MATTERS OF THE RECORD

The problem with the Paleozoic

Shanan E. Peters

Shanan E. Peters. Department of Geological Sciences and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109. E-mail: shananp@umich.edu

Accepted: 13 December 2006

Unfossiliferous marine sedimentary rocks of Phanerozoic age are known to all field-oriented paleontologists. These troublesome units are often encountered in the field, perhaps cursed roundly for a moment or two, and usually shrugged off in pursuit of the next fossiliferous interval. Paleontologists tend not to discuss barren units, and they rarely publish on the absence of a fauna from what appears to be unaltered marine rock. But aren't barren marine sediments revealing something important about their paleoenvironment and possibly about the paleoenvironments of conformably adjacent fossil-bearing units? Shouldn't paleontologists be just as interested in knowing the locations and ages of unfossiliferous sediments as they are fossiliferous strata?

In this essay, I discuss the possible environmental significance of barren marine sediment and present preliminary data to suggest that its frequency may have varied considerably during the Phanerozoic. I also present evidence to suggest that this variation is associated with shifts in the prevailing location of preserved marine sediment accumulation from expansive epicontinental seas to comparatively narrow continental shelves. Finally, I propose that such shifts in the physiographic contexts of marine shelf habitats and their preserved sediments are associated with oceanographic effects that have greatly influenced environmental and biological evolution, the character of the fossil record, and our perception of marine biodiversity and macroevolution at many different temporal and spatial scales.

Nobody Home: Causes

In the short time that I knew Jack Sepkoski, he told me at least twice about all of his fa-

© 2007 The Paleontological Society. All rights reserved.

vorite Cambrian formations. He was particularly fond of puzzling over those unaltered marine sedimentary rocks that contained no, or exceedingly few, body fossils. The absence of skeletal material might, he reasoned, be the result of taphonomic or diagenetic loss. After all, it is widely appreciated that dissolution can substantially modify the diversity and composition of fossil assemblages (e.g., Cherns and Wright 2000). The wholesale removal of skeletal material was not, however, a satisfying explanation for many unfossiliferous units because, even in the most extreme taphonomic and diagenetic settings, skeletonized animals are generally expected to leave at least some remnants behind. Although Sepkoski would never completely dismiss the possibility that dissolution was important, and for good reason (e.g., Reaves 1986), he would always conclude that "no, it's much more likely that there's just nobody home."

Sepkoski's quip about "nobody home" probably rings true for the majority of barren marine sediments. Although pre-compaction carbonate dissolution can remove all traces of calcareous skeletal material (e.g., Reaves 1986; Schovsbo 2001), lithology, sedimentary structures, stratigraphic context, and occasional characteristic body fossils (Byers 1977; Gaines and Droser 2003) or ichnofossils (Byers 1977; Savrda and Bottjer 1986; Föllmi and Grimm 1990) often betray the fact that unfossiliferous sediments accumulated in environments that were inhospitable to most metazoans. What environmental factors might prevent the successful recruitment of skeletonized benthic animals for prolonged periods of time and therefore promote the accumulation of barren marine sediments?

The most geographically widespread environmental factor is probably oxygen depletion (Rhoads and Morse 1971; Byers 1977; Levin 2003). Many benthic marine animals have unique physiological or behavioral adaptations to cope with low oxygen concentrations (e.g., Diaz and Rosenberg 1995; Levin 2003), but intense or prolonged hypoxia can nonetheless result in the complete extermination of benthic metazoans and the spread of persistent "dead zones" on the ocean floor (e.g., Nordberg et al. 2001; Rabalais et al. 2002; Helly and Levin 2004). Because hypoxia is promoted by biologically mediated oxidation of organic matter in the water column, it is most prevalent in bottom waters located below the wind-mixed surface layer in regions of high productivity (Levin 2003) and in restricted basins with poor circulation and stratified water columns (Rhoads and Morse 1971; Byers 1977; Kamykowski and Zentara 1990; Tyson and Pearson 1991a; Wignall 1994).

Although humans are often implicated in many cases of marine hypoxia (Levin 2003), there are presently over 10⁶ km² of shelves that are naturally hypoxic owing to incursions of permanent oceanic thermoclines and their associated oxygen minimum zones (OMZs) as well as to precipitation and runoff-induced salinity stratification (Helly and Levin 2004). Thus, despite the important role that humans play in promoting hypoxia (Diaz and Rosenberg 1995; Diaz 2001), large areas would experience episodic hypoxia even in the absence of humans (Diaz and Rosenberg 1995; Diaz 2001; Rabalais et al. 2002; Sorokin 2002; Levin 2003; Helly and Levin 2004; Osterman et al. 2005).

Low dissolved oxygen concentration is probably the most geographically widespread factor that can result in the accumulation of significant quantities of barren marine sediment, but unusual salinity can also exclude metazoans for extended periods of time. Unlike hypoxia, hypersalinity typically occurs in well-mixed, shallow-water settings, such as rimmed carbonate platforms and arid marginal marine environments. Brackish water within estuaries and other humid, marginal marine embayments may also contain a relatively depauperate benthic fauna, but because many taxa are uniquely adapted to variably brackish conditions (e.g., Fürsich 1993), brackish water alone is usually insufficient to exclude benthic organisms for long periods of time.

Water-mass properties, such as oxygen concentration and, to a lesser degree, salinity, are important factors that control the abundance and diversity of benthic animals, but if sedimentation rates are high enough to dilute skeletal input or if sedimentary processes themselves preclude successful benthic recruitment, then unfossiliferous sediment may also accumulate under fully normal marine conditions. Depositional settings with the necessary subsidence and sedimentation rates to exclude benthic organisms typically are found only in regions of active tectonic faulting, such as the pull-apart basins in southern California (e.g., Kidwell 1988), and in pro-deltaic settings in foreland basins.

All three proximal causes of barren marine sediment in the rock record, namely hypoxia, salinity, and sedimentation, are directly controlled by circulation patterns on and adjacent to shelves, precipitation patterns over the shelf and adjacent landmasses, and temperature. These parameters, in turn, are controlled by climate and shelf physiography (Fig. 1). Because hypoxia can be promoted by many different factors, it is likely to be a prevalent, but by no means exclusive, cause of barren marine sediment in the geologic record. It is of course also likely that several factors might combine so as to effectively exclude benthic organisms even when any one factor by itself would be insufficient to prevent the successful recruitment of skeletonized benthos.

Nobody Home: Temporal Patterns

"Paleozoic black shales indicate by their contained faunas and lithologic associations the prevalence of somewhat abnormal, toxic bottom conditions that either impoverished or completely prevented all bottom life ... over vast areas and throughout long intervals of time" Ruedemann (1935: p. 90).

