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Marine productivity changes during the end-Permian crisis and Early Triassic recovery

Jun Shen^{a,b}, Shane D. Schoepfer^c, Qinglai Feng^{a,*}, Lian Zhou^a, Jianxin Yu^d, Huyue Song^{b,d},
Hengye Wei^{b,e}, Thomas J. Algeo^{a,b,d,**}

^a State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences, Wuhan, Hubei 430074, PR China

^b Department of Geology, University of Cincinnati, Cincinnati, OH 45221-0013, USA

^c Department of Earth and Space Sciences, University of Washington, Seattle, WA 98195, USA

^d State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, Hubei 430074, PR China

^e Department of Earth Science, East China Institute of Technology, Nanchang, Jiangxi, Nanchang 330013, PR China

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ABSTRACT

The latest Permian mass extinction (LPME) coincided with major changes in the composition of marine plankton communities, yet little is known about concurrent changes in primary productivity. Earlier studies have inferred both decreased and increased productivity in marine ecosystems immediately following the end-Permian crisis. Here, we assess secular and regional patterns of productivity variation during the crisis through an analysis of the burial fluxes of three elemental proxies: total organic carbon (TOC), phosphorus (P), and biogenic barium (Ba_{bio}). Primary productivity rates appear to have increased from the pre-crisis Late Permian through the Early Triassic in many parts of the world, although the South China Craton is unusual in exhibiting a pronounced decline at that time. Most of the 14 Permian–Triassic study sections show concurrent increases in sediment bulk accumulation rates, suggesting two possible influences linked to subaerial weathering rate changes: (1) intensified chemical weathering, resulting in an increased riverine flux of nutrients that stimulated marine productivity, and (2) intensified physical weathering, leading to higher fluxes of particulate detrital sediment to continental shelves, thus enhancing the preservation of organic matter in marine sediments. An additional factor, especially in the South China region, may have been the intensified recycling of bacterioplankton-derived organic matter in the ocean-surface layer, reducing the export flux rather than primary productivity *per se*. The ecosystem stresses imposed by elevated fluxes of nutrients and particulate sediment, as well as by locally reduced export fluxes of organic matter, may have been important factors in the ~2- to 5-million-year-long delay in the recovery of Early Triassic marine ecosystems.

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* Corresponding author.

** Corresponding author at: State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences, Wuhan, Hubei 430074, PR China
E-mail addresses: qinglaifeng@cug.edu.cn (Q. Feng), thomas.algeo@uc.edu (T.J. Algeo).

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1. Introduction

1.1. Marine productivity changes during the Permian–Triassic crisis

The latest Permian mass extinction (LPME) was the largest biotic crisis of the Phanerozoic, resulting in an ~90% loss of species-level biodiversity among marine invertebrates (Erwin et al., 2002; Yin et al., 2012; Clapham, 2013). This event was accompanied by major changes in the composition of marine phytoplankton (Xie et al., 2005; Knoll et al., 2007; Payne and van de Schootbrugge, 2007; Lei et al., 2012; Shen et al., 2013a) and zooplankton communities (Feng and Algeo, 2014), suggesting a far-reaching restructuring of the marine trophic system. The end-Permian crisis was followed by an extended, ~2 to 5-Myr-long interval of delayed recovery in marine ecosystems (Payne et al., 2004; Chen and Benton, 2012) that may have been related to repeated major environmental perturbations (Algeo et al., 2011a; Retallack et al., 2011) and/or sustained elevated Earth-surface temperatures (Sun et al., 2012; Romano et al., 2013). These biotic developments played out against a backdrop of widespread marine anoxia (Wignall and Twitchett, 1996; Isozaki, 1997; Bond and Wignall, 2010) and unsettled conditions in the marine C and S cycles (Payne et al., 2004; Bottrell and Newton, 2006; Richoz et al., 2012; Song et al., 2014).

