Expansion of photic-zone euxinia during the Permian–Triassic biotic crisis and its causes: Microbial biomarker records

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Abstract

The incursion of euxinic waters into the ocean-surface layer is hypothesized to have been an important killing agent during the end-Permian mass extinction. However, both the causes and extent of oceanic euxinia during this crisis remain poorly known, making assessment of its role in the mass extinction difficult. Here, we document the distribution of aryl isoprenoids

(AI), which are biomarkers of obligate anaerobic green sulfur bacteria (Chlorobiaceae) that are indicative of photic-zone euxinia, in 12 Permian-Triassic Boundary (PTB) sections with a wide distribution globally. Profiles of AI abundance for the 12 study sections show significant spatio-temporal variation. No AIs were identified in the shallowest sections, but AIs are present both prior to and following the mass extinction in intermediate-depth sections and following the mass extinction in deep-water sections. This pattern suggests a combination of upward and oceanward expansion of photic-zone euxinia during the PTB crisis, possibly fueled by elevated riverine nutrient fluxes as a consequence of climatic warming, terrestrial ecosystem destruction, and enhanced erosion. This hypothesis is supported by the close association of AIs with elevated abundances of moretanes and dibenzofuran (DBF), which are biomarkers for terrestrial erosion. Expansion of oceanic euxinia at intermediate water depths may have established a long-term reservoir that fed episodic incursions of H₂S-bearing waters into shallow-marine environments, delaying the recovery of marine ecosystems during the Early Triassic. The biomarker records of the present study thus provide significant evidence of terrestrial-marine linkage during the PTB crisis.

1. Introduction

The end-Permian mass extinction (EPME) was the most severe biotic crisis in the Phanerozoic, killing over 90% of marine invertebrate species ([Erwin et al., 2002](#)). The eruption of the Siberian Traps Large Igneous Province is widely regarded as the ultimate cause of this biocrisis ([Campbell et al., 1992](#); [Kamo et al., 2003](#); [Reichow et al., 2009](#);

Svensen et al., 2009; Korte et al., 2010), but the direct killing mechanism remains controversial, with hypotheses invoking marine anoxia (Wignall and Twitchett, 1996; Isozaki, 1997), hypercapnia (Knoll et al., 2007), global cooling (Joachimski et al., 2012; Romano et al., 2013), and ocean acidification (Hinojosa et al., 2012; Clarkson et al., 2015), among other possibilities. Although early claims of whole-ocean anoxia (e.g., Wignall and Twitchett, 1996; Isozaki, 1997) have been disproven (e.g., Algeo et al., 2011a), more recent studies have shown that the Permian-Triassic boundary (PTB) interval was widely associated with a shift toward more reducing marine environmental conditions (Grice et al., 2005a; Kump et al., 2005; Kaiho et al., 2006; Hays et al., 2007; Riccardi et al., 2007; Gorjan et al., 2007; Algeo et al., 2007, 2008; Meyer and Kump, 2008; Takahashi et al., 2014). However, spatial patterns of marine redox variation (i.e., related to proximity and water depths) have been addressed to only a limited degree in a few studies (e.g., Feng and Algeo, 2014).

Among the various types of geochemical proxies used in paleoredox studies, biomarkers are important for their ability to discern photic-zone euxinia (PZE), i.e., sulfidic conditions within the surface layer of the ocean (Grice et al., 2005a; Xie et al., 2005, 2007; Chen et al., 2015). Certain photosynthetic microbes are obligate anaerobes, requiring both sunlight and H₂S, e.g., green sulfur bacteria (GSB) and purple sulfur bacteria (PSB) (Whiteside and Grice, 2016). GSB produce isorenieratane and chlorobactane, as well as aryl isoprenoids (AI) as diagenetic breakdown products, and PSB produce okenane, all of which are characteristic indicators of PZE (Summons and Powell, 1986, 1987; Grice et al., 1996; Whiteside and Grice, 2016).

GSB biomarkers have been reported from a number of PTB sections (e.g., Grice et al.,

2005a; Xie et al., 2005, 2007; Hays et al., 2007, 2012; Algeo et al., 2012), which indicates that at least portions of the global ocean were euxinic during the end-Permian crisis. However, the spatio-temporal distribution of GSB biomarkers in PTB sections has not been investigated in detail, leaving the relationship between oceanic euxinia and the end-Permian mass extinction unclear. Here, we present biomolecular records from multiple locales representing a range of water depths in order to investigate the spatial and temporal distribution of PZE during the end-Permian crisis. Additionally, we examine the relationship of PZE to changes in terrestrial weathering fluxes and tropical sea-surface temperatures (SSTs) in order to gain insights regarding the factors controlling the development of PZE during this crisis. The present study includes new biomarker data for five PTB sections (Bulla in northern Italy, and Laolongdong, Cili, Shangsi, and Chaohu in South China) as well as published biomarker data for seven other PTB sections with a broad global distribution.

2. Study sections

We examined 12 PTB marine sections from all major Permian-Triassic oceans, including the Panthalassa, Paleo-Tethys, and Neo-Tethys oceans (Table 1; Fig. 1C). These sections can be catalogued into three types according to sedimentary water depths: (1) shallow platform sections above fair-weather wave base (i.e., water depths <50 m, and commonly <20 m; cf. Brett et al., 1993), including Bulla in northern Italy and Laolongdong and Cili in South China, (2) intermediate shelf/ramp sections located between fair-weather wave base and storm wave base (i.e., ~50-200 m water depth), including Huangzhishan (Kaiho et al., 2012) and Meishan

in South China (Grice et al., 2005a; Cao et al., 2009), the Perth Basin of Western Australia (Thomas et al., 2004; Grice et al., 2005a), Kap Stosch in Greenland (Hays et al., 2012), Spitsbergen (Nabbefeld et al., 2010b), and the Peace River Basin (Hays et al., 2007) and West Blind Fiord in Canada (Algeo et al., 2012), and (3) deep shelf/ramp sections (>200 m water depth), including Shangsi and Chaohu in South China (Fig. 1C). Background details for each section are given below.

2.1. Shallow platform sections

The Bulla section (Southern Alps, northern Italy) was located in the western Paleo-Tethys during the Permian-Triassic transition (Fig. 1). PTB strata belong to the uppermost Bellerophon Formation (Bulla Member) and lower Werfen Formation (Tesero Member). The former consists of gray and dark-gray fossiliferous limestone and dolostone interbedded with siltstone, sandstone and gypsum, whereas the latter comprises oolitic grainstone (Farabegoli et al., 2007). These facies accumulated on a shallow carbonate platform (ca. <10 m water depth) (cf. Hine, 1977). The EPME, which is marked by sharp declines in fossil abundance and biodiversity and the appearance of small ooids, is located at the base of the Tesero Member (Gorjan et al., 2007). The extinction horizon consists of mixed terrigenous-calcareous material and exhibits hummocky cross-bedding and wave ripples, pointing to high-energy storm sedimentation in an area proximal to sources of terrigenous clastics. The PTB is located 1.30 m above the base of the Tesero Member based on the first occurrence of the conodont *Hindeodus parvus* (Perri, 1991).

The Laolongdong section (Chongqing Province, China) was located on the paleo-western margin of the Yangtze Platform (South China Craton), facing the Paleo-Tethys Ocean (Liao et al., 2010; Fig. 1). The Upper Permian consists of skeletal limestone of the Changxing Formation that is sharply overlain by microbialite, with the contact between these two units corresponding to the EPME horizon (Ezaki et al., 2003; Kershaw et al., 2012). The occurrence of microbialite implies water depths of ~20-40 m, and the absence of terrigenous sediment indicates an open-marine setting far removed from land areas. The conodont *H. parvus* has been recovered from the uppermost part of the microbialite, which is overlain by Lower Triassic laminated mudstone of the Feixianguan Formation (Wignall and Hallam, 1996).

The Cili section (Hunan Province, China) was located on the paleo-western margin of the Yangtze Platform (Fig. 1). The PTB succession consists of muddy limestone and skeletal packstone/grainstone below the EPME horizon (Wang et al., 2009; Yang et al., 2011; Luo et al., 2013, 2014) and thrombolitic calcimicrobialite with limited fossil content (mainly microgastropods, microconchids, ostracods, and conodonts) above the EPME horizon (Ezaki et al., 2003; Wang et al., 2009; Yang et al., 2011, 2015a, b). The Cili section was far from contemporaneous landmasses, thus shielding it from terrestrial influences (Luo et al., 2013). The PTB is located in the upper part of the microbialite (Yang et al., 2011).

2.2. Intermediate shelf/ramp sections

The Perth Basin section (Western Australia) was located in a silled basin in the eastern

Neo-Tethys during the Permian-Triassic transition (Fig. 1). A detailed study of the litho-, bio-, and carbon-isotope stratigraphy as well as palynofacies and biomarkers of the Hovea Member of the Kockatea Shale was published by [Thomas et al. \(2004\)](#). The Hovea Member consists of two units: (1) fossiliferous black mudstone, sandy siltstone, and shelly storm beds of the lower Inertinitic Interval, in which charcoal and wood fragments dominate the organic fraction; and (2) dark brownish-gray, finely laminated mudstone and thin limestone of the upper Sapropelic Interval, in which amorphous marine algal organic matter is dominant. Well-preserved fossils, locally intense bioturbation, and shelly storm beds suggest deposition at water depths of ~20-50 m ([Thomas et al., 2004](#)). The EPME horizon and PTB are located approximately at the contact of the Inertinitic and Sapropelic intervals.

