

Prolonged Permian–Triassic ecological crisis recorded by molluscan dominance in Late Permian offshore assemblages

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The end-Permian mass extinction was the largest biotic crisis in the history of animal life, eliminating as many as 95% of all species and dramatically altering the ecological structure of marine communities. Although the causes of this pronounced ecosystem shift have been widely debated, the broad consensus based on inferences from global taxonomic diversity patterns suggests that the shift from abundant brachiopods to dominant molluscs was abrupt and largely driven by the catastrophic effects of the end-Permian mass extinction. Here we analyze relative abundance counts of >33,000 fossil individuals from 24 silicified Middle and Late Permian paleocommunities, documenting a substantial ecological shift to numerical dominance by molluscs in the Late Permian, before the major taxonomic shift at the end-Permian mass extinction. This ecological change was coincident with the development of fluctuating anoxic conditions in deep marine basins, suggesting that numerical dominance by more tolerant molluscs may have been driven by variably stressful environmental conditions. Recognition of substantial ecological deterioration in the Late Permian also implies that the end-Permian extinction was the climax of a protracted environmental crisis. Although the Late Permian shift to molluscan dominance was a pronounced ecological change, quantitative counts of 847 Carboniferous–Cretaceous collections from the Paleobiology Database indicate that it was only the first stage in a stepwise transition that culminated with the final shift to molluscan dominance in the Late Jurassic. Therefore, the ecological transition from brachiopods to bivalves was more protracted and complex than their simple Permian–Triassic switch in diversity.

end-Guadalupian extinction | modern fauna | paleoecology | Paleozoic fauna

The Permian–Triassic mass extinction was one of the most dramatic faunal transitions in the evolution of marine animal life (1–3), altering the composition of benthic communities and ultimately paving the way for present-day marine ecosystems. Compilations of marine animal diversity have shown that the phyletic transition from diverse rhynchonelliform brachiopods to diverse molluscs occurred at the Permian–Triassic boundary (2–4), coincident with the end-Permian mass extinction event. That concurrence has been used to argue that the mass extinction was the primary cause of the ecological change by eliminating previously dominant brachiopods and allowing molluscs to rise to dominance (2). However, because ecological changes are not necessarily synchronous with taxonomic changes (5, 6), the tacit assumption that the shift to abundant molluscs paralleled the well known shift to diverse molluscs may not be accurate. Similar taxonomic richness data have been used to argue that the end-Permian mass extinction was a catastrophic and abrupt event confined to the immediate boundary interval (7, 8), occurring in <1 million years (9). Although an earlier extinction has been recognized at the end of the Middle Permian (the end-Guadalupian extinction), it was a separate event, distinct from the end-Permian crisis (10, 11). However, recognition of ecological deterioration before the mass extinction event has not

been possible because of a lack of quantitative paleoecological studies from Late Permian marine fossil assemblages.