Ruedemann's (1935) observations characterize a few familiar manifestations of the oxygen-deficient bottom-water conditions that commonly result in the accumulation of thick,



FIGURE 1. Causes of barren marine sediment (excluding dissolution). Arrows indicate direction of forcing, but not magnitude or nature of interaction. Shelf physiography subsumes tectonic context of shelves, bathymetric profiles, geometry, geographic position, and characteristics of adjacent oceanic water masses and currents. Climate includes both global and local effects. Circulation includes exchange of water between the shelf and open ocean as well as wind-driven mixing. Oval boxes list some of the general signal types that may be unique to each proximal cause of barren sediment. Strat., stratification of the water column; O_2 sol., oxygen solubility.

organic-rich, unfossiliferous sedimentary successions (Rhoads and Morse 1971; Byers 1977). Two aspects of Ruedemann's comments are particularly noteworthy. First, he specifically highlights the Paleozoic as a time that is characterized by such deposits. Second, he notes that "toxic bottom conditions" are commonly widespread and geologically long lived. Although Ruedemann's perceptions must have been colored by his work on graptolites from the well-known Paleozoic mudstones of the Appalachian foreland basin, his commentary makes a testable prediction regarding the frequency of unfossiliferous marine sediment over geologic time.

To indirectly evaluate the possibility that "toxic bottom conditions," as evidenced by unfossiliferous marine sediment, may have decreased in frequency during the Phanerozoic, I searched the Georef bibliographic index first for the term "unfossiliferous" and then for the term "fossiliferous" occurring anywhere in a citation (searches conducted in March 2006). I then read the abstracts of the recovered references (extending only back to 1957) to determine whether the referenced sediments were marine and to determine their geologic age. If age was given to period and the unit was determined to be marine in origin (either explicitly or by inference), one unit was scored for all of the relevant time periods listed in the reference.

According to the Georef search, there is a decline in the frequency of unfossiliferous units from a Phanerozoic high in the Ordovician to a low in the Paleogene (Fig. 2A). This decline is broadly similar to Phanerozoic sea level estimates (Miller et al. 2005) and the history of continental flooding (Fig. 2A, gray line) (Ronov 1994). Although the time series of unfossiliferous sediment (Fig. 2A) suggests that there may have been significant temporal changes in the prevalence of environmental conditions favoring the accumulation of barren marine sediment, it is also possible that the pattern is controlled by preserved rock



FIGURE 2. Number of marine sedimentary rock units described as "unfossiliferous" and "fossiliferous" in a Georef search versus geologic time. A, Number of unfossiliferous units binned by period and measured per million years. Percent continental flooding from Ronov (1994) shown on same axis in gray. B, Number of fossiliferous units binned by period and measured per million years.

quantity, the history of which has already been shown to reflect the history of continental flooding (Peters 2006). However, contrary to the hypothesis that any arbitrary compilation from the published literature will yield a time series that reflects rock quantity, the time series for fossiliferous references (Fig. 2B) differs substantially from that for unfossiliferous references (Fig. 2A). This suggests that there may be real temporal variation in the ratio of fossiliferous to unfossiliferous marine sediment and that this variation may in part be related to continental flooding.

If the frequency of unfossiliferous unit ref-

erences is a reasonable (albeit imperfect) proxy for the general extent and persistence of inhospitable bottom waters, then the results shown in Figure 2 suggest that average shelf environments may have changed during the Phanerozoic and that this change is causally related to the extent of continental flooding. But is there any evidence to suggest that Paleozoic and Cenozoic sediments selected at random from the geologic record represent, on average, different basin types or environments?

To address this question, I used two data sets to estimate the frequency of water depths among Paleozoic and Cenozoic marine fossil assemblages. The first is from Bush and Bambach (2004), who focused on Phanerozoic alpha diversity in level-bottom (i.e., non-reef/ bioherm) fossil assemblages that were initially compiled irrespective of depth zone. The second data set derives from the Paleobiology Database (PBDB) Marine Invertebrate Working Group. A total of 35,691 PBDB marine collections were downloaded (http://paleodb. org) in April 2006 and then parsed into depth bins on the basis of the paleoenvironment field given for each collection. The depth frequency distributions of PBDB Paleozoic and Neogene collections were then binned temporally and environmentally in such a way as to be directly comparable to the analysis of Bush and Bambach (2004).

In both the Bush and Bambach (2004) and the PBDB compilations, the depth frequency distributions for Paleozoic and Cenozoic fossil assemblages are consistently different from one another (Fig. 3). Specifically, most Paleozoic assemblages derive from near storm wave base in what Bush and Bambach (2004) termed "open shelf" settings, whereas Cenozoic assemblages derive primarily from more onshore and marginal marine environments.

The PBDB data make it possible to track the frequency of a depth zone during the Phanerozoic. The time series for deep and shallow PBDB collections differ substantially from one another (Fig. 4A; see caption for included environments), and the ratio of marginal marine collections to deeper shelf collections increases dramatically toward the Recent (Fig. 4B). Although it is conceivable that this pattern re-



FIGURE 3. Total number of Paleozoic (Pz, Ordovician-Devonian, solid line) and Neogene (Ng, dashed line) fossil assemblages sampled from different depth zones. A, Assemblage data from Bush and Bambach (2004). Depth zones given by Bush and Bambach (2004) are (e1) shorelines, (e2) nearshore shelf, (e3) open shelf, (e4) distal open shelf, (e5) outer shelf margin. Estimated position of average storm wave base (swb) is shown by dashed line. B, Percent collections in the PBDB Marine Invertebrate Working Group for the Pz (4742 total collections) and Ng (1198 total collections). Environmental bin e1 corresponds to PBDB marginal marine, coastal, and foreshore collections, e2 corresponds to PBDB shallow subtidal and shoreface collections, e3 corresponds to PBDB deep subtidal and lower shoreface collections, e4 corresponds to PBDB offshore collections, and e5 corresponds to PBDB slope and basinal collections.

flects systematic environmental error in the PBDB, the time series for the number of deep shelf collections mirrors global sea level (Miller et al. 2005) and the number of unfossiliferous unit references (Fig. 2A), and the time series for the number of marginal marine collections resembles the number of fossiliferous unit references (Fig. 1B) and the history of marine genus richness (Sepkoski 2002; curve not shown).

What might account for the observed dif-



FIGURE 4. Number of Paleobiology Database (PBDB) collections from deep water and marginal marine environments versus geologic time. A, Absolute time series. Solid line labeled "deep" includes collections identified as deep subtidal, transition zone/lower shoreface, offshore, basinal, slope, and submarine fan. Dashed line labeled "marginal" includes collections designated as coastal, marginal marine, estuary/bay, paralic, lagoonal, peritidal, and foreshore. Compare the deep curve to the curve for continental flooding (Fig. 2A) and compare the marginal curve to the number of fossiliferous Georef references (Fig. 2B). B, Ratio of marginal to deep PDBD collections over time.

ferences in the depth frequency distributions of Cenozoic and Paleozoic fossil assemblages (Fig. 3) as well as for different temporal patterns in the frequency of marginal and deeper shelf collections (Fig. 4)? I argue here that the most likely explanation is a shift in the average location of deposition of preserved marine sediment from broad epicontinental seas in the Paleozoic to narrow continental margins



Late Ordovician expansive epeiric seas

Early Miocene narrow continental shelves



in the Cenozoic (Fig. 5; see caption for definitions used here). Such a shift in the average tectonic and physiographic context of marine shelf habitats is likely to be associated with many important oceanographic effects, some of which may explain aspects of the results shown in Figures 2-4 as well as other temporal patterns in the quantity and lithological composition of sedimentary rocks (e.g., Ronov 1978; Ronov et al. 1980; Veizer and Ernst 1996; Peters 2006). The physiography of marine shelves exerts important first-order controls on water-mass properties, and these are important for many reasons, but here I will focus on their relevance to the evolution and preservation of marine animals.