The Spitsbergen section (Lusitaniadalen, Svalbard, Norway) was deposited in an epicontinental shelf sea located in the boreal region during the Permian-Triassic transition (Fig. 1; [Nabbefeld et al., 2010b](#)). This Upper Permian section (Fig. 3) is divided into two units: (1) a lower unit consisting of well-bioturbated, fine-medium-grained, greenish glauconite-rich sandstones, and (2) an upper unit composed of laminated, dark gray mudstones, with occasional thin, ripple-laminated sandstone beds ([Mørk et al., 1999](#)). Depositional water depths of ~100 m are inferred based on sedimentologic features, e.g., glauconite, which forms mainly in mid-shelf environments at depths >50 m ([Chafetz and Reid, 2000](#)), and siltstone and sandstone beds with ripple lamination indicating open-shelf storm influence, typically at depths of ~50-100 m (cf. [Brett et al., 1993](#)). The EPME is located approximately at the contact between the lower and upper units.

The Peace River Basin section (western Alberta, Canada) is an Apexco drillcore that

represents a site on the northwestern margin of Pangaea (Hays et al., 2007; Fig. 1). The thin uppermost Permian and thicker Lower Triassic strata (Fig. 3) consist of silty, partially bioturbated mudstone, cross-stratified siltstone with low-angle bedsets, and very fine-grained sandstone. These characteristics imply storm influence on a continental shelf above storm wave base (water depths of ~50-100 m). The conodonts *Clarkina taylorae* and *H. parvus* were found in the upper part of parasequence G1, in association with a large negative carbon isotope excursion, constraining the location of the PTB (Hays et al., 2007).

The Kap Stosch section (east-central Greenland) was deposited at the margin of the Boreal Ocean during the Permian-Triassic transition (Fig. 1; Teichert et al., 1972; Hays et al., 2012). The uppermost Permian to lowermost Triassic succession shows an abrupt transition from dark shale and siltstone to medium grayish-brown arkosic sandstone at the level of the EPME (Teichert et al., 1972; Fig. 3 and 5). The Permian sediments were deposited in an open-shelf setting that shallowed into the earliest Triassic. Average water depths are estimated at ~80-120 m.

The West Blind Fjord section (Ellesmere Island, Arctic Canada) is located on the margin of the Sverdrup Basin (Fig. 1), part of the larger Boreal Ocean region (Algeo et al., 2012). The measured section consists of 24 m of medium-bedded black to white spiculitic cherts of the Lindström Formation and thinly bedded siliceous shales of the Blind Fiord Formation deposited in a slope setting at water depths of ~100-200 m. The EPME and PTB, are placed at 10.2 m and ~13 m, respectively, above the Lindström-Blind Fiord formation contact.

The Huangzhishan section (Zhejiang Province, China) was located on the paleo-northwestern margin of the Yangtze Platform of the South China Block (Fig. 1). The

PTB succession comprises four units: (1) bioclastic limestone of the Changxing Formation, (2) alternating calcareous mudstone and muddy limestone of the Huangzhishan Formation, (3) mudstone and marlstone of the Yinkeng Formation, and (4) alternating calcareous mudstone and argillaceous limestone of the Helongshan Formation (Chen et al., 2009; Kaiho et al., 2012). The succession shows a sharp transition from high-energy, open-platform facies of the uppermost Changxing Formation to low-energy, restricted-marine facies of the lowermost Huangzhishan Formation (Chen et al., 2010). Average water depths are estimated as ~40-80 m. The EPME horizon is placed at the base of the Huangzhishan Formation, and the PTB at the first appearance of the conodont *H. parvus* (base of Bed 25) (Chen et al., 2009).

The Meishan section (Zhejiang Province, China), which is the Global Stratotype Section and Point (GSSP) of the PTB, was located on the paleo-northwestern margin of the South China Craton (Yin et al., 2001; Fig. 1). The latest Permian Changxing Formation comprises medium- to thin-bedded bioclastic limestone, representing a proximal carbonate ramp setting (Zhang et al., 1996; He et al., 2005; Song-HJ et al., 2007). The earliest Triassic Yinkeng Formation consists of greenish mudstone interbedded with thin marlstone, representing a deepening-upward succession (Chen et al., 2007, 2015; Tian et al., 2014). With evidence of both shallow- and deep-water faunal assemblages, water depths have been interpreted as ranging from ~30 to 100 m (Yin et al., 2001; He et al., 2005; Chen et al., 2010; Kaiho et al., 2012; Song-HY et al., 2013). The EPME is located at the base of Bed 25 and the PTB in the middle of Bed 27 (Yin et al., 2001).

2.3. Deep shelf/ramp sections

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200 The Shangsi section (Sichuan Province, China) was located on the paleo-southwestern
201 margin of the South China Craton (Fig. 1; [Wignall et al., 1995](#); [Lai et al., 1996](#); [Nicoll et al.,](#)
202 [2002](#); [Jiang et al., 2011](#)). The PTB interval comprises two units: (1) the Dalong Formation,
203 which consists of black siliceous limestone interbedded with siliceous mudstone, and (2) the
204 Feixianguan Formation, which consists mainly of gray carbonaceous mudstone ([Li et al.,](#)
205 [1986](#); Fig. 3 and 6). The Shangsi section was deposited in deeper waters of the partially
206 restricted Guangyuan-Liangping Bay at estimated water depths of ~200-300 m ([Yin et al.,](#)
207 [2014](#)). The EPME coincides with the Dalong-Feixianguan formation contact, and the PTB
208 with the first occurrence of *H. parvus* ~22 cm above this contact ([Jiang et al., 2011](#)).

209 The Chaohu section (Anhui Province, China) was deposited on the paleo-northwestern
210 margin of the South China Craton (Fig. 1; [Zhao et al., 2007](#); [Tong and Zhao, 2011](#)). It is a
211 composite of three closely spaced sections at West Majiashan (Permian-Triassic boundary
212 beds), West Pingdingshan (basal Griesbachian to Smithian), and South Majiashan (Smithian
213 to Spathian). It consists of dark siliceous mudstone of the Upper Permian Dalong Formation
214 and yellowish-green calcareous mudstone interbedded with mudstone and white claystone of
215 the Lower Triassic Yinkeng Formation. Both litho- and biofacies data suggest that uppermost
216 Permian to lowermost Triassic strata represent a deep ramp setting with water depths up to
217 ~200-400 m ([Chen et al., 2010, 2011](#)). The EPME is placed at the Dalong-Yinkeng formation
218 contact and the PTB ~18 cm above this contact ([Yin et al., 2014](#)).

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220 **3. Material and methods**

Samples for biomarker analysis were collected from five sections: Bulla (northern Italy), and Laolongdong, Cili, Shangsi, and Chaohu (South China) (Fig. 1). Each sample (~500 g) was trimmed to remove visible veins and weathered surfaces, broken into small pieces (~1 cm³), washed in ultrapure water three times, oven-dried overnight, and then rinsed with dichloromethane (DCM). Small pieces of each sample were ground to ~150 mesh powder that was processed by accelerated solvent extraction using a solvent mixture of 9:1 dichloromethane: methanol and concentrated via rotary evaporation, with activated copper being added to remove elemental sulfur. Extracts were fractionated by activated silica gel chromatography (using silica gel baked at 500 °C for 6 h) and separated into three fractions by sequential elution: a saturated hydrocarbon fraction (*n*-hexane), an aromatic hydrocarbon fraction (80 % *n*-hexane: 20 % dichloromethane), a polar fraction (50 % dichloromethane: 50 % methanol). All fractions were dried under a nitrogen purge.

Aryl isoprenoids (AI) in the aromatic fraction were analyzed by gas chromatography (GC) and gas chromatography-mass spectrometry (GC-MS). An Agilent 6890 gas chromatograph linked to an Agilent 5973 mass selective detector equipped with an SLB-5MS capillary column (30 m × 0.25 mm internal diameter; film thickness 0.25 µm) was used for AI analysis. Samples were injected while oven temperature was held constant at 70 °C and the injector programmed to 320 °C. The oven then followed a temperature program of 3 °C min⁻¹ to a final temperature of 300 °C, which was held constant for 30 min. Helium was used as the carrier gas, the ionization energy of the mass spectrometer was set at 70 eV, and the scan range was from 50 to 550 amu. Aromatic quantification was achieved by comparison of peak

areas with an internal standard (chrysene-d). Organic compounds were identified on the basis of mass spectra and retention time of well-characterized samples, per standard protocols (e.g., [Grice et al., 2005a](#)).

4. Results

Although the three shallow platform sections (Bulla, Cili, and Laolongdong) record the EPME and an accompanying sharp lithologic change from skeletal limestone to calcimicrobialite or oolitic limestone, none of these sections yields AIs within the Permian-Triassic transition interval (Fig. 4). At Bulla, high DBF ratios (0.6-0.9) were detected at the EPME horizon, whereas most samples from lowermost Triassic strata exhibit intermediate DBF ratios (mostly 0.4-0.5). The C₃₀ moretane/hopane (C₃₀M/C₃₀HP) ratios vary within a narrow range (0.14-0.19). At Cili, DBF ratios show a slight increase below the EPME horizon (to ~0.4-0.5) and then decrease abruptly at the PTB to values of ~0.2. C₃₀M/C₃₀HP ratios are less than 0.12, varying around 0.10. At Laolongdong, DBF ratios vary within a low, narrow range (mostly 0-0.2), and C₃₀M/C₃₀HP ratios are less than 0.2.

