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Permian marine paleoecology and its implications for large-scale decoupling of brachiopod and bivalve abundance and diversity during the Lopingian (Late Permian)

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Abstract

The transition during the Permian–Triassic interval from brachiopod-rich benthic marine assemblages to communities with diverse molluscs has been well constrained by measures of global taxonomic richness but its ecological context has not been studied using quantitative relative abundance data. New relative abundance data from Early, Middle, and Late Permian silicified fossil assemblages from offshore shelf carbonate environments indicate that molluscs increased significantly in relative abundance, from 0.8% in the Middle Permian (Guadalupian) to 65.4% in the Late Permian (Lopingian). These numerical changes are accompanied by increases in the abundance of infaunal bivalves and motile gastropods in the Late Permian. Although this ecological change was coincident with the end-Guadalupian extinction, a new global diversity compilation indicates that the overall genus-level severity of that biotic crisis was substantially lower than previous estimates. The pronounced ecological shift was instead concurrent with the onset of deep-marine anoxic or euxinic conditions around the Guadalupian–Lopingian boundary, suggesting that increased environmental variability in proximity to the deep water mass may have given eurytopic molluscs a competitive advantage over more stenotopic brachiopods. However, the lack of global changes in relative genus richness implies dramatic decoupling of global taxonomic and local ecological processes. The pronounced increase in molluscan abundance and alpha diversity in the silicified assemblages contrasts with their unchanged global taxonomic richness and may also have resulted from increased environmental stress in offshore shelf environments. These results demonstrate that the ecological transition from the brachiopods to molluscs was more complex than inferred from global measures of taxonomic richness and imply that initial stages of Permo–Triassic environmental deterioration may have been responsible for the decoupling of local ecological from global taxonomic processes during the dramatic Late Permian rise of the Modern Fauna.
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1. Introduction

The end-Permian mass extinction, the most severe crisis in the Phanerozoic (Erwin, 2006), and its associated faunal shift from the brachiopod-rich Paleozoic Fauna to the molluscan Modern Fauna (Gould and Calloway, 1980; Sepkoski, 1981) represent a fundamental change in the taxonomic structure and ecological architecture of marine animal ecosystems. The dramatic shift in relative global richness at the genus or family level, from Paleozoic brachiopod-rich assemblages to post-Paleozoic mollusc-rich assemblages, was also accompanied by a significant

increase in alpha diversity (Bambach, 1977), a shift towards mobile and infaunal organisms (Stanley, 1968; Bambach et al., 2002), and an increased occupation of ecospace in the marine realm (Bambach, 1983). This iconic "brachiopod–bivalve transition" has been attributed to the severe effects of the end-Permian biotic crisis (Gould and Calloway, 1980), differing physiological tolerances between brachiopods and molluscs (Steele-Petrovic, 1979), or competitive interactions between the two groups (Sepkoski, 1996). However, because of the close association of the faunal transition with the end-Permian mass extinction, it has generally been accepted that the severe effects of the biotic crisis forcibly dismantled brachiopod-rich assemblages that had dominated for 250 m.y. of the Paleozoic, opening benthic ecospace and new niches for molluscs and ultimately giving rise to modern-style marine ecosystems.

Detailed compilations of genus richness at the global scale indicate that the transition between the Paleozoic Evolutionary Fauna and the Modern Fauna was an abrupt switch at the Permian–Triassic boundary, coincident with the end-Permian mass extinction (Gould and Calloway, 1980; Sepkoski, 1996). The large magnitude and abrupt timing of this diversity shift has fueled a tacit assumption that the ecological shift in relative abundance between rhynchonelliform brachiopods and molluscs was synchronous with taxonomic changes and that it was also caused by the severe effects of the end-Permian biotic crisis. Although ecological dominance (as measured by relative abundance) does appear broadly correlated with global taxonomic richness at large temporal scales (Clapham et al., 2006; Madin et al., 2006), documented instances of decoupled taxonomic and ecological behavior over shorter timescales (e.g., McKinney et al., 1998) caution against the assumption of synchroneity during the end-Permian crisis. The ecology of the Permian–Triassic transition has been comprehensively investigated only in Early Triassic fossil assemblages (e.g., Schubert and Bottjer, 1995; Boyer et al., 2004; Fraiser and Bottjer, 2004; Fraiser and Bottjer, 2005), whereas the ecological structure of Permian fossil assemblages, and Late Permian (Lopingian) assemblages in particular, remains largely unknown.

This comparative lack of Middle and Late Permian abundance data, with only a single Middle Permian study (Waterhouse, 1987) and one from nearshore Late Permian environments (Hollingworth and Pettigrew, 1988), has troubling implications for the assumed abrupt Permian–Triassic ecological transition given the recognition of potentially important environmental and biotic crises in the Middle and Late Permian (Guadalupian–Lopingian interval). The end-Guadalupian extinction, occurring at the end of the Capitanian Stage of the Middle Permian about 8 m.y. prior to the end-Permian crisis, may have eliminated as many as 60% of marine invertebrate genera and perhaps preferentially affected members of the Paleozoic Fauna (Stanley and Yang, 1994). There were additional environmental changes during the Guadalupian–Lopingian interval (e.g., Isozaki, 1997) that may also have influenced the ecological transition between rhynchonelliform brachiopods and molluscs.

There is some circumstantial evidence to suggest that the Permian–Triassic ecological transition between the Paleozoic and Modern faunas may have been more protracted than previously assumed from global diversity metrics. Late Paleozoic onshore–offshore diversity patterns (Fig. 1) indicate that bivalves were becoming more diverse before the end-Permian mass extinction and expanding their range into a wider spectrum of shelf environments through the Early and Middle Permian (Sepkoski and Miller, 1985; Miller, 1988). This increased offshore diversification among bivalves may also be correlated with a Permian increase in their abundance and ecological importance relative to rhynchonelliform brachiopods. If true, the correlation may imply that at least part of the ecological transition in relative abundance between the Paleozoic and Modern faunas may also have occurred before the end-Permian
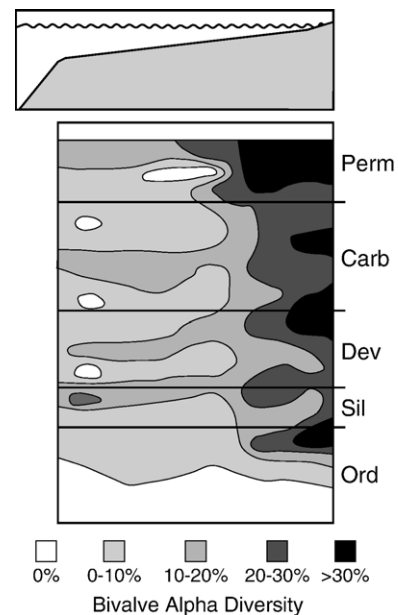

Fig. 1. Onshore–offshore diversity pattern for Paleozoic bivalves. Shaded contours indicate the relative within-assemblage (alpha) diversity of bivalves, indicating a distinct offshore expansion of diverse bivalve assemblages in the Permian. Modified from Miller (1988).

mass extinction. There was also a gradual decrease in gastropod size through the Guadalupian–Lopingian interval (Payne, 2005), culminating in the predominance of small individuals in the Permian–Triassic extinction interval and the Early Triassic (Twitchett, 2001; Price-Lloyd and Twitchett, 2002; Fraiser and Bottjer, 2004). This long-term size diminution may have resulted from increasing but low levels of environmental stress, potentially a precursor to the environmental crisis that caused the end-Permian mass extinction and prolonged Early Triassic recovery.

This study reports quantitative counts and size data from silicified Permian fossil assemblages in order to constrain the nature and timing of the ecological transition from the brachiopod-rich Paleozoic Fauna to the molluscan Modern Fauna. Integration of this new Middle and Late Permian data with previously published Early Triassic quantitative information will indicate whether the shift in relative abundance was synchronous with the taxonomic change, as previously assumed, or if the two were decoupled and the ecological switch began earlier and was more protracted. In particular, the ecological structure of Late Permian assemblages is compared to Early and Middle Permian assemblages as well as Early and Middle Triassic assemblages to examine the correlation between taxonomic and ecological change, investigate the ecological consequences of the end-Guadalupian extinction, and test for environmental or ecological deterioration prior to the end-Permian biotic crisis.