Changes in marine productivity rates during the Permian–Triassic transition have been the subject of much speculation without development of a consensus to date. Arguments for reduced primary productivity in the aftermath of the LPME have been based on drastically diminished fossil abundance (Twitchett, 2001; Payne, 2005; Twitchett, 2007), reductions in body size (the “Lilliput effect”) in many clades including molluscs (Twitchett, 2007), conodonts (Luo et al., 2008), sponges (Liu et al., 2013), and brachiopods (He et al., 2007, 2010), and negative excursions in marine carbonate $\delta^{13}\text{C}$ profiles (Rampino and Caldeira, 2005). On the other hand, arguments for increased primary productivity have been based on an increased frequency of organic-rich mudstones (Kakuwa, 1996; Suzuki et al., 1998), positive excursions in marine carbonate $\delta^{13}\text{C}$ profiles (Suzuki et al., 1998; Horacek et al.,

2007), and enhanced carbon-isotope depth gradients in Lower Triassic limestones (Meyer et al., 2011). The lack of agreement among these diverse records may indicate that many, and perhaps all, of them are not primarily related to variations in marine productivity.

A more quantitative approach to evaluation of marine productivity changes based on the fluxes of productivity-related sedimentary components has been developed in recent studies. Algeo et al. (2010) calculated organic carbon burial fluxes for Japanese deep-sea sections, showing significant increase just prior to and, possibly, following the end-Permian extinction event. These changes were accompanied by a major decline in radiolarian (zooplankton) productivity, probably due to upward expansion of the oceanic oxygen-minimum zone (Feng and Algeo, 2014). Algeo et al. (2013) undertook a more comprehensive analysis of 40 Permian–Triassic boundary (PTB) sections with a near-global distribution, back-calculating the organic carbon sinking flux to the sediment–water interface based on transfer functions accounting for diagenetic losses of organic matter due to aerobic and anaerobic respiration. They determined that sections in the South China region almost uniformly recorded a >50% decline in organic carbon burial during the end-Permian crisis, but that sections elsewhere showed variable changes with an average increase of ~400% that they attributed to a comparable increase in average bulk sediment accumulation rates.

Various proxies have been used to estimate paleomarine productivity, including carbon isotopes, biomineral fluxes, and elemental concentrations or fluxes (Zonneveld et al., 2010). The concentrations or fluxes of productivity-related elements have been widely used in this capacity owing to their ease of measurement and inferred relationship to primary productivity, especially organic carbon (Pedersen and Calvert, 1990; Canfield, 1994; Tyson, 2005), phosphorus (Filippelli and Delaney, 1996; Schenau and De Lange, 2001; Schenau et al., 2005), and biogenic barium (Dehairs et al., 1980, 1987; Dymond et al., 1992; see also reviews by Tribouillard et al. (2006); Calvert and Pedersen (2007). Schoepfer et al. (2014, this volume) examined the correlation of sedimentary fluxes of these three proxies to primary productivity in modern marine systems, establishing relationships that we apply in

the present study to an analysis of paleoproductivity during the Permian–Triassic transition.

The analysis below examines changes in productivity proxies in 14 PTB sections with a wide global distribution. The sections chosen for this study represent a wide diversity of depositional settings and facies, allowing us to explore patterns of productivity change linked to the LPME and Early Triassic recovery of marine ecosystems. The present study differs from that of Algeo et al. (2013) in (1) utilizing phosphorus (P) and biogenic barium (Ba_{bio}) in addition to organic carbon as productivity proxies, (2) making use of the recent analysis of modern systems by Schoepfer et al. (2014) to quantitatively estimate paleoproductivity, and (3) reconstructing productivity variation through a ~5-Myr interval spanning the Changhsingian Stage of the Late Permian through the Induan and early Olenekian stages of the Early Triassic, rather than for just the PTB *sensu stricto*.