The Epeiric Sea Effect

The results presented above (combined with a moment's reflection on the history of continental flooding and the nature of the geologic record) suggest that most surviving Paleozoic marine sediment accumulated in low-latitude (e.g., Allison and Briggs 1993), expansive epicontinental seas, and that most surviving Cenozoic sediment accumulated along higher-latitude, narrow continental shelves that were more directly exposed to the open ocean (Fig. 5). Conditions prevailing within many epeiric seas would have been fundamentally different from those characterizing otherwise similar marine environments located along narrow shelf margins. In particular, low-latitude epeiric seas would have been conducive to the development of unusual water-mass characteristics and sedimentation patterns, and I suggest here that such environmental factors may be at least partly responsible for the accumulation of most unfossiliferous sediment as well as for the overall similarity of history of unfossiliferous sediment (Fig. 1) to the history of continental flooding (Ronov 1994).

Expansive epeiric seas of the type that char-

acterized much of the Paleozoic and the Jurassic-Cretaceous have no close modern analogues, and few oceanographic studies have systematically explored the expected watermass properties of epeiric seas. Nevertheless, several authors have pointed out the oceanographic differences between narrow continental shelves and epicontinental seaways, and some of the most consistent and important differences involve the expected frequency and extent of bottom-water hypoxia. For example, Tyson and Pearson (1991a) summarize the causes of hypoxia on modern shelves, argue that most epeiric seas must have been subject to episodic hypoxia, and offer an actualistic model for its development in epeiric seas. Allison and Wright (2005) and Algeo et al. (2007) emphasize the non-actualistic aspects of epeiric seas and offer what the latter study calls a "superesturarine model" for the development of widespread salinity anomalies and concomitant hypoxia in thin bottom-water layers. Some of the basic features of these models that are most relevant to paleobiology, along with a few modifications and additions, are briefly outlined below.

Hypoxia in Epeiric Seas.—The frequency and intensity of hypoxia in any epeiric sea would have been controlled by boundary conditions specific to the physiography of the seaway and adjacent water masses as well as to local climate, just as it is on modern shelves (Algeo et al. 2007). However, two factors are consistently important on long time scales: (1) sea level rises that establish widespread seaways with water depths capable of supporting pycnoclines on at least a temporary basis, and (2) cyclicity on annual and Milankovitch timebands in temperature, productivity, freshwater input, and storm-driven mixing of the water column. Tidal mixing may also serve as an important deterrent of stratification on many continental shelves (Algeo et al. 2007), but tidal amplitudes were probably negligible in most large epeiric seas (e.g., Allison and Wright 2005; Wells et al. 2005).

The combination of, and interactions between, sea level changes and climate likely resulted in at least seasonal development of a pycnocline and concomitant hypoxia in thin bottom-water layers over vast areas in many epeiric seas, particularly those located at low latitudes. Because wind-driven mixing is critical to preventing stratification of the water column and therefore the development of hypoxia in shallow (<200 m) water settings, then even if Milankovitch forcing resulted in no substantial changes in sea level, its influence on storm frequency or intensity could have an oceanographic effect in offshore settings that is equivalent to sea level change. Seasonality and climatic variations would have been particularly effective promoters of hypoxia in epeiric seas located at low latitudes, such as those that dominated during much of the Paleozoic.

Hypoxia would tend to develop initially in the deepest basins, some of which could potentially have permanent thermoclines and therefore permanently anoxic bottom waters, and then spread outward across the shelf in response to sea level rise or changes in mixing parameters. This is comparable to what Wignall (1994) called the "expanding puddle model" because of the potentially sharp, waterline-like oxycline that would intersect the seafloor, possibly filling subtle seafloor topography and contributing to strong faunal patchiness both regionally and locally (e.g., Brett 1999).

It is obvious, but important to point out, that oxygen concentration varies continuously from anoxic to fully oxic, and that hypoxia in epeiric seas must also have varied in intensity, frequency, duration, and distribution depending upon a large number of boundary conditions, including circulation patterns, water depths, nutrient supplies, storm intensities, freshwater inputs, mean annual temperature (e.g., Keeling and Garcia 2002), and even the concentration of oxygen in the atmosphere (e.g., Berner et al. 2003). Barren, laminated "black shales" represent but one end-member in a continuum of bottom-water oxygen conditions, and the absence of a stereotypic "anoxic" facies cannot be interpreted as evidence for the absence of episodic hypoxia. This is particularly true because all sedimentological, geochemical, and biological signatures of brief bouts of hypoxia could be overprinted during intervals of normal oxygen concentration.

Biotic Consequences of Hypoxia.-Seasonal

hypoxia, modulated by longer-wavelength cyclicity in water depth or storm intensity, productivity, and temperature could have resulted in the widespread mortality of benthic marine animals on an annual or longer-term basis over vast areas in many epeiric seas. The recovery of benthic communities from these hypoxic episodes would have been difficult and much slower than their initial extermination (e.g., Stachowitsch 1991). Moreover, in epeiric seas that experienced frequent hypoxia, only opportunistic, rapidly dispersing taxa with short life cycles would have been able to colonize the seafloor during temporary improvements, possibly resulting in the preservation of single, nearly monospecific, settlement cohorts within otherwise mostly barren sediment. Slowly growing, longer-lived taxa would generally have been excluded from such environments altogether. More persistently hypoxic environments would have promoted specialization and morphological/ physiological adaptation, and this has been observed in the fossil record (e.g., Savrda and Bottjer 1987; Gaines and Droser 2003; Henderson 2004).

Rhodes and Morse (1977), Tyson and Pearson (1991a), Wignall (1994), Levin (2003), and others provide comprehensive summaries of the many dramatic effects that hypoxia can have on the behavior, diversity, composition, and abundance of benthic organisms, and I refer the reader to these excellent sources for more information. It is worth noting, however, that most of these references focus on the biotic characteristics of persistently hypoxic or even anoxic environments, such as those located beneath permanent OMZs and recorded by black shales. However, because hypoxia is likely to have been transient over wide areas in many epeiric seas, the presence of rather diverse and abundant stenotopic benthic organisms does not necessarily preclude the possibility that a marine community was influenced by episodic hypoxia. Brief episodes brought about by unusually low storm frequency/intensity (low mixing), peaks in productivity (high oxygen consumption), or freshwater pulses (enhanced stratification) could have resulted in the wholesale or selective extermination of benthic animals over vast areas of seafloor. Thus, even in sediments that yield abundant and well-preserved marine animals, hypoxia may have resulted in the episodic extermination and reestablishment of entire benthic communities (e.g., Boesch and Rabalais 1991).

A Possible Example of Hypoxia in an Epeiric Sea Setting.—The richly fossiliferous Cincinnatian Series of the Cincinnati Arch region accumulated in an epeiric sea that is typically thought of as being "normal marine" in character. However, much of this thick succession of mudstone, siltstone, and carbonate accumulated in a terrigenous sediment-catching epeiric sea separated by hundreds of kilometers from the open ocean. Episodic hypoxia may have been common in this depositional setting, and I suggest that some features of the stratigraphy and taphonomy of the type Cincinnatian Series may have been influenced by cyclical variation in the frequency and intensity of widespread hypoxia, particularly in offshore sediments that contain well-preserved fossil assemblages.

