

PALEOZOIC (CAMBRIAN THROUGH DEVONIAN) ANOXITROPIC BIOTOPES

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Abstract

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The oxygen-poor to denitrified waters of modern oceans provide an analog for open ocean conditions which contained the Early Paleozoic "graptolite" biotope. Certain euphausiids, other zooplankton and fish, as demonstrated in the Eastern Tropical Pacific, are found concentrated in and about denitrified waters. The boundary zone between oxic and denitrified waters show intense organismal growth due to the increased chemical availability of nutrients as reduced nitrogen compounds. Such waters are areally limited in the present cold and well-ventilated modern ocean. The distribution patterns showing attraction to low or oxygen-depleted waters (*anoxitropy*) in these modern open marine faunas suggest that Early Paleozoic plankton and nekton, preserved in lithofacies formed under low oxygen or anoxic conditions, could have been similarly attracted to the more extensive ancient denitrified and anoxic waters. The major Paleozoic faunal groups, in order of their occupation of the niche, include agnostid and olenid trilobites, graptoloid graptolites, styliolinids, thin-shelled bivalves, small orthocone nautiloids, and early ammonoids. The expansion of low-oxygen to anoxic waters across the shelves during warm climates in the Early Paleozoic may be correlated with major evolutionary radiations in the graptolites and possibly in the early ammonites.

Introduction

In Early into Middle Paleozoic oceans, two facies dominate: the shelly facies with mostly benthic organisms requiring oxygenated waters generally associated with sandstones, limestones, and bioturbated shales; and the graptolite facies with planktic or passive organisms found in laminated unbioturbated black shales. Fossils found in the shelly facies rarely occur in the graptolite facies; although graptolite facies organisms may be found as a minor component of certain shelly facies rocks. This separation implies distinct environmental conditions for each facies. Due to extinctions and replacements of most of the graptolite facies organisms and the lack of extensive modern black shale lithofacies, the environ-

mental conditions of these biofacies and lithofacies are difficult to study using modern analogs. Accordingly, the origins of the graptolitic biofacies and its related black shale lithofacies have been the subject of speculation (Bulman, 1970; Pettijohn, 1975). Bulman (1970) in his analysis of the environmental conditions under which the "graptolite facies" accumulated, suggested that "the essential condition is the complete lack of bottom circulation so that dissolved oxygen, soon exhausted, cannot be replenished; while a high proportion of decaying organic matter may be contributed by animal and plant remains falling from superficial aerated layers." Erdtmann (1982) noted that preservation of delicate graptolite peridermal structures suggests that both living conditions and sites of

fossilization were removed from vigorous wave action and from oxygenated bottom waters which could have permitted active predation and scavenging by benthic organisms. This view is supported by the evidence that most black graptolite-bearing shales commonly are characterized by fine-scale laminations, absence of evidence of bioturbation, and locally abundant pyrite (Pettijohn, 1975, p. 282). There also is a spatial separation of these facies as the occurrences of graptoloid or planktic graptolites indicates that they were most abundant in outer shelf and slope waters (Berry, 1974); whereas the shelly biofacies are near-shore shallow water to inter-tidal.

That the graptolite lithofacies is not restricted to the life-span of the floating or graptoloid graptolites has been discussed by Berry (1962, 1974) and House (1975) who recognized black shales of the graptolite facies type in Cambrian and Devonian stratal sequences respectively. Cambrian "graptolite facies" strata bear primarily agnostid trilobites (Berry, 1974; Ludvigsen et al., 1986). Ludvigsen et al. (1986) found that dark, laminated mudstones that formed on Late Cambrian continental slopes contain almost exclusively olenid and agnostid trilobites. The agnostids are considered planktic; whereas certain olenids probably were swimmers. Berry (1974) noted that the planktic graptolites appear in black, thinly laminated shales with agnostids in the Cambro-Ordovician transition interval. Ultimately, planktic graptolites replaced agnostid and olenid trilobites in that facies formed on the continental slope in the Ordovician. The Devonian "graptolite facies" strata bear, in layers stratigraphically above those containing the last graptoloid graptolites, styliolinids (notably *Nowakia*, Lutke, 1979), slender orthocone nautiloids, some ammonoids (House, 1975), thin-shelled bivalves, and certain ostracods (Rabien, 1956). Thus, the Paleozoic "graptolite facies" rocks bear remains of planktic organisms other than graptolites in strata both younger and older than those formed in the life span of the planktic graptolites.