Results and Discussion

Our quantitative counts of silicified Middle and Late Permian fossil assemblages [Fig. 1; see also [supporting information \(SI\)](#) and ref. 12] provide direct evidence to demonstrate that, in contrast to the Permo–Triassic taxonomic transition and contrary to previous assumptions (2), the shift in relative abundance between rhynchonelliform brachiopods and molluscs occurred during the Guadalupian–Lopingian interval in offshore tropical carbonates. For comparison purposes, relative abundance data for all assemblages were normalized to include only rhynchonelliform brachiopods, bivalves, and gastropods because of the fluctuating abundance of accessory faunal components (most commonly crinoid ossicles and stenolaemate bryozoan fragments) and the inherent taphonomic problems involved in counting those groups. When normalized, rhynchonelliform brachiopods have a mean abundance of 99.2% (range 97.8–100%), whereas bivalves only comprise 0.6% (range 0–2.1%) and gastropods 0.2% (range 0–1.9%) of the average Middle Permian assemblage (Fig. 2A). In contrast, Late Permian fossil assemblages, collected from similar carbonate lithologies deposited in similar offshore environments below storm wave base, contain a mixed brachiopod–mollusc fauna markedly different from that found in Middle Permian samples (Fig. 2A). Gastropods are the most abundant component in the samples (mean 48.4%, range 13.2–88.6%), whereas rhynchonelliform brachiopods comprise only 34.6% of the individuals (range 1.2–84.1%), and bivalves account for 17.0% (range 0.6–34.7%) in an average assemblage. This dramatic shift in numerical dominance also was accompanied by a pronounced change in the ecological structure of benthic communities, from extreme dominance by sessile, pedically attached (56.2%), and reclining (36.8%) epifaunal suspension-feeding individuals in the Middle Permian to an abundance of motile herbivores/detritivores (47.4%) in the Late Permian (Fig. 2B). Infaunal individuals (primarily shallow suspension-feeding bivalves) were absent from most Middle Permian assemblages (mean abundance < 0.01%) but increased dramatically to 7.2% in the Late Permian samples. Motile forms (some infaunal bivalves and most gastropods) increased in abundance from 0.06% in the Middle Permian to comprise a majority in the Late Permian assemblages (54.6%).

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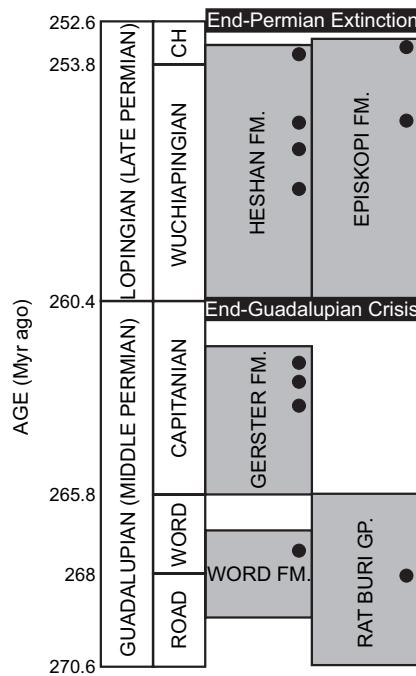


Fig. 1. Permian timescale showing age of sampled formations, approximate age of silicified fossil assemblages (filled circles) used in this study, and timing of the end-Guadalupian biotic crisis and end-Permian mass extinction. Absolute ages are based on ref. 37. Road, Roadian; Word, Wordian; Ch, Changhsingian.

Taphonomic and Biogeographic Biases. Although these results from geographically distinct Middle and Late Permian localities imply that the transition was a real, global phenomenon, the observed changes may not reflect a true ecological shift if taphonomic biases during silicification greatly decreased the abundance of aragonitic genera (especially gastropods) in Middle Permian assemblages. Given that aragonite preservation is enhanced by early diagenetic silicification (13), it seems unlikely that the Middle Permian assemblages from the Gerster Formation in Nevada, which underwent silicification before or early during sediment compaction and record fine details such as brachiopod punctae, would have all suffered from extensive aragonite dissolution, whereas similarly silicified Late Permian samples from Greece and China did not. Finally, there was also a pronounced increase in the abundance of calcitic-shelled bivalves between the Middle and Late Permian samples, implying that the dominance of molluscs in the Late Permian does not simply represent increased preservation of aragonitic components. However, even if Middle Permian assemblages were biased against species with aragonitic shells, our conclusion that the brachiopod–mollusc ecological transition predated the end-Permian mass extinction would still remain valid.

It is also possible that these observed ecological changes between Middle Permian samples from the western United States and Late Permian samples from Greece and China represent geographic variations between eastern Panthalassa and the Tethys Sea, rather than a global change. However, several other quantitative counts support the conclusion that the observed Guadalupian–Lopingian ecological change is a real phenomenon in tropical carbonate environments. Our counts from a single silicified sample from Khao Phrik in Thailand (14) indicate that brachiopods were numerically dominant, accounting for 87.9% of the assemblage, although the depositional environment was shallower than our other field samples. In addition, previously published thin-section point counts of latest

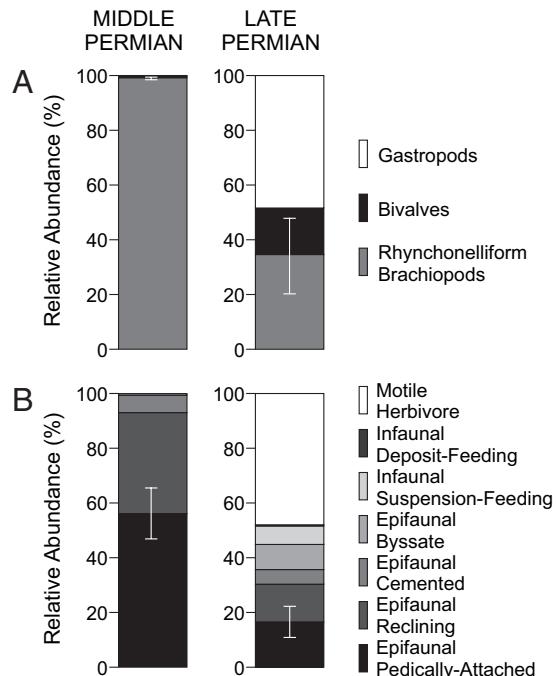


Fig. 2. Ecological changes in silicified Middle and Late Permian fossil samples. (A) Normalized mean abundance of rhynchonelliform brachiopods, bivalves, and gastropods from silicified field samples. (B) Mean proportional abundance of ecological guilds in Middle and Late Permian silicified assemblages. Error bars indicate 95% confidence intervals.

Capitanian fossiliferous carbonates from Guangxi Province (China) record abundant brachiopods and no molluscs (15), strikingly similar to Middle Permian North American samples and significantly different from Late Permian samples also from China. Brachiopods were also numerically dominant in temperate siliciclastic deposits from the Bowen basin (Queensland, Australia), comprising 79.5% of seven quantitative samples from the Wordian and Capitanian (16). These data strongly imply that biogeographic differences in community ecology between Tethys and eastern Panthalassa were minor and that the ecological shift from Middle Permian to Late Permian tropical carbonate assemblages was a widespread phenomenon.

Implications for the Brachiopod–Mollusc Transition. The brachiopod–bivalve transition traditionally has been viewed as a single abrupt event at the Permian–Triassic boundary, based on inferences from global diversity data (2). However, the recognition here of a substantial decrease in the relative abundance of brachiopods during the Guadalupian–Lopingian interval implies that the ecological shift was more complex than indicated by diversity data. The role of the Guadalupian–Lopingian shift in the broader context of the brachiopod–bivalve transition can be assessed by incorporating quantitative abundance data from the primary literature (culled from the Paleobiology Database, www.paleodb.org) for the Carboniferous through Cretaceous interval. A total of 847 collections with >100 specimens, including the 24 collections described here and other silicified collections in ref. 12, constrain changes in the relative abundance of brachiopods (Fig. 3). The transition from abundant brachiopods in the Carboniferous through Middle Permian (80% in 129 Carboniferous assemblages, 70% in 75 Early Permian assemblages, and 86% in 23 Middle Permian assemblages) to a more even brachiopod–mollusc mix in the Late Permian is apparent. During the Early and Middle Permian, brachiopods were less abundant globally than in the silicified offshore carbonates due

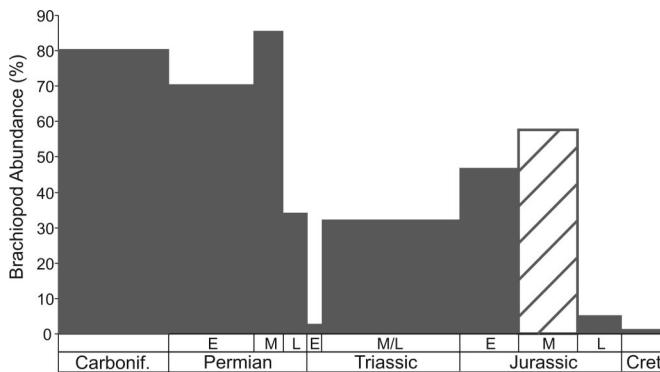


Fig. 3. Relative abundance of rhynchonelliform brachiopods (normalized to include only brachiopods, bivalves, and gastropods) from 847 quantitative assemblages from the Carboniferous through Cretaceous, indicating the two-stage Middle–Late Permian and Middle–Late Jurassic transitions. Middle Jurassic abundance (indicated by hatched pattern) may be overestimated.

to the inclusion of more mollusc-dominated inner shelf and siliciclastic samples, but the magnitude of the Middle–Late Permian ecological change is still substantial.

As documented by other studies (17–19), the end-Permian mass extinction had a massive short-term ecological impact, with Early Triassic assemblages containing almost no brachiopods (mean abundance in 40 assemblages is 2.5%). However, brachiopods rebounded to comprise 30–50% of Middle/Late Triassic through Early Jurassic assemblages (Middle/Late Triassic, $n = 31$; Early Jurassic, $n = 161$), similar to their Late Permian abundance of 34.6%. Although the Triassic and Early Jurassic assemblages are not silicified and likely underestimate gastropod abundance (and therefore overestimate the abundance of brachiopods), the quantitative data indicate that brachiopods were comparatively abundant in the early Mesozoic, especially with respect to their Early Triassic low. However, early Mesozoic brachiopod assemblages were overwhelmingly dominated by pedically attached individuals (especially spiriferinids), in contrast to the mixture of pedunculate and reclining late Paleozoic forms, indicating that the end-Permian extinction had a major impact on brachiopod guild structure. The final stage in the brachiopod–bivalve transition occurred between the Middle and Late Jurassic (although their Middle Jurassic abundance is biased somewhat by the inclusion of many monospecific brachiopod-only reef assemblages), with brachiopods decreasing to 5% ($n = 247$) in the Late Jurassic and finally to <1% by the Cretaceous ($n = 87$) (Fig. 3). The recognition of the two-phase change (Middle–Late Permian and Middle–Late Jurassic) in relative abundance confirms the importance of the end-Guadalupian interval for the brachiopod–bivalve transition.

Timing and Cause. This dramatic global change in ecological dominance, where rhynchonelliform brachiopods decreased in mean abundance from 99.2% to only 34.6% in our silicified samples, occurred at some point between the Capitanian (likely early or mid-Capitanian based on samples from Nevada) and mid-Wuchiapingian, indicating that it was approximately coincident with the end-Guadalupian extinction (10, 11) ≈8 million years before the end-Permian crisis (Fig. 1). It therefore seems reasonable that the moderately severe taxonomic effects of the end-Guadalupian extinction may have triggered the ecological shift in much the same manner as previously inferred for the end-Permian crisis. However, our sampling-standardized analysis of brachiopod and mollusc global taxonomic richness for the Guadalupian and Lopingian (Fig. 4) indicates that, after rarefaction, Lopingian genus richness among brachiopods, bivalves, and gastropods is no more than 30% lower than Guadalupian

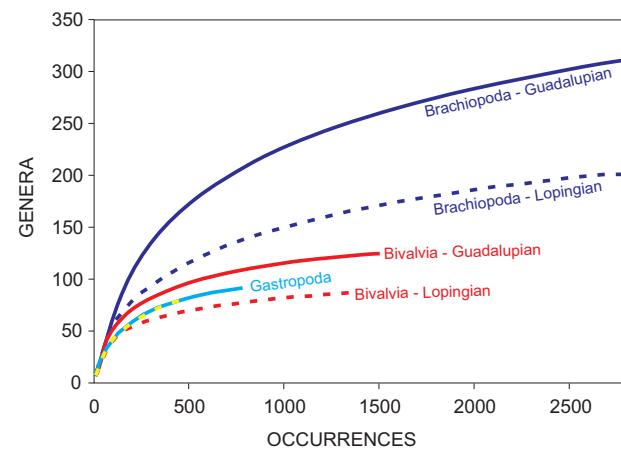


Fig. 4. Sampling-standardized genus richness during the Guadalupian–Lopingian interval. Generic richness rarefaction curves for rhynchonelliform brachiopods, bivalves, and gastropods for the Guadalupian (solid lines) and Lopingian Series (dashed lines) are shown. The rarefaction curve for Lopingian gastropods overlaps the Guadalupian line. Brachiopod rarefaction curves are truncated, and only the initial 2,700 occurrences are displayed for comparison purposes.

richness. Genus-level extinction in the Capitanian Stage ranges from 25% to 35% for rhynchonelliform brachiopods, bivalves, and gastropods. This relative taxonomic stability at the global scale is consistent with a study of brachiopod extinctions in south China, which indicates low and unchanged standing extinction rates in the Capitanian after sampling standardization (20). The moderate global diversity decrease instead likely resulted from habitat loss due to a tectonically driven reduction in marine deposition in regions such as western North America, eastern Australia, the Ural Mountains, and north China (21). Although overall global marine diversity did decrease, the fact that brachiopods remained approximately twice as diverse as either gastropods or bivalves in the Lopingian contrasts markedly with the pronounced ecological shift in local relative abundance, indicating decoupling of diversity and ecology (5) during the Lopingian interval (12).

There was a biotic crisis affecting fusulinids (11, 22) and an ecological crisis in reef communities (23) at the end of the Guadalupian, but consistent relative global taxonomic richness, moderately elevated extinction rates after sampling standardization, and the absence of an extinction peak (at least among brachiopods) in south China and other Tethyan localities (20, 21) imply that the crisis was not a pronounced mass extinction event affecting brachiopods or molluscs. Therefore, it is not likely that the Guadalupian–Lopingian interval of maximum ecological change was driven by the rather muted taxonomic turnover in brachiopods and molluscs, although both may have been symptoms of a common cause. The increased dominance of molluscs in the Late Permian also did not result from a radiation of new taxa with new evolutionary innovations, as the same bivalve and gastropod genera that were abundant in the Late Permian were also present in earlier time intervals.

Instead, the ecological shift and minor biotic crisis may have been related to environmental changes during the Guadalupian–Lopingian interval that altered the competitive interactions between rhynchonelliform brachiopods and molluscs. Many bivalves and gastropod species are better adapted than brachiopods to withstand fluctuating and physically stressful environmental conditions, such as salinity, turbulence, or oxygen levels, because of their mobility and more efficient gas exchange and active metabolism (24). These broader environmental tolerances are thought to have played a significant role in fostering higher

molluscan diversity and abundance in stressful and variable nearshore environments throughout the Paleozoic (25). The expansion of mollusc-dominated assemblages from nearshore environments in the Early and Middle Permian to span the width of tropical carbonate shelves in the Late Permian may imply increased levels of environmental stress that favored the more eurytopic molluscs and was coincident with the onset of deep-marine euxinia around the Guadalupian–Lopingian boundary (26, 27). It is plausible that the comparative proximity of the deep euxinic water mass to these offshore shelf environments may have resulted in low-level fluctuations of oxygen and/or hydrogen sulfide levels that produced a sufficiently variable environment to favor molluscs over the more stenotopic brachiopods in offshore settings, without being severe enough to cause major global changes in biodiversity. However, it is also possible that the end-Guadalupian and end-Permian ecological shifts correspond to two discrete episodes of environmental stress, similar to the two discrete crises affecting fusulinids and reefs (11, 23). There was a sea-level lowstand at the Guadalupian–Lopingian boundary (28), but the eustatic regression itself did not cause extinctions among marine invertebrates (20, 21) and therefore also may not have triggered the pronounced ecological shifts. Prolonged environmental stress during the Lopingian also is indicated by changes in the onshore–offshore distribution of bryozoans (29) and the occurrence of pathological foraminiferal morphotypes (30). In addition, the competitive superiority of molluscs under long-term fluctuating conditions of lowered oxygen levels during the Lopingian is also consistent with their preferred survivorship during the end-Permian mass extinction (1, 31), as that biotic crisis was largely caused by the expansion of the deep euxinic water mass into shallow marine environments (32). Recognition of long-term stress also does not negate the possibility of two discrete events, as both prolonged and episodic factors may have contributed to Late Permian biotic and ecological changes.