1.2. Elemental proxies for paleoproductivity

Total organic carbon (TOC) concentrations depend, in part, on the flux of organic matter reaching the sediment and, in part, on the redox conditions at and just below the sediment–water interface (Pedersen and Calvert, 1990; Canfield, 1994; Schoepfer et al., 2014). The sinking flux of organic carbon is commonly proportional to the export flux, i.e., the rate of organic carbon sinking out of the euphotic zone, although it tends to show a weaker or non-existent relationship to primary productivity itself owing to sometimes intense recycling of organic matter within the ocean-surface layer (Sigman and Hain, 2012; Schoepfer et al., 2014). Once organic matter arrives at the sediment–water interface, its fate depends on the redox conditions in the upper part of the sediment column. A higher percentage of organic carbon is preserved under reducing conditions than under oxic conditions, although this difference diminishes sharply with increasing sedimentation rates (Pedersen and Calvert, 1990; Canfield, 1994; Tyson, 2005).

Phosphorus (P) concentrations can show a good relationship to marine productivity owing to its close association with organic carbon (Schenau et al., 2005; Schoepfer et al., 2014). The fate of P in the burial environment depends strongly on sediment redox conditions. If sediment pore waters are entirely reducing, P that is remineralized during decay of organic matter tends to diffuse out of the sediment back into the water column (Föllmi, 1996; Algeo and Ingall, 2007), resulting in quite low sediment P concentrations even in high productivity areas (Kraal, 2010). On the other hand, decay in or upward diffusion into oxic sediment porewaters commonly results in P being adsorbed onto Fe(III)-oxyhydroxides (Schenau and De Lange, 2001; Algeo and Ingall, 2007; Schoepfer et al., 2014). P adsorbed in this manner tends to be converted later in the deep diagenetic environment to authigenic phosphate phases (Anderson et al., 2001). Marine systems characterized by high rates of productivity and having persistently suboxic or variably fluctuating redox conditions are the most prone to high accumulation rate of P (PAR) (Algeo and Ingall, 2007).

Biogenic barium (Ba_{bio}) is a potential proxy for export productivity owing to formation of authigenic barite in sinking organic particles or aggregates (Dehairs et al., 1980, 1987, 1992; Jaccard et al., 2013). Seawater is nearly saturated with respect to the mineral barite, and a local increase in sulfate concentration on the surfaces of sinking organic particles due to oxidation of H_2S from particle interiors causes barite precipitation. Authigenic barite has a relatively high preservation potential in the sediment, especially under oxic to suboxic conditions, with an average preservation rate of ~30% (Dymond et al., 1992). For this reason, Ba_{bio} commonly shows a strong correlation to nutrient content and/or productivity of ocean-surface waters (Dehairs et al., 1980, 1992; Schoepfer et al., 2014). However, under reducing conditions, authigenic barite may be reductively dissolved and lost to the water column through diffusion out of the sediment (Dymond et al., 1992).

2. Materials and methods

2.1. Study sections

For this study, we chose 14 sections with a wide global distribution (Fig. 1) and representing a range of water depths from shallow-platform or shelf to deep-ocean (Fig. 2A). The sections can be arranged into four regional groupings. For the South China Craton, two sections represent shallow shelf or platform settings (Zuodeng and Nih Tao) and five represent deep-ramp or basinal settings (Chaohu, Daxiakou, Dongpan, Shangsi, and Xinmin; Fig. 1B). The non-Chinese Tethyan region is represented by two sections (Guryul Ravine and Mud), the N&W Pangean region by four intermediate to deepwater sections (Spitsbergen, Kap Stosch, West Blind Fiord, and Opal Creek), and the Panthalassic region by a single abyssal section (Gujo-Hachiman; Fig. 1A). The dominant lithologies vary geographically: mainly carbonates throughout the Tethyan region (with the exception of Chaohu and Dongpan, which is dominated by calcareous mudstone, muddy carbonate, and chert), but mainly siliciclastics in the N&W Pangean and Panthalassic regions. However, all sections show a shift toward more clay-rich compositions in the Early Triassic as a consequence of intensified weathering and elevated fluxes of detrital sediment from continents (Fig. 2B; Algeo and Twitchett, 2010).