One of the best-known examples of the spectacular preservation that can characterize offshore and deep subtidal deposits within the type Cincinnatian are articulated specimens of Flexicalymene. This medium-sized (up to about 7 cm) calymenid trilobite is often found in dense aggregations within blue-gray mudstones ("butter shales"; Hunda et al. 2006), some of which can be traced for tens of kilometers (Brett et al. 2007). Many of the individuals within these aggregations are wholly articulated (including in-place hypostomes) and display numerous postures, including enrollment (Fig. 6). One common interpretation is that these assemblages formed during the deposition of distal tempestites that rapidly smothered trilobites in life and escape positions (e.g., Hughes and Cooper 1999). However, articulated Flexicalymene individuals are often distributed throughout 40-100 cm thick mudstone intervals that contain subtle centimeter-scale and finer bedding features, and there appears to be no consistent association between articulated trilobites and storm-generated sedimentary features (Schumacher and Shrake 1997; Hunda et al. 2006).

Even if articulated Flexicalymene specimens



FIGURE 6. *Flexicalymene* aggregation of four articulated individuals preserved in pyrite-bearing gray mudstone from the type Cincinnatian Series in Ohio. It is here hypothesized that episodic bouts of hypoxia resulted in the death of trilobites and other benthic animals in many epicontinental settings. Subsequent burial by modest quantities of sediment preserved the dead animals in fantastic death poses (shown here), modified death poses, or as scattered carcasses in various states of decay and disarticulation. See text for further explanation and for discussion of similar hypoxia-related enrollment among modern horseshoe crabs (Fisher 1977). Individual specimen at lower left side of photo has been removed from the matrix and turned upside down in order to reveal the enrolled specimen located directly beneath the partially prone individual. Specimen and photo courtesy of Kenneth D. Karns.

could be consistently linked to centimeterscale graded silt and mud beds, it seems unlikely that an entire community of trilobites with lengths of 5 cm or more could be rendered helpless by burial in what must have been rather modest amounts of suspended fine-grained sediment (generally much less than 10 cm, even after correction for compaction). Moreover, fully articulated specimens of Isotelus, an asaphid trilobite reaching over 30 cm in length, also occur in enrolled and flat postures within similar muddy intervals (Schumacher and Shrake 1997). It is unlikely that these giants were overly sensitive to burial by the modest quantities of sediment that are often suggested by detailed microstratigraphic studies (Schumacher and Shrake 1997; Hunda et al. 2006), particularly because some trilobites, including calymenids and asaphids, are known to be capable burrowers (e.g., Osgood 1970; Cherns et al. 2006).

In many cases of trilobite Konservat-Lagerstätte, such as the Cincinnatian trilobite beds, enrolled specimens are common. For example, Hunda et al. (2006) reported an enrollment frequency of 42% among *Flexicalymene* in a single mudstone interval (56% if partial enrollment is included). Although enrollment is often interpreted as a defensive posture assumed in response to the physical burial process, Fisher (1977, personal communication 2006) has shown that small horseshoe crabs can easily escape when buried by at least several body lengths of fine sediment. When subject to hypoxia, however, these same horseshoe crabs will enroll in a fashion that is similar to that of trilobites and remain so even when shallowly buried. If hypoxia persists, the animals will die in an enrolled posture on the surface or beneath a thin layer of sediment. Partly because of the experiments conducted by Fisher (1977), enrollment among some trilobites has been interpreted as a behavioral response to hypoxia by Fisher and subsequently by other authors (e.g., Speyer 1990). This hypothesis is supported by studies that have identified beds of enrolled trilobites as being particularly prevalent in pyritic mudstone facies indicative of hypoxia (Speyer and Brett 1986).

In the hypoxia model for trilobite Lagerstätte (and other deposits that contain articulated multi-element skeletons buried beneath relatively thin mud drapes), all animals that succumbed to hypoxia would be lying undisturbed (and not disturbing one another) in death postures on the seafloor. The entire assemblage could then be buried by one or more storm-induced mud transport events, or it could be left exposed, only to undergo eventual decay, disarticulation, and dispersal by scavengers during the next normal oxygen phase or by currents during the next large storm. Cyclic alternations between favorable and hypoxic conditions would result in the accumulation of significant quantities of sediment with comparable fine-scale sedimentologic and taphonomic signatures. Under this model, there need be no consistent relationship between storm-induced sedimentary structures and articulated or incipiently decaying benthic organisms, but any widespread hypoxia-related death assemblage can be preserved only if it is buried, and rapid burial beneath a silt/mud tempestite, transported in suspension over wide areas along submarine nepheloid layers (e.g., Kohrs et al. 2007), is a very probable scenario.

Paleozoic Lagerstätte of all types should be reevaluated for ichnological, sedimentological, and taphonomic evidence of hypoxia as the primary killing mechanism and later burial beneath thin tempestites as the entombing mechanism. Distinguishing between the obrution and hypoxia models may seem like a subtle distinction in taphonomic mode, but it is of great importance in understanding the water-mass properties in which the preserved taxa lived and evolved and for determining the potential influence and scope of the Epeiric Sea Effect in structuring benthic marine communities.

Stratigraphic Consequences of Hypoxia.—Given the possibility of widespread hypoxia in the Cincinnati Arch region, it is interesting to hypothesize that meter-scale cyclicity in faunal composition within the Cincinnatian (e.g., Holland et al. 2000; Miller et al. 2001; Webber 2002), and other similar units with cyclicity manifested by the abundance and composition of skeletal material (e.g., Brett et al. 2006), might be influenced by the effects of cyclic hypoxia as well as changes in bottom-current energy and the frequency of sediment transport events.

During times of more frequent or intense hypoxia, poorly fossiliferous sediments containing only those taxa that were able to cope, or that had short generation times permitting them to take advantage of brief intervals of normal oxygen concentration, would accumulate. Less frequent or less intense hypoxia would, by contrast, permit the establishment of communities with lower hypoxia tolerances and would typically support a higher density of individuals. In this situation, shelly lags or skeletal grainstones and packstones with a generally different taxonomic composition from interbedded, less fossiliferous sediments would accumulate (see Tsujita et al. 2006 for an example of this phenomenon in the Devonian Arkona Shale). The thicknesses of each facies (sparingly fossiliferous fine-grained sediment versus higher carbonate content and more shell beds) would be largely indicative of the average amount of time spent in each state (frequent/intense hypoxia versus more oxygenated conditions), and it would be possible to have oscillations between end-members on the shortest time and thickness scales.

Interestingly, many of the same factors that would contribute to cyclicity in hypoxia, such as Milankovitch forcing of climate (see above), would also influence wave energy at the sediment-water interface and it is therefore likely that hypoxia would be acting in conjunction with bottom current energy to structure sedimentologic and taxonomic signatures. During periods of weaker storms, hypoxia would generally be more widespread and intense owing to weaker mixing of the water column, and this would promote the accumulation of less fossiliferous sedimentary intervals consisting of relatively fine-grained sediment. Periods of shallower water or stronger storms would be characterized by less frequent bottom-water hypoxia and would produce more fossiliferous sedimentary intervals, more winnowed and amalgamated storm beds, and coarser grain sizes. Disentangling the relative contributions of hypoxia and wave energy at the sediment-water interface may prove difficult, but it should be possible with detailed microstratigraphic taphonomic, ichnologic, and paleoecological studies because hypoxia makes many testable predictions at these much finer stratigraphic scales (e.g., see Wignall 1994 and references therein).