Berry and Wilde (1978), Berry et al. (1987),

Wilde and Berry (1982, 1984, 1986), Wilde (1987) have applied fundamental principles of physical and chemical oceanography, based upon observations of modern oceanic environments to distinguish those oceanic environments in which strata typical of the "graptolite facies" could have formed. This series of papers indicates that the Early Paleozoic oceans were anoxic beneath the surface wind-mixed layer and when sea level rose during warm climates anoxic waters invaded the outer shelf. During glacial intervals in the Late Ordovician or cool climates in the Devonian, the waters beneath the pycnocline were ventilated by deep circulation driven by the sinking of cold oxic waters at high latitudes. A similar mechanism drives the ventilation and circulation in the modern deep ocean. An oceanographic model is proposed here for the environmental conditions in which graptolite facies organisms lived in the Lower Paleozoic. This model offers an explanation for the separation of both graptolite biofacies and black shale lithofacies from that of the shelly facies.

Modern environmental analogs of the graptolite facies

Chemical oceanography of transitional (oxic to anoxic) waters

Potential modern analogs of oceanic environments in which the "graptolite facies" formed are limited in extent because the modern oceans are well ventilated and circulation is rapid in the modern inter-glacial climate (Munk, 1966). The modern ocean is truly anoxic in very limited areas such as fjords, small basins in the Baltic, the Black Sea, and the Cariocao Trench (Richards, 1965; Deuser, 1975; Demaison and Moore, 1980). Such anoxic areas are formed due to special conditions blocking extensive interchange with the aerated open ocean usually by shallow sills. However, there are relatively extensive areas of the modern open ocean that have little or no oxygen and are transitional between oxic and anoxic waters. In such waters

slowly metabolizing organisms or migrating transient higher organisms survive. Areas of modern oceans in which an oxic surface layer is underlain by near anoxia in the pycnocline are present in the Eastern Tropical Pacific (ETP) (Anderson, 1982), the northern Arabian Sea in the Indian Ocean (Qasim, 1982), and seasonally in areas of coastal upwelling as off the western coasts of California (Mullins et al., 1985) and Namibia (Calvert and Morris, 1977). In these waters, oxic chemical reactions cease at oxygen concentrations below 0.22 ml/l (Devol, 1978). Below this concentration and to an negative oxygen equivalent of about -1 ml/l (Wilde, 1987) nitrogen compounds are consumed as an "oxidant" in chemical reactions in the process of denitrification (Stumm and Morgan, 1970; Curtis, 1983; Hashimoto et al., 1983. Dugdale et al. (1977) described denitrification in the ETP as a process of reduction of NO_3 to N_2 or N_2O by bacteria and the use of nitrate as a hydrogen acceptor when oxygen concentrations are too low for its use as an oxidant (see also discussion in Richards, 1965; Goering, 1968; Anderson et al., 1982; Blackburn, 1983). When NO_3 is consumed by denitrification, then SO_4 is the next abundant hydrogen acceptor in sea water (Stumm and Morgan, 1970; Richards, 1965). This sulfate reduction would occur in truly anoxic waters with the anoxic respiration of H_2S as the end product. Of significant importance is that during denitrification, reduced nitrogen compounds preferred by plankton (Eppley et al., 1969) are produced, increasing nitrogen nutrient availability without the sulfide toxicity of the more anoxic sulfate reduction. In the modern ocean, sulfidic conditions normally are not reached in the open ocean due to vertical advection of oxygen from the well ventilated deep waters which nitrify the waters in the lower pycnocline back to oxic conditions. However, Dugdale et al. (1977, p. 606) reported that during dinoflagellate blooms "denitrification can occur so strongly in the open sea that hydrogen sulfide is found in the water column". In the Lower Paleozoic, during warmer climates with less ventilated deep waters, the

core of what now is the oxygen minimum zone probably was anoxic. In this case denitrified waters were transitional between the surface oxic water and sulfidic rich anoxic waters in the pycnocline (Wilde and Berry, 1986; Wilde, 1987). Thus, in the Paleozoic, denitrified waters may contain an attractive food source just overlying the toxic sulfide rich waters of truly anoxic oceanic environments. This suggests not only the possibility of a unique biotope there, but also explains the preservation of planktic organisms as fossils in the underlying black shale lithofacies.