2.1.1. Chaohu, Anhui Province, China

The Chaohu area is located on the northern margin of the South China Craton (Fig. 1B) and represents deposition in a deep-ramp setting at water depths of ~300–500 m (Fig. 2A; Tong et al., 2002; Chen et al., 2010). The well-exposed Early Triassic strata around Chaohu have been the subject of many biostratigraphic, sedimentologic, and geochemical studies (Zhao et al., 2002; Tong et al., 2004; Zhao et al., 2004; Tong et al., 2007a, 2007b; Zhao et al., 2007; Guo et al., 2008; Gui et al., 2009). The West Pingdingshan section was proposed as a candidate for the Global Boundary Stratotype Section and Point (GSSP) of the Induan–Olenekian Boundary (Tong et al., 2004). In this study, we integrated three sections (West Majiashan, West Pingdingshan, and South Majiashan) to generate a composite section spanning most of the Lower Triassic. Our composite section begins in the pre-crisis upper Changhsingian stage, which consists of siliceous mudstone of the Dalong Formation assigned to the *Clarkina changxingensis* Zone. The overlying Lower Triassic Yinkeng Formation consists of interbeds of calcareous mudstone and argillaceous limestone comprising ~28 m of Griesbachian strata and ~13 m of Dienerian strata. Up section, the Smithian-age Helongshan Formation consists mainly of calcareous mudstone, and the Spathian-age Nanlinghu Formation consists mainly of limestone with a few calcareous mudstone interbeds. The entire succession has been subdivided into ~14 conodont zones offering a high level of stratigraphic resolution (Tong and Zhao, 2005; Tong et al., 2007a; Zhao et al., 2007).

2.1.2. Daxiakou, Hubei Province, China

The Daxiakou section was deposited on the northern margin of the South China Craton (Fig. 1B) in a deep-shelf setting at water depths of ~200–300 m (Lai et al., 2001; Zhao et al., 2005) (Fig. 2A). It has been the subject of many biostratigraphic, sedimentologic, and geochemical studies (Wang and Xia, 2004; Zhao et al., 2005; Tong et al., 2007b; Wang et al., 2008; Li et al., 2009; Zhang et al., 2009a, 2009b; Hong et al., 2011; Shen et al., 2012a; Wu et al., 2012; Shen et al., 2013b; Zhao et al., 2013). The Daxiakou section ranges from the upper Middle Permian to the upper Lower Triassic. The Permian strata contain the upper Maokougian (~28 m), the Wuchiapingian (~44 m), and the Changhsingian stages (~92 m). The Maokougian and Wuchiapingian are composed of limestone of the Maokou Formation and Wujiaping Formation (Wang et al., 2008), and the Changhsingian consists of the Changxing Formation (dominated by limestone) in the lower part and the Dalong Formation (composed of mudstone and shale, with