All five of the intermediate shelf/ramp sections at non-Chinese sites contain AIs in elevated abundances both prior to and following the EPME (Fig. 5). A short, sharp spike of C₁₉ AIs was observed immediately above the EPME in the Perth Basin. In the same section, the benzo(e)pyrene / $\sum$ (benzo(a)pyrene + benzo(e)pyrene (BeP/(BaP+BeP)) ratios decrease sharply at the EPME, reflecting a decline of terrestrial organic matter inputs ([Grice et al., 2007](#)). At Spitsbergen, the AI, DBT, and DBF profiles show similar trends around the EPME

horizon, and there is a positive relationship among these proxies in the Lower Triassic interval (Nabbefeld et al., 2010a). Similar results for the Peace River Basin were reported by Hays et al. (2007) and Nabbefeld et al. (2010a): the highest abundances of all proxies are found around the EPME, and a positive correlation among these proxies is observed in the Lower Triassic. At Kap Stosch, AI peaks near the base of the section and correlates positively with DBT below the PTB (Nabbefeld et al., 2010a; Hays et al., 2012). The relatively deep water West Blind Fjord section yields low AI concentrations ($<0.008 \mu\text{g/g TOC}$) that show positive covariation with $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$.

Similar biomarker patterns are shown by intermediate shelf/ramp sections in South China. Huangzhishan exhibits relatively low AI values (mostly $<0.004 \mu\text{g/g TOC}$) that peak at the EPME and in the lowermost Triassic (Kaiho et al., 2012; Fig. 5). At Meishan, there is a strong positive relationship between AI and $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$ (Fig. 5), as documented by Cao et al. (2009) and Xie et al. (2007). Two episodes of elevated AI and $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$ values can be observed, with the first episode coincident with the EPME horizon and the second occurring within the lowermost Triassic *I. isarcica* Zone.

The deep shelf/ramp sections (Chaohu and Shangsi) yield abundant AIs following the EPME but only minor quantities (Chaohu) or none at all (Shangsi) prior to the EPME (Fig. 6). The deep sections thus resemble the intermediate sections in showing evidence for PZE following the mass extinction but differ in lacking evidence for PZE prior to the biocrisis. As for Meishan, the $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$ profile at Shangsi shows a first peak at the EPME and a second peak within the *I. isarcica* Zone. At Chaohu, the DBT/phenanthrene (Phe) and AI profiles show almost synchronous changes in the lowermost Triassic.

Biomarkers for PZE commonly covary positively with those for terrigenous organic matter inputs (i.e., DBF) within the narrow EPME-PTB interval, but not in stratigraphically lower or higher beds. For example, samples from the EPME-PTB interval at Shangsi show strong positive covariation of $C_{30}M/C_{30}HP$ with AI ($r^2 = 0.72$; Fig. 7A). These covariation patterns imply a causal relationship between GSB blooms and terrigenous organic matter inputs to continental shelves during the latest Permian. In Section 5.3, we hypothesize that land-derived nutrient fluxes stimulated marine phytoplankton productivity, triggering the development of PZE in mid-shelf settings and its oceanward expansion into deeper-water areas during the peak of the biocrisis.

To summarize, AI concentrations in continental shelf settings show a significant relationship to depositional water depths. On the South China Craton, AIs increase from shallow to intermediate settings (e.g., from Huangzhishan to Meishan) and then decrease from intermediate to deep settings (e.g., from Meishan to Shangsi and Chaohu; Fig. 8). A similar pattern is observed for the non-Chinese sections: AI concentrations increase from near-zero in the shallow Bulla section to relatively high values in the intermediate to deep Peace River Basin and Kap Stosch sections (Fig. 8). On the other hand, the development of PZE among intermediate-depth sections does not show any relationship to paleogeographic factors such as paleolatitude or ocean-basin location (i.e., Panthalassa versus Tethys).

5. Discussion

5.1. Biomarker proxies for green sulfur bacteria

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310 Green sulfur bacteria (GSB), which are common within stratified basins, estuaries, lakes,
311 and coastal embayments, are obligate anaerobic bacteria whose metabolism requires both
312 sunlight and H₂S (Grice et al., 1996; Grice et al., 2005b; Sinninghe Damsté and Schouten,
313 2006; Overmann, 2008). They synthesize special aromatic carotenoids such as chlorobactene
314 and isorenieratene, along with a range of other pigments including bacteriochlorophyll-c, -d,
315 and -e (Fig. 2) (Overmann and Tuschak, 1997). During diagenesis, these aromatic carotenoids
316 are usually converted to geologically much more stable counterparts, chlorobactane and
317 isorenieratane. Therefore, the presence of these compounds in sediments are convincing
318 evidence for green sulfur bacterial productivity and, thus, photic zone euxinia (Naeher and
319 Grice, 2015; Plet et al., 2016). These biomarkers have been found in a number of PTB
320 sections, including the Perth Basin (Grice et al., 2005a), Kap Stosch (Hays et al., 2012), the
321 Peace River Basin (Hays et al., 2007), and Meishan (Grice et al., 2005a; Cao et al., 2009).

322 During thermal diagenesis, these compounds can be further cleaved into aryl isoprenoids
323 (AIs). As AIs can also be produced through decay of the carotenoid pigment β -carotene
324 (Koopmans et al., 1996), they are not uniquely diagnostic of GSB in the absence of other
325 evidence. One way to differentiating these two sources of AIs is via their carbon isotopic
326 compositions: GSB are generally enriched in ¹³C due to the reversed (or reductive)
327 tricarboxylic acid (TCA) cycle used during carbon fixation (Summons and Powell, 1986,
328 1987). Unfortunately, the low AI concentrations of the study sections prevented acquisition of
329 $\delta^{13}\text{C}$ data. On the other hand, isorenieratane was found in association with AIs--at Shangsi,
330 these compounds covary with $r^2 = 0.60$ (Fig. 7B)--suggesting that aryl isoprenoids were

mainly sourced from isorenieratene and, thus, are strongly indicative of a GSB precursor.

5.2. Expansion of photic-zone euxinia during the Permian-Triassic transition

It is unlikely that differences in AI concentrations among the study sections were caused by variable diagenesis as they all exhibit low to moderate thermal maturity levels according to Rock-Eval data and biomarker maturity parameters, e.g., Bulla ($T_{\max} < 445\text{ }^{\circ}\text{C}$), Laolongdong ($22\text{S}/(22\text{S}+22\text{R})$ of C_{31} homohopanes = 0.56-0.64), Cili ($T_{\text{S}}/(T_{\text{S}}+T_{\text{M}}) \approx 0.5$), Shangsi ($T_{\max} \approx 425\text{ }^{\circ}\text{C}$), and Chaohu ($22\text{S}/(22\text{S}+22\text{R})$ of C_{31} homohopanes = 0.56-0.61). Systematic relationships were also not observed between AI concentrations and TOC, e.g., Bulla exhibits TOC up to 2 % but zero AIs, and both Kap Stosch and Shangsi exhibit high AI concentrations with low TOC (mainly 0.2-0.9 %). Thus, differences in the concentrations of pigment degradation products do not appear to reflect thermal maturity or TOC content.

The spatio-temporal pattern of GSB biomarkers in the study sections (Figs. 4-6) suggests a major expansion of PZE during the PTB transition (Fig. 8). Prior to the EPME, relatively stable euxinia existed in limited areas on some continental shelves, as shown by non-zero AI abundances in the Huangzhishan, Meishan, Peace River Basin, and Kap Stosch sections, all of which were located at intermediate water depths (~20-200 m; Table 1). At the same time, shallow-water sections such as Bulla and Cili, and deep-water sections such as Shangsi and Chaohu show no evidence of PZE. Following the EPME, shallow-water sections continue to show no evidence of PZE. Rather, these sections exhibit low $\text{S}/\text{C}_{\text{org}}$ ratios, large framboidal pyrite diameters, and low trace-element concentrations in the post-extinction microbialite that

are indicative of oxic-dysoxic conditions (Liao et al., 2010; Loope et al., 2013; Song-HY et al., 2014). At water depths of <20 m, it is likely that any hydrogen sulfide that was generated locally or advected from remote sources was rapidly oxidized to sulfate. However, the post-EPME interval is characterized by GSB blooms in the photic zone of both intermediate and deep-water sections, indicating an oceanward expansion of the areas in which PZE existed. Thus, areas of continental shelf or carbonate platform shallower than ~20 m were probably not subject to sustained euxinic conditions, and intensification of photic-zone euxinia during the PTB crisis was expressed as oceanward expansion of a wedge-shaped mass of sulfide-bearing, oxygen-depleted water (Fig. 8).

Both in continental shelf and carbonate platform settings, the concentration of AIs in intermediate and deep sections rose rapidly following the EPME, generally peaking prior to the PTB (Figs. 5-6). In the Peace River Basin, West Blind Fiord, Shangsi, and Chaohu, a second peak of AI abundance is observed in the Lower Triassic. These peaks may represent a globally correlative event during the earliest Triassic, although this potential event needs further confirmation through identification in additional sections.