Biological oceanography in modern denitrified waters

Both the oceanographic and biological conditions have been studied extensively in the denitrified waters of the Eastern Tropical Pacific. Wooster and Cromwell (1958) and Wyrski (1967) described the physical conditions. Eppley et al. (1968), Longhurst (1967), Brinton (1962, 1980), and Judkins (1980) described plankton, primarily euphausiid zooplankton distribution in relationship with depth and areal extent of oxygen-deficient waters in the ETP. Gallardo (1963, 1977) and Menzies et al. (1973) reviewed benthic life found where the oxygen-poor waters intersect the bottom in the ETP off Peru. Douglas (1981) and Mullins et al. (1985) described oceanic and biologic developments in the oxygen-minimum zone in the California coastal upwelling system. Thompson et al. (1985) described benthic life where the oxygen-poor waters formed during upwelling off Central California intersect the sea floor.

Faunal concentrations

Mullins et al. (1985) noted that "the density of all major invertebrate groups with the exception of calcareous molluscs, is greatest along the upper edge of the central California oxygen minimum zone". Brinton (1980) found three distinct types of euphausiid behavior in the oxygen minimum zone in the ETP. In one type, the euphausiids migrated daily in and out

of the core of the oxygen minimum. Another euphausiid group skirted the lowest oxygen content waters, but was abundant at the edge of the oxygen-poor waters. A third group concentrates symmetrically at the upper and lower edges of the oxygen minimum zone. Mullins et al. (1985, p. 491) noted "the edges or boundaries of the oxygen-minimum zone (OMZ) are 'hot spots' of increased biogeochemical activity". The enhanced biological activity is explained by the increased availability of nitrogen due to denitrification at the edges of the OMZ. The edges of the OMZ's may be preferred sites of increased biological activity because of greater nutrient concentration plus larger food supplies in the form of bacteria" (Mullins et al., 1985, p. 464).

Dugdale et al. (1977) suggested productivity was high enough in dinoflagellate blooms in the ETP to completely consume nitrate to produce total denitrification. Holligan et al. (1984) also noted dinoflagellate blooms in denitrified waters off both the Peru and west African coasts. Holmes et al. (1957), Reid (1962) and Banse (1964) reviewed primary productivity and faunal occurrence data and concluded both phytoplankton and zooplankton were especially abundant in the waters of the ETP.

Anoxitrophic indigenous faunas

McGowan (1971) demonstrated that the planktonic and nektonic species in the Pacific show six unique geographical distribution patterns, including the ETP. Brinton (1980), in his review of the euphausiids of the ETP, indicated these zooplankton comprise a distinctive biogeographic provincial fauna that has remained relatively stable for a considerable length of time. Brinton (1980, p. 126) suggested that this "temporal stability in the extreme environmental features combined with high nutrient availability" are factors in controlling the unique aspects of the ETP euphausiid fauna. Ebeling (1962) noted that the ETP comprises one of the four major zoogeographic provinces of fish in tropical waters. Blackburn et al. (1970) pointed out that the unique euphausiid fauna of the ETP attracted

intense tuna foraging. This relationship illustrates that active nekton are attracted to denitrified waters for the purpose of predation.

Longhurst (1967) and Youngbluth (1975) analyzed the life habits of zooplankton living in waters at the northern margins of the ETP. There, whole populations of copepods and euphausiids migrate vertically daily, spending daytime hours at depth in waters with an oxygen content of only about 0.25 ml/l. Brinton (1980, p. 180) found that certain euphausiids spend the day at depths of 200–400 m in oxygen-poor waters, but migrate upward at night as much as 300 m to the surface waters to alleviate the oxygen debt they incurred during the day. Teal and Carey (1967) showed in the laboratory that the euphausiid *Euphausia mucronata* could respire in waters in which oxygen was barely detectable. This and other laboratory studies (Childress, 1968) indicate that some species could live in waters with very little oxygen content. Such organisms that feed in oxygen-poor waters would be "anoxitrophic".

The imprint of the denitrification zone on bottom sediments

Thompson et al. (1985) discussed benthic conditions under the central California coastal upwelling system. Gallardo (1963, 1977) described benthic life in oxygen-poor waters off the Peru–Chile coast. Coles (in Menzies et al., 1973) documented benthic life where denitrified waters intersected the sea floor off Peru–Chile.

Thompson et al. (1985) found evidence of burrowers in bottom sediments in environments in which the oxygen content was as low as 0.1 ml/l. "Environments having oxygen values between 0.3 and 0.5 ml/l were found to contain abundant animal populations capable of completely homogenizing bottom sediments" (Thompson et al., 1985, p. 178). Calvert (1964) found laminated, non-bioturbated sediment in the Gulf of California where the oxygen content was below 0.2 ml/l. Savrda et al. (1984) noted that laminated, non-biotur-

bated sediment occurs in southern California borderland basins where the oxygen content falls below 0.15 ml/l. From these data, Thompson et al. (1985) suggested that laminated, non-bioturbated sediment, that would be considered characteristic of anoxic conditions, could occur when oxygen concentrations were 0.1 ml/l or less. Following Rhoades and Morse (1971) and Byers (1977), Thompson et al. (1985, fig.15) used the term "dysaerobic" to describe burrowed sediment where the oxygen content was from 0.1 to 0.3 ml/l. In addition, Thompson et al. (1985, p. 178) found calcareous shelled organisms in sediments where the oxygen in bottom waters was as low as 0.3 ml/l. Savrda and Bottjer (1987) have called this situation the "exaerobic" zone as a boundary between dysaerobic and anaerobic conditions based on the occurrence of the Miocene bivalve *Anadara montereyana*. Clearly, in both sediments and overlying waters, organisms can function when the oxygen content is as low as 0.1 ml/l. Non-bioturbated, laminated sediments must occur in truly anoxic environments. Further, the observational evidence of organismal activity in oxygen-poor but nutrient rich waters indicates that a zonation exists between truly oxic and truly anoxic waters. In modern benthic environments, the lower limit of oxic waters is indicated by the disappearance of calcareous shelled organisms at an oxygen concentration of about 0.3 ml/l, which is close to the value of the cessation of oxygen oxidation at 0.22 ml/l (Devol, 1978). From 0.3 to 0.1 ml/l oxygen, non-shelled burrowers may function. Brinton's (1980) analysis of euphausiid groups in oxygen-poor waters in the ETP also show faunal zonation reflective of oxygen content of the oceans.

Early to Middle Paleozoic anoxygenic organisms

Fossil analogs

The presence of abundant and unique zooplankton in denitrified waters at the cores of modern oxygen minimum zones suggest this

niche also could have been filled by zooplankton uniquely adapted to low to no oxygen levels in the Cambrian through Devonian, where such waters were more wide-spread than in the modern well-ventilated ocean. We suggest that the unique fauna generally restricted to the "graptolite" lithofacies such as agnostid trilobites, planktic graptolites, styliolinids such as *Nowakia*, and possibly thin-shelled ostracods and certain ammonites were at least part time inhabitants of Paleozoic denitrified waters below the surface mixed layer. Such organisms living in or attracted to mildly anoxic waters thus would be "anoxygenic". If the anoxygenic organisms additionally fed in these waters, they also would be anoxygenic as are certain modern euphausiids from the Eastern Tropical Pacific described above.

From the Cambrian through the Devonian, agnostid trilobites, graptoloid graptolites, styliolinids, and entomozoecid ostracods most commonly are preserved in laminated, non-bioturbated sediments (black shale facies). Such organisms are preserved rarely in other lithofacies associated with undoubted oxic, chiefly benthic, faunas. The organisms of the graptolite facies are planktic, nekto-planktic, and nektonic so undoubtedly lived in the water above their eventual site of preservation in sediment. The preservation of the graptolitic facies organisms in black shales suggests a proximity to anoxic conditions, which may reflect the anoxygenicity shown by modern euphausiids in the ETP. By analogy with the indigenous faunas of the ETP, graptolite facies organisms potentially could migrate downward into denitrified waters for food then upward into more oxic waters to respire. While in denitrified waters, such organisms could avoid predation from active nekton requiring truly oxic waters. Figure 1 shows the postulated living conditions in the water column for this biofacies from the base of low oxygen waters into the transition denitrified zone between oxic and toxic sulfide-rich anoxic waters. The thickness, depth, and position of the niche off-shore changed with climatic conditions. As Wilde's (1987) model shows, the

