

Taxonomic composition and environmental distribution of post-extinction rhynchonelliform brachiopod faunas: Constraints on short-term survival and the role of anoxia in the end-Permian mass extinction

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ABSTRACT

Marine taxonomic losses during the end-Permian mass extinction were driven by physiological stresses from ocean warming, acidification, and anoxia that ultimately resulted from CO₂ release from Siberian Traps flood volcanism. Despite abundant proxy evidence for anoxia, its role is not well resolved because the timing and selectivity of the extinction are better explained by warming and ocean acidification. We studied the taxonomic composition and spatial and temporal distribution of brachiopod-rich post-extinction faunas, which contain short-lived Permian survivors that lived at a key time during and immediately after the peak of the extinction, to elucidate the controls on survival and the role of anoxia. Holdover brachiopods primarily belong to extinct families and orders, not to long-term survivors, and their probability of short-term survival was a function of pre-extinction metapopulation size. Although short-term survival appears to have been stochastic, likely because of intraspecific variation in tolerance within larger metapopulations, opportunistic and possibly dysaerobic-tolerant genera thrived locally. Rhynchonelliform brachiopod distribution was patchy, both environmentally and temporally. They were more abundant in shallow-water settings, consistent with an oxygenated habitable zone, and their local demise often corresponded with the local development of low-oxygen conditions. Thus, although warming and acidification may have been the primary triggers of taxonomic loss, the addition of spatially and temporally variable anoxic conditions exacerbated physiological stress and contributed to ultimate extinction of short-lived survivors. The combination of the three stresses—warming, acidification, and anoxia—which act synergistically to negatively affect respiratory physiology of marine invertebrates, may explain the severity of the end-Permian extinction and provides a sobering analogue for modern ocean acidification and anoxic dead zones.

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1. Introduction

The end-Permian mass extinction, which eliminated 80% of marine invertebrate genera, was the most severe example of a CO₂-driven extinction, providing a deep-time analogue for modern ocean warming, acidification, and hypoxia (Payne and Clapham, 2012). The extinction had a simple trigger—eruption of the Siberian Traps flood basalts—but the chain of events that followed was complex and included ocean warming (Joachimski et al., 2012), anoxia or euxinia (Wignall and Twitchett, 1996; Grice et al., 2005; Bond and Wignall, 2010; Brennecke et al., 2011), and probable ocean acidification (Fraiser and Bottjer, 2007a; Knoll et al., 2007; Payne et al., 2010; Clapham and Payne, 2011), all of which were potential kill mechanisms during the crisis. Although all three stresses were likely involved, particularly

because of the synergistic negative effects of warming, acidification, and hypoxia (Pörtner et al., 2005a), the precise role of each remains poorly understood. Because the kill mechanisms acted on the respiratory physiology of marine invertebrates, through effects on aerobic scope and extracellular acid–base balance, the end-Permian and similar extinctions (e.g., Guadalupian, end-Triassic, and Toarcian) are considered to be physiologically-driven crises (Payne and Clapham, 2012). Constraining the timing and effects of anoxia and acidification will help refine predictions about the consequences of physiologically-driven crises and also help explain how and why the Permian extinction triggered major ecological changes such as the rise of the molluscan-dominated Modern Fauna (Fraiser and Bottjer, 2005, 2007b).

Despite the severity and tempo of the end-Permian crisis, short-lived surviving taxa, including rhynchonelliform brachiopods, are found in post-extinction “mixed faunas” around the world (Fig. 1; Teichert et al., 1970; Sheng et al., 1984; He and Shen, 1991; Shen et al., 1995; Chen et al., 2005). Those assemblages, containing

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a mixture of short-lived Permian survivors and typical Early Triassic taxa, occupied an approximately 500 kyr interval after the initial pulse of extinction when taxonomic losses continued at an elevated rate (Shen et al., 2011). Because mixed faunas represent communities living during the extinction interval, their temporal and environmental distribution record a signal of fluctuating environmental stresses and their taxonomic composition may be able to constrain the relative susceptibility of groups to physiological stresses and elucidate factors that promoted survival.

We studied post-extinction faunas in Italy, south China, and the western United States and compiled a global database of rhynchonelliform brachiopod occurrences to examine the relationship between short-term brachiopod survivors and environmental stresses in the Permian–Triassic interval. Here, we document the temporal and bathymetric distribution of surviving brachiopods to test the “habitable zone” hypothesis for extinction survival (Beatty et al., 2008) and constrain the role of anoxia in the end-Permian mass extinction. We also statistically test short-term selectivity patterns to determine the traits that enabled Permian brachiopod genera to survive past the onset of extinction, and to test if mixed faunas acted as a bridge between Permian and Triassic brachiopod lineages. Understanding the controls on mixed fauna composition and distribution will not only help reconstruct environment deterioration in the Permian–Triassic interval but will also provide insights into the susceptibility of marine invertebrates to combined physiological stresses in times of warming, acidification, and anoxia.

2. Methods

We used a combination of quantitative paleoecology of bulk fossil samples collected from measured sections, facies analysis to determine paleoenvironmental distribution, and analysis of global occurrence data from the Paleobiology Database (www.paleodb.org). The relative abundance of surviving rhynchonelliform brachiopods was also quantified from bulk samples from the Tesero and Bulla sections in Italy (one sample from each section) and in thin sections from the Blacktail Creek section in Montana (14 samples in a 50 m-thick measured section). Counts from Tesero and Bulla involved disaggregating the rock and counting and identifying all fossils larger than 1 mm in size to genus level. Because of fragmentation of fossils in samples from Blacktail Creek, we made thin sections and assigned all fragments larger than 1 mm to a higher-level taxonomic group (e.g., Bivalvia, Gastropoda, Lingulida, Rhynchonelliformea, Echinodermata). We counted all fragments in the field of view and repeated the process in different areas of the thin section until reaching a total of 100 fragments (some had

fewer than 100 counts because of sparse fossil density). Finally, we assessed the depositional environment of each sample through field observations of lithological characteristics and sedimentary structures, and through microfacies analysis of thin sections (for Blacktail Creek samples). In south China, we collected samples from the Liangfengya section in Chongqing, using the same methods as applied in Italy, to assess the stratigraphic range of surviving rhynchonelliform brachiopods.

We used data from the Paleobiology Database (www.paleodb.org) to measure changes in abundance and geographic range and to test the importance of organism- and population-level traits in short-term survivorship. The data included 3601 taxonomic occurrences, excluding questionably assigned genera (qualified by ? or *) from 895 Changhsingian and Griesbachian collections, downloaded on March 31, 2012 (supplementary data). We divided the occurrences into pre-extinction Changhsingian and post-extinction, which includes the latest Changhsingian *Clarkina meishanensis* zone (or correlatives) and the Griesbachian, and coded each genus as a short-term survivor (if it occurred in post-extinction holdover faunas) and/or a long-term survivor (if it belonged to a family that survived past the Griesbachian—no genus survived past that time). Metapopulation size, a measure of the global abundance of a genus, was estimated from the number of occurrences per genus and geographic range was calculated as the maximum great-circle distance spanned by the occurrences of a genus. Finally, we approximated the thermal limits of each genus by calculating the mean paleolatitude of its occurrences, a proxy for preferred temperature (e.g., Clapham, 2010), and the equator-to-pole latitudinal range (calculated by subtracting the paleolatitude of the furthest equatorial occurrence from the paleolatitude of the furthest poleward occurrence), a proxy for thermal tolerance. Latitudinal range is an imperfect measure, however, because the genus could instead contain multiple highly stenothermal species, but on average it may roughly approximate the physiological tolerance of a genus (Pörtner et al., 2005b). Because these traits are mutually correlated, particularly the range and abundance traits, we used multiple logistic regression (e.g., Clapham and Payne, 2011) to determine the effect of each trait on survivorship while accounting for the effects of the other confounding traits.

3. Results

3.1. Taxonomic composition

Brachiopods in post-extinction faunas, with the exception of the disaster taxon “*Lingula*” (Rodland and Bottjer, 2001), primarily belonged to Permian orders and families that did not play a role in the later



Fig. 1. Paleogeographic map showing location of post-extinction fauna localities discussed in the text. Areas marked by black circles include data from the literature and our own field data; gray circles are based only on data from the literature.

Triassic recovery. The spiriferid *Orbicoelia*, common in south China (Chen et al., 2006), Italy (Posenato, 2009), Oman (Twitchett et al., 2004), Pakistan (Grant, 1970), and the western United States (Girty, in Mansfield, 1927; Newell and Kummel, 1942), was the most widespread genus and, along with *Paracrurithyris* from post-extinction faunas in south China (Chen et al., 2005), was the last member of its order. Faunas in south China were dominated by the last members of the order Productida, such as *Tethyochonetes*, *Paryphella*, and *Spinomarginifera* (Chen et al., 2005, 2006), whereas the last orthotetids, including *Ombonia*, *Orthothetina*, and *Teserina*, were common in Italy and Hungary, in western Tethys (Posenato, 2009, 2011). Although productids were dominant in south China, they were also found elsewhere; *Spinomarginifera* occurred in Italy (Chen et al., 2006) and Pakistan (Grant, 1970), and *Tethyochonetes*, characteristic of the Lopingian in south China, occurred in the “*Waagenites*” bed fauna in Tibet (Shen et al., 2006).

Brachiopod orders that went extinct (Orthida, Orthotetida, Productida, and Spiriferida) comprised nearly 85% of taxonomic occurrences in the post-extinction faunas. *Paryphella*, *Tethyochonetes*, *Spinomarginifera*, and *Orbicoelia*, all members of extinct orders, alone accounted for more than 40% of all brachiopod occurrences. In contrast, more typically Mesozoic orders were only sparse contributors in post-extinction faunas. Spiriferinids were absent from the post-extinction collections recorded in the Paleobiology Database and terebratulids were extremely rare (e.g., Grant, 1970; Chen et al., 2009). Athyrids such as *Araxathyris* and rhynchonellids were somewhat more common; in particular, the genus *Prelissorhynchia* occurred in south China and Oman (Twitchett et al., 2004; Chen et al., 2005).

The Paleozoic aspect of the post-extinction assemblages and extreme rarity of taxa representing long-term survivors suggest that holdover faunas did not serve as a bridge linking Permian to Triassic brachiopod clades. We used multiple logistic regression to test how other traits, such as abundance, geographic range, preferred temperature (using preferred latitude as a proxy), and temperature tolerance (using latitudinal range as a proxy), controlled short-term survivorship. Global abundance, or metapopulation size, was the only trait of the four to significantly affect survivorship; Changhsingian genera with more occurrences were significantly more likely to occur in post-extinction faunas than were rare Changhsingian genera. Geographic range, mean paleolatitude, or paleolatitudinal range did not predict short-term survival.

3.2. Environmental distribution

3.2.1. Western United States

The basal part of the Dinwoody Formation at Blacktail Creek contains the holdover brachiopod *Orbicoelia* in a 50 m-thick shallowing-upward succession, from outer ramp mudstone and siltstone to skeletal packstone and grainstone representing inner ramp shoal deposits (Fig. 2). Fossils are sparse in the outer ramp setting but the typical Early Triassic bivalve *Claraia* is present at some horizons. In contrast, shell fragments are the dominant constituent in the inner ramp shoal deposits, where they are represented primarily by echinoderms and rhynchonelliform brachiopods. Fragmentation is extreme, but all identifiable brachiopod fragments belong to the genus *Orbicoelia*, a Permian survivor that was a common member of post-extinction faunas worldwide, and identifiable echinoderm fragments are from echinoids.

Because fragmentation precludes counting of specimens from bulk samples or in outcrop, we assessed the relative abundance of higher-level taxonomic groups through thin section censuses. The lowest sample, from a limestone nodule about 20 m above the base-Dinwoody unconformity, is strongly dominated by bivalve fragments (Fig. 2). The broad and thin shell morphology suggests that the bivalves are most likely *Claraia*, as observed in outcrop. Bivalve fragments are also common in the lowest limestone bed at 36.5 m in

the section, along with small gastropods and lingulid brachiopods. Substantial micritization of skeletal fragments implies deposition in shallow water within the photic zone. Lingulid and bivalve fragments also dominate sample 3, a packstone bed located at 44 m in the section. Samples 4–11, however, are composed nearly entirely of rhynchonelliform brachiopod and echinoderm fragments; lingulids are present but rare in most samples and bivalves and gastropods appear sporadically. All observed brachiopod shells are impunctate and appear smooth, consistent with the identification of *Orbicoelia* in outcrop. Pseudopunctate productids, found in post-extinction faunas in Tethys, and punctate spiriferinids or terebratulids were not observed. Echinoid spines were the most recognizable echinoderm fragment in thin section; however, some abraded plate fragments could also represent crinoids or ophiuroids. The coarse-grained and mud-poor nature of the sediments (grainstone and packstone), combined with the fragmentation of skeletal material and increasing amount of fine quartz sand, support deposition in very shallow-water shoals in the inner ramp.

3.2.2. Italy

Post-extinction faunas in the Italian Dolomites (western Tethys) also contain *Orbicoelia* and other Permian holdover brachiopods in post-extinction strata (Neri and Pasini, 1985; Chen et al., 2006; Posenato, 2009, 2011). Rhynchonelliform brachiopods were most common at the Tesero section and *Orbicoelia* dominated our sample T7 (70% of specimens). Other workers have found similar dominance by rhynchonelliform brachiopods at Tesero. *Orbicoelia* was also dominant in sample CNT10 (86% of specimens) reported by Posenato (2009), while the orthotetid brachiopod *Teserina* (Posenato, 2011) comprised more than 90% of specimens in Posenato's sample CNT11A. Echinoid plates and spines are common in our sample but bivalves and gastropods are rare, both in our samples and in the samples reported by Posenato (2009). Lateral bed transitions from the fossiliferous marlstone or wackestone units to ooid packstone and grainstone imply that these communities inhabited muddy or muddy carbonate substrates between ooid shoals in a high-energy, restricted inner ramp setting.

The fauna at the Bulla section is preserved immediately above the Tesero oolite in a thin, marly siliciclastic unit with carbonate nodules (Fig. 3). Posenato (2009) identified *Eumorphotis*, one of the most common Early Triassic bivalve genera, as the dominant genus, comprising nearly 90% of the specimens in sample BU9-10. *Warthia* (formerly “*Bellerophon*”), a short-lived Permian survivor, was also present (8.5% of specimens), whereas Permian brachiopods *Orbicoelia* and *Ombonia* were exceedingly rare. Our sample B10, collected from the same horizon, was also strongly dominated by *Eumorphotis* (95%) and contained rare gastropods and Permian brachiopods. Bulla records a more distal setting than the Tesero section but was still located in a shallow-marine, inner-ramp environment.

The Sass di Putia post-extinction fauna is also preserved in a thin marly unit above the Tesero oolite, and the bulk sample collected by Posenato (2009) is nearly entirely composed of *Eumorphotis* (98.4% of specimens) (we do not have samples from Sass di Putia). No echinoids or rhynchonelliform brachiopods were reported by Posenato (2009). Sass di Putia records deposition in an open-marine, most likely mid-ramp, environment (Posenato, 2009).

3.2.3. South China

South China contains post-extinction faunas at dozens of P/T boundary sections (Sheng et al., 1984; Chen et al., 2005), including nearly 20 genera of rhynchonelliform brachiopods co-occurring with characteristic Triassic bivalves such as *Claraia* and *Eumorphotis* (He and Shen, 1991; Shen et al., 1995; Chen et al., 2005, 2009). *Orbicoelia*, the dominant brachiopod in many faunas elsewhere, is also widespread in South China, but holdover faunas are more strongly dominated by productids such *Tethyochonetes* and *Paryphella* (Chen et

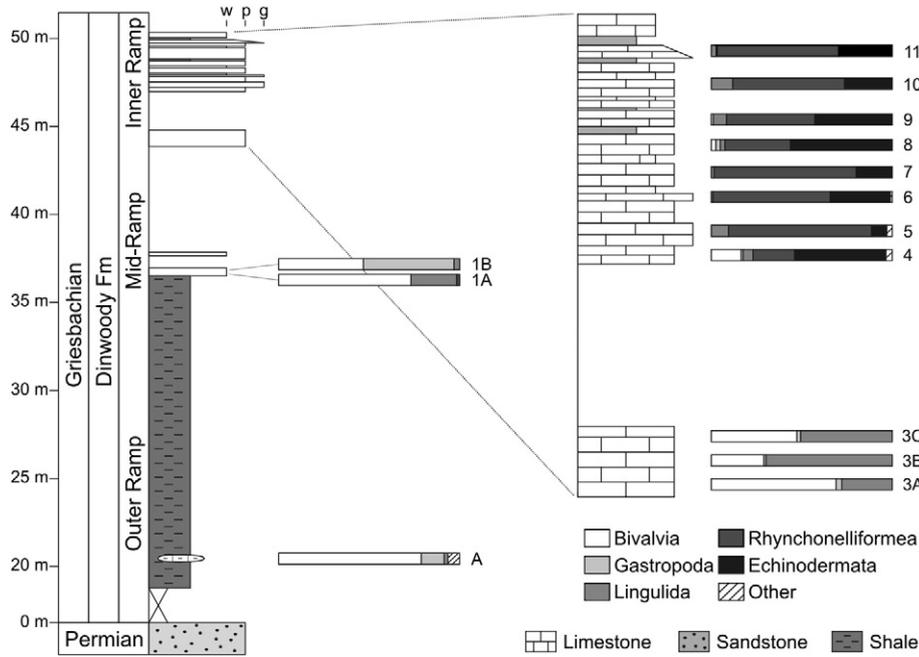


Fig. 2. Stratigraphic section and faunal composition of the basal Dinwoody Formation at Blacktail Creek, Montana. The formational contact is unconformable at this section, but the age of the basal Dinwoody Formation is uncertain. Note change of scale in the basal 20 m (covered at this section). The detailed section on the right is an expanded view of the upper 7 m of the measured section. Filled rectangles show the proportional abundance of five major faunal groups in thin section censuses. Other includes cephalopods, ostracods, and microconchids.

al., 2005, 2010). Rhynchonelliform brachiopods are numerically dominant in all environments in the lower Yangtze River region, from mid-ramp to basin, although they are less dominant at the shallowest section (Huangzhishan), deposited above storm wave base (Chen et al., 2010). These faunas typically had low diversity, with diversity increasing in the shallower, mid-ramp environment (Chen et al., 2010). Other comparatively diverse assemblages (for the Early Triassic) also occurred in very

shallow water environments above wave base and contained short-lived Permian survivors such as the bivalve *Astartella* (Hautmann et al., 2011), but lack Permian holdover brachiopods.

3.2.4. Other regions

Post-extinction faunas are widespread along the Gondwanan margin of Tethys, in Oman, the Salt Range of Pakistan, and in Kashmir. In

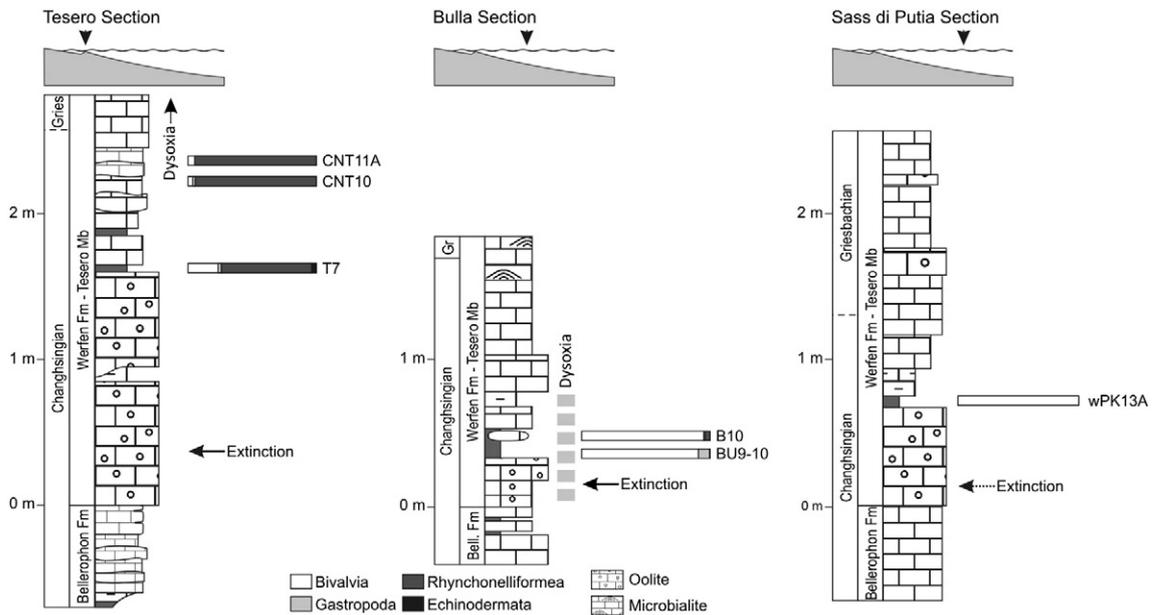


Fig. 3. Stratigraphic section and faunal composition of the Permian–Triassic boundary interval at sections in Italy. Schematic profiles at the top show the relative bathymetric position of each section (more details are discussed in the text). The extinction level is marked in each section, based on quantitative assessment at Tesero and Bulla (Groves et al., 2007) and by correlation at Sass di Putia. The position of the Permian–Triassic boundary is approximate at Tesero and Sass di Putia. Filled rectangles show the proportional abundance of four major faunal groups from our bulk sample counts (T7 and B10) and from Posenato (2009; CNT10, CNT11A, BU9–10, and wPK13A). The exact stratigraphic level of samples CNT10 and CNT11A in our section is approximate because of rapid lateral facies variations at Tesero.

Oman, a fauna containing the Permian brachiopods *Orbicoelia* and *Prelissorhynchia* occurs in shallow-marine limestones deposited on an isolated seamount (Krystyn et al., 2003; Twitchett et al., 2004). In contrast to the bathymetric pattern in the western United States and Italy, brachiopods were more abundant in the upper part of a deepening-upwards succession in Oman, although the entire unit was deposited in shallow conditions (Krystyn et al., 2003; Twitchett et al., 2004). The Kathwai Member is the lowest post-extinction strata in the Salt Range (Pakistan) and contains a fairly diverse fauna of rhynchonelliform brachiopods, including *Orbicoelia* and *Spinomarginifera* (Grant, 1970). The dolomitic lithology, planar cross-bedding, and presence of desiccation cracks suggest that the basal part of the unit was deposited in a peritidal setting (Kummel and Teichert, 1970). In contrast, the Kashmir fauna, which contains productid brachiopods like *Spinomarginifera* in association with the characteristic Early Triassic bivalve *Claraia* (Teichert et al., 1970), is found in shell beds in a dominantly fine-grained siliciclastic succession. Some of the shell beds are graded and fragmented, suggesting deposition in a mid-ramp setting below typical fair-weather wave base but where intermittent storms could rework the sediment (Brookfield et al., 2003).

3.3. Temporal distribution

The end-Permian extinction began approximately 100 kyr before the biostratigraphic P/T boundary and had a duration of about 200 kyr, extending into the basal Triassic Griesbachian substage, although taxonomic losses persisted even later into the Griesbachian (Shen et al., 2011). Holdover faunas occupied the interval following the peak of extinction and range in age from latest Changhsingian to Griesbachian (Sheng et al., 1984; Chen et al., 2005). Despite the global synchronicity of the extinction peak (Payne and Clapham, 2012), the temporal distribution of brachiopod-rich faunas varied markedly in different regions (Fig. 4).

In the Meishan and Huangzhishan sections of south China, post-extinction Permian brachiopods range from the latest Changhsingian *Clarkina meishanensis* zone to the mid-Griesbachian *Isarcicella isarcica* zone (Chen et al., 2006, 2009). Most surviving taxa, such as the dominant *Tethyochonetes* and *Paryphella*, were restricted to the latest Changhsingian or to the Griesbachian *Hindeodus parvus* zone;

only the spiriferids *Orbicoelia* and *Paracrurithyris*, the rhynchonellid *Prelissorhynchia*, and the orthid *Acosarina* survived to the *isarcica* zone (Chen et al., 2006). The Liangfengya and Beifengjing sections in southwestern China also contain a similar post-extinction fauna dominated by *Tethyochonetes* and *Paryphella* in strata of the *meishanensis* and *parvus* zones (beds 31–34; Shen and He, 1991; Yuan and Shen, 2011), but rhynchonelliform brachiopods were not found in strata higher in the section in our sampling. If taxa such as *Paracrurithyris* survived to the *isarcica* zone at these sections, they must have been rare.

No Griesbachian rhynchonelliform brachiopods are known from post-extinction faunas in western Tethys, despite their local abundance in post-extinction Changhsingian strata. The nearly-ubiquitous hold-over brachiopod *Orbicoelia* and several genera of orthotetids occurred at the Balvány North section in Hungary (Posenato et al., 2005) and in the Italian Dolomites (Posenato, 2009), but have not been found above the first occurrence of *Hindeodus parvus* in those sections.

The more diverse assemblages of surviving brachiopods were also confined to post-extinction Changhsingian strata, correlated to the *meishanensis* zone, in peri-Gondwanan sites (Shen et al., 2006). In the Salt Range of Pakistan, all rhynchonelliform brachiopods except *Orbicoelia* occurred only in the basal 10–20 cm of the Kathwai member (Grant, 1970). *Orbicoelia* ranged nearly 2 m higher, however, to the top of the Kathwai dolomite (Grant, 1970), which is correlated with the *carinata* zone (Wignall et al., 1996). Like in Pakistan, most surviving brachiopods occurred in the post-extinction Changhsingian E1 member of the Khunamuh Formation and only two genera persisted to the *parvus* zone (Shen et al., 2006). A similar pattern is observed in nearby sections in Tibet (Wignall and Newton, 2003; Shen et al., 2006). Although the fauna of the “*Waagenites*” bed at the Selong Xishan section was initially interpreted as reflecting a later, diachronous end-Permian extinction (Wignall and Newton, 2003), it is actually a holdover fauna containing the typical brachiopod *Tethyochonetes* in post-extinction strata within the latest Changhsingian *Mesogondolella sheni* conodont zone (Shen et al., 2006). Brachiopods have not been recorded from the *parvus*-zone *Otoceras* bed but other Permian holdovers, such as the foraminifera *Colaniella*, may persist to that level (Wignall and Newton, 2003). In contrast, surviving brachiopods were absent in the earliest

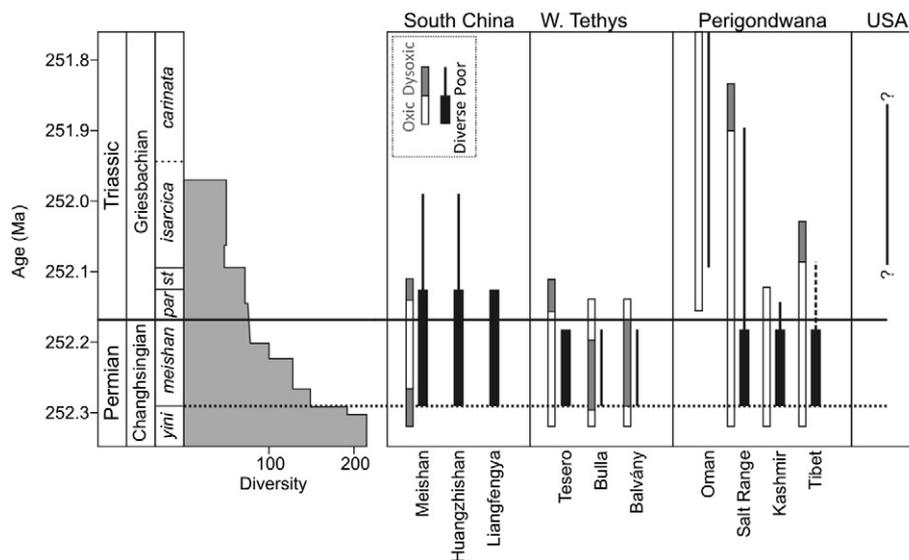


Fig. 4. Compilation of the temporal distribution of rhynchonelliform brachiopods in faunas from south China, western Tethys, Perigondwana, and the western USA based on our field data (black bars) and literature data (gray bars, see text). Thick bars indicate comparatively diverse brachiopod assemblages and thin lines are faunas containing only *Orbicoelia* or *Paracrurithyris*. The age of conodont zones is taken from Shen et al. (2011) but is approximate for the *carinata* zone and top of the Griesbachian. Conodont zones: *yini* = *Clarkina yini*; *meishanensis* = *C. meishanensis*; *par.* = *Hindeodus parvus*; *st.* = *Isarcicella staeschei*; *isarcica* = *I. isarcica*; *carinata* = *Clarkina carinata*.

Griesbachian in Oman but *Orbicoelia* and *Prelistorhynchia* were extremely abundant in the later Griesbachian *isarcica* and *carinata* zones (Krystyn et al., 2003; Twitchett et al., 2004).

In the western United States, the surviving brachiopod *Orbicoelia* ranged well above the base of the Dinwoody Formation. At Blacktail Creek, its highest occurrence is 50 m above the base in our samples, while Newell and Kummel (1942) reported “*Mentzelia*” (= *Orbicoelia*) from 100 to 120 m above the base of the formation at a section at MacDouglas Pass, Wyoming. The age of these faunas is more difficult to determine in the absence of conodont biostratigraphy from each section, but the *parvus* zone typically occurs in the basal few meters of the Dinwoody Formation in Idaho, Wyoming, and southern Montana (Paull and Paull, 1994). Although Dinwoody Formation sections are typically much more expanded than sections in Tethyan localities, occurrences 50–100 m above the base of the formation suggests that the *Orbicoelia* faunas could date to the *isarcica* or *carinata* zone, or even younger.

4. Discussion

4.1. Biotic controls on faunal composition

The occurrence of brachiopod-rich faunas within the extinction interval raises the possibility that these short-lived survivors persisted beyond the onset of the crisis because they were less vulnerable to the physiological stresses from increased temperature, ocean acidification, and hypoxia. If true, the composition of post-extinction faunas may provide information about the nature or selectivity of extinction stresses.

There does not appear to be a relationship between short- and long-term survivorship during the Permian extinction, however. First, genera found in holdover faunas belong primarily to Permian orders that did not persist beyond the Griesbachian. Second, genera were not significantly more likely to belong to families that survived to the Middle Triassic than to families that went extinct (Fisher's exact test, $p = 0.32$). Finally, only metapopulation size (number of global occurrences) during the pre-extinction Changhsingian was a significant control on short-term survival (Table 1). These results imply that holdover brachiopods simply represent a subset of the Changhsingian fauna where temporary survival was governed primarily by metapopulation size, rather than by organism-level traits. Larger metapopulations are more likely to contain genetic variability or subgroups with different tolerances (Somero, 2010). Thus, short-term survival was primarily stochastic, driven by greater chance for adaptation in large metapopulations, and the composition of the faunas does not have implications for extinction selectivity.

The importance of metapopulation size does not imply that organism-level traits were unimportant in controlling the composition of mixed faunas. Most genera were more widespread in the pre-extinction Changhsingian than in the post-extinction faunas (Fig. 5A). It is unlikely that this signal is an artifact because the geographic extent of sampling is nearly unchanged across the boundary (27 of 120 equal-area bins contain marine invertebrate data in the Changhsingian versus 25 in the Griesbachian). Instead, the decreases in geographic range likely reflect actual restrictions in distribution during the extinction

interval. Three genera, *Orbicoelia*, *Tethyochonetes*, and *Prelistorhynchia*, substantially expanded their ranges in the holdover faunas (Fig. 5A), while *Orbicoelia* and *Tethyochonetes* (along with *Paryphella*) also increased in relative commonness (calculated as the proportion of occurrences) in the post-extinction interval (Fig. 5B). In contrast to the preferential survival of common genera, there was actually a significant negative rank-order correlation between range increases and Changhsingian commonness (Spearman $\rho = -0.4$, $p = 0.035$) and between commonness increases and Changhsingian range (Spearman $\rho = -0.71$, $p < 0.001$).

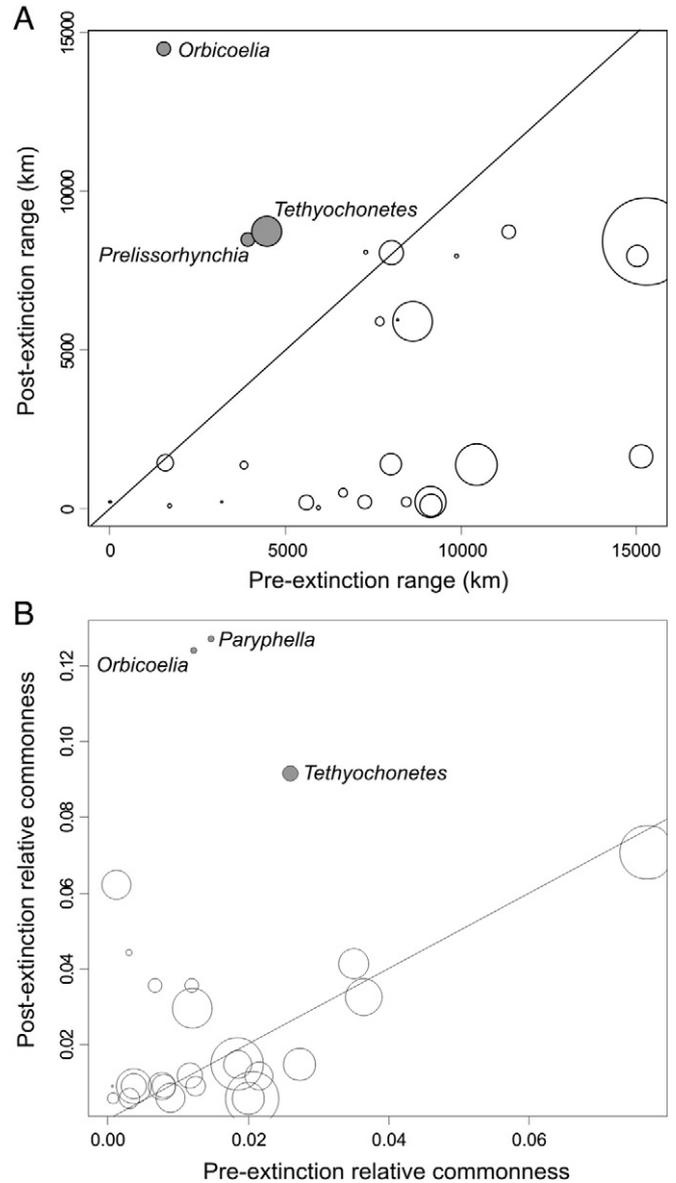


Fig. 5. Changes in rhynchonelliform brachiopod range and abundance across the end-Permian mass extinction. A. Pre-extinction and post-extinction geographic ranges (maximum great-circle distance) of surviving brachiopod genera. The size of circles corresponds to the global abundance (number of occurrences) of the genus in pre-extinction Changhsingian strata, indicating a significant negative rank-order correlation between size of range change and pre-extinction abundance (Spearman $\rho = -0.4$, $p = 0.035$). B. Pre-extinction and post-extinction relative abundance (proportion of all rhynchonelliform brachiopod occurrences) of surviving brachiopod genera. The size of circles corresponds to pre-extinction geographic range, indicating a significant negative rank-order correlation between abundance increases and pre-extinction range (Spearman $\rho = -0.71$, $p < 0.001$). Labeled points highlight genera with large range increases and large increases in relative abundance.

Table 1

Effects of geographic range (maximum linear distance in km), latitudinal range (in degrees), mean latitude, and abundance (number of occurrences) on survivorship from the Changhsingian to Griesbachian.

	Log-odds ratio	Standard error	P value
Geographic range	0.0001	0.00008	0.236
Latitudinal range	0.011	0.017	0.524
Mean latitude	-0.02	0.011	0.072
Abundance	0.058	0.013	<0.0001

Those trends suggest that *Orbicoelia*, *Tethyochonetes*, and to a lesser extent *Paryphella* and *Prelissorhynchia*, had particular traits that enabled them to thrive, at least compared to other rhynchonelliform brachiopods, in the post-extinction faunas. *Tethyochonetes* belongs to the Rugosochonetidae, a family that includes many other opportunistic taxa (e.g., Alexander, 1977; Simanaukas and Cisterna, 2000; Campi and Shi, 2002, 2005). Ambocoeliid spiriferids, such as *Orbicoelia*, were also eurytopic taxa that were common constituents of dysaerobic communities in the late Paleozoic (Kammer et al., 1986). Thus, although overall short-term survivorship was largely governed by metapopulation size, certain opportunistic taxa, characterized by small body size and likely by tolerance of dysaerobic conditions, proliferated during the stressful extinction interval before ultimately being driven to extinction (Campi and Shi, 2005; Chen et al., 2005; Posenato, 2009, 2011).

Post-extinction faunas in paleoequatorial localities (Italy, south China) contain genera also found in pre-extinction faunas in those regions, but the same is not true in higher-latitude sites such as the Salt Range or Tibet. There, holdover brachiopods instead belong to genera common in pre-extinction paleoequatorial regions (especially south China) such as *Orbicoelia*, *Spinomarginifera* and *Tethyochonetes*. Paleolatitude was not a significant predictor of short-term survival, so it is plausible that south China may have been a major source of holdover genera because it had a large carbonate platform area that would have hosted large brachiopod metapopulations. Migration of genera to higher-latitude regions, for example from south China to the Salt Range, is also consistent with the effects of climate warming during the extinction interval (e.g., Shen et al., 2006).

4.2. Environmental controls on -faunal distribution

The environmental and temporal distribution of rhynchonelliform brachiopods in post-extinction faunas also has implications for the nature of stresses during the extinction. Brachiopods were present from peritidal to basinal environments (Chen et al., 2005) but, on average, were more abundant in settings above wave base. *Orbicoelia* was dominant in shoreface shoals in the Dinwoody Formation and in the Tesero oolite along with *Teserina*. Similarly, the comparatively diverse Salt Range holdover fauna occurred in cross-stratified peritidal dolomites, although other brachiopods lived in sub-wave base environments, in Kashmir and the Huangzhishan and Meishan sections in China for example. The prevalence of surviving brachiopods, particularly dysaerobic-tolerant opportunists, in shallow-marine sections, although not an absolute restriction, is consistent with the “habitable zone” hypothesis (Beatty et al., 2008) that local expansion of the oxygen-minimum zone may have more frequently disrupted communities in offshore environments.

The temporal distribution of brachiopod-rich faunas was variable, persisting to the late Griesbachian in some regions but not beyond the post-extinction Changhsingian in others. Most brachiopods were restricted to the post-extinction Changhsingian (*meishanensis-praeaparus* zone or correlatives) and fewer than five genera, most notably the spiriferids *Orbicoelia* and *Paracrurithyris*, survived past the early Griesbachian. Although the apparently diachronous disappearance of holdover faunas may have been exacerbated by Signor-Lipps effects, particularly because the last surviving brachiopods would have been rare, local disappearances coincided with diachronous geochemical evidence for environmental disruption. In particular, brachiopod-dominated faunas occurred in settings interpreted as oxygenated and often disappeared with the onset of low-oxygen conditions in local sections, whereas bivalve-dominated faunas were more common where there is evidence for dysoxia.

Although there is no available proxy evidence for oxygen levels at the Blacktail Creek section, pyrite framboid sizes from correlative beds at the Paris Canyon section indicate dysoxic conditions in more distal settings (Bond and Wignall, 2010). The laminated and largely unfossiliferous nature of basal outer ramp siltstones at Blacktail

Creek, containing only infrequent beds dominated by *Claraia*, is consistent with intermittent oxygen restriction like that inferred at Paris Canyon. In contrast, inner ramp environments where *Orbicoelia* was dominant were likely oxic because wind mixing would have maintained oxygenation of shallow waters in contact with the atmosphere (Beatty et al., 2008). It is not possible to link the local disappearance of *Orbicoelia* to environmental disturbance because of facies changes at the Blacktail Creek section. *Orbicoelia* dominates the first limestone unit but was not found in the stratigraphically higher limestone; however, its disappearance occurred during the intensifying distal and unfossiliferous shale succession and cannot be constrained precisely.

Rhynchonelliform brachiopods had a similar distribution and range in Italian sections. Most evidence for oxygenation in Italy comes from the Bulla section, where pyrite framboid size and S/C ratios suggest dysoxic conditions in the lower part of the Tesero Oolite horizon (Gorjan et al., 2007). Bond and Wignall (2010) also used pyrite framboids to infer lower dysoxic conditions in samples through the entire Tesero Oolite at Bulla. Brachiopods were rare at the dysoxic Bulla locality, which was instead dominated by bivalves (especially *Eumorphotis*). Rhynchonelliform brachiopods such as *Orbicoelia* and *Teserina* were, however, highly abundant at the shallower Tesero locality, which was likely well-oxygenated for much of its deposition. A pyrite-rich unit above the highest brachiopod-rich sample at Tesero has been interpreted as a euxinic marine deposit by Wignall and Hallam (1992), although not based on framboid sizes or geochemical proxies, suggesting that final disappearance of brachiopods may have coincided locally with onset of low-oxygen conditions.

Other regions in Tethys exhibit a similar relationship between brachiopod abundance and evidence for low-oxygen conditions. The final disappearance of most brachiopods, except for *Orbicoelia* and *Paracrurithyris*, occurred near the end of the *parvus* zone at Meishan and Huangzhishan in south China, before a second episode of environmental disruption (Xie et al., 2005, 2007) and a second pulse of photic-zone euxinia (Grice et al., 2005). In the Selong section of Tibet, the first evidence for oxygen-deficient conditions is in the mid-Griesbachian, but also coincides with the local demise of the holdover foraminifera, although the brachiopods disappeared earlier (Wignall and Newton, 2003). The last brachiopods disappeared during the late Griesbachian *carinata* zone in Oman and the Salt Range, also related to a later onset of low-oxygen conditions in those regions (Wignall et al., 1996; Krystyn et al., 2003; Twitchett et al., 2004). Prior to that, rhynchonelliform brachiopods were highly abundant in well-oxygenated shallow-marine deposits (Twitchett et al., 2004).

Thus, the spatio-temporal distributions of post-extinction faunas and low-oxygen conditions were both diachronous, but the coincidence between holdover disappearance and development of dysoxia in many regions strongly implicates low oxygen levels as a major contributor in the demise of short-lived Permian brachiopod survivors. This complex distribution of post-extinction faunas is consistent with a spatially variable and intermittent, rather than global and persistent, distribution of anoxia during the Permian–Triassic interval (Wignall et al., 1996; Bond and Wignall, 2010). Furthermore, global shallow-marine anoxia, although not explicitly invoked in extinction models, is unlikely because oxygen-deficient conditions could only be sustained where excess nutrient supply, likely from enhanced continental weathering (Algeo et al., 2011), counteracted wind-driven mixing to expand the oxygen minimum zone into the photic zone (Meyer et al., 2008). Warming-driven ocean stratification and deoxygenation would also have expanded the area with reduced oxygen concentrations (Keeling et al., 2010; Song et al., in press). The observed diachronous onset and duration of anoxia, and the resulting complex spatio-temporal distribution of holdover brachiopods, is expected given that the size of the pre-existing nutrient inventories and oxygen minimum zone would be spatially variable, as would the intensity of weathering and nutrient influx.

4.3. The role of anoxia in the Permian mass extinction

Anoxia and euxinia have long been linked with the end-Permian extinction (e.g., Wignall and Twitchett, 1996) but evidence for euxinic conditions before the extinction at Meishan (Cao et al., 2009) and the lack of evidence for anoxia during the extinction level at other sections (e.g., Wignall and Hallam, 1993; Wignall et al., 1996; Wignall and Newton, 2003) imply that it could not have been the primary or only kill mechanism (Payne and Clapham, 2012). The synchronous onset of extinction and the taxonomic selectivity are also inconsistent with anoxia as the primary stress (Payne and Clapham, 2012); instead temperature warming and ocean acidification associated with Siberian Traps volcanism were likely more important triggers (Fraiser and Bottjer, 2007a; Knoll et al., 2007; Clapham and Payne, 2011; Hinojosa et al., 2012; Joachimski et al., 2012).

If increased temperature and ocean acidification were the direct triggers, what then was the role of anoxia in the extinction, given the broad correspondence between brachiopod disappearance and onset of low-oxygen conditions at many sections? The answer lies in the physiological mechanisms through which climate warming, ocean acidification, and anoxia stressed marine invertebrates. The end-Permian extinction was a physiological crisis (Knoll et al., 2007; Payne and Clapham, 2012) in that selectivity was largely governed by the metabolism and respiratory physiology of the affected taxa based on the principle of oxygen and capacity-limited thermal tolerance (Pörtner, 2010). In marine ectotherms, metabolic oxygen demand increases with increasing temperature, imposing thermal limits on performance and survival when it outstrips the rate at which oxygen can be supplied (Pörtner, 2010). Increased temperatures negatively influence performance even before lethal limits are reached because the increasing mismatch between oxygen demand and supply limits the amount of energy that can be devoted to other biological activities (Pörtner, 2001; Pörtner et al., 2005a). Furthermore, in addition to negatively influencing shell calcification (Ries et al., 2009; Kroeker et al., 2010), increased PCO₂ has metabolic consequences by reducing the efficiency of oxygen transport in many marine invertebrates, further exacerbating the mismatch between oxygen demand and supply (Pörtner et al., 2004, 2005a). In organisms already stressed by elevated oxygen demand driven by increased temperature and diminished supply driven by increased PCO₂, a reduction in dissolved oxygen availability, to a point, would have acted synergistically to intensify the physiological stress (Pörtner et al., 2005a). Species with a larger aerobic scope (excess oxygen supply available for growth and reproduction) are less vulnerable to those synergistic stresses (Pörtner, 2010), consistent with the selective survival and Early Triassic dominance of genera with higher metabolic rates (Clapham and Payne, 2011). The intensity and/or duration of dysoxic conditions was also likely greater during the extinction interval than before, but even if it was unchanged the additional reduction in oxygen availability could have pushed the already stressed surviving brachiopods, with their low metabolic rates and small aerobic scopes, to extinction. Extremely low oxygen concentrations, below levels to which most organisms are able to regulate metabolic oxygen consumption (Childress and Seibel, 1998), would have favored dominance by different organisms with specialized low-oxygen adaptations, and are a plausible cause of monotaxic *Claraia* assemblages.

5. Conclusions

The success of opportunistic and potentially dysaerobic-tolerant rhynchonelliform brachiopods and their dominance in shallow, wave-influenced environments, along with the close coincidence of brachiopod demise and the onset of anoxia, all imply an important role for anoxia in the development and extinction of holdover faunas. The physiological effects of increased temperatures and elevated PCO₂

were the primary triggers of the Permian extinction, but the composition and distribution of brachiopod-rich faunas elucidate the synergistic role played by spatially and temporally variable anoxia, which exacerbated the mismatch between elevated metabolic oxygen demand and reduced supply. Local and intermittent expansion of low-oxygen waters onto the shallow continental shelf during the latest Changhsingian and Griesbachian, perhaps as long as 500 ka after the onset of extinction, was responsible for continuing stress and ultimately contributed to the extinction of short-lived survivors that populated post-extinction faunas. The short-lived survival and ultimate demise of Permian–Triassic holdover faunas highlight the additive effects of anoxia-related stress on top of pre-existing thermal and acidification stresses, providing analogues for the possible outcome from expansion of low-oxygen “dead zones” in today’s warming and increasingly acidic oceans.

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Appendix A. Supplementary data

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