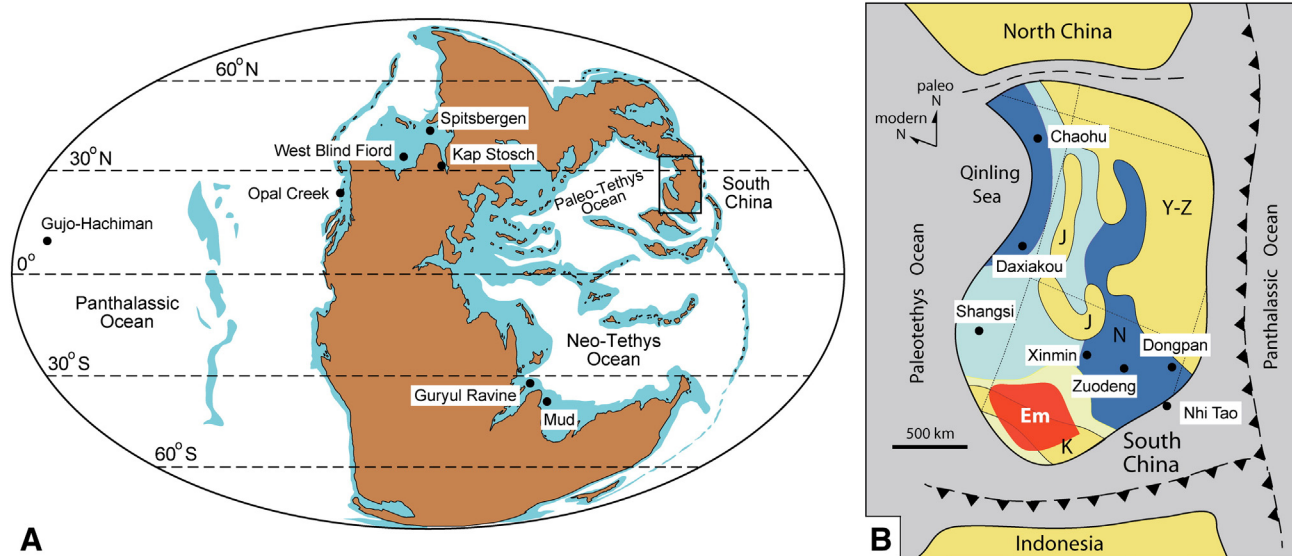


Fig. 1. Paleogeography of world (A) and South China Craton (B) at the Permian–Triassic boundary (~252 Ma). The rectangle in A shows location of inset map B. Locations are shown for the study sites on the South China Craton (Chaohu, Daxiakou, Shangsi, Dongpan, Xinmin, Zuodeng, and Nhi Tao), in the Neotethys Ocean (Guryul Ravine, Mud), on the northern and western Pangean margins (West Blind Fiord, Spitsbergen, Kap Stosch, and Opal Creek), and in the Panthalassic Ocean (Gujo-Hachiman). Abbreviations in B: Em = Emeishan flood basalts, J = Jiangnan Uplift, K = Khamdian Uplift, N = Nanpanjiang Basin, and Y–Z = Yunkai–Zhemu uplifts. Paleogeography of world from <http://jan.ucc.nau.edu/~rcb7/>; map of South China Craton from [Scotese and Langford \(1995\)](#) and [Stampfli and Borel \(2001\)](#).

scattered interbeds of marl and volcanic ash) in the upper part (Wang and Xia, 2004; Shen et al., 2013b). The Triassic strata contain the Griesbachian (~15 m), Dienerian (~19 m), and lower Smithian substages (~32 m), and consist of argillaceous limestone and mudstone deposits of the Daye Formation (Figs. 3 and 6, Tong et al., 2007b). Biostratigraphic studies have produced a detailed conodont biozonation for this section (Tong et al., 2007b).

2.1.3. Dongpan, Guangxi Province, China

The Dongpan section was deposited on the southern margin of the South China Craton (Fig. 1B). An abundance of radiolarians in siliceous mudstones document a deep-shelf depositional environment at water depths of ~300–500 m (Fig. 2A; He et al., 2005, 2007; Feng et al., 2007). This section has been the subject of paleoecological and biostratigraphic studies of numerous fossil groups, including radiolarians (Feng and Gu, 2002; He et al., 2005; Feng et al., 2007; Jin et al., 2007; Wu and Feng, 2008), sponges (Liu et al., 2008, 2013), conodonts (Luo et al., 2008), forams (Gu et al., 2005), brachiopods (He et al., 2007), and bivalves (He et al., 2005). The geochemistry of the section was analyzed by Shen et al. (2012b). The section comprises the upper Changhsingian stage (~8 m), which consists of chert and siliceous mudstone of the Dalong Formation, and the lower Griesbachian substage (~4 m), which consists of mudstone of the Daye Formation (Shen et al., 2012b). Radiolarians in the Upper Permian part of the section indicate an assignment to the *Albaillella yaoi*–*A. degradans* Zone, but only a few fauna (e.g., the ammonoid *Ophiceras*, He et al., 2005) have been found in the Lower Triassic beds (Figs. 3 and 6, Feng et al., 2007).