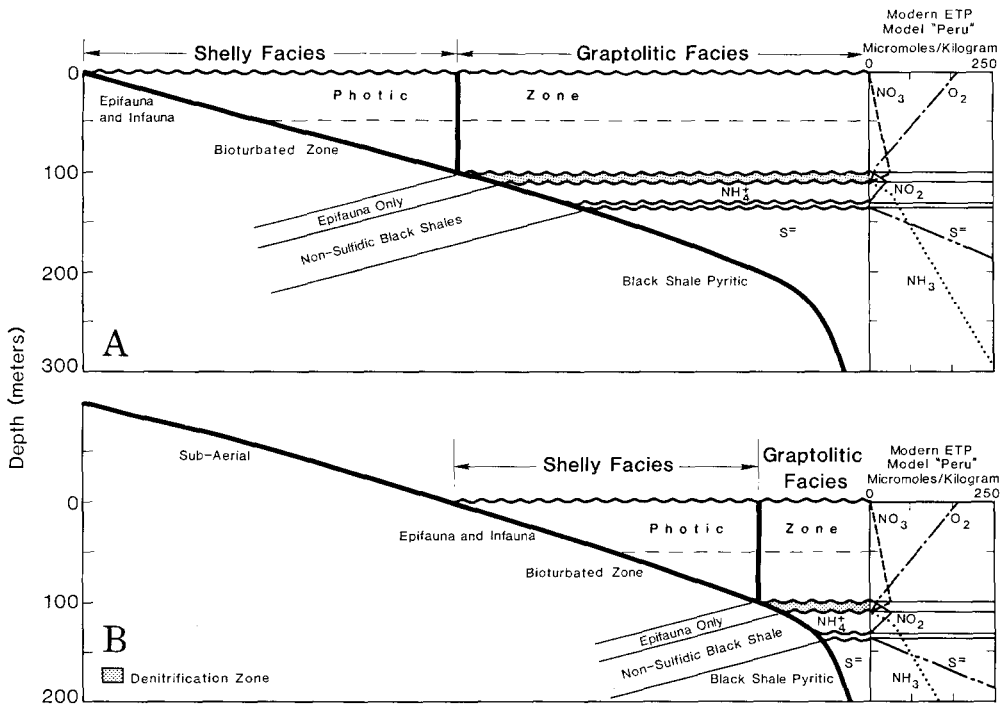


Fig.1. Proposed relationships in the equatorial Early Paleozoic among shelly and graptolite biofacies, shelly and black shale lithofacies, and chemical oceanography (Modified from Berry et al., 1987). Chemical model (Redfield et al., 1963, p. 46) uses modern surface values in the ETP (Anderson, 1982), but with no deep ventilation. A. Conditions for warm climates and high stands of sealevel. B. Conditions for cold climates and low stands of sealevel.

thickness of the non-oxic but non-sulfidic transitional layer, where denitrification occurs, can fluctuate with oxygen conditions in the pycnocline related to circulation and the source and origin of deep water masses. Thus, the greatest extent of the niche, both areally and vertically, would occur during warm climates with lower oxygen saturation values and higher stands of sea level. Periodic cold and cooler periods accompanied with the progressive ventilation of deep water would contract the niche resulting in extinctions or faunal reductions. Significant faunal changes or replacements would be seen in the more complete fossil record of the subsequent warm interval.

Berry et al. (1987) discussed the potential effect on the evolution of graptolites with changes in thickness and depth of the denitrification zone. If denitrified waters were present within the photic zone during times of poor ventilation, primary productivity would

increase with the attendant increase of zooplankton. This would enhance the development of large many-branched graptolites taking advantage of the abundant food supply. If denitrified waters sank below the photic zone due to increased ventilation in the surface layers, zooplankton adapted to living in oxygen-poor waters would have to migrate periodically upward into the photic zone and/or partially subsist on detritus. Thus colonies that developed the ability to migrate vertically and those with upward facing zooids would have an advantage in feeding. The evolutionary changes in graptolites from the Early Ordovician through the Early Devonian from (a) many-branched to few to single branched forms and from (b) pendant to biserial and finally uniserial scandant colonies may reflect the adaptation to the sinking of the denitrification zone to well below the photic zone in the top of the pycnocline due to progressive ventilation of the oceans.