5.3. Enhanced terrestrial erosion as a trigger for expansion of photic-zone euxinia

A number of aromatic hydrocarbon compounds derived from higher land plants are useful for assessing inputs of terrigenous organic matter to marine systems (e.g., Xie et al., 2007; Nabbefeld et al., 2010a). Fenton et al. (2007) showed that increased DBT and DBF correlated with spikes in the spores and pollen of woody plants, suggesting that lignin from

woody plants is a source of DBT and DBF. Other studies have linked DBF and its derivatives to dehydrated polysaccharides (Pastorova et al., 1994), which are extremely abundant in leaf litter and soil and, hence, can potentially serve as an indicator of enhanced soil erosion and terrestrial inputs to marine systems (Sephton et al., 2005). The ratio of DBF/(DBT+DBF+F) (where F stands for “fluorences”) has been used as an indicator of land-derived organic matter, with higher values indicative of enhanced soil erosion (Wang and Visscher, 2007). Other biomarker proxies for terrestrial inputs include (1) the C₃₀M/C₃₀HP ratio, with higher values indicative of enhanced terrestrial inputs, as in the EPME horizon at Meishan (French et al., 2012; Xie et al., 2007), and (2) the BeP/(BaP+BeP) ratio, with lower values indicative of enhanced terrestrial inputs, as in the EPME horizon of the Perth Basin (Grice et al., 2007).

Both in mid-shelf (e.g., Spitsbergen, Peace River Basin, Kap Stosch, West Blind Fiord) and inner-shelf settings (e.g., Huangzhishan, Meishan), intermediate-depth sections show a strong positive relationship between land-derived organic matter and GSB blooms (Fig. 5). An important observation is that, prior to the EPME, proxies for terrestrial inputs had already increased slightly in many of these sections (e.g., Huangzhishan, Meishan, and Spitsbergen), indicating that destruction of terrestrial ecosystems and soil erosion preceded the marine biotic crisis (cf. Sephton et al., 2005). Evidence for enhanced terrigenous inputs prior to the marine crisis can also be seen at Schuchert Dal in eastern Greenland (Fenton et al., 2007), where high abundances of DBT, DBF, and BP are found up to 6 m below the EPME horizon. Even in deep-water settings such as at Shangsi, an increase in C₃₀M/C₃₀HP below the EPME horizon (Fig. 6) suggests the influence of terrestrial ecosystem collapse on marine systems. In fact, all of the intermediate and deep sections of the present study that exhibit high AIs

following the EPME are associated with elevated abundances of moretanes, DBF, and DBT, i.e., biomarkers that are diagnostic of terrestrial erosion and soil inputs.

Elevated riverine nutrient fluxes may have been triggered by rapid soil erosion during the end-Permian crisis and subsequently sustained by enhanced terrestrial erosion under high $p\text{CO}_2$ conditions in the post-extinction greenhouse climate (Algeo et al., 2011b; Sun et al., 2012). Enhanced terrestrial erosion during the PTB transition has been documented on the basis of biomarker evidence, i.e., DBT, DBF, retene, and moretane concentrations (Sephton et al., 2005; Xie et al., 2007), sediment fluxes (Algeo and Twitchett, 2010), and Sr isotopes (Korte et al., 2003; Sedlacek et al., 2014). High riverine nutrient fluxes would have stimulated marine primary productivity during the latest Permian to earliest Triassic (Algeo et al., 2011b, 2013; Shen et al., 2015; Wei et al., 2015). According to paleoceanographic modeling results, widespread oceanic anoxia and PZE are likely to have developed if riverine phosphate fluxes during the PTB crisis reached $\sim 10\times$ the modern value (Meyer et al., 2008; Winguth and Winguth, 2012). We infer that expansion of euxinia at that time was triggered by a pulse of land-derived nutrients to continental shelves, as suggested by positive covariation of $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$ with AI concentrations (Fig. 7).

5.4. Global warming as a trigger for expansion of photic-zone euxinia

Although the majority of the study sections show a clear relationship between enhanced terrestrial weathering inputs and increased frequency of GSB blooms, there are some exceptions, e.g., the Perth Basin. Low AI abundances in uppermost Permian strata of the

Perth Basin, despite large terrestrial inputs including abundant wood and charcoal (Thomas et al., 2004), suggest that there were other factors influencing GSB activity other than increased nutrient inputs. An abrupt rise of tropical seawater temperatures during the EPME crisis, as documented by conodont apatite oxygen isotope compositions (Joachimski et al., 2012; Sun et al., 2012), may have been the immediate cause of expansion of PZE, as inferred also for the end-Triassic mass extinction (Jaraula et al., 2013). The links between global warming and expansion of PZE include decreased solubility of oxygen in warmer ocean-surface waters (Kennett and Stott, 1991; Kaiho, 1994) as well as an enhanced hydrologic cycle and terrestrial weathering rates (Meyer and Kump, 2008; Algeo et al., 2011b). During the latest Permian in the Perth Basin, global climatic warming led to more humid conditions in the southern subtropics, as shown by pollen and spore records (Hermann et al., 2012). As a consequence, increased riverine discharge into the Perth Basin would have intensified water-column stratification and, thus, stimulated GSB blooms during the end-Permian crisis. These considerations reflect the dominant role that global warming played in the aftermath of the EPME, although its specific effects depended on local paleogeographic and -oceanographic factors. Moreover, with regard to the transition from terrestrial-dominated to algal-dominated organic matter during the EPME crisis proposed by Grice et al. (2007), high marine primary productivity caused by increased land-derived nutrient inputs may have been an important factor.

5.5. Role of hydrogen sulfide in the marine mass extinction

Many studies have inferred that oceanic euxinia was an important killing agent during the end-Permian biocrisis (Wignall and Twitchett, 1996; Isozaki, 1997; Kato et al., 2002; Grice et al., 2005a; Algeo et al., 2007; Hays et al., 2007; Knoll et al., 2007; Riccardi et al., 2007; Meyer and Kump, 2008; Brennecka et al., 2011). Despite the lack of biomarker evidence for PZE in shallow-marine sections of this study, other geochemical proxies have been used to infer the development of at least transient euxinia in some shallow-water PTB sections. At Bulla in northern Italy, small pyrite framboids in oolitic grainstone of the Tesero Member suggest that euxinic conditions existed at the time of the EPME (Bond and Wignall, 2010). At Nhi Tao in northern Vietnam, framboidal pyrite layers appear exactly at the level of the EPME horizon and continue several meters upsection, suggesting a series of brief but possibly intense incursions of H₂S onto this shallow carbonate platform (Algeo et al., 2007, 2008). Such short-term incursions of sulfidic waters into the ocean surface layer would have been possible if a long-term reservoir of H₂S-rich waters existed at intermediate water depths (Feng and Algeo, 2014; this study). The absence of biomarker evidence for PZE in the shallow-water sections of the present study may reflect the briefness of such sulfidic incursions into the ocean-surface layer, after which H₂S would have been rapidly oxidized to sulfate and may not have persisted long enough to have allowed an obligate anaerobic community to become established.

In addition, expanding areas of seafloor euxinia from both upper continental slopes (in response to oceanic OMZ expansion; Algeo et al., 2011a; Schoepfer et al., 2013) and mid-shelf regions (in response to nutrient loading; this study) may have created a ‘euxinic pincher’ that effectively killed off marine benthos over a wide range of water depths (perhaps

<100 m to >500 m). The shallowest regions of the ocean (<20 m) may have been affected by episodic shallowing of the chemocline (i.e., ‘chemocline upward excursions’ of [Kump et al., 2005](#)) or eruptions of H₂S into ocean-surface waters. Alternatively, much of the biotic stress in ocean-surface waters may have been due to intense climatic warming ([Sun et al., 2012](#); [Song-HJ et al., 2014](#)). Whatever mechanism is invoked must have operated quickly because fossil records demonstrate that extinction rates were low (<30 %) prior to the EPME and suddenly spiked to ~90 % at the EPME ([Song-HJ et al., 2012](#)). The speed with which this extinction event occurred is consistent with a pulse of nutrients derived from global warming and terrestrial ecosystem destruction causing rapid expansion of mid-shelf PZE.

6. Conclusions

Aryl isoprenoids (AI), biomarkers typical of obligate anaerobic green sulfur bacteria (Chlorobiaceae), were detected in 12 Permian-Triassic boundary sections globally. Profiles of AI abundance from these study sections reveal significant spatio-temporal variation, documenting the development of photic-zone euxinia (PZE) before, during, and after the end-Permian mass extinction (EPME). No AIs were identified in the shallowest sections, but AIs are present in large amounts both prior to and following the mass extinction in intermediate-depth sections and following the mass extinction in deep-water sections, a pattern that is consistent with an oceanward expansion of PZE in the aftermath of the EPME. This expansion may have been fueled by an enhanced riverine nutrient flux as a result of global warming, terrestrial ecosystem destruction, and soil erosion, although intensified

oceanic stratification as a function of climatic warming may have been a contributing factor.

Marine euxinia is likely to have been a major player in the end-Permian mass extinction. Generation of a long-term reservoir of euxinic waters at intermediate ocean depths would have created the potential for episodic shallowing of the chemocline or eruptions of sulfidic waters into the ocean-surface layer. A major event of this type may have caused a rapid kill-off of shallow-marine benthos during the end-Permian mass extinction, and episodic expansion of PZE following the EPME may have been a factor delaying the recovery of Early Triassic marine ecosystems.

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References

[Algeo, T.J., Twitchett, R.J., 2010. Anomalous Early Triassic sediment fluxes due to elevated](#)

weathering rates and their biological consequences. *Geology* 38, 1023–1026.