Conclusions

The primary conclusion from this study is that initial stages of molluscan ecological dominance occurred before the end-Permian mass extinction, earlier than previously assumed (2, 4). The ecological transition to dominant molluscs occurred in a stepwise fashion, beginning around the Guadalupian–Lopingian boundary and concluding with a second abundance shift in the Late Jurassic. This complex ecological change contrasts with the taxonomic transition, which was fundamentally a single shift at the Permian–Triassic boundary (2). The increased abundance of bivalves and gastropods in the Late Permian may reflect their competitive advantage in fluctuating and more stressful environmental conditions, possibly related to the development of deep-water euxinia at the Middle–Late Permian boundary. The variable environmental conditions that began during the end-Guadalupian transition and favored molluscan dominance ultimately culminated in the catastrophic end-Permian mass extinction, demonstrating that, although the extinction's effects on global biodiversity were rapid and abrupt, the Permian–Triassic ecological crisis was considerably more protracted.

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Materials and Methods

To assess the tempo of ecological change before the end-Permian mass extinction, we made counts of fossil abundance from silicified bulk samples collected from individual, thin (<20 cm) limestone shell beds (lime mudstone to wackestone) recording deposition in offshore paleoenvironments in the Middle Permian (Guadalupian) and Late Permian (Lopingian) (12). Sampling was concentrated in offshore environments (below wave base) to minimize confounding environmental factors and capture any changes in the relative abundance of brachiopods and molluscs, as onshore settings were already mollusc-dominated through much of the Paleozoic (25). Depositional environment was assessed from detailed bed-by-bed measured stratigraphic sections and thin section analysis, using standard criteria (33). Taphonomic indicators (34) were also applied in the field to recognize and remove overly mixed or time-averaged shell accumulations. All fossils were replaced by early diagenetic silicification and were etched from the limestone matrix by using 3 M hydrochloric acid, followed by identification to genus level with all individuals counted for each sample by using the “Minimum Number of Individuals” (MNI) method (35). Early diagenetic silicification preserves an excellent record of the original community, including molluscs with aragonitic skeletal composition that may be dissolved in nonsilicified biotas (13). Six Late Permian samples were collected from the Heshan Formation at Heshan (Guangxi Province, China) and six from the Episkopi Formation at Hydra (Greece) (Fig. 1), yielding a total of 3,861 individuals. Eight Middle Permian samples (2,563 individuals) were obtained from the Gerster Formation in northeastern Nevada, and three previously collected Middle Permian samples (26,582 individuals) from the Word Formation, Glass Mountains (TX) were examined at the National Museum of Natural History (Washington, DC). An additional Middle Permian sample (752 individuals) from the early Guadalupian Rat Buri Group at Khao Phrik (Thailand), likely deposited in shallower inner-shelf settings, was counted at the Royal Ontario Museum in Toronto (ON, Canada). Additional quantitative data for the Carboniferous–Cretaceous interval was culled from the Paleobiology Database (www.paleodb.org) by using 847 collections sampled from a single bed or group of beds and including >100 counted specimens (collection information is in ref. 36).

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