2.1.4. Nhi Tao, Vietnam

The Nhi Tao section was on the southern margin of the South China Craton during the Permian–Triassic transition (Fig. 1B; Lepvrier et al., 2004). It was an isolated carbonate platform within the Nanpanjiang Basin deposited at water depths of ~10–30 m (Fig. 2A). The section has been the subject of both biostratigraphic and geochemical studies (Doan et al., 2004; Nguyen et al., 2004; Algeo et al., 2007a; Son et al., 2007; Algeo et al., 2008a). The 7.2-m-thick section consists of limestones of the uppermost Changhsingian Dong Dang Formation and lowermost Griesbachian Hong Ngai Formation, the latter containing microbial framestones (Figs. 3 and 6; Algeo et al., 2007a).

2.1.5. Shangsi, Sichuan Province, China

The Shangsi section was located on the northwestern margin of the South China Craton (Fig. 1B). Its lithologies and faunas indicate deposition in a deep shelf environment at water depths of ~200–500 m (Fig. 2A, Wignall et al., 1995). This section offers one of the most detailed records of events during the Permian–Triassic transition and was proposed as a candidate for the GSSP of the PTB (Lai et al., 1996). Studies of its biostratigraphy, lithofacies, geochronology, and geochemistry have been undertaken (Li et al., 1986; Heller et al., 1988; Zhou and Kyte, 1988; Wignall et al., 1995; Lai et al., 1996; Nicoll et al., 2002; Mundil et al., 2004; Riccardi et al., 2006, 2007; Jiang et al., 2011; Shen et al., 2011, 2013a). The interval of the present study spans the upper Wuchiapingian stage through lower Griesbachian substage (Fig. 3; Li et al., 1986; Lai et al., 1996; Jiang et al., 2011). The Wuchiapingian and Changhsingian (~28 m) consist of chert, calcareous mudstone, and argillaceous limestone of the Dalong Formation, and the Griesbachian (~3 m) is composed of calcareous mudstone with volcanic tuff interbeds that are assigned to the Feixianguan Formation (Lai et al., 1996). *C. orientalis* was recovered from the Wuchiapingian beds, *C. yini* and *C. meishanensis* from the Changhsingian beds, and *C. taylorae* from the Griesbachian beds (Figs. 3 and 6; Nicoll et al., 2002; Jiang et al., 2011).

2.1.6. Xinmin, Guizhou Province, China

The Xinmin section is located within the Nanpanjiang Basin, on the southern margin of the South China Craton (Fig. 1B). Its lithologies and faunas indicated deposition in a deep shelf setting at water depths of ~200–500 m (Fig. 2A; Shen et al., 2013c). Detailed geochemical and fauna studies have been undertaken (Shen et al., 2012a, 2013a, 2013c). The upper Changhsingian (~8 m) consists of siliceous mudstone and limestone of the Dalong Formation, which has yielded *C. changxingensis* and *C. meishanensis* zones. The lower Griesbachian (~3 m) consists of mudstone of the Daye Formation, containing only a few bivalves (Figs. 3 and 6; Shen et al., 2013c). Numerous volcanic ash beds are found throughout the section (Shen et al., 2012a, 2013a).

2.1.7. Zuodeng, Guizhou Province, China

The Zuodeng section was located on the Great Bank of Guizhou (Fig. 1B), a large, isolated carbonate platform in the Nanpanjiang Basin (Tong et al., 2007b). It represents a shallow shelf environment with