Algeo, T.J., Ellwood, B.B., Nguyen, T.K.T., Rowe, H., Maynard, J.B., 2007. The Permian–Triassic boundary at Nhi Tao, Vietnam: evidence for recurrent influx of sulfidic watermasses to a shallow-marine carbonate platform. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 304–327.

Algeo, T.J., Shen, Y., Zhang, T., Lyons, T., Bates, S., Rowe, H., Nguyen, T., 2008. Association of ^{34}S -depleted pyrite layers with negative carbonate $\delta^{13}\text{C}$ excursions at the Permian–Triassic boundary: Evidence for upwelling of sulfidic deep-ocean water masses. *Geochem. Geophys. Geosyst.* 9e.

Algeo, T.J., Kuwahara, K., Sano, H., Bates, S., Lyons, T., Elswick, E., Hinnov, L., Ellwood, B., Moser, J., Maynard, J.B., 2011a. Spatial variation in sediment fluxes, redox conditions, and productivity in the Permian–Triassic Panthalassic Ocean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 65–83.

Algeo, T.J., Chen, Z.Q., Fraiser, M.L., Twitchett, R.J., 2011b. Terrestrial–marine teleconnections in the collapse and rebuilding of Early Triassic marine ecosystems. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 1–11.

Algeo, T.J., Henderson, C.M., Ellwood, B., Rowe, H., Elswick, E., Bates, S., Lyons, T., Hower, J.C., Smith, C., Maynard, B., 2012. Evidence for a diachronous Late Permian marine crisis from the Canadian Arctic region. *Geol. Soc. Am. Bull.* 124, 1424–1448.

Algeo, T.J., Henderson, C.M., Tong, J., Feng, Q., Yin, H., Tyson, R., 2013. Plankton and productivity during the Permian–Triassic boundary crisis: An analysis of organic carbon fluxes. *Glob. Planet. Chang.* 105, 52–67.

529 Bond, D.P., Wignall, P.B., 2010. Pyrite framboid study of marine Permian–Triassic boundary
530 sections: a complex anoxic event and its relationship to contemporaneous mass
531 extinction. *Geol. Soc. Am. Bull.* 122, 1265–1279.

532 Brennecka, G.A., Herrmann, A.D., Algeo, T.J., Anbar, A.D., 2011. Rapid expansion of
533 oceanic anoxia immediately before the end-Permian mass extinction. *Proc. Natl. Acad.*
534 *Sci. USA* 108, 17631–17634.

535 Brett, C.E., Boucot, A.J., Jones, B., 1993. Absolute depths of Silurian benthic assemblages.
536 *Lethaia* 26, 25–40.

537 Campbell, I., Czamanske, G., Fedorenko, V., Hill, R., Stepanov, V., 1992. Synchronism of the
538 Siberian Traps and the Permian-Triassic boundary. *Science* 258, 1760–1763.

539 Cao, C., Love, G.D., Hays, L.E., Wang, W., Shen, S., Summons, R.E., 2009. Biogeochemical
540 evidence for euxinic oceans and ecological disturbance presaging the end-Permian mass
541 extinction event. *Earth Planet. Sci. Lett.* 281, 188–201.

542 Chafetz, H., Reid, A., 2000. Syndepositional shallow-water precipitation of glauconitic
543 minerals. *Sed. Geol.* 136, 29–42.

544 Chen, Z.Q., Tong, J., Kaiho, K., Kawahata, H., 2007. Onset of biotic and environmental
545 recovery from the end-Permian mass extinction within 1-2 million years: A case study of
546 the Lower Triassic of the Meishan section, South China. *Palaeogeogr. Palaeoclimatol.*
547 *Palaeoecol.* 252, 176–187.

548 Chen, Z.Q., Tong, J., Zhang, K., Yang, H., Liao, Z., Song, H.J., Chen, J., 2009.
549 Environmental and biotic turnover across the Permian–Triassic boundary on a shallow
550 carbonate platform in western Zhejiang, South China. *Austral. J. Earth Sci.* 56, 775–797.

- Chen, Z.Q., Tong, J., Liao, Z.T., Chen, J., 2010. Structural changes of marine communities over the Permian–Triassic transition: ecologically assessing the end-Permian mass extinction and its aftermath. *Glob. Planet. Chang.* 73, 123–140.
- Chen, Z.Q., Tong, J., Fraiser, M.L., 2011. Trace fossil evidence for restoration of marine ecosystems following the end-Permian mass extinction in the Lower Yangtze region, South China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 449–474.
- Chen, Z.Q., Yang, H., Luo, M., Benton, M.J., Kaiho, K., Zhao, L.S, Huang, Y., Zhang, K.X., Fang, Y., Jiang, H.S., Qiu, H., Li, Y., Tu, C.Y., Shi, L., Zhang, L., Feng, X.Q., Chen, L., 2015. Complete biotic and sedimentary records of the Permian-Triassic transition from Meishan section, South China: ecologically assessing mass extinction and its aftermath. *Earth-Sci. Rev.* 149, 63–103.
- Clarkson, M.O., Kasemann, S.A., Wood, R.A., Lenton, T.M., Daines, S.J., Richoz, S., Ohnemueeller, F., Meixner, A., Poulton, S.W., Tipper, E.T., 2015. Ocean acidification and the Permo-Triassic mass extinction. *Science* 348, 229–232.
- Erwin, D.H., Bowring, S.A., Jin, Y., 2002. End-Permian mass extinctions: a review. In: Koeberl, C., MacLeod, K.G. (Eds.), *Catastrophic Events and Mass Extinctions: Impacts and Beyond*: Boulder, Colorado, Geological Society of America Special Paper 356, pp. 363–383.
- Ezaki, Y., Liu, J., Adachi, N., 2003. Earliest Triassic microbialite micro-to megastructures in the Huaying area of Sichuan Province, South China: implications for the nature of oceanic conditions after the end-Permian extinction. *Palaios* 18, 388–402.
- Farabegoli, E., Perri, M.C., Posenato, R., 2007. Environmental and biotic changes across the

573 Permian–Triassic boundary in western Tethys: the Bulla parastratotype, Italy. *Glob.*
 574 *Planet. Chang.* 55, 109–135.

575 Feng, Q., Algeo, T.J., 2014. Evolution of oceanic redox conditions during the Permo-Triassic
 576 transition: Evidence from deepwater radiolarian facies. *Earth-Sci. Rev.* 137, 34–51.

577 Fenton, S., Grice, K., Twitchett, R.J., Böttcher, M.E., Looy, C.V., Nabbefeld, B., 2007.
 578 Changes in biomarker abundances and sulfur isotopes of pyrite across the
 579 Permian–Triassic (P/Tr) Schuchert Dal section (East Greenland). *Earth Planet. Sci. Lett.*
 580 262, 230–239.

581 French, K.L., Tosca, N.J., Cao, C., Summons, R.E., 2012. Diagenetic and detrital origin of
 582 moretane anomalies through the Permian–Triassic boundary. *Geochim. Cosmochim. Acta*
 583 84, 104–125.

584 Gorjan, P., Kaiho, K., Kakegawa, T., Niitsuma, S., Chen, Z.Q., Kajiwara, Y., Nicora, A., 2007.
 585 Paleoredox, biotic and sulfur-isotopic changes associated with the end-Permian mass
 586 extinction in the western Tethys. *Chem. Geol.* 244, 483–492.

587 Grice, K., Schaeffer, P., Schwark, L., Maxwell, J.R., 1996. Molecular indicators of
 588 palaeoenvironmental conditions in an immature Permian shale (Kupferschiefer, Lower
 589 Rhine Basin, north-west Germany) from free and S-bound lipids. *Org. Geochem.* 25,
 590 131–147.

591 Grice, K., Cao, C., Love, G.D., Böttcher, M.E., Twitchett, R.J., Grosjean, E., Summons, R.E.,
 592 Turgeon, S.C., Dunning, W., Jin, Y., 2005a. Photic zone euxinia during the
 593 Permian–Triassic superanoxic event. *Science* 307, 706–709.

594 Grice, K., Twitchett, R.J., Alexander, R., Foster, C., Looy, C., 2005b. A potential biomarker

595 for the Permian–Triassic ecological crisis. *Earth Planet. Sci. Lett.* 236, 315–321.

596 Grice, K., Nabbefeld, B., Maslen, E., 2007. Source and significance of selected polycyclic
597 aromatic hydrocarbons in sediments (Hovea-3 well, Perth Basin, Western Australia)
598 spanning the Permian–Triassic boundary. *Org. Geochem.* 38, 1795–1803.

599 Hays, L.E., Beatty, T., Henderson, C.M., Love, G.D., Summons, R.E., 2007. Evidence for
600 photic zone euxinia through the end-Permian mass extinction in the Panthalassic Ocean
601 (Peace River Basin, Western Canada). *Palaeoworld* 16, 39–50.

602 Hays, L.E., Grice, K., Foster, C.B., Summons, R.E., 2012. Biomarker and isotopic trends in a
603 Permian–Triassic sedimentary section at Kap Stosch, Greenland. *Org. Geochem.* 43,
604 67–82.

605 He, W., Feng, Q., Gu, S., Jin, Y., 2005. Changxingian (Upper Permian) radiolarian fauna from
606 Meishan D section, Changxing, Zhejiang, China, and its possible paleoecological
607 significance. *J. Paleontol.* 79, 209–218.

608 Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D., Weissert, H.,
609 Roohi, G., Yaseen, A., 2012. Climatic oscillations at the onset of the Mesozoic inferred
610 from palynological records from the North Indian Margin. *J. Geol. Soc. London* 169,
611 227–237.

612 Hine, A.C., 1977. Lily Bank, Bahamas: history of an active oolite sand shoal. *J. Sed. Res.* 47,
613 1554–1582.

614 Hinojosa, J.L., Brown, S.T., Chen, J., DePaolo, D.J., Paytan, A., Shen, S.Z., Payne, J.L.,
615 2012. Evidence for end-Permian ocean acidification from calcium isotopes in biogenic
616 apatite. *Geology* 40, 743–746.

Isozaki, Y., 1997. Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea. *Science* 276, 235–238.

Jaraula, C.M., Grice, K., Twitchett, R.J., Böttcher, M.E., LeMetayer, P., Dastidar, A.G., Opazo, L.F., 2013. Elevated $p\text{CO}_2$ leading to Late Triassic extinction, persistent photic zone euxinia, and rising sea levels. *Geology* 41, 955–958.

Jiang, H., Lai, X., Yan, C., Aldridge, R.J., Wignall, P., Sun, Y., 2011. Revised conodont zonation and conodont evolution across the Permian-Triassic boundary at the Shangsi section, Guangyuan, Sichuan, south China. *Glob. Planet. Chang.* 77, 103–115.

Joachimski, M.M., Lai, X., Shen, S., Jiang, H., Luo, G., Chen, B., Chen, J., Sun, Y., 2012. Climate warming in the latest Permian and the Permian–Triassic mass extinction. *Geology* 40, 195–198.

Kaiho, K., 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology* 22, 719–722.

Kaiho, K., Kajiwarra, Y., Chen, Z.Q., Gorjan, P., 2006. A sulfur isotope event at the end of the Permian. *Chem. Geol.* 235, 33–47.

Kaiho, K., Oba, M., Fukuda, Y., Ito, K., Ariyoshi, S., Gorjan, P., Riu, Y., Takahashi, S., Chen, Z.Q., Tong, J., 2012. Changes in depth-transect redox conditions spanning the end-Permian mass extinction and their impact on the marine extinction: Evidence from biomarkers and sulfur isotopes. *Glob. Planet. Chang.* 94, 20–32.

Kamo, S.L., Czamanske, G.K., Amelin, Y., Fedorenko, V.A., Davis, D.W., Trofimov, V.R., 2003. Rapid eruption of Siberian flood-volcanic rocks and evidence for coincidence with the Permian–Triassic boundary and mass extinction at 251 Ma. *Earth Planet. Sci. Lett.*

639 214, 75–91.

640 Kato, Y., Nakao, K., Isozaki, Y., 2002. Geochemistry of Late Permian to Early Triassic
641 pelagic cherts from southwest Japan: implications for an oceanic redox change. *Chem.*
642 *Geol.* 182, 15–34.

643 Kershaw, S., Crasquin, S., Li, Y., Collin, P.Y., Forel, M.B., Mu, X., Baud, A., Wang, Y., Xie,
644 S., Maurer, F., 2012. Microbialites and global environmental change across the
645 Permian–Triassic boundary: a synthesis. *Geobiology* 10, 25–47.

646 Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., Fischer, W.W., 2007. Paleophysiology
647 and end-Permian mass extinction. *Earth Planet. Sci. Lett.* 256, 295–313.

648 Koopmans, M.P., Köster, J., Van Kaam-Peters, H.M., Kenig, F., Schouten, S., Hartgers,
649 W.A., de Leeuw, J.W., Sinninghe Damsté, J.S., 1996. Diagenetic and catagenetic
650 products of isorenieratene: molecular indicators for photic zone anoxia. *Geochim.*
651 *Cosmochim. Acta* 60, 4467–4496.

652 Korte, C., Kozur, H.W., Bruckschen, P., Veizer, J., 2003. Strontium isotope evolution of Late
653 Permian and Triassic seawater. *Geochim. Cosmochim. Acta* 67, 47–62.

654 Korte, C., Pande, P., Kalia, P., Kozur, H.W., Joachimski, M.M., Oberhänsli, H., 2010.
655 Massive volcanism at the Permian–Triassic boundary and its impact on the isotopic
656 composition of the ocean and atmosphere. *J. Asian Earth Sci.* 37, 293–311.

657 Kump, L.R., Pavlov, A., Arthur, M.A., 2005. Massive release of hydrogen sulfide to the
658 surface ocean and atmosphere during intervals of oceanic anoxia. *Geology* 33, 397–400.

659 Lai, X.L., Yang, F.Q., Hallam, A., Wignall, P., 1996. The Shangsi section, candidate of the
660 global stratotype section and point of the Permian–Triassic boundary. In: Yin, H.F. (Ed.),

The Palaeozoic-Mesozoic Boundary Candidates of Global Stratotype Section and Point of the Permian–Triassic Boundary. China University of Geosciences Press, Wuhan, pp. 113–124.

Li, Z.S., Zhan, L.P., Zhu, X.F., Zhang, J.H., Jin, R., Liu, G., Sheng, H., Shen, G., Dai, J., Huang, H., 1986. Mass extinction and geological events between Paleozoic and Mesozoic era. *Acta Geol. Sin.* 60, 1–15.

Liao, W., Wang, Y., Kershaw, S., Weng, Z., Yang, H., 2010. Shallow-marine dysoxia across the Permian–Triassic boundary: Evidence from pyrite framboids in the microbialite in South China. *Sediment. Geol.* 232, 77–83.

Loope, G.R., Kump, L.R., Arthur, M.A., 2013. Shallow water redox conditions from the Permian–Triassic boundary microbialite: The rare earth element and iodine geochemistry of carbonates from Turkey and South China. *Chem. Geol.* 351, 195–208.

Luo, G., Wang, Y., Grice, K., Kershaw, S., Algeo, T.J., Ruan, X., Yang, H., Jia, C., Xie, S., 2013. Microbial–algal community changes during the latest Permian ecological crisis: Evidence from lipid biomarkers at Cili, South China. *Glob. Planet. Chang.* 105, 36–51.

Luo, G., Algeo, T.J., Huang, J., Zhou, W., Wang, Y., Yang, H., Richoz, S., Xie, S., 2014. Vertical $\delta^{13}\text{C}_{\text{org}}$ gradients record changes in planktonic microbial community composition during the end-Permian mass extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 396, 119–131.

Meyer, K.M., Kump, L.R., 2008. Oceanic euxinia in Earth history: causes and consequences. *Annu. Rev. Earth Planet. Sci.* 36, 251–288.

Meyer, K.M., Kump, L., Ridgwell, A., 2008. Biogeochemical controls on photic-zone euxinia

during the end-Permian mass extinction. *Geology* 36, 747–750.

Monteiro, F., Pancost, R., Ridgwell, A., Donnadieu, Y., 2012. Nutrients as the dominant control on the spread of anoxia and euxinia across the Cenomanian–Turonian oceanic anoxic event (OAE2): Model–data comparison. *Paleoceanogr.* 27, PA4209, doi:10.1029/2012PA002351.

Mørk, A., Elvebakk, G., Forsberg, A.W., Vigran, J.O., Weitschat, W., 1999. The type section of the Vikinghogda Formation: a new Lower Triassic unit in central and eastern Svalbard. *Polar Res.* 18, 51–82.

Nabbefeld, B., Grice, K., Summons, R.E., Hays, L.E., Cao, C., 2010a. Significance of polycyclic aromatic hydrocarbons (PAHs) in Permian/Triassic boundary sections. *Applied Geochem.* 25, 1374–1382.

Nabbefeld, B., Grice, K., Twitchett, R.J., Summons, R.E., Hays, L., Böttcher, M.E., Asif, M., 2010b. An integrated biomarker, isotopic and palaeoenvironmental study through the Late Permian event at Lusitaniadalen, Spitsbergen. *Earth Planet. Sci. Lett.* 291, 84–96.

Naeher, S., Grice, K., 2015. Novel 1H-Pyrrole-2, 5-dione (maleimide) proxies for the assessment of photic zone euxinia. *Chem. Geol.* 404, 100–109.

Nicoll, R.S., Metcalfe, I., Wang, C.Y., 2002. New species of the conodont genus *Hindeodus* and the conodont biostratigraphy of the Permian–Triassic boundary interval. *J. Asian Earth Sci.* 20, 609–631.

Overmann, J., 2008. Ecology of phototrophic sulfur bacteria. In: Hell, R., Dahl, C., Knaff, D.B., Leustek, T. (Eds), *Sulfur Metabolism in Phototrophic Organisms*. Springer, Berlin/Heidelberg, pp. 375–396.

705 Overmann, J., Tuschak, C., 1997. Phylogeny and molecular fingerprinting of green sulfur
706 bacteria. *Arch. Microbiol.* 167, 302–309.

707 Pastorova, I., Botto, R.E., Arisz, P.W., Boon, J.J., 1994. Cellulose char structure: a combined
708 analytical Py-GC-MS, FTIR, and NMR study. *Carbohydr. Res.* 262, 27–47.

709 Perri, M., 1991. Conodont biostratigraphy of the Werfen Formation (Lower Triassic),
710 Southern Alps, Italy. *Boll. Soc. Paleontol. Ital.* 30, 23–46.

711 Plet, C., Grice, K., Pagès, A., Ruebsam, W., Coolen, M., Schwark, L., 2016.
712 Microbially-mediated fossil-bearing carbonate concretions and their significance for
713 palaeoenvironmental reconstructions: A multi-proxy organic and inorganic geochemical
714 appraisal. *Chem. Geol.* 426, 95–108.

715 Reichow, M.K., Pringle, M., Al'Mukhamedov, A., Allen, M., Andreichev, V., Buslov, M.,
716 Davies, C., Fedoseev, G., Fitton, J., Inger, S., 2009. The timing and extent of the eruption
717 of the Siberian Traps large igneous province: Implications for the end-Permian
718 environmental crisis. *Earth Planet. Sci. Lett.* 277, 9–20.

719 Riccardi, A., Kump, L.R., Arthur, M.A., D'Hondt, S., 2007. Carbon isotopic evidence for
720 chemocline upward excursions during the end-Permian event. *Palaeogeogr.*
721 *Palaeoclimatol. Palaeoecol.* 248, 73–81.

722 Romano, C., Goudemand, N., Vennemann, T.W., Ware, D., Schneebeli-Hermann, E., Hochuli,
723 P.A., Brühwiler, T., Brinkmann, W., Bucher, H., 2013. Climatic and biotic upheavals
724 following the end-Permian mass extinction. *Nat. Geosci.* 6, 57–60.

725 Schoepfer, S.D., Henderson, C.M., Garrison, G.H., Foriel, J., Ward, P.D., Selby, D., Hower,
726 J.C., Algeo, T.J., Shen, Y., 2013. Termination of a continent-margin upwelling system at

the Permian–Triassic boundary (Opal Creek, Alberta, Canada). *Glob. Planet. Chang.* 105, 21–35.

Sedlacek, A.R., Saltzman, M.R., Algeo, T.J., Horacek, M., Brandner, R., Foland, K., Denniston, R.F., 2014. $^{87}\text{Sr}/^{86}\text{Sr}$ stratigraphy from the Early Triassic of Zal, Iran: Linking temperature to weathering rates and the tempo of ecosystem recovery. *Geology* 42, 779–782.

Sephton, M.A., Looy, C.V., Brinkhuis, H., Wignall, P.B., De Leeuw, J.W., Visscher, H., 2005. Catastrophic soil erosion during the end-Permian biotic crisis. *Geology* 33, 941–944.

Shen, J., Schoepfer, S.D., Feng, Q.L., Zhou, L., Yu, J., Song, H.Y., Wei, H.Y., Algeo, T.J., 2015. Marine productivity changes during the Permian–Triassic boundary crisis and Early Triassic recovery. *Earth-Sci. Rev.* 149, 136–162.

Shen, S.-Z., Crowley, J.L., Wang, Y., Bowring, S.A., Erwin, D.H., Sadler, P.M., Cao, C.-Q., Rothman, D.H., Henderson, C.M., Ramezani, J., 2011. Calibrating the end-Permian mass extinction. *Science* 334, 1367–1372.

Sinninghe Damsté, J.S., Schouten, S., 2006. Biological markers for anoxia in the photic zone of the water column. In: Volkman, J. (Ed.), *Marine Organic Matter: Biomarkers, Isotopes and DNA. The Handbook of Environmental Chemistry*. Springer, Berlin/Heidelberg, pp. 127–163.

Song, H.J., Tong, J.-N., Zhang, K.-X., Wang, Q.-X., Chen, Z., 2007. Foraminiferal survivors from the Permian–Triassic mass extinction in the Meishan section, South China. *Palaeoworld* 16, 105–119.

Song, H.J., Wignall, P.B., Tong, J., Yin, H., 2012. Two pulses of extinction during the

749 Permian–Triassic crisis. *Nature Geosci.* 6, 52–56.

750 Song, H.J., Wignall, P.B., Chu, D., Tong, J., Sun, Y., Song, H., He, W., Tian, L., 2014.

751 Anoxia/high temperature double whammy during the Permian–Triassic marine crisis and

752 its aftermath. *Sci. Rep.* 4, 4132e.

753 Song, H.Y., Tong, J., Algeo, T.J., Horacek, M., Qiu, H., Song, H.J., Tian, L., Chen, Z.Q., 2013.

754 Large vertical $\delta^{13}\text{C}_{\text{DIC}}$ gradients in Early Triassic seas of the South China craton:

755 Implications for oceanographic changes related to Siberian Traps volcanism. *Glob.*

756 *Planet. Chang.* 105, 7–20.

757 Song, H.Y., Tong, J., Tian, L., Song, H.J., Qiu, H., Zhu, Y., Algeo, T.J., 2014. Paleo-redox

758 conditions across the Permian–Triassic boundary in shallow carbonate platform of the

759 Nanpanjiang Basin, South China. *Sci. China D: Earth Sci.* 57, 1030–1038.

760 Summons, R.E., Powell, T.G., 1986. Chlorobiaceae in Palaeozoic seas revealed by biological

761 markers, isotopes and geology. *Nature* 319, 763–765.

762 Summons, R., Powell, T., 1987. Identification of aryl isoprenoids in source rocks and crude

763 oils: biological markers for the green sulphur bacteria. *Geochim. Cosmochim. Acta* 51,

764 557–566.

765 Sun, Y., Joachimski, M.M., Wignall, P.B., Yan, C., Chen, Y., Jiang, H., Wang, L., Lai, X.,

766 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338,

767 366–370.

768 Svensen, H., Planke, S., Polozov, A.G., Schmidbauer, N., Corfu, F., Podladchikov, Y.Y.,

769 Jamtveit, B., 2009. Siberian gas venting and the end-Permian environmental crisis. *Earth*

770 *Planet. Sci. Lett.* 277, 490–500.

771 Takahashi, S., Yamasaki, S.-i., Ogawa, Y., Kimura, K., Kaiho, K., Yoshida, T., Tsuchiya, N.,
 772 2014. Bioessential element-depleted ocean following the euxinic maximum of the
 773 end-Permian mass extinction. *Earth Planet. Sci. Lett.* 393, 94–104.

774 Teichert, C., Kummel, B., 1972. Permian–Triassic boundary in the Kap Stosch area, east
 775 Greenland. *Bull. Canadian Petrol. Geol.* 20, 659–675.

776 Thomas, B., Willink, R., Grice, K., Twitchett, R., Purcell, R., Archbold, N., George, A., Tye,
 777 S., Alexander, R., Foster, C., 2004. Unique marine Permian–Triassic boundary section
 778 from Western Australia. *Austral. J. Earth Sci.* 51, 423–430.

779 Tian, S.F., Chen, Z.Q., Huang, C.J., 2014. Orbital forcing and sea-level changes in the earliest
 780 Triassic of the Meishan section, South China. *J. Earth Sci. (China Univ. Geosci.-Wuhan)*
 781 25, 64–73.

782 Tong, J., Zhao, L., 2011. Lower Triassic and Induan-Olenekian Boundary in Chaohu, Anhui
 783 Province, South China. *Acta Geol. Sin. (English edition)* 85, 399–407.

784 Wang, C., Visscher, H., 2007. Abundance anomalies of aromatic biomarkers in the
 785 Permian–Triassic boundary section at Meishan, China—evidence of end-Permian
 786 terrestrial ecosystem collapse. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 291–303.

787 Wang, Q., Tong, J., Song, H.J., Yang, H., 2009. Ecological evolution across the
 788 Permian/Triassic boundary at the Kangjiaping Section in Cili County, Hunan Province,
 789 China. *Sci. China D: Earth Sci.* 52, 797–806.

790 Wei, H.Y., Shen, J., Schoepfer, S.D., Krystyn, L., Richoz, S., Algeo, T.J., 2015.
 791 Environmental controls on marine ecosystem recovery following mass extinctions, with
 792 an example from the Early Triassic. *Earth-Sci. Rev.* 149, 108–135.

793 Whiteside, J.H., Grice, K., 2016. Biomarker records associated with mass extinction events.
 794 *Annu. Rev. Earth Planet. Sci.* 44, in press.

795 Wignall, P.B., Hallam, A., Lai, X.L., Yang, F.Q., 1995. Palaeoenvironmental changes across
 796 the Permian/Triassic boundary at Shangsi (N. Sichuan, China). *Historical Biology* 10,
 797 175–189.

798 Wignall, P., Hallam, A., 1996. Facies change and the end-Permian mass extinction in SE
 799 Sichuan, China. *Palaio* 11, 587–596.

800 Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction.
 801 *Science* 272, 1155–1158.

802 Winguth, C., Winguth, A.M.E., 2012. Simulating Permian–Triassic oceanic anoxia
 803 distribution: implications for species extinction and recovery. *Geology* 40(2), 127–130.

804 Xie, S., Pancost, R.D., Yin, H., Wang, H., Evershed, R.P., 2005. Two episodes of microbial
 805 change coupled with Permo/Triassic faunal mass extinction. *Nature* 434, 494–497.

806 Xie, S., Pancost, R.D., Huang, J., Wignall, P.B., Yu, J., Tang, X., Chen, L., Huang, X., Lai, X.,
 807 2007. Changes in the global carbon cycle occurred as two episodes during the
 808 Permian–Triassic crisis. *Geology* 35, 1083–1086.

809 Yang, H., Chen, Z.Q., Wang, Y., Tong, J., Song, H.J., Chen, J., 2011. Composition and
 810 structure of microbialite ecosystems following the end-Permian mass extinction in South
 811 China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 111–128.

812 Yang, H., Chen, Z.Q., Ou, W.Q., 2015a. Microconchids from microbialites near the
 813 Permian–Triassic boundary in the Zuodeng section, Baise area, Guangxi Zhuang
 814 Autonomous Region, South China and their paleoenvironmental implications. *J. Earth*

Sci. (China Univ. Geosci.-Wuhan) 26, 157–165.

Yang, H., Chen, Z.Q., Wang, Y., Ou, W.Q., Liao, W., Mei, X., 2015b. Microconchids from microbialite ecosystem immediately after end-Permian mass extinction: ecologic selectivity and implications for microbialite ecosystem structure. *Lethaia* 48, 497–508.

Yin, H.F., Zhang, K.X., Tong, J.N., Yang, Z.Y., Wu, S.B., 2001. The global stratotype section and point (GSSP) of the Permian–Triassic boundary. *Episodes* 24, 102–114.

Yin, H.F., Jiang, H., Xia, W., Feng, Q., Zhang, N., Shen, J., 2014. The end-Permian regression in South China and its implication on mass extinction. *Earth-Sci. Rev.* 137, 19–33.

Zhang, K., Tong, J., Yin, H., Wu, S., 1996. Sequence stratigraphy near the Permian–Triassic boundary at Meishan section, South China. In: Yin, H.F. (Ed.), *The Palaeozoic–Mesozoic Boundary Candidates of Global Stratotype Section and Point of the Permian–Triassic Boundary*. China University of Geosciences Press, Wuhan, pp. 72–83.

Zhao, L.S., Orchard, M.J., Tong, J.N., Sun, Z.M., Zuo, J.X., Zhang, S.X., Yun, A.L., 2007. Lower Triassic conodont sequence in Chaohu, Anhui Province, China and its global correlation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 24–38.

Figure captions

Fig. 1. Latest Permian paleogeography of world (A) and South China block (B), showing locations of the study sections: LLD – Laolongdong, CL – Cili, BL – Bulla, PRB – Peace River Basin, WBF – West Blind Fjord, KS – Kap Stosch, SP – Spitsbergen, PB – Perth Basin.

MS – Meishan, HZS – Huangzhishan. SS – Shangsi, CH – Chaohu. Note that, relative to its modern orientation (A), the South China craton was rotated nearly 90° counter-clockwise during the latest Permian (B); all references in the text to compass orientations are based on Permian-Triassic paleogeography. Estimated water depths for study sections in continental shelf (C) and ramp settings (D). FWWB – fair-weather wave base, SWB – storm wave base.

Fig. 2. (Top) Molecular structure of aromatic carotenoids (chlorobactene and isorenieratene). (Middle) Breakdown sequence leading to AIs. (Bottom) Structures of moretanes, fluorenes, DBF, DBT, BaP, and BeP.

Fig. 3. Stratigraphic ranges of the study sections (vertical stripes indicate uncertain age ranges) (modified from [Shen et al., 2015](#)). Abbreviations for biozones: *C.* = *Clarkina*, *H.* = *Hindeodus*, *I.* = *Isarcicella*, *N.* = *Neoclarkina*.

Fig. 4. Profiles of the abundance of aryl isoprenoids (AI, µg/g TOC) derived from green sulfur bacteria and the relative abundance of DBF (i.e., DBF/(DBF+DBT+F)) derived from terrestrial organic matter inputs. The blue and red lines represent the EPME and PTB horizons, respectively. Data source: [this study](#). Abbreviations for biozones (based on conodonts except as noted): *L. p.* and *U. p.* – lower and upper *Hindeodus praeparvus*, *H. p.* – *H. parvus*, *Pa.-Co.* – *Palaeofusulina-Colaniella* (foraminifer), *I. i.* – *Isarcicella isarcica*, *I. s.* – *I. staeschei*, *C. y.* – *Clarkina yini*.

Fig. 5. Profiles of the abundance of aryl isoprenoids (AI, $\mu\text{g/g TOC}$) derived from green sulfur bacteria and data derived from terrestrial organic matter inputs (i.e., DBF abundance). Data sources: Peace River Basin (Hays et al., 2007), Kap Stosch (Hays et al., 2012), Spitsbergen (Nabbefeld et al., 2010b), West Blind Fiord (Algeo et al., 2012), Perth Basin (Grice et al., 2005a; Thomas et al., 2004), Huangzhishan (Kaiho et al., 2012), Meishan (AI from Cao et al., 2009; $\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$ from Cao et al., 2009 (yellow) and Xie et al., 2007 (white)). Conodont zones: *C. m.* – *Clarkina meishanensis*, *H. c.* – *Hindeodus changxingensis*, *I. l.* – *Isarcicella lobata*, *H. t.* – *H. typicalis*, *C. ch.* – *C. changxingensis*, *C. t.* – *C. taylorae*, *M. s.* – *Mesogondolella sheni*, *C. h.* – *C. ch.* – *C. hauschkei*–*C. changxingensis*. Other details as in Figure 2.

Fig. 6. Profiles of the abundance of aryl isoprenoids (AI, $\mu\text{g/g TOC}$) derived from green sulfur bacteria and data derived from terrestrial organic matter inputs (i.e., DBF abundance). Data sources: Chaohu (Kaiho et al., 2012; red points, this study), Shangsi (this study). AI and DBT abundances for Chaohu have been normalized to phenanthrene (Phe). Other details as in Figure 2.

Fig. 7. Relationship of aryl isoprenoids (AI, $\mu\text{g/g TOC}$) to moretanes ($\text{C}_{30}\text{M}/\text{C}_{30}\text{HP}$) (A) and isorenieratane ($\mu\text{g/g TOC}$) to AI ($\mu\text{g/g TOC}$) (B) at Shangsi (SS). The blue and red dots represent pre-EPME and post-EPME samples, respectively.

Fig. 8. Expansion of photic-zone euxinia during the Permian-Triassic biotic crisis. Gray and

881 green shaded areas represent euxinia in the pre-EPME and post-EPME intervals, respectively

882 (A and B); black dots represent primary productivity (C, D, and E).

883

884

885 Table 1. Paleogeographic and paleoenvironmental characteristics of the 12 study sections

886

Figure1

Land
 Alluvial facies
 Neritic clastic facies
 Carbonate platform
 Basin

Figure2

Figure3

Figure4

Figure5

Figure6

Figure7

Figure8

Table1

Sections	Paleogeographic settings	Lithology of the PTB beds (<i>C. yini</i> - <i>I. isarcia</i> zones)	Water depth change up section	Environmental interpretation	Estimated water depth	Principal references
Bulla, northern Italy	western Tethys	Thick bedded bioclastic limestone to thin bedded oolitic limestone beds	Shallowing	near the FWWB	~20-30 m	Gorjan et al., 2007,2008; Farabegoli et al., 2007 Wang et al., 2009; Luo et al., 2013 Wu et al., 2006; Liu et al., 2010; Liao et al., 2010
Cili, South China	eastern Tethys	Massive reef like bioclastic limestone to massive microbialites and oolites	Deepening	near the FWWB	~20-40 m	
Laolongdong, South China	eastern Tethys	Thick bedded to massive bioclastic limestone to massive microbialites	Deepening	near the FWWB	~20-40 m	
Huangzhishan, South China	eastern Tethys	Medium-thick bedded bioclastic limestone to thin-medium bedded muddy limestone with claystone and mudstone	Deepening	upper part of FWWB-SWB zone	~40-80 m	Chen et al., 2009
Hovea-1, Perth Basin, Australia	northern margin of Gondwana	Mudstone, sandy siltstone and shelly storm beds to finely laminated mudstone and thin bedded limestone	Deepening	lower part of FWWB-SWB	~20-50 m	Thomas et al., 2004
Spitsbergen, Norway	shelf sea in Boreal Ocean	Sandstone with few mudstone to mudstone with sandstone, and thin bedded limestone	Deepening	near the SWB	~ 60-80 m	Mørk et al., 1999; Nabbefeld et al., 2010
Peace River Basin, Arctic Canada	northwestern margins of Pangea	Silty mudstone to Sandstone	Shallowing	near the SWB	~80-100 m	Hays et al., 2007
Kap Stosch	margin of Boreal Ocean (Greenland)	Shale and Siltstone to sandstone	Shallowing	near the SWB	~80-100 m	Hays et al., 2012
Meishan, South China	eastern Tethys	Medium-thick bedded bioclastic limestone to Thin bedded clay beds; thin bedded mudstone/shale; medium bedded limestone	Deepening	FWWB-SWB zone	~80-100m	Zhang et al., 1996; Chen et al., 2007, 2015; Tian et al., 2014
West Blind Fjord, Arctic Canada	Boreal Ocean basin	Chert to sandstone and siltstone	Shallowing	Below the SWB	~100-200 m	Algeo et al., 2012
Shangsi, South China	eastern Tethys	Thin bedded siliceous limestone to clay beds and thin bedded carbonaceous mudstone	Shallowing	inner shelf basin	~200-300 m	Wignall et al., 1999; Song-HJ et al., 2012; Lei et al., 2012

Chaohu, South
China

eastern Tethys

Thin bedded siliceous
Mudstone to medium bedded
carbonaceous limestone and claystone

Shallowing

inner shelf basin

~200-400m

Chen et al., 2011;
Song-HY et al., 2013