2. Methods

Quantitative counts of silicified fossil abundance were made from bulk samples collected from individual, thin (< 20 cm) limestone (primarily lime mudstone or wackestone) shell beds. Sample size varied from 1 to 15 kg, depending on the size and density of fossils, in order to yield an average of 200–400 specimens per locality. Where possible, replicate samples were collected along the extent of the outcrop (Bennington, 2003). The depositional environment (nearshore, inner shelf — above fair weather wave base, middle shelf — below fair weather wave base, or outer shelf — below storm wave base) of each sample was assessed from detailed bed-by-bed measured sections and thin section analysis using standard sedimentological criteria (e.g., Bottjer and Jablonski, 1988). Taphonomic indicators (Kidwell and Holland, 1991) were applied in the field to recognize and remove overly time averaged or spatially mixed shell accumulations. The resulting data set (see Supplementary data) includes quantitative counts and size data of 8897 individuals from 25 field collections and 31,871 individuals from six museum collections, including the first reported abundance information from Late Permian fossil assemblages from offshore environments. Five Early Permian samples (2473 individuals) were collected from southern and central Nevada (Bird Spring, Pequop, and Loray Formations); eight Middle Permian samples (2563 individuals) were collected from northeastern Nevada (Gerster Formation, Capitanian (Henderson and Mei, 2000)); and 12 Late Permian samples (3861 individuals) were collected from Hydra, Greece (six samples from the Episkopi Formation, Wuchiapingian–Changhsingian (Nestell and Wardlaw, 1987; Jenny et al., 2004)) and Heshan, China (six samples from the Heshan Formation, Wuchiapingian–Changhsingian (Shao et al., 2003)). In addition to the field samples, fossils from six west Texas localities were counted at the Smithsonian National Museum of Natural History: three Early Permian samples from the Hess Formation, Taylor Ranch Member (Kungurian; 5289 individuals) and three Middle Permian samples from the Word Formation between the Willis Ranch and Appel Ranch members (Wordian; 26,582 individuals). All collecting localities were situated in or near the tropical belt during the Permian (Fig. 2).

Fossils were well silicified by early diagenetic silica replacement and were etched from the limestone matrix using 3 M hydrochloric acid, identified to genus level, and all individuals counted for each sample using the "Minimum Number of Individuals" (MNI) method (Gilinsky and Bennington, 1994). Early diagenetic silicification preserves an excellent record of the original community, including molluscs with aragonitic skeletal composition that may be diagenetically dissolved in non-silicified biotas (Cherns and Wright, 2000). The life habit of each genus, based on their functional morphology, was recorded. Bivalves were classified as epibyssate, infaunal suspension-feeding, infaunal deposit-feeding, or cementing. Rhynchonelliform brachiopods were classified as pedically-attached, reclining (free-resting), or cementing. The dimensions of each complete specimen were also measured using calipers; only specimens 2.5 mm or larger were counted and measured. The mean size of brachiopods and bivalves was calculated from the geometric mean of length and width for each specimen (Aberhan et al., 2006), in order to account for shape variations between the two groups. Gastropod size was quantified using shell height to allow comparison with published Early Triassic data. Fossils in the Smithsonian collections were also counted using the MNI method but their sizes were not measured. Although all specimens were counted for field collections and most for museum collections, the relative abundance information presented here has been
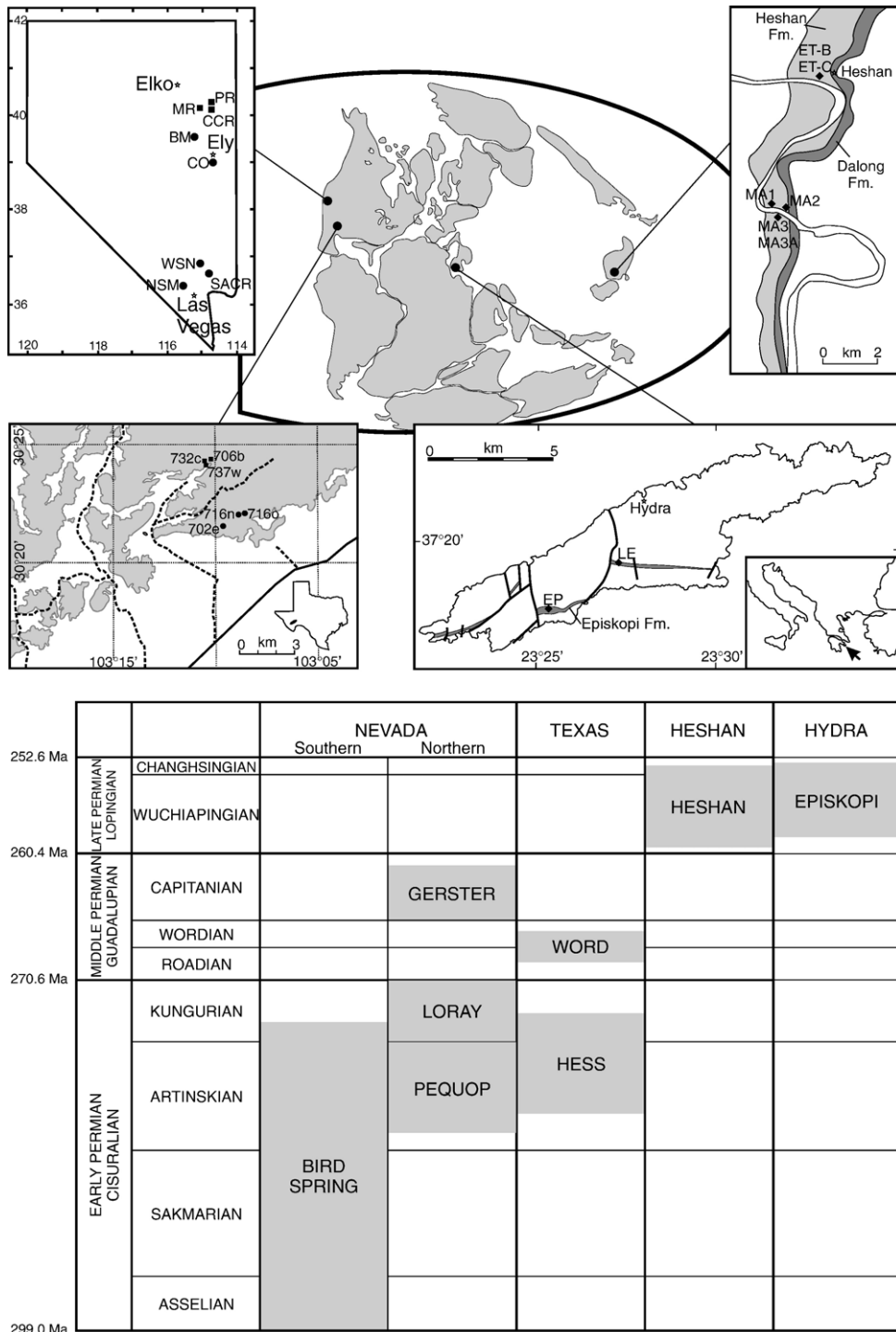
Fig. 2. Location map showing the paleogeographic (base map), modern locations (inset), and age of sampled formations of the bulk samples used for paleoecological analysis. Texas inset map modified from Cooper and Grant (1972), Hydra inset map modified from Grant et al. (1991), and Heshan inset map modified from Rigby et al. (1995).

normalized to include only rhynchonelliform brachiopods, bivalves, and gastropods because of taphonomic biases during silicification of bryozoans and problems involved in counting organisms like bryozoans and crinoids, and because bryozoans and crinoids were not retained with the Smithsonian collections.

3. Results

3.1. Early Permian onshore–offshore abundance patterns

Although onshore–offshore diversity patterns imply increasing molluscan importance through the Permian (Sepkoski and Miller, 1985; Miller, 1988), it is not clear that environmental trends in relative abundance parallel those diversity trends. Onshore–offshore abundance patterns were investigated from eight Early Permian fossil assemblages, spanning an environmental range from nearshore peritidal to outer shelf, near the shelf-slope break, in conjunction with previously published information (e.g., Yancey and Stevens, 1981). Four samples were collected from onshore environments (one from nearshore peritidal dolomite and three from inner shelf normal-marine limestones) and four samples were derived from offshore settings (three from below fair weather wave base in the middle shelf and one from below storm wave base on the outer shelf).

The nearshore sample (BM), collected from the Kungurian Loray Formation in the Butte Mountains of central Nevada (Mayou, 1967), exclusively contains molluscs (primarily bivalves and gastropods, with a single scaphopod). The assemblage contains 1059 individuals and is strongly dominated by individuals of the nuculoid bivalve *Nuculavus levatiformis* (63.2% of the assemblage), along with the gastropods *Amphiscapha proxima* (22.7%) and *Euphemites crenulates* (8.5%). Rare constituents include *Schizodus* sp. (3.8%) and *Orthonema* sp. (1%), with several other gastropods also comprising less than 0.5% of the census. Both bivalve species were infaunal — *Nuculavus* was an infaunal deposit-feeder while *Schizodus* was a shallow suspension-feeder.

The inner shelf appears to have contained a more heterogeneous mosaic of communities (Fig. 3), where molluscs remained numerically dominant but members of the Paleozoic Fauna such as rhynchonelliform brachiopods, crinoids, and stenolaemate bryozoans were also abundant. Sample CO, collected from the Artinskian Pequop Formation in the Egan Range of east-central Nevada, is dominated by gastropods (57.4%), with abundant brachiopods (36.1%) and rare bivalves (6.5%). Gastropod dominance is even stronger in sample SACR, from the Artinskian Bird Spring Formation in the southern Arrow Canyon Range (Plas, 1972). A diverse group of gastropods, dominated by *Glyptospira arelela* (69.6%), comprise 98% of the assemblage; bivalves (1.8%) and brachiopods (0.2%) are both rare. In contrast, sample

NSM, from the Early Permian Bird Spring Formation in the northern Spring Mountains, contains a relatively equitable mixture of rhynchonelliform brachiopods (47.3%), bivalves (37.9%), and gastropods (14.8%). Brachiopods in these inner shelf samples are primarily represented by pedically-attached terebratulids such as *Dielasma* (30.2% of sample CO, 21.8% in sample NSM, and the only brachiopod from SACR) and athyridids such as *Composita* (11.1% in NSM) and *Hustedia* (10.7% in NSM). Pedunculate spiriferids and rhynchonellids are also present but reclining productid genera and cementing productids or orthotetids are not found in any inner shelf samples (Fig. 3). Infaunal suspension-feeding bivalves dominate samples SACR and CO (*Astartella*, *Permophorus*, and *Schizodus*) but epibyssate genera such as *Septimyalina* and *Heteropecten* are most abundant in sample NSM (Fig. 3). Only a single deposit-feeding bivalve individual (*Nuculavus levatiformis*) was recovered from sample SACR.

Whereas brachiopods and molluscs were both abundant in inner shelf assemblages, offshore settings were overwhelmingly dominated by rhynchonelliform brachiopods, which have a mean abundance of 98.3% in the four middle and outer shelf samples (Fig. 4). Molluscs never comprise more than 3% (mean bivalve abundance 0.7%, mean gastropod abundance 1%). In contrast to the heterogeneous nature of inner shelf assemblages, the composition of offshore samples is remarkably stable: rhynchonelliform brachiopods comprise 96.9–99.1% of the samples while bivalves account for 0.4–1.4% and gastropods 0.5–1.8%. Brachiopods with a free-resting life position are more abundant in offshore samples, accounting for 72.7% of the brachiopods in sample USNM716o (e.g., *Oncosarina whitei*, *Peniculauris imitata*) and 52.8% in sample USNM716n (e.g., *Oncosarina whitei*, *Linoproductus undatus*), both from Texas (Fig. 4). Other assemblages, like the inner shelf samples, are dominated by pedically-attached genera, comprising 88.9% of brachiopods in sample WSN (e.g., *Orbicoelia wampensis*, *Hustedia culcitula*, *Composita* cf. *apheles*) from the Asselian Bird Spring Formation in the Las Vegas Range, Nevada (Mills and Langenheim, 1987) and 88.8% in sample USNM702e (e.g., *Rhipidomella hessensis*, *Hustedia cepacea*, *Composita apsidata*) from Texas (Hess Formation). Cementing forms are generally rare, but the productids *Eolyttonia* sp. and *Acritosia peculiaris* compose 7.2% of the brachiopods in sample USNM716o. Because bivalves are rare in these offshore samples, it is difficult to assess the relative abundance of epifaunal and infaunal forms. Sample USNM702e contains 23 bivalve individuals, 82.6% of which are epibyssate myalinids or pectinoids. However, the shallow infaunal
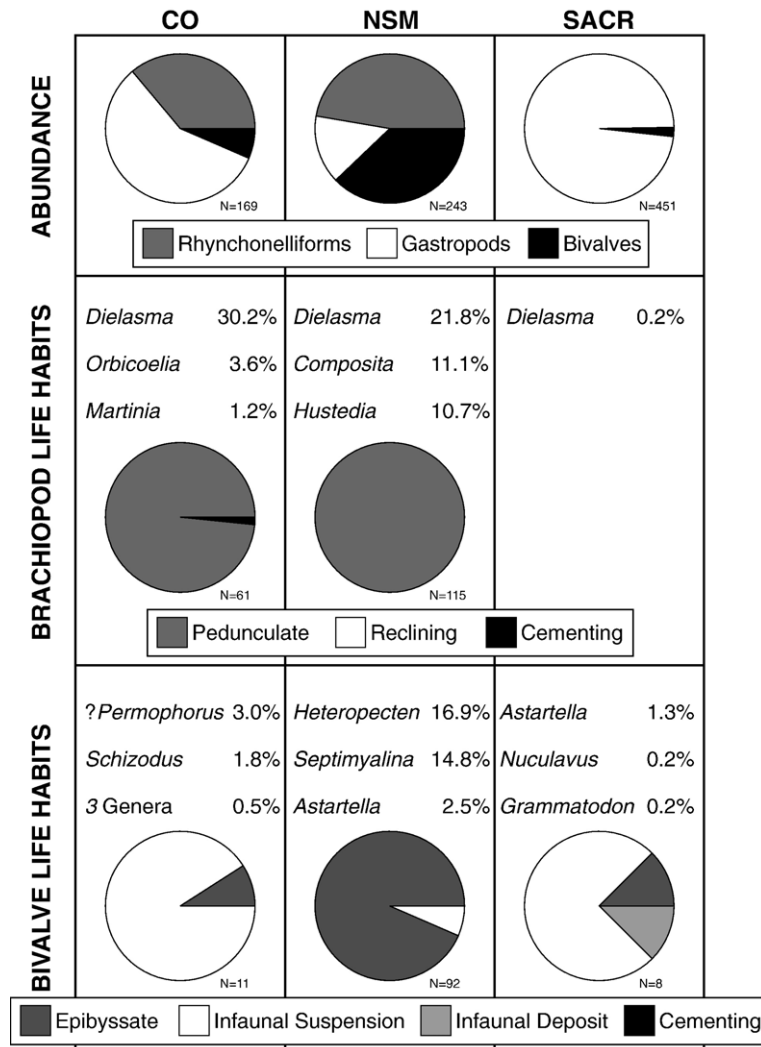
Fig. 3. Normalized relative abundance of rhynchonelliform brachiopods, bivalves, and gastropods in onshore (nearshore and inner shelf) assemblages. The relative abundance of the three most abundant brachiopods and bivalves are shown along with the relative proportion of life habits in each group. Sample CO is from northeastern Nevada; samples NSM and SACR are from southern Nevada.

genus *Astartella* is the only bivalve (2 individuals) in sample WSN and accounts for two of the three bivalve individuals in sample USNM716o. Similarly, *Schizodus* cf. *supaiensis* and another unidentified infaunal suspension-feeding individual were the only bivalves in sample 716n. Like in the inner shelf assemblages, only a single deposit-feeding nuculoid bivalve (from sample USNM702e) was present in the offshore assemblages.

These results are consistent with onshore–offshore ecological trends previously reported from shallow water assemblages (Yancey and Stevens, 1981) and demonstrate that environmental changes in diversity (Miller, 1988) are paralleled by similar changes in abun-

dance (Fig. 5). Molluscs were extremely dominant in nearshore environments and abundant in inner shelf settings but extremely rare in offshore assemblages on carbonate shelves, similar to the diversity patterns where molluscan-rich assemblages were typically found in onshore environments (Sepkoski and Miller, 1985; Miller, 1988). Diverse brachiopods were largely restricted to middle and outer shelf settings, although mollusc-rich assemblages were often found in slope, basinal, and dysaerobic settings in the late Paleozoic (Kammer et al., 1986; Miller, 1988). The dominance of pedically-attached terebratulid and athyridid brachiopods in shallow settings and the increased importance of reclining productid genera in many offshore assemblages are
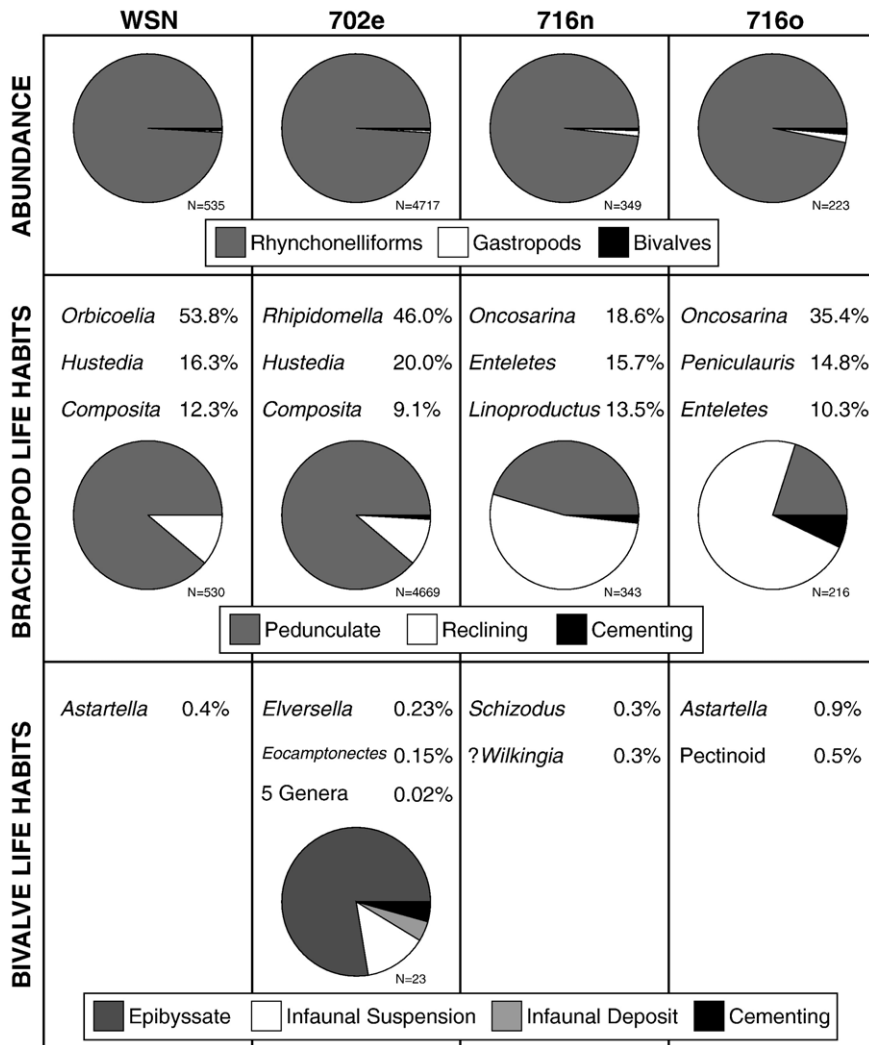
Fig. 4. Normalized relative abundance, life habits, and list of abundant genera for Early Permian offshore (middle and outer shelf) assemblages. Sample WSN is from southern Nevada, all other samples are from west Texas.

also consistent with bathymetric trends in brachiopod abundance documented from Pennsylvanian assemblages (Pérez-Huerta and Sheldon, 2006). Environmental patterns in bivalve ecology are less clear because of the low sample size in offshore assemblages, but it is apparent at least that infaunal deposit-feeding nuculoid bivalves dominated nearshore assemblages, whereas normal marine environments may have had a mixture of infaunal suspension-feeding and epifaunal genera. Like the overall patterns, these trends are broadly similar to those recognized from diversity metrics, with free-burrowing deposit-feeding bivalves most diverse in extreme nearshore environments and epibyssate and infaunal suspension-feeding forms most diverse in inner shelf settings (Miller, 1988).

3.2. Middle to Late Permian ecological changes

Onshore–offshore diversity compilations indicate that molluscs, and bivalves in particular, were becoming more diverse in offshore environments through the Permian (e.g., Sepkoski and Miller, 1985; Miller, 1988). Given that onshore–offshore trends in relative abundance during the Early Permian broadly correlate with those diversity trends, as shown above, examination of temporal changes in ecological dominance may reveal shifts in the Paleozoic and Modern fauna before the end-Permian extinction. In addition, as molluscs were already abundant in onshore environments by the Early Permian and continued to be dominant in the Late Permian (Hollingworth and Pettigrew, 1988), sampling

was concentrated in offshore (middle and outer shelf) settings for the Middle and Late Permian in order to capture the interface between the evolutionary faunas.

Like offshore assemblages during the Early Permian, the 11 Middle Permian samples from northeastern Nevada and west Texas display minimal variation in the relative abundance of brachiopods, bivalves, and gastropods (Fig. 6), and are strongly dominated by rhynchonelliform brachiopods (mean abundance 99.2%, range 97.8%–100%). The relative abundances of bivalves (0.6%) and gastropods (0.2%) also did not change significantly from the Early Permian. Although the overall abundance of higher-level clades is remarkably consistent, there are large variations in the abundance of brachiopod genera and life habits (Fig. 6). Many Middle Permian assemblages are numerically dominated by pedically-attached brachiopods (78.7%–83.7% in five samples from the Gerster Formation of northeastern Nevada), primarily the spiriferinid *Xestotrema pulchrum* and the athyridid *Composita mira*. The reclining productids *Dyoros* (*Dyoros*) *convexus*, *Rhamnaria kingorum*, and *Echinauris lateralis* are most abundant in samples USNM732c and USNM737w from west Texas, in which free-resting individuals comprised 73.5% and 69.9%, respectively. Reclining individuals also dominate several of the Gerster Formation assemblages (54.1% of sample CCR and 60.5% of sample MR), represented by *Yakovlevia multistriata*, *Echinauris subhorrida*, and *Dyoros* sp. Sample USNM706b contains a nearly equal mix of pedically-attached (e.g., *Spiriferella gravis*, *Hustedia pugilla*), reclining (e.g., *Dyoros* (*Dyoros*) *planiextensus*, *Paucispinifera quadrata*, *Rhamnaria kingorum*),

and cemented (e.g., *Heteralosia hystricula*, *Cyclacantharia kingorum*) brachiopod individuals. Although bivalves are rare in all samples, it appears that epibyssate forms dominated in these offshore carbonate settings (Fig. 6). Only epifaunal pectinoid bivalves (primarily *Aviculopecten*) are present in the Gerster Formation samples. Sample USNM732c is also exclusively dominated by epibyssate individuals, containing only *Guizhoupecten cheni* and *Cyrtorostra varicostata*. Epifaunal bivalves account for 66.2% of the individuals in sample USNM706b, dominated by *Cyrtorostra varicostata*, *Leptodesma* sp., and *Procostatoria gloveri*. Infaunal suspension-feeders (e.g., *Astartella*, *Schizodus texanus*, *Permophorus*) comprise 20.8% while cementing individuals (e.g., *Prospondylus acinetus*, *Pegmavalvula gloveri*) represent 11.7%.

The similarities between Early Permian and Middle Permian offshore carbonate samples are quite striking, both in terms of the relative abundance of brachiopods and molluscs and the proportional representation of brachiopod life habits. The relative abundance of rhynchonelliform brachiopods in the Middle Permian (99.2%) is higher than their Early Permian abundance (98.3%), but not significantly (*t*-test, $p = 0.07$). Similarly, the abundance of bivalves in the Middle Permian (0.57%) is indistinguishable ($p = 0.70$) from their abundance in the Early Permian (0.70%). However, gastropods (Middle Permian 0.20% vs. Early Permian 1.0%) are significantly less abundant in Middle Permian samples ($p = 0.03$), largely because of their absence from assemblages from the Gerster Formation. Both Early and Middle Permian offshore settings contained a
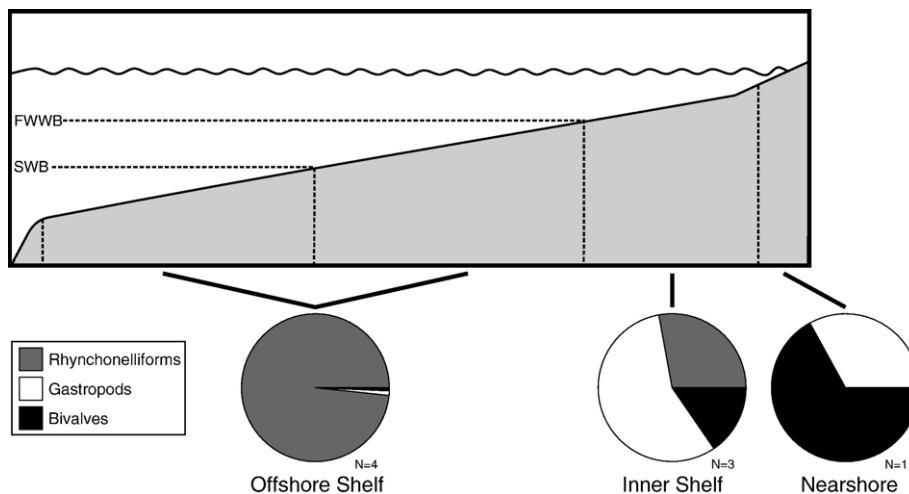