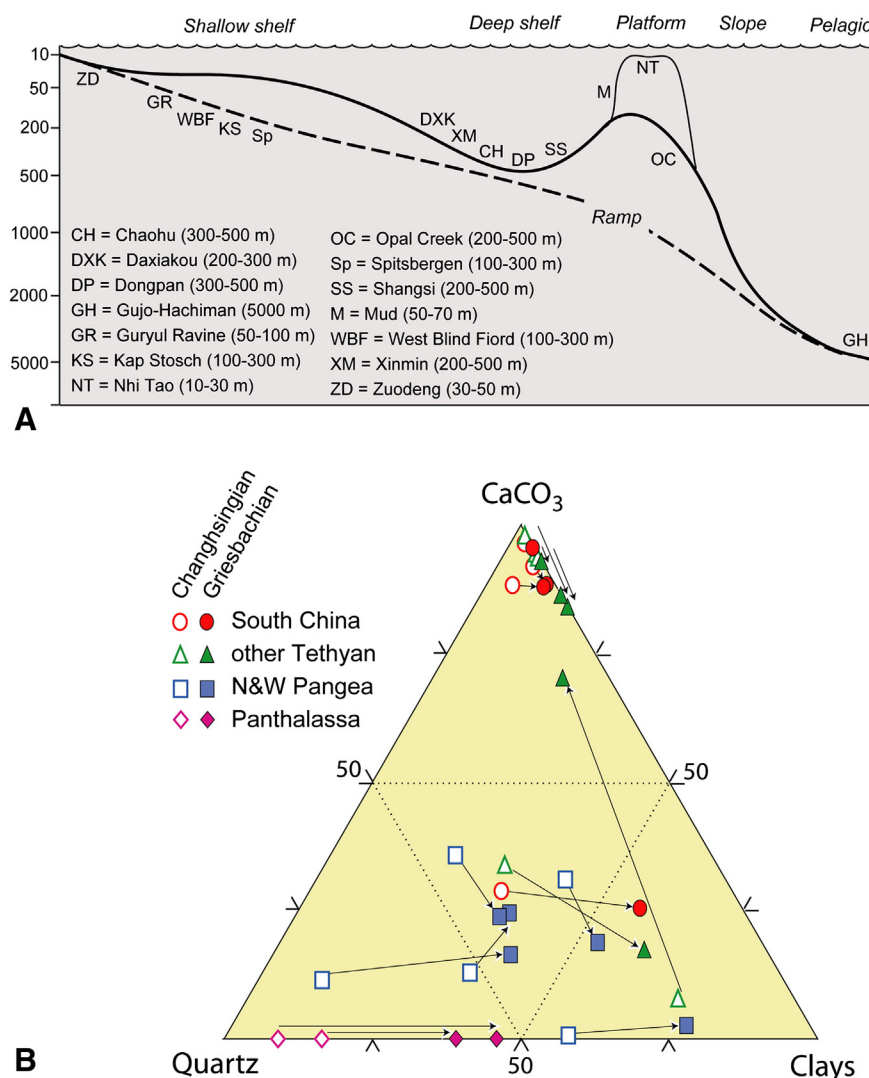


Fig. 2. (A) Location of study sections within a generalized depositional profile. See text for discussion of individual sections. (B) Changes in mineralogy from the Changhsingian (Late Permian) to the Griesbachian (Early Triassic) of the study sections; note the general shift toward more clay-rich compositions in the Early Triassic (from Algeo and Twitchett (2010)).

water depths of ~30–50 m (Fig. 2A; Lehrmann et al., 2007; Yin et al., 2014). The section comprises the upper Changhsingian Heshan Formation (~22 m) and Lower Triassic Luolou Formation (~87 m). The latter contains strata of Griesbachian through mid-Spathian age and has been the subject of detailed conodont biostratigraphic studies (Figs. 3 and 6, Tong et al., 2007b).

2.1.8. Guryul Ravine, Kashmir, India

The Guryul Ravine section was located in the southern Neo-Tethys Ocean (Fig. 1A) and was deposited in a carbonate ramp setting at water depths of ~50–100 m (Fig. 2A; Brookfield et al., 2003). It was proposed as a candidate for the GSSP of the PTB (Kapoor, 1996) and has been the subject of much research (Baud et al., 1996; Kapoor, 1996; Wignall et al., 1996; Orchard and Krystyn, 1998; Brookfield et al., 2003; Kozur, 2003; Korte and Kozur, 2005; Shen et al., 2006; Algeo et al., 2007b; Brookfield et al., 2013). It contains the Upper Permian Zewan and Lower Triassic Khunamuh formations (Brookfield et al., 2003). The present study interval ranges from the upper Changhsingian (~10 m) to the upper Griesbachian (~11 m) (Figs. 3 and 7; Algeo et al., 2007b). It has been extensively studied biostratