publications' on these criteria, because an earlier requirement for conventional printing no longer applies. This can create several difficulties. In the first place there is nothing to prevent a statement of intent on the part of, say, a research student, becoming a formal proposition of a taxon which he or she, or the scientific community, may come to regret. Newsletters do not have the kind of refereeing procedures which act as some kind of filter for taxonomy. We know of several examples where taxa have surfaced in newsletters and never attained formal publication. It would be even more regrettable if newsletters became a potential base for 'battles of priority'. Anybody who has worked with the more obscure publications of the last century will have experienced the nightmares of trying to establish relative dates at a time when taxonomic skirmishes were commoner. The answer to these problems is obvious: newsletters should be excluded as valid publications for taxonomic purposes. The same remarks apply to other informal publications, such as abstracts for meetings, papers of IGCP working groups, and the like.

Fortunately the *Code* (Article 8b) does allow for a disclaimer to be included in any organ which will mean that it is 'not published within the meaning of the Code' At the moment few if any of the informal newsletters include such a disclaimer. We would urge the editors of all informal stratigraphic or palaeontological newsletters to include a disclaimer in a prominent position on the cover. An appropriate wording might be: 'This newsletter is not deemed to be a valid publication for formal taxonomic purposes' (see ICZN Article 8b). This would settle the matter. There is, of course, no reason why some other kinds of information should not be quoted from newsletter sources – stratigraphic distributions or new occurrences being obvious examples.

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