Transgression and regression and extinctions

Fortey (1984) and Berry et al. (1987) drew attention to the relationship between transgression and regression across continental shelves of the Ordovician and graptolite flowerings and extinctions. Fortey (1984) showed that Early Ordovician world-wide transgressions were linked with marked radiations among the graptolites whereas global regressions were linked with graptolite extinctions. Berry et al. (1987) noted that below the surface mixed-layer (ca. 100 m) during Ordovician transgressions, oxygen-poor, denitrified, and anoxic water would spread across the shelf. This would result in two distinct lithofacies and related biofacies (Fig.1). Sediments shallower than 100 m would have oxic overlying waters and would be closest to shore with the attendant possibility of high rates of sedimentation and coarser sediments. Such conditions would support the typical Paleozoic "shelly" biofacies. Plankton localized in denitrified waters would be deeper and further offshore than the shelly fauna. Accordingly, upon death they would sink into the denitrified and anoxic waters and would be preserved in the offshore "black shale" facies. If these plankton behaved as euphausiids in the modern ETP and lived part-time in oxic waters to recuperate from oxygen deficiency, this would explain the occasional occurrence of "black shale" fauna with shallower "shelly" faunas.

During warm, equable climates and relatively high stands of sea level, large portions of the middle and outer continental shelf would have been overlain by denitrified and possibly anoxic waters (Berry et al., 1987). Wilde (1987) demonstrated the fluctuations with depth of the various redox zones as a function of climate. During cool and glacial intervals, such as in the Late Ordovician and the Devonian, sea level would regress and the denitrified and anoxic waters would withdraw off the shelf onto the slope. Wilde and Berry (1984, 1986) noted that global oceanic overturn is possible at either the beginning or end of a glacial interval, as a result of the shift in the

source of the major oceanic water masses. An oceanic overturn at the onset of glaciation after a long interval of high sea level and anoxic water on the shelf could advect toxic sulfide-rich waters into the overlying perennial wind-mixed oxic upper ocean causing mass kills of both oxic and denitrification zone faunas.

Early Devonian graptolite facies commonly include increasing numbers of styliolinids with time (Lutke, 1979). After the extinction of graptolites, styliolinids persist in the "graptolite" lithofacies (Rabien, 1956; House, 1975). Potentially, the tiny, conical styliolinids may have been more motile or their shells offered better protection from new predators such as nektonic ammonites than was available to the graptolites.

House (1975) found Devonian ammonites in dark shales that formed on the margins of basins that were anoxic at the center. The Devonian ammonites may have swum into the denitrified waters overlying the anoxic waters to feed as do modern tuna in the ETP. The facies relationship of Devonian ammonites to dark shales suggests they were linked to oxygen-poor waters by food. House (1985) reviewed eight ammonoid extinctions in the interval from the Early Devonian into the Carboniferous. Chlupac and Kukal (1986) provided a detailed description of three of these extinctions in the Barrandian. The data suggests that the Devonian ammonite extinctions may have been related to relatively rapid sea level changes; although House (1985) noted that precise global correlation between sea level changes and ammonoid extinctions was not possible at present. If the ammonite groups that became extinct were linked nutritionally to the denitrified waters, then sea level and climatic changes which modify the depth and thickness of denitrified waters also may be correlated with major extinctions and radiations among the ammonites.

The appearance and proliferation of nektonic faunas, the extinction of graptolites and the reduction among other planktic faunas in the graptolite facies in the Devonian may

reflect the diminution of denitrified and anoxic waters due to progressive ventilation of the oceans (Berry and Wilde, 1978).

Summary

The oxygen-poor, denitrified waters seen in limited regions in the modern ocean provide a modern ecological analog for faunas found in the "graptolite" lithofacies. Modern organismal distributions, particularly observed in the Eastern Tropical Pacific, show a close link between euphausiid zooplankton and certain fish to redox conditions. This implies that Early Paleozoic zooplankton and nekton, found preserved almost exclusively in low oxygen and anoxic lithofacies could have responded similarly to redox conditions in the water column. The major faunal groups potentially related to denitrified waters include agnostid trilobites, graptoloid graptolites, styliolinids, thin shelled bivalves, certain ostracods, orthocone nautiloids, and some nektonic ammonites. Figure 2 shows the occupants of this biotope with time for the Lower Paleozoic.