Salinity in Epeiric Seas.—Hypoxia is not the only environmental stress that would have been widespread in many epeiric sea settings. Carbonate platforms in the Paleozoic, such as the expansive Great American Carbonate Bank (Cambro-Ordovician) and the continentscale carbonate platforms and ramps of the Silurian, were maintained at or near sea level for millions of years (e.g., Ginsburg 1982). The water masses on these shallow platforms and ramps were probably often restricted from open-ocean circulation by virtue of marginal buildups or their sheer geographic scale. In such settings, high water temperatures, elevated salinity, and rapid salinity changes owing to alternating high evaporation and rainfall probably prevented all but algal and microbial life from becoming established. It is probably for this reason that many platform carbonate successions contain barren, cryptalgal laminated, shallow subtidal to peritidal carbonates that are both devoid of benthic animal remains and similar to those found in salinity-stressed modern tropical carbonate buildups (e.g., Fagerstrom and Weidlich 2005).

Although shallow carbonate platforms in the Paleozoic were certainly capable of supporting diverse benthic communities, it is also true that extensive carbonate platforms were frequently subjected to anomalously high or fluctuating salinities. As with hypoxia, these two end-members bracket a continuum in the frequency and magnitude of episodically stressful salinity conditions. At any particular point in space, normal and stressful conditions are likely to have alternated in time such that barren intervals come to be interbedded with fossiliferous strata. Changes in the geometry of carbonate environments from platforms to more openly circulating ramps are also likely to have resulted in important water-mass changes, and such changes have been linked to the abundance of crinoids in the fossil record (Kammer and Ausich 2006).

High salinity may have prevailed on many expansive carbonate platforms during the Paleozoic, but low salinity may have been an even more pernicious problem in many epeiric seas. Allison and Wright (2005) argue for the development of extensive freshwater lenses in epeiric seas and describe the environmental changes they promote. In particular, they point out that salinity stratification, in combination with weak tidal mixing, can result in shallow-water hypoxia. The ponding of brackish water within epeiric seas is therefore likely to have imposed salinity stresses that both directly and indirectly influenced the abundance and diversity of marine animals.

Sedimentation in Epeiric Seas.—During times of high continental flooding and expansive epicontinental seas, most of the world's siliciclastic sediment load would have been transported by rivers onto shallow shelves spanning hundreds of kilometers. Some of this sediment would have been trapped in rapidly subsiding foreland basins, but much of it would have been dispersed by storm waves (which form effective base level) over wide areas. Suspended sediment, transported directly from rivers or resuspended during storms, would contribute not only to productivity in the water column and therefore to bottom-water hypoxia, but also to the near simultaneous smothering of wide areas as storm-transported sediment encountered and then spread along pycnoclines before finally settling.

As for hypoxia and salinity, it is likely that expansive epicontinental seas promoted different sediment transport dynamics than otherwise similar narrow continental shelves, and that such dynamics are relevant to the distribution and abundance of benthic organisms. The comparative sedimentology of narrow shelves versus widespread epicontinental seas needs to be explored more thoroughly before evolutionary hypotheses can be adequately formulated and then tested in the field.

The Cenozoic Contrast.—In contrast to the epeiric sea-dominated Paleozoic, most Cenozoic marine sediments, and other Phanerozoic time intervals characterized by low levels of continental flooding, represent "bathtub rings" that were deposited on narrow continental margins with a comparatively small area of deeper shelf. Most of these narrow shelf environments would have been more freely circulating with the open ocean and less prone (but by no means immune) to episodic stratification and concomitant hypoxia. Estuarine and other restricted marine environments are certainly present in many Cenozoic sequences, and numerous sedimentary basins during sea level lowstands could have been prone to unusual water-mass characteristics and strong stratification, but, on average, shelf environments of the type that characterize the Cenozoic are quite unlike those that dominated during the Paleozoic. The oceanographic consequences of such critical changes in marine shelf physiography cannot go unrecognized by ecological and evolutionary studies of the fossil record.

The Epeiric Sea Effect: Macroevolutionary Consequences

The macroevolutionary consequences of temporal shifts in the average character of marine shelf habitats and their preserved sediments (the Epeiric Sea Effect) are twofold. First, because these shifts reflect, at least in part, real changes in the relative proportions of fundamentally different types of marine habitats, at least one important aspect of the environmental mosaic upon which marine animal evolution occurred must have changed. Second, because at any point in time benthic animals would have been influenced by the Epeiric Sea Effect, temporal patterns derived from the aggregate fossil record may not be evolutionary or ecological trends per se, but may instead reflect differential environmental sampling (i.e., empirical temporal patterns reflect spatial patterns). It is also possible that real evolutionary or ecological patterns might result only from shifting relative proportions of habitats in an otherwise constant environmental mosaic (see Rhoads and Morse 1977: Fig. 5 for an illustration of the basic idea). Here, I briefly discuss these issues and suggest approaches to overcoming some of the potential empirical problems imposed by the Epeiric Sea Effect.

Macroevolutionary Consequences.—The potential macroevolutionary consequences of the expansion and contraction of epeiric seas and their unique shallow marine environments have been discussed for some 60 years (e.g., Newell 1949, 1952; Valentine and Moores 1970; Johnson 1974; Schopf 1974; Simberloff 1974). Most of these discussions have focused on species-area effects and the possibility that mass extinctions may have been induced by the elimination of shallow marine environments and associated "perched" endemic faunas. There is now good quantitative evidence to suggest that such factors have indeed exercised a first-order control on global biodiversity and on rates of extinction and origination during the Phanerozoic (Peters 2005), and that similar processes can affect the composition and evolution of marine faunas on million-year time scales within individual depositional basins (e.g., Bowersox 2005). However, few studies have addressed the potential large-scale macroevolutionary significance of the Epeiric Sea Effect in terms of changes in the character of marine shelf habitats in general.

We have much to learn about the specific environmental conditions that would have prevailed in most epeiric seas, but there is abundant evidence to suggest that hypoxia would have been particularly widespread and frequent (Tyson and Pearson 1991a; Allison and Wright 2005; Algeo et al. 2007). Because hypoxia probably occurred on short, even seasonal, time scales in many epeiric seas, living at or above the sediment-water interface could have conferred a substantial survival advantage over being infaunal. In fact, at the onset of hypoxia, modern infaunal stenoxic benthic organisms extend from the sediment and eventually remove themselves completely in order to reach upward into the water column, and mobile taxa will aggregate on topographic highs or climb on top of one another to escape the benthic boundary layer (Tyson and Pearson 1991a). The dominance of epibenthic taxa, shallow bioturbation, and vertical watercolumn tiering (Ausich and Bottjer 1982; Bottjer and Ausich 1986) in many Paleozoic communities may therefore partially reflect the fact that elevation above the sediment-water interface is a very effective way for benthic animals to minimize the impacts of bottom-water hypoxia.