Fig. 5. Onshore–offshore trends in the normalized mean abundance of rhynchonelliform brachiopods, bivalves, and gastropods in the Early Permian. Pie diagrams represent the mean abundance from the constituent assemblages in each environmental bin (individual assemblages shown in Figs. 3 and 4).
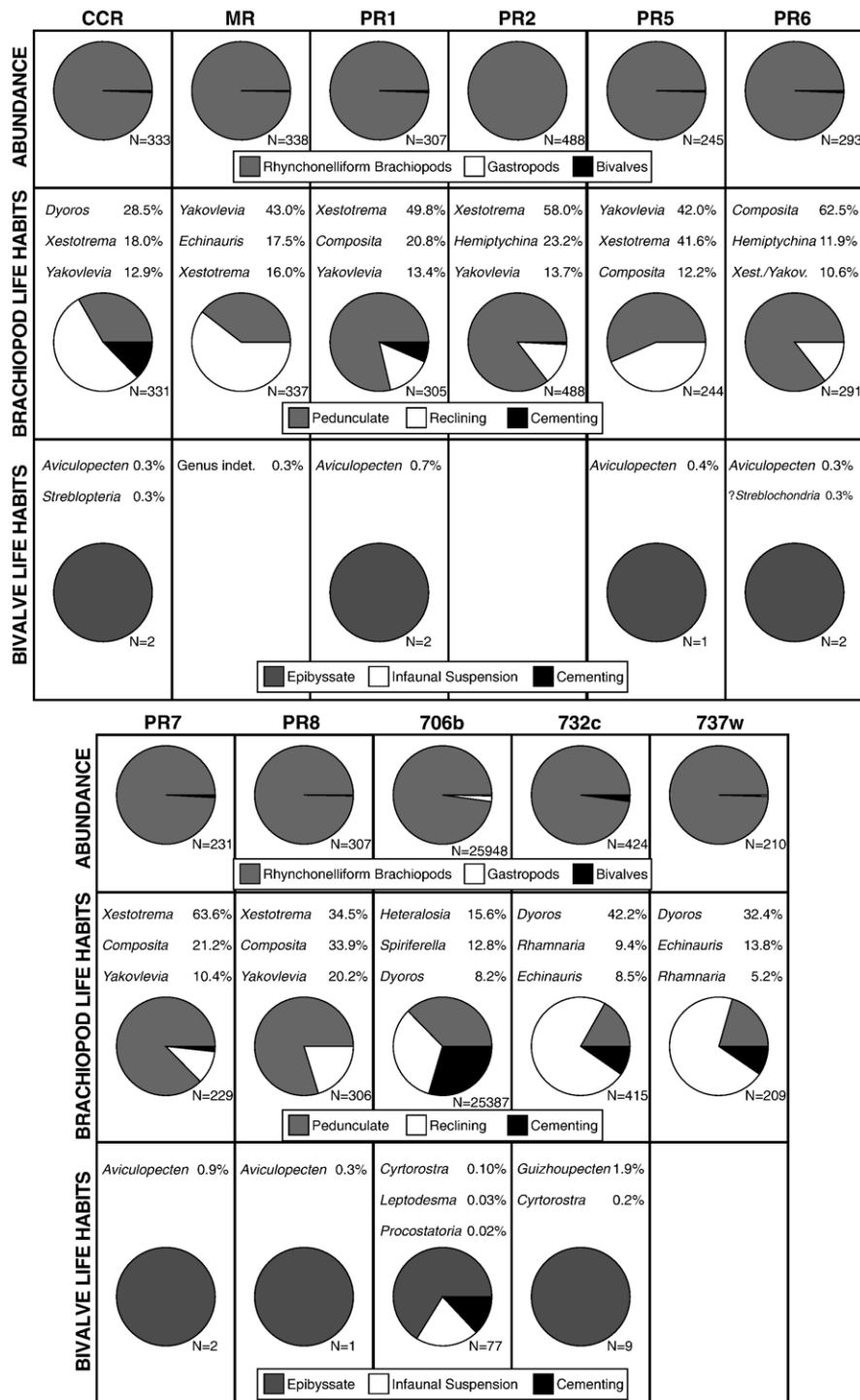
Fig. 6. Normalized relative abundance, life habits, and list of abundant genera for Middle Permian offshore (middle shelf) assemblages from Nevada (Capitanian) and Texas (samples USNM706b, USNM732c, USNM737w; Wordian).

heterogeneous mixture of pedically-attached and reclining brachiopod genera, but the overall proportion of each life habit category was also essentially unchanged

from the Early to Middle Permian. Pedically-attached individuals decreased slightly (but not significantly) in mean abundance from 60.8% to 56.4% ($p = 0.80$),
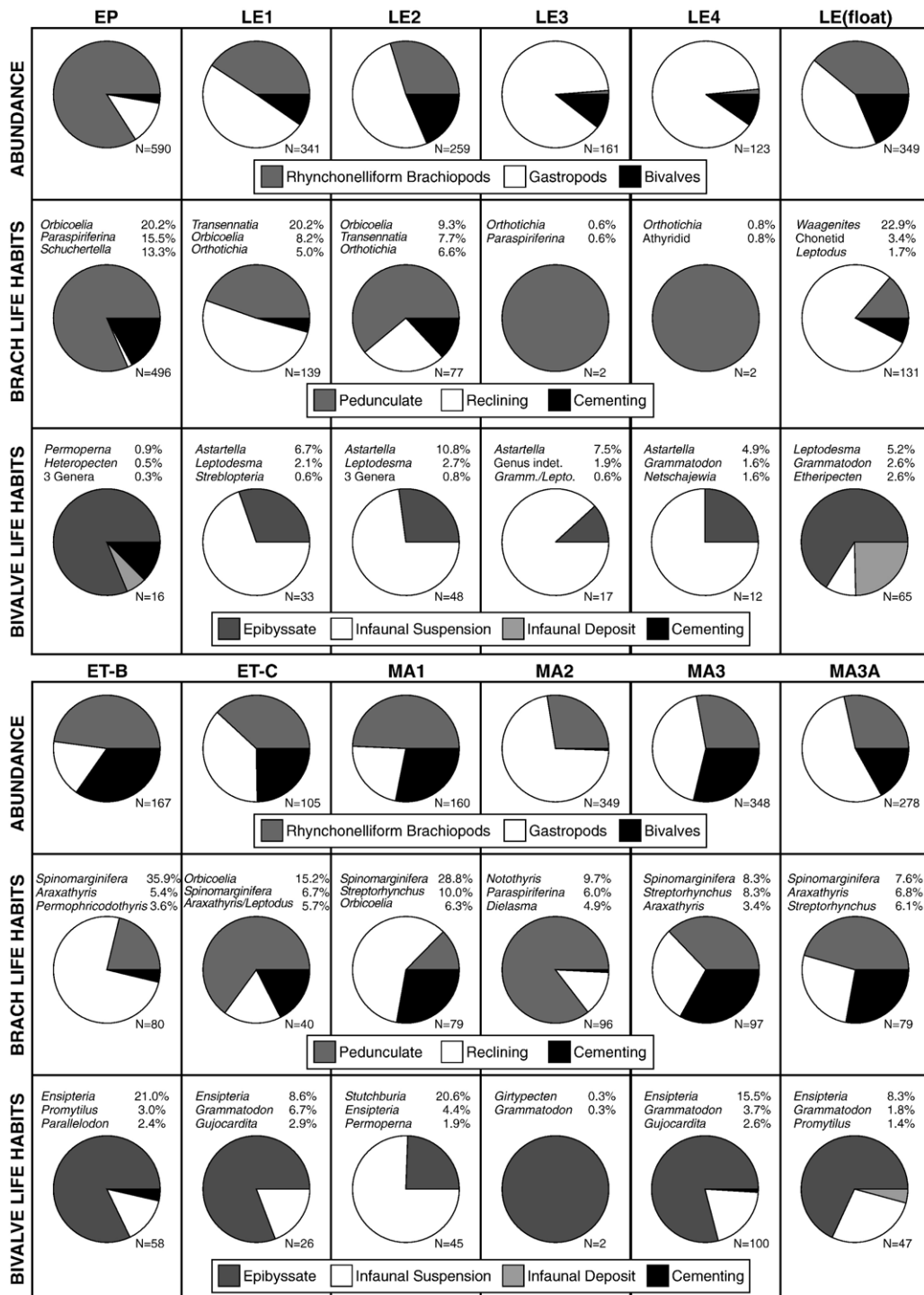
Fig. 7. Normalized relative abundance, life habits, and list of abundant genera for Late Permian offshore (middle and outer shelf) assemblages. Upper panel includes assemblages from Greece (mostly Changhsingian, except EP which is Wuchiapingian); lower panel contains assemblages from China (mostly Wuchiapingian, except MA2 which is Changhsingian).

reclining forms increased from 36.7% to 37.1% ($p=0.98$), and cementing specimens increased in mean abundance from 2.5% to 6.4% ($p=0.42$). It appears based on the studied samples that epibyssate forms are more abundant in the Middle Permian assemblages. However, because of the low number of bivalves in the

assemblages, it is not possible to rigorously test whether the relative abundance of life habits changed between the Early and Middle Permian.

In contrast to the uniformly high abundance of rhynchonelliform brachiopods in Early-Middle Permian offshore settings, Late Permian samples from Hydra (Greece; Episkopi Formation) and Heshan (south China; Heshan Formation) contain a mixture of co-dominant brachiopods and molluscs (Fig. 7). Rhynchonelliform brachiopods have a mean abundance of 34.6%, but comprise as much as 84.1% (sample EP, Hydra) and as little as 1.2% (sample LE3, Hydra) of a given assemblage, although most often they have an abundance of 27%–49%. Bivalves range in abundance from 0.6% to 34.7%, with a mean abundance of 17.0%, whereas gastropods are the most abundant component, accounting for 48.4% of a typical assemblage (range 13.2%–88.6%). Pedically-attached brachiopods remain the most abundant life habit (Fig. 7), accounting for 47.4% of all brachiopod individuals, including the athyridid *Araxathyris* in Heshan and the spiriferid *Orbicoelia* at Heshan and Hydra. Reclining productids such as *Spinomarginifera lopingensis* (Heshan) and *Transennatia* (Hydra) are also important, with a mean abundance of 36.7%. Cementing genera are common (mean abundance, 15.9%), primarily due to the abundance of the orthotetid *Streptorhynchus* in many samples from the Heshan Formation. Bivalves were approximately evenly divided between epibyssate forms such as *Ensipteria*, *Leptodesma*, *Grammatodon*, and *Promytilus* (mean abundance 52.4%) and infaunal suspension-feeders such as *Stutchburia*, *Gujocardita*, and *Astartella* (mean abundance 42.9%). Infaunal deposit-feeders (nuculoid genera such as *Palaeoneilo*, *Phestia*, and *Nuculopsis*) have a mean abundance of 3.2% with cementing individuals such as *Pegmavalvula* and "*Lopha*" (*sensu* Nakazawa and Newell (1968)) comprising 1.6%.

These results indicate that there was substantial ecological change from extreme brachiopod dominance in Middle Permian offshore carbonates to a more equitable mixture of co-dominant brachiopods and molluscs in similar environments during the Late Permian. The abundance changes among rhynchonelliform brachiopods (99.2% to 34.6%), bivalves (0.6% to 17%), and gastropods (0.2% to 48.4%) are all highly significant (Mann–Whitney *U*-test, $p < 0.001$). The increased abundance of cementing brachiopods (from 6.4% to 15.9%) was also significant (*t*-test, $p = 0.04$), but the dominance of pedically-attached (56.4% to 47.4%; $p = 0.46$) and reclining (37.1% to 36.7%; $p = 0.97$) individuals did not change significantly. As infaunal suspension-feeding bivalves are apparently

absent from most Middle Permian samples, it is tempting to argue that their high abundance in the Late Permian indicates a pronounced shift in bivalve life habits. Although it is possible that infaunal bivalves increased in abundance in the Late Permian, the low sample size in many Middle Permian assemblages (often only a single bivalve individual) precludes rigorous evaluation of their abundance changes.

3.3. Temporal trends in fossil size

The prevalence of small organisms in the aftermath of the end-Permian mass extinction is thought to be a result of stressful environmental conditions (Twitchett, 2001; Payne, 2005), implying that similar trends towards decreased fossil size before the extinction may be an indicator of low-level background environmental stress during the Late Permian. However, Late Permian brachiopods are in fact slightly larger (mean size 8.76 mm, $n = 876$) than Middle Permian specimens from northeastern Nevada (mean size 8.12 mm, $n = 1610$), while the largest Middle Permian brachiopod (40.3 mm) is the same size as the largest Late Permian individual (40.7 mm) (Fig. 8). Middle Permian
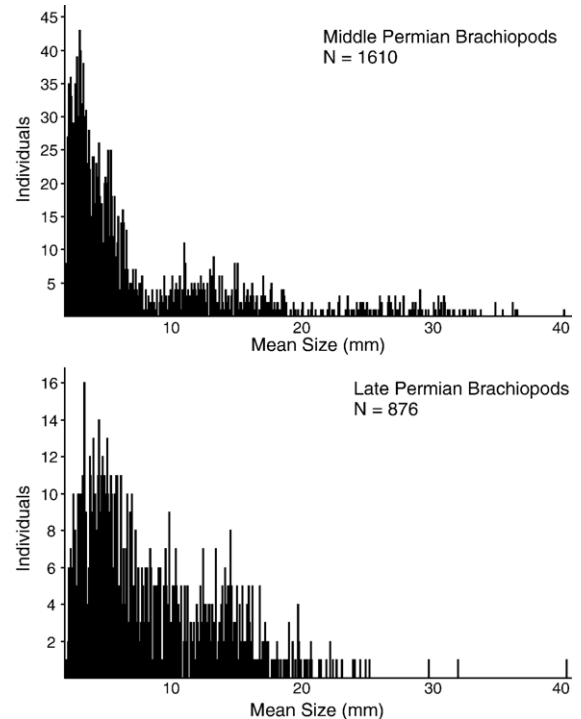

Fig. 8. Size–frequency histograms (geometric mean of shell length and width) for complete, unbroken brachiopods from Middle Permian silicified samples from Nevada (upper) and Late Permian silicified samples from Hydra and Heshan (lower).

brachiopods also displayed a more strongly skewed distribution, with small individuals predominating to a greater degree than in Late Permian assemblages, as the median size of Middle Permian brachiopods was 5.19 mm compared to 7.14 mm in the Late Permian. The extreme rarity of bivalves in Middle Permian offshore assemblages precludes size comparison with Late Permian bivalves. However, bivalves were significantly smaller than rhynchonelliform brachiopods in the Late Permian. The mean size of rhynchonelliform brachiopods was 8.76 mm ($n=876$) compared to only 6.76 mm ($n=269$) for bivalves ($p<0.001$) (Fig. 9).

One of the most dramatic examples of the "Lilliput effect" during the end-Permian mass extinction is the dominance of tiny gastropods in the Early Triassic (Fraiser and Bottjer, 2004; Payne, 2005). Microgastropods (individuals smaller than 1 cm in height) comprise 99% of all measured specimens ($n=376$) in the Early Triassic Sinbad Limestone and the largest specimen is only 18.8 mm in height (Fraiser and Bottjer, 2004), although some Early Triassic gastropods reached heights of slightly more than 20 mm (Wheeley and Twitchett, 2005). This extreme microgastropod dominance (97% of specimens > 2.5 mm in size) contrasts markedly with Early Permian assemblages from similar
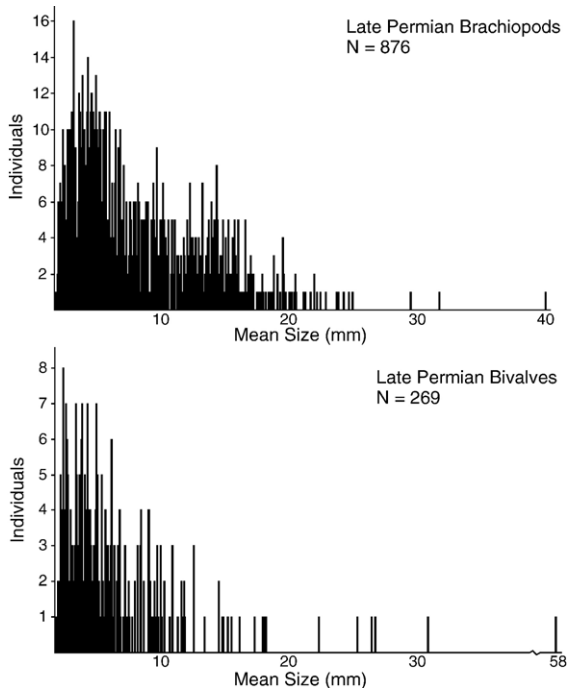

Fig. 9. Size–frequency histograms (geometric mean of shell length and width) for complete, unbroken Late Permian rhynchonelliform brachiopods (upper) and bivalves (lower), both from silicified samples from Hydra and Heshan.

environmental settings (Fig. 10). In Early Permian inner shelf samples, 6.1% of gastropods ($n=521$) are larger than 1 cm and the mean height is 6.05 mm. The largest Early Permian gastropod in this study (a specimen of *Omphalotrochus* from sample CO) is 59.2 mm tall and two other individuals are greater than 30 mm in size. In contrast, the size–frequency distribution of gastropods from offshore settings in the Late Permian differs significantly from those Early Permian inner shelf gastropods and instead is remarkably similar to Early Triassic onshore samples. The mean Late Permian gastropod height, based only on specimens 2.5 mm or larger, is 4.63 mm — significantly smaller than the mean gastropod size in the Early Permian. Only 3.05% of gastropod individuals are 1 cm or more in height ($n=1310$), essentially identical to the ∼ 3% abundance of macrogastropods in the > 2.5 mm size fraction during the Early Triassic (Fraiser and Bottjer, 2004), and the maximum gastropod size is 23.4 mm, again similar to the maximum Early Triassic gastropod size (Wheeley and Twitchett, 2005). Although larger gastropods (greater than 50 mm in height) are present in Late Permian inner shelf samples (Pan and Erwin, 2002), the prevalence of microgastropods in the studied samples implies that the Early Triassic microgastropod dominance may have had its origin in deep shelf environments during the Late Permian.

4. Decoupling of local and global processes

The substantial change in the relative abundance of rhynchonelliform brachiopods and molluscs occurred between the Capitanian (Middle Permian) and mid-Wuchiapingian (Late Permian), broadly coincident with the end-Guadalupian extinction (Stanley and Yang, 1994). However, a new global diversity compilation for the Middle and Late Permian, taking advantage of the large amount of published data on Lopingian fossils in the past decade and including data for most marine invertebrate groups (Table 1), reveals that the end-Guadalupian extinction was not the major crisis suggested by previous studies (e.g., Stanley and Yang, 1994). Additional data for ammonoids was obtained from Leonova (2002), bryozoans from Gilmour and Morozova (1999), crinoids from Webster (2002), and trilobites from Owens (2003), supplemented with more recent literature. Genus-level extinction intensity (using ranged-through diversity excluding stratigraphic singletons) was only 28.1% in the Capitanian Stage, when 197 of 702 genera became extinct (Table 1). Although higher than the preceding Wordian Stage, the true extinction intensity may even have been lower, as apparent extinctions in the
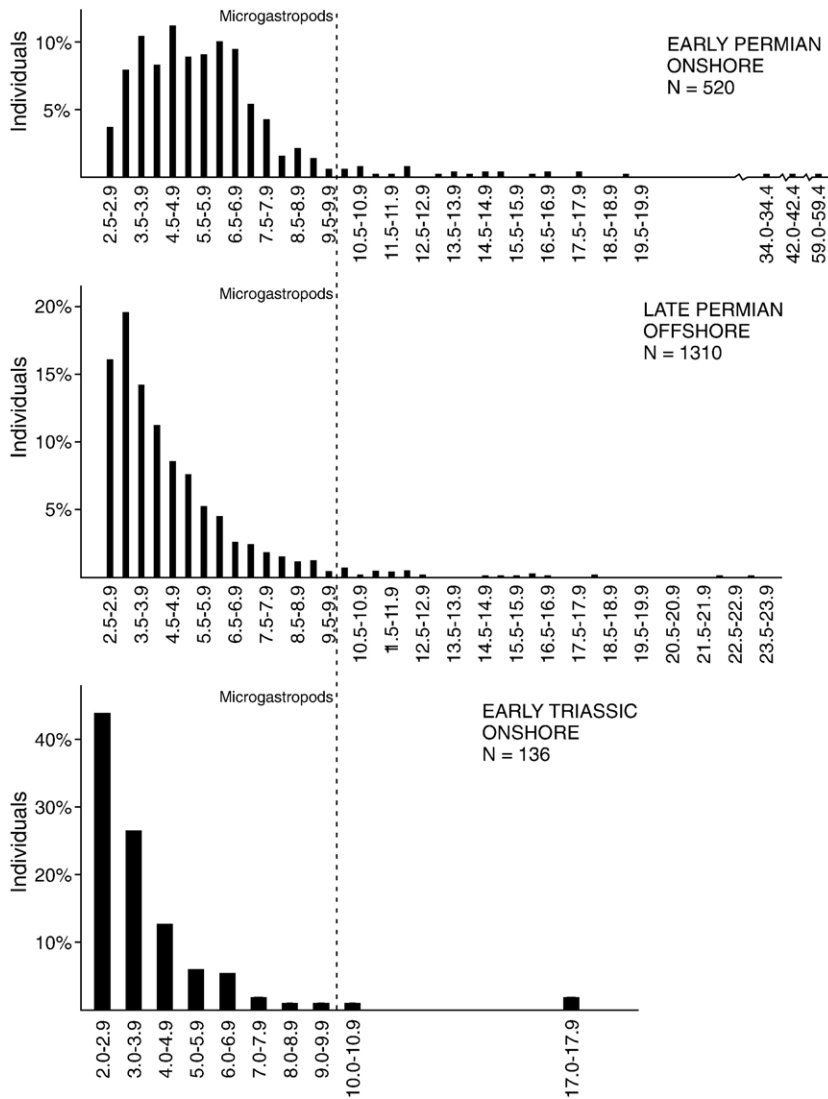
Fig. 10. Size–frequency histograms (shell height) for Early Permian gastropods from onshore environments (Nevada silicified samples), Late Permian gastropods from offshore environments (Hydra and Heshan silicified samples), and Early Triassic gastropods from onshore environments. Early Permian graph modified from Fraiser and Bottjer (2004) to include only specimens larger than 2 mm.

Capitanian may have been exacerbated by a pronounced decrease in preserved marine rocks in the Late Permian (Shen and Shi, 2002). The relative global genus richness of rhynchonelliform brachiopods, bivalves, and gastropods was also essentially unchanged from the Wordian through Wuchiapingian (Table 1), indicating that the pronounced ecological change was not accompanied by a severe global biotic crisis. However, there was a significant change in mean relative within-assemblage richness (alpha diversity) that was approximately correlated with the changes in relative abundance (Fig. 11). In addition to these changes in relative alpha diversity, the absolute within-assemblage genus richness of both

bivalves and gastropods increased substantially in the Late Permian (to 8 genera from 1.1 and to 12.3 genera from 0.1, respectively), while the mean genus richness of rhynchonelliform brachiopods (9.4 genera vs. 11.5 in the Middle Permian) only decreased slightly. The approximate correlation between local abundance and genus richness, combined with the unchanged global genus richness, indicates strong decoupling of local ecological and global taxonomic processes in the Late Permian. This is the most extensive example of large-scale decoupling recognized in the fossil record, affecting the taxonomic and ecological transitions between evolutionary faunas, but differs from previously-recognized instances of

Table 1
Ranged-through genus richness and extinctions for the Wordian, Capitanian, and Wuchiapingian stages

	Wordian			Capitanian			Wuchiapingian		
	Div.	Ext.	%	Div.	Ext.	%	Div.	Ext.	%
Brachiopods	281	24	8.5%	281	74	26.3%	223	56	25.1%
Bivalves	103	10	9.7%	97	29	29.9%	73	10	13.7%
Gastropods	92	17	18.5%	72	17	23.6%	58	7	12.1%
Sponges	62	8	12.9%	56	8	14.3%	53	2	3.8%
Corals	60	13	21.7%	48	16	33.3%	33	21	63.6%
Bryozoans	89	12	13.5%	77	32	41.6%	45	22	48.9%
Crinoids	20	15	75.0%	5	0	0.0%	5	4	80.0%
Ammonoids	48	21	43.8%	35	17	48.6%	20	13	65.0%
Nautiloids	23	2	8.7%	21	0	0.0%	30	1	3.3%
Trilobites	20	10	50.0%	10	4	40.0%	6	1	16.7%
TOTAL	798	132	16.5%	702	197	28.1%	546	137	25.1%

decoupling in which local abundance diverged from both local and global taxonomic richness (McKinney et al., 1998; Strömberg, 2005).

It is not known what general conditions promote decoupling between diversity and abundance. Decoupling of bryozoan abundance and richness occurred in the aftermath of the end-Cretaceous mass extinction (McKinney et al., 1998), whereas the spread of grasslands occurred later than their taxonomic diversification and corresponded with climate drying (Strömberg, 2005). The decoupling of local and global processes in Late Permian offshore carbonate environments may have resulted from a variety of factors, including taphonomic biases in global diversity compilations, environmental variations in the timing of the brachiopod–mollusc transition, or differences in beta diversity (encompassing variables such as geographic range of individual genera) between brachiopods and molluscs.

It is possible that increased alpha diversity of molluscs in Late Permian silicified assemblages reflects a real global change in taxonomic richness but that the global diversity compilation does not capture this shift because of the large contribution from unsilicified biotas that may suffer from diagenetic loss of those molluscan taxa (e.g., Cherns and Wright, 2000). Although such a taphonomic bias may have affected nonsilicified assemblages, especially influencing the relative abundance of gastropods, several lines of evidence suggest it is unlikely that the global diversity compilation was significantly influenced in most cases. First, nearly all brachiopod, bivalve, or gastropod genera known from silicified samples are also found in nonsilicified samples during a given stage, suggesting that silicification itself did not have a major influence on their global taxonomic richness (although gastropods are more dependent on excellent preservation, including but not restricted to silicification). Second, global taxonomic richness does

not vary substantially between stages with abundant silicification and those where most molluscs are known from unsilicified assemblages. This may be because the use of ranged-through diversity tends to smooth out variations due to changing abundance of silicified collections by extending the range of some genera between those stages with abundant silicification. This smoothing effect and the lack of correlation between the
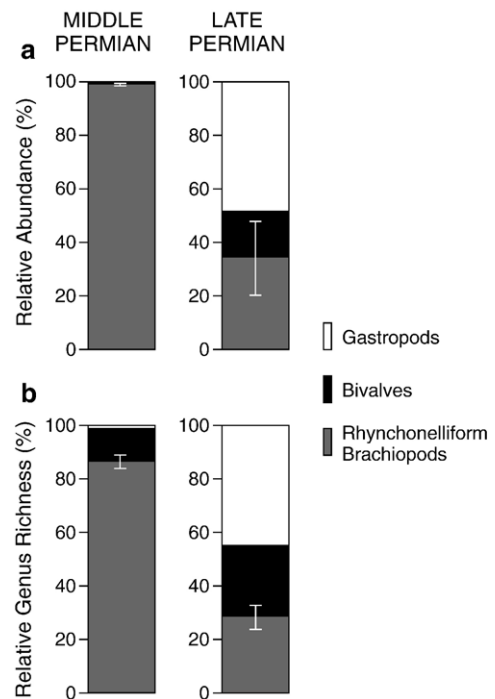

Fig. 11. Local taxonomic richness and abundance. (a) Mean relative abundance of rhynchonelliform brachiopods, bivalves, and gastropods in the Middle Permian and Late Permian samples. (b) Relative within-assemblage richness (alpha diversity) of rhynchonelliform brachiopods, bivalves, and gastropods in the Middle Permian and Late Permian samples. Error bars indicate 95% confidence intervals.

number of silicified assemblages and global taxonomic richness (either the total or relative richness of molluscs) strongly implies that silicification does not significantly influence the global compilation. This suggests that global compilations produce broadly accurate estimates of global diversity and the decoupling in carbonate assemblages between local ecology and global taxonomic richness is a real phenomenon.

Apparent decoupling during the Late Permian may simply reflect the fact that molluscs were diverse in tropical carbonate environments but remained rare in temperate and/or siliciclastic settings. In this scenario, relatively constant global taxonomic richness during the Middle-Late Permian interval could have been maintained by stability in a broad spectrum of environments, with changes in tropical carbonates only contributing a small amount to overall change. This would imply that molluscan ecological dominance first began in these tropical carbonate environments during the Late Permian and spread to other settings at a later time. However, as the tropics, both today and in the Permian, tend to have substantially greater diversity than temperate regions (Pianka, 1966; Powell, 2005), any changes in alpha diversity in the tropics, especially one as pronounced as the Late Permian increase in molluscan within-assemblage genus richness documented here, would be expected to have a significant impact on global compilations. Published faunal lists also indicate that molluscs were comparatively diverse relative to brachiopods in temperate regions and siliciclastic settings in the Late Permian (Nakazawa et al., 1975; Hollingworth and Pettigrew, 1988), demonstrating that the shift in alpha diversity in tropical carbonates is likely representative of changes in alpha diversity worldwide.

Given that the decoupling between local and global processes appears to be a real phenomenon in the Late Permian and does not reflect differences between tropical carbonate settings and the global ecosystem, it is instead possible temporal changes in the geographic distribution of individual mollusc genera (i.e., changes in beta diversity) contributed to the decoupling of their local diversity and global genus richness. Limited data suggest that individual bivalve genera were relatively cosmopolitan in the Wuchiapingian and may have been more broadly distributed than Wordian bivalves. Wordian bivalves are recorded from 18 regions worldwide, and 13.4% of genera occur at four or more of those localities. In contrast, 23% of Wuchiapingian bivalves occur at four or more stations, despite the fact that only 14 regions were included. If true, this broadened distribution would enable bivalves to increase their alpha diversity as previously endemic or geographically localized genera spread to colonize a wider range and more assemblages in the Late Permian. Global genus richness would not change substantially because many of those genera were present in earlier time intervals but were simply restricted to a narrower geographic or environmental range.

5. Causes of the ecological shift

Decoupling of local ecological processes from global taxonomic change during the Guadalupian–Lopingian transition from abundant brachiopods to dominant molluscs indicates that the ecological change was not associated with severe taxonomic effects during an extinction event. The marked shift in relative abundance is not a taphonomic artifact, as all samples are well-silicified during early diagenesis and no unsilicified shells or molds of dissolved specimens were observed in the field or in thin section. In addition, the pronounced increase among a variety of groups with different shell mineralogy and microstructure (i.e., calcitic bivalves and aragonitic gastropods) implies that the ecological change is a real phenomenon. The dramatic increase in molluscan abundance during the Late Permian was also not likely caused by intrinsic biological processes, such as acquisition of evolutionary innovations that allowed molluscs to radiate in the Lopingian, as the dominant genera in the Lopingian samples were also present in older time intervals. Rather, extrinsic environmental factors may have been a more important influence on relative abundance, by mediating the competitive interaction between molluscs and rhynchonelliform brachiopods.

As molluscs have more active metabolisms and greater food requirements than rhynchonelliform brachiopods (Thayer, 1986; Bambach, 1993; Rhodes and Thompson, 1993), it is possible that an increase in productivity in offshore carbonate environments gave molluscs a competitive advantage in the Lopingian. A similar relationship between productivity and community structure has been observed in the modern Adriatic Sea, where Paleozoic Fauna organisms dominate in nutrient-poor regions while the Modern Fauna is abundant in areas of higher productivity (McKinney and Hageman, 2006). Although there is no direct evidence for an increase in productivity during the Guadalupian–Lopingian interval, there was a general increase in marine productivity through the late Paleozoic (Martin, 1996; Martin, 2003) that may have triggered an abrupt regime shift at a critical nutrient threshold (e.g., Scheffer et al., 2001; Scheffer and Carpenter, 2003). However, a nutrient-triggered shift,

whether a regime change or driven by an end-Guadalupian productivity increase, would have caused markedly diachronous ecosystem change that occurred earlier in high-productivity regions such as upwelling zones and much later in oligotrophic shelf regions. Although there is only sparse quantitative information, the combination of abundance data presented here and qualitative assessments from other regions tentatively appears to indicate approximately synchronous ecological change, suggesting that nutrients were not the primary driver of the ecological shift.

Bivalves and gastropods are both also better adapted than rhynchonelliform brachiopods to thrive in harsh or fluctuating environmental conditions (Steele-Petrovic, 1979), and this eurytopic habit was largely responsible for their abundance in more rigorous nearshore and inner shelf habitats during the Paleozoic (Sepkoski and Miller, 1985). Increasing environmental stress or variability in offshore carbonate habitats during the Late Permian may have given molluscs a competitive advantage over the more stenotopic brachiopods, although it is unlikely that the same shallow-water environmental stresses (including salinity and physical disturbance from storm events) would have acted in these relatively quiet offshore settings in the Late Permian. However, the Guadalupian–Lopingian transition was marked by the onset of anoxia in deep ocean settings (Isozaki, 1997) and the occurrence of fluctuating euxinia in some Wuchiapingian-aged basinal environments (Nielsen and Shen, 2004). The proximity of this anoxic or euxinic water mass to outer regions of the shelf may have resulted in fluctuating lowered oxygen concentrations and generally increased levels background environmental stress.

The striking similarities in relative abundance structure between Late Permian offshore shelf communities from China and Greece and the Early Permian inner shelf assemblages from Nevada are consistent with the effects of increased environmental stress in Late Permian offshore carbonates. Both contain a relatively equitable mixture of rhynchonelliform brachiopods (27.9% in Early Permian onshore assemblages, 34.6% in Late Permian offshore), bivalves (15.4% and 17.0%, respectively), and gastropods (56.7% and 48.4%). Both were also characterized by a heterogeneous mosaic of community types, with some strongly dominated by gastropods, some with abundant brachiopods and gastropods with rare bivalves, and others containing co-dominant brachiopods and molluscs. For example, Early Permian sample SACR contains 98% gastropods, similar to samples LE3 (88.2% gastropods) and LE4 (88.6%) from the Late Permian of Hydra. Likewise,

Early Permian sample NSM (47.3% brachiopods, 37.9% bivalves, 14.8% gastropods) has Late Permian offshore equivalents such as sample ET-B from Heshan (47.9% brachiopods, 34.7% bivalves, 17.4% gastropods). The expansion of habitats in the Late Permian in which molluscs, such as bivalves, had a competitive advantage is also consistent with the potentially more cosmopolitan nature of bivalve genera in Wuchiapingian. The broad occurrence of environmentally variable conditions in Late Permian offshore shelf environments may have expanded the size of favorable habitat area for molluscs, facilitating dispersal and colonization of molluscan genera over a much wider geographic area. In addition, size similarities between Late Permian offshore gastropods and Early Triassic onshore individuals, in terms of the proportion of microgastropods, the mean size, and the maximum individual size, are consistent with causation by similar mechanisms, such as proximity to euxinic water masses, and may imply that the environmental stress that caused the end-Permian mass extinction (e.g., Grice et al., 2005) and contributed to the delayed Early Triassic recovery began in deep shelf environments during the Late Permian.

6. Conclusions

Changes in relative abundance in offshore benthic communities reveal that the first stage in the ecological transition from the rhynchonelliform brachiopod-dominated Paleozoic Fauna to the molluscan Modern Fauna occurred between the Middle and Late Permian, in contrast to the abrupt diversity switch at the Permian–Triassic boundary. The dramatic increase in molluscan abundance, from 1% to 65% in these offshore assemblages, was paralleled by a similar increase in the abundance of motile gastropods and, potentially, infaunal bivalves. The increase in molluscan dominance reflects a substantial shift in their environmental range, expanding from their onshore roots in the Early Permian to gain widespread dominance in many shelf environments in the Late Permian. Late Permian offshore communities were very similar to Early Permian onshore communities, in that both appear to have contained a heterogeneous mosaic of mixed mollusc–brachiopod assemblages, in contrast to the rather homogeneous extreme brachiopod dominance in Early and Middle Permian offshore settings.

The coincidence of the ecological change with the onset of deep ocean euxinia at the end of the Middle Permian and the striking similarity of Late Permian offshore samples to Early Permian onshore assemblages implies that the ecological structure of Late Permian communities may have been influenced more

strongly by environmental variability than Middle Permian offshore assemblages. Eurytopic molluscs may have had a competitive advantage in Late Permian offshore assemblages if those environments were intermittently affected by stress from proximity to the deep euxinic water mass. This correlation between ecological change and onset of deep-water euxinia, as well as the lack of a corresponding global change in taxonomic richness, indicates pronounced decoupling of local and global phenomena in the Late Permian and implies that the dramatic faunal shift did not result from a major biotic crisis. Instead, competition and the environmental and biotic factors that influence competitive interactions were likely the primary factors driving ecological change in the Guadalupian–Lopingian interval.

Decoupling of local ecological processes from global taxonomic richness may have also been caused by the same environmental factors that promoted ecological change during the Late Permian. Increased environmental variability and physical stress resulted in expanded habitat space that was favorable for molluscs and may have contributed to the wider geographic range of individual bivalve genera in the Late Permian. The prevalence of more cosmopolitan bivalves in the Late Permian may be indicative of changes in beta diversity that allowed a pronounced increase in within-assemblage diversity while maintaining relatively stable global taxonomic richness.

These results also indicate that the ecological transition between rhynchonelliform brachiopods and molluscs was much more protracted and complex than previously assumed based on diversity metrics. The potential link between ecological change and the onset of deep marine anoxia or euxinia, the primary cause of the end-Permian mass extinction, implies that the ecological dominance of molluscs in the Late Permian was a precursor to the severe biotic crisis and abrupt shift in global taxonomic richness at the end-Permian mass extinction. It also indicates that abrupt taxonomic crisis and rapid loss of marine biodiversity during the end-Permian extinction were actually part of a prolonged ecological crisis that spanned much of the Late Permian and Early Triassic and began with the initial stages of molluscan ecological dominance around the Guadalupian–Lopingian boundary.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2007.02.003.

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