Agnostid and olenid trilobites dominated this habitat until the proposed cold interval of the Late Cambrian (Frakes, 1979) when their numbers were reduced. The graptoloid graptolites were prominent in the biotope from the Cambrian-Ordovician boundary interval until the extinction of the group by the late Early Devonian. Massive extinctions and restriction of graptolitic faunas coincided with the Late Ordovician glaciation, but they re-radiated during the warmer Silurian. Nekto-planktic styliolinids developed in the Early Devonian and outlived the graptolites. These styliolinids with nektonic ammonoids occupied the anoxic biotope until its marked areal and vertical reduction during the Permo-Carboniferous glaciation. Competition from and even predation by these more free swimming and shelled forms may have hastened the end of the graptolites. The affinities of the styliolinids with benthic oxic forms and the oxygen requirements of the nektonic habit suggest that styliolinids and early ammonites only opportunistically grazed organisms in the denitrification zone while it lasted. Their primary

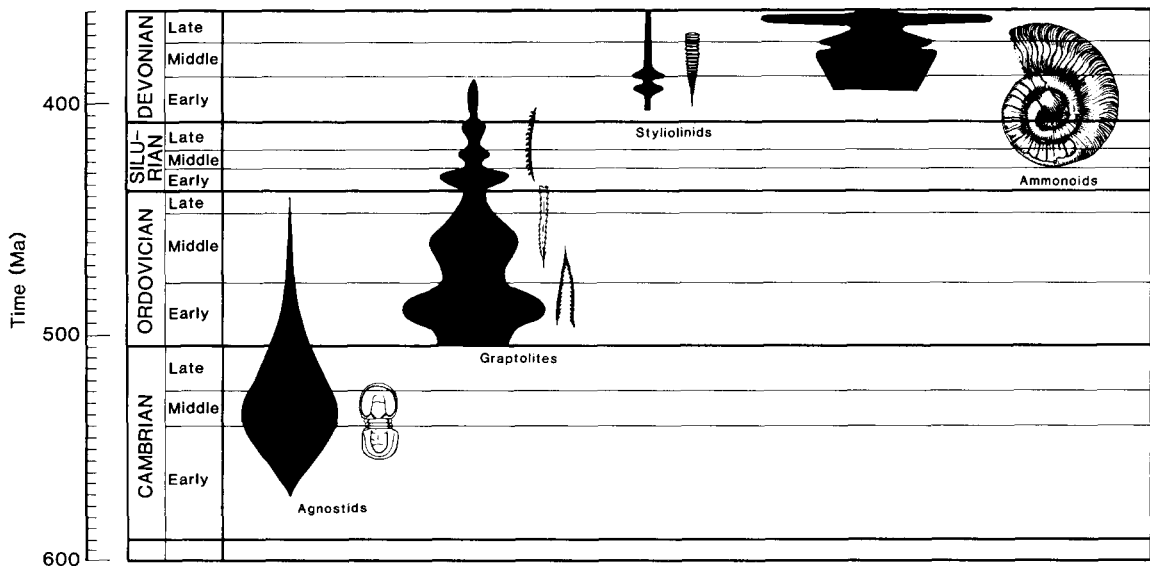


Fig.2. Distribution of graptolite or anoxic biotopes in the Early Paleozoic. Time intervals from Harland et al. (1982). Relative abundance of species level derived for (1) agnostids: Whittington (1954); (2) graptolites: Berry (this paper); (3) styliolinids: Lutke (1979); and (4) ammonoids: House (1985). Representative figured organisms are not to scale. Drawings are modified from (a) agnostids: Moore (1959); (2) graptolites: Bulman (1970); (3) styliolinids: Lutke (1979); and (4) ammonoids: Moore (1957).

habitat must have been oxic waters. Thus the graptolites may have been the last major organismal group principally linked trophically to the denitrification zone.

The spread of low-oxygen to anoxic waters across the shelves in the Early Paleozoic can be correlated with major evolutionary radiations among the graptolites (Fortey, 1984; Berry et al., 1987) and possibly among the ammonites (House, 1975). More study of organismal distributions in relation to redox conditions as well as detailed faunal investigations of "graptolite" facies rocks is needed to better understand the origin of "black shale" faunas.

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