In support of this hypothesis, Brett (1984) and Frest et al. (1999) have noted that longstemmed Devonian crinoids are particularly abundant in dysoxic facies lacking surface dwellers like brachiopods, bryozoans, and other shorter-stemmed crinoids, and that long-stemmed crinoids are not so abundant in more oxygenated and crowded benthic communities where the traditional view of niche partitioning would predict strong selective pressure for vertical tiering. Because swimming predators often take advantage of the effects that hypoxia has on benthic prey (e.g., Pihl et al. 1992; Rabalais et al. 2002), an epifaunal, vertically positioned life habit would have been a particularly effective strategy to deal with frequent hypoxia before the evolution of abundant durophagous predators (Signor and Brett 1984; Baumiller and Gahn 2004).

Although widespread hypoxia in epeiric seas may have been stressful for many benthic animals, it may also have afforded an important opportunity in the form of an effective, if episodically costly, means of escaping predators. Benthic marine invertebrates that were able to cope with hypoxia could have actively sought out these environments to aggregate in during vulnerable stages of their life history (e.g., reproduction and molting), to exploit little-used resource pools, or to escape predators with higher oxygen demands. "Oxygen refugia" have been demonstrated to reduce rates of predation in some freshwater fish (e.g., Chapman et al. 1995) and it is likely that marine invertebrates use similar avoidance strategies, either actively or opportunistically (Levin 2003). Precarious tradeoffs associated with life near the oxycline would contribute to the frequent mortality (and subsequent spectacular preservation) of densely aggregated, fully articulated individuals of trilobites (e.g., Gaines and Droser 2003) and other taxa, but it is possible that such episodic risks would be offset by the persistent advantage of having a refugium from predators with higher oxygen demands.

Episodic hypoxia would also tend to favor rapidly developing taxa that are able to take advantage of boom-bust oxygen cycles. Unless possessing unique physiological adaptations, slowly developing, high-biomass taxa would be at a disadvantage in hypoxia-prone epeiric seas. Stenotopic taxa may therefore tend to be restricted to, and evolve in, regions that were rarely, if ever, subject to water column stratification and hypoxia. In fact, the tendency for higher taxa to originate in nearshore settings (e.g., Jablonski et al. 1983; Jablonski and Bottjer 1991) has been specifically related to sea level highstands and the prevalence of stressful hypoxia in offshore epeiric sea settings (Jacobs and Lindberg 1998). It is therefore possible that hypoxia in widespread epeiric seas has affected environmental patterns of clade origination and diversification, thereby influencing the familiar onshore-offshore patterns of faunal distribution (e.g., Sepkoski and Miller 1985).

Biases.—Given the potential of the Epeiric Sea Effect to substantially impact the restructure benthic marine communities, there is a danger in any paleontological study of confounding spatial and environmental patterns with temporal evolutionary phenomena. Fully accounting for the Epeiric Sea Effect is, however, a challenging task because the environmental stresses related to water-mass properties can be difficult to identify without appealing to the fossil assemblages themselves, a strategy that would lead to circular reasoning in any study of fossil biodiversity.

The difficulty of identifying and fully controlling for the Epeiric Sea Effect, combined with the lack of clearly defined biological expectations, makes most studies of Phanerozoic marine biodiversity problematical to interpret in terms of their evolutionary significance (e.g., Bambach 1977; Sepkoski 1988; Alroy et al. 2001; Powell and Kowalewski 2002; Fraiser and Bottjer 2004; Peters 2004; Bush and Bambach 2004; and many other similar studies). Comparisons between Paleozoic and Cenozoic fossil assemblages (e.g., Bush and Bambach 2004) are particularly prone to bias in the direction of increasing diversity simply because of the much greater prevalence of samples narrow continental shelves than from epeiric seas, but shorter-term studies (e.g., Peters 2004), and even studies that focus on just one stratigraphic section, are also subject to profound bias due to shifting water-mass effects.

One potentially powerful approach to controlling for the Epeiric Sea Effect would be to limit all comparisons to fossil assemblages that derive from similar oceanographic settings. This could be accomplished by consulting paleogeographic maps and analyzing samples that come from continental margins facing the open ocean separately from those that derive from interior epicontinental seas. Perhaps more effectively, paleogeographic reconstructions could be used to identify regions that are expected, on purely physical grounds, to have comparable oceanographic parameters and then appropriate paleontological samples could be sought out in those regions. Although an effective first step, this approach is not failsafe because many factors can cause strong Epeiric Sea Effects besides geographic location (see discussion above), and it would still be necessary to control for absolute water depth, taphonomy, diagenesis, and other sample-specific factors that can confound biodiversity patterns.

Summary

The problem with the Paleozoic is that, on average, Paleozoic marine sediments derive from expansive epicontinental seas that were markedly environmentally different from those found on narrow, open-ocean-facing continental margins. Episodic hypoxia in siliciclastic environments, salinity variations on carbonate platforms, freshwater lenses within shallow and expansive epeiric seas, and other water-mass properties may have structured many benthic animal communities, including those that are typically considered diverse and "normal marine." This is not to suggest that all epeiric sea environments were inhospitable or harsh, but rather that taxa living in epeiric seas would have been subject to a different suite of environmental conditions than those living in otherwise similar shelf settings located along narrow continental margins. The general influences that basin configurations, circulation patterns, and climate have on biologically essential water-mass properties and sedimentation patterns are collectively referred to as the "Epeiric Sea Effect."

Paleobiological studies that control only for water depth, lithology, taphonomy, diagenesis, and other similar sample-specific factors do not address the Epeiric Sea Effect and are therefore subject to substantial biases that can only be overcome by additional paleo-oceanographic control. However, the Epeiric Sea Effect does not just impose an important environmental sampling bias that has largely been ignored by paleobiologists interested in largescale macroevolutionary patterns. Instead, changes in the degree of continental flooding have forced real shifts in the average character of shelf habitats over time, and these shifts are likely to have had many important evolutionary, taphonomic, and stratigraphic consequences. This has long been recognized by field-oriented paleontologists, but it is now necessary to begin incorporating these insights into larger-scale macroevolutionary studies.

Fully accounting for the environmental effects of expanding and contracting epeiric seas and testing the evolutionary and ecological consequences of sea level changes and the resultant formation and destruction of unique epeiric sea habitats requires (1) quantifying the shifting geographic, tectonic, and environmental contexts of preserved marine sediments; (2) documenting the distribution of fossil organisms within the environmental mosaic of the sedimentary rock record; and (3) developing rigorous field tests to estimate paleo-water-mass properties and to effectively disentangle the relative contributions of hypoxia, salinity, and sedimentation in controlling the composition, abundance, and evolution of marine life.

Acknowledgments

I thank C. Badgley, M. Foote, B. Gaines, and B. Wilkinson for feedback on early drafts of this manuscript. C. E. Brett and S. Holland provided insightful reviews that greatly improved this manuscript. T. Baumiller served as managing editor. Acknowledgment is made to the donors of the American Chemical Society Petroleum Research Fund for partial support of this research and to the Michigan Society of Fellows. This work also partially supported by National Science Foundation EAR 0544941. This is Paleobiology Database Publication 51.

Literature Cited

Algeo, T. J., P. H. Heckel, J. B. Maynard, R. C. Blakey, and H. Rowe. 2007. Modern and ancient epicontinental seas and the superestuarine circulation model of marine anoxia. *In C.* Holmden and B. Pratt, eds. Geology of epeiric seas. Geological Association of Canada (in press).

- Allison, P. A., and D. E. G. Briggs. 1993. Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. Geology 21:527–530.
- Allison, P. A., and V. P. Wright. 2005. Switching off the carbonate factory: a-tidality, stratification and brackish wedges in epeiric seas. Sedimentary Geology 179:175–184.
- Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M Raup, K. Roy, J. J. Sepkoski Jr., M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Sciences USA 98:6261–6266.
- Ausich, W. I., and D. J. Bottjer. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. Science 216:173–174.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology 3:152–167.
- Baumiller, T. K., and F. J. Gahn. 2004. Testing predator-driven evolution with Paleozoic crinoid arm regeneration. Science 305:1453–1455.
- Berner, R. A., D. J. Beerling, R. Dudley, J. M. Robinson, and R. A. Wildman Jr. 2003. Phanerozoic atmospheric oxygen. Annual Review of Earth and Planetary Sciences 31:105–134.
- Boesch, D. F., and N. N. Rabalais. 1991. Effects of hypoxia on continental shelf benthos: comparisons between the New York Bight and the Northern Gulf of Mexico. Pp. 27–34 *in* Tyson and Pearson 1991b.
- Bottjer, D. J., and W. I. Ausich. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. Paleobiology 12:400–420.
- Bowersox, J. R. 2005. Reassessment of extinction patterns of Pliocene mollusks from California and environmental forcing of extinction in the San Joaquin Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 221:55–82.
- Brett, C. E. 1984. Autecology of Silurian pelmatozoan echinoderms. Special Papers in Palaeontology 32:87–120.
- . 1999. Wenlockian fossil communities in New York State and adjacent areas paleontology and paleoecology. Pp. 592– 637 in A. J. Boucot and J. D. Lawson, eds. Paleocommunities: a case study from the Silurian and Lower Devonian (World and Regional Geology 11). Cambridge University Press, New York.
- Brett, C. E., P. A. Allison, C. J. Tsujita, D. Soldani, and H. A. Moffat. 2006. Sedimentology, taphonomy, and paleoecology of meter-scale cycles from the Upper Ordovician of Ontario. Palaios 21:530–547.
- Brett, C. E., R. H. Kohrs, and B. Kirchner. 2007. Paleontological event beds from the Upper Ordovician of Ohio and northern Kentucky and the limits of high-resolution stratigraphy. *In C.* Holmden and B. Pratt, eds. Geology of epeiric seas. Geological Association of Canada (in press).
- Bush, A. M., and R. K. Bambach. 2004. Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. Journal of Geology 112:625–642.
- Byers, C. W. 1977. Biofacies patterns in euxinic basins: a general model. *In* H. E. Cook and P. Enos, eds. Deep-water carbonate environments: Society of Economic Paleontologists and Mineralogists Special Publication 25:5–17.
- Chapman, L. J., L. S. Kaufman, C. A. Chapman, and F. E. McKenzie. 1995. Hypoxia tolerance in twelve species of East African cichlids: potential for low oxygen refugia in Lake Victoria. Conservation Biology 9:1274–1287.

- Cherns, L., and V. P. Wright. 2000. Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. Geology 28:791–794.
- Cherns, L., J. R. Wheeley, and L. Karis. 2006. Tunneling trilobites: habitual infaunalism in an Ordovician carbonate floor. Geology 34:657–660.
- Diaz, R. J. 2001. Overview of hypoxia around the world. Environmental Quality 30:275–281.
- Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology Annual Review 33:245–303.
- Fagerstrom, J. A., and O. Weidlich. 2005. Biologic response to environmental stress in tropical reefs: lessons from modern Polynesian coralgal atolls and Middle Permian sponge and *Shamovella*-microbe reefs (Capitan Limestone USA). Facies 51: 501–515.
- Fisher, D. C. 1977. Mechanism and significance of enrollment in xiphosurans (Chelicerata, Merostomes). Geological Society of America Abstracts with Programs 9:264–265.
- Föllmi, K. B., and K. A. Grimm. 1990. Doomed pioneers: gravity flow deposition and bioturbation in marine oxygen-deficient environments. Geology 18:1069–1072.
- Fraiser, M. L., and D. J. Bottjer. 2004. The non-actualistic Early Triassic gastropod fauna: a case study of the Lower Triassic Sinbad Limestone Member. Palaios 19:259–275.
- Frest, T. J., C. E. Brett, and B. J. Witzke. 1999. Caradocian-Gedinnian echinoderm associations of central and eastern North America. World and Regional Geology 11:638–783.
- Fürsich, F. T. 1993. Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. Lethaia 26:327–346.
- Gaines, R. R., and M. L. Droser. 2003. Paleoecology of the familiar trilobite *Elrathia kingii*: an early exaerobic zone inhabitant. Geology 31:941–944.
- Ginsburg, R. N. 1982. Actualistic depositional models for the Great American Bank (Cambro-Ordovician). International Congress on Sedimentology 11:114.
- Helly, J. J., and L. A. Levin. 2004. Global distribution of naturally occurring marine hypoxia continental margins. Deep-Sea Research Part I 51:1159–1168.
- Henderson, R. A. 2004. A mid-Cretaceous association of shell beds and organic-rich shale: bivalve exploitation of a nutrientrich, anoxic sea-floor environment. Palaios 19:156–169.
- Holland, S. M., A. I. Miller, and D. L. Meyer. 2000. High-resolution correlation in apparently monotonous rocks: Upper Ordovician Kope Formation. Palaios 15:73–80.
- Hughes, N. C., and D. L. Cooper. 1999. Paleobiologic and taphonomic aspects of the "granulosa" trilobite cluster, Kope Formation (Upper Ordovician, Cincinnati region). Journal of Paleontology 73:306–319.
- Hunda, B. R., N. C. Hughes, and K. W. Flessa. 2006. Trilobite taphonomy and temporal resolution in the Mt. Orab Shale Bed (Upper Ordovician, Ohio, U.S.A.). Palaios 21:26–45.
- Jablonski, D., and D. J. Bottjer. 1991. Environmental patterns in the origins of higher taxa: the post-Paleozoic fossil record. Science 252:1831–1833.
- Jablonski, D., J. J. Sepkoski Jr., D. J. Bottjer, and P. M. Sheehan. 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. Science 222:1123–1125.
- Jacobs, D. K., and D. R. Lindberg. 1998. Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. Proceedings of the National Academy of Sciences USA 95:9396–9401.
- Johnson, J. G. 1974. Extinction of perched faunas. Geology 2: 479-482.

- Kammer, T. W., and W. I. Ausich. 2006. The "age of crinoids": a Mississippian biodiversity spike coincident with widespread carbonate ramps. Palaios 21:238–248.
- Kamykowski, D., and S.-J. Zentara. 1990. Hypoxia in the world ocean as recorded in the historical data set. Deep-Sea Research 37:1861–1874.
- Keeling, R. F., and H. E. Garcia. 2002. The change in oceanic O_2 inventory associated with recent global warming. Proceedings of the National Academy of Sciences USA 99:7848–7853.
- Kidwell, S. M. 1988. Taphonomic comparison of passive and active continental margins: Neogene shell beds of the Atlantic coastal plain and northern Gulf of California. Palaeogeography, Palaeoclimatology, Palaeoecology 63:201–223.
- Kohrs, R., C. E. Brett, and N. O'Brien. 2007. Sedimentology of Upper Ordovician mudstones from the Cincinnati Arch region, Ohio/Kentucky: toward a general model of mud event deposition. In P. I. McLaughlin, C. E. Brett, S. L. Taha Mc-Laughlin, and J. Bazeley, eds. Stratigraphic renaissance in the Cincinnati Arch: implications for Upper Ordovician paleontology and paleoecology. Cincinnati Museum Center Special Publication 2 (in press).
- Levin, L. A. 2003. Oxygen minimum zone benthos: adaptation and community responses to hypoxia. Oceanography and Marine Biology 41:1–45.
- Miller, A. I., S. M. Holland, D. L. Meyer, and B. F. Dattilo. 2001. The use of faunal gradient analysis for intraregional correlation and assessment of changes in sea-floor topography in the type Cincinnatian. Journal of Geology 109:603–613.
- Miller, K. J., M. A. Kominz, J. V. Browning, J. D. Wright, G. S. Mountain, M. E. Katz, P. J. Sugarman, B. S. Cramer, N. Christie-Blick, and S. F. Pekar. 2005. The Phanerozoic record of global sea-level change. Nature 310:1293–1298.
- Newell, N. D. 1949. Periodicity in invertebrate evolution. Geological Society of America Bulletin 60:1911–1912.
- ——. 1952. Periodicity in invertebrate paleontology. Journal of Paleontology 26:371–385.
- Nordberg, K., H. L. Filipsson, M. Gustafsson, R. Harland, and P. Ross. 2001. Climate, hydrographic variations and marine benthic hypoxia in Koljo Fjord, Sweden. Journal of Sea Research 46:187–200.
- Osgood, R. G. 1970. Trace fossils of the Cincinnati area. Palaeontographica Americana 6:281–444.
- Osterman, L. E., R. Z. Poore, P. W. Swarzenski, and R. E. Turner. 2005. Reconstructing a 180 yr record of natural and anthropogenic induced low-oxygen conditions from Louisiana continental shelf sediments. Geology 33:329–332.
- Peters, S. E. 2004. Evenness of Cambrian-Ordovician benthic marine communities in North America. Paleobiology 30:325– 346.
- 2005. Geologic constraints on the macroevolutionary history of marine animals. Proceedings of the National Academy of Sciences USA 102:12326–12331.
- 2006. Macrostratigraphy of North America. Journal of Geology 114:391–412.
- Pihl, L., S. P. Baden, R. J. Diaz, and L. C. Shaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Marine Biology 112:349–361.
- Powell, M. G., and M. Kowalewski. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. Geology 30:331–334.
- Rabalais, N. N., E. Turner, and W. J. Wiseman Jr. 2002. Gulf of Mexico hypoxia, a.k.a. "the dead zone." Annual Review of Ecology and Systematics 33:235–363.
- Reaves, C. M. 1986. Organic matter metabolizability and calcium carbonate dissolution in nearshore marine muds. Journal of Sedimentary Petrology 56:486–494.

- Rhoads, D. C., and J. W. Morse. 1971. Evolutionary and ecologic significance of oxygen-deficient basins. Lethaia 4:413–428.
- Ronov, A. B. 1978. The Earth's sedimentary shell. International Geology Review 24:1313–1363.
- ——. 1994. Phanerozoic transgressions and regressions on the continents: a quantitative approach based on areas flooded by the sea and areas of marine and continental deposition. American Journal of Science 294:777–801.
- Ronov, A. B., V. E. Khain, A. N. Balukhovsky, and K. B. Seslavinsky. 1980. Quantitative analysis of Phanerozoic sedimentation. Sedimentary Geology 25:311–325.
- Ruedemann, R. 1935. Ecology of black mud shales of eastern New York. Journal of Paleontology 9:79–91.
- Savrda, C. E., and D. J. Bottjer. 1986. Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. Geology 14:306–309.
- ——. 1987. The exaerobic zone, a new oxygen-deficient marine biofacies. Nature 327:54–56.
- Schopf, T. J. M. 1974. Permo-Triassic extinctions: relation to seafloor spreading. Journal of Geology 82:129–143.
- Schovsbo, N. H. 2001. Why barren intervals? A taphonomic case study of the Alum Shale and its faunas. Lethaia 34:271–285.
- Schumacher, G. A., and D. L. Shrake. 1997. Paleoecology and comparative taphonomy of an *Isotelus* (Trilobita) fossil lagerstätten from the Waynesville Formation (Upper Ordovician, Cincinnatian Series) of southwestern Ohio. Pp. 131–161 *in* C. E. Brett and G. C. Baird, eds. Paleontological events: stratigraphic, ecological, and evolutionary implications. Columbia University Press, New York.
- Sepkoski, J. J., Jr. 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology 14:221–234.
- ——. 2002. A compendium of fossil marine animal genera. Bulletins of American Paleontology 363:560.
- Sepkoski, J. J., Jr., and A. I. Miller. 1985. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. Pp. 153–190 *in* J. W. Valentine, ed. Phanerozoic diversity patterns: profiles in macroevolution. Princeton University Press, Princeton, N.J.
- Signor, P. W., III, and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. Paleobiology 10: 229–245.
- Simberloff, D. S. 1974. Permo-Triassic extinctions: effects of area on biotic equilibrium. Journal of Geology 82:267–274.
- Sorokin, Y. I. 2002. The Black Sea: ecology and oceanography. Backhuys, Leiden.
- Speyer, S. E. 1990. Enrollment in trilobites. Pp. 450–455 in A. J. Boucot, ed. Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam.
- Speyer, S. E., and C. E. Brett. 1986. Trilobite taphonomy and Middle Devonian taphofacies. Palaios 1:312–327.
- Stachowitsch, M. 1991. Anoxia in the Northern Adriatic Sea: rapid death, slow recovery. Pp. 119–130 *in* Tyson and Pearson 1991b.
- Tsujita, C. J., C. E. Brett, M. Topor, and J. Topor. 2006. Evidence of high-frequency storm disturbance in the Middle Devonian Arkona Shale, southwestern Ontario. Journal of Taphonomy 4:49–68.
- Tyson, R. V., and T. H. Pearson. 1991a. Modern and ancient continental shelf anoxia: an overview. Pp. 1–26 *in* Tyson and Pearson 1991b.
- Tyson, R. V., and T. H. Pearson, eds. 1991b. Modern and ancient continental shelf anoxia. Geological Society of London Special Publication 58.
- Valentine, J. W., and E. M. Moores. 1970. Plate-tectonic regulation of faunal diversity and sea level: a model. Nature 228: 657–659.

- Veizer, J., and R. E. Ernst. 1996. Temporal patterns of sedimentation: Phanerozoic of North America. Geochemistry International 33:64–76.
- Webber, A. J. 2002. High-resolution faunal gradient analysis and an assessment of the causes of meter-scale cyclicity in the type Cincinnatian Series (Upper Ordovician). Palaios 17:545–555.
- Wells, M. R., P. A. Allison, G. J. Hampson, M. D. Piggott, and C. C. Pain. 2005. Modeling ancient tides: the Upper Carboniferous epi-continental seaway of Northwest Europe. Sedimentology 52:715–735.
- Wignall, P. B. 1994. Black shales. Oxford Monographs on Geology and Geophysics No. 30. Clarendon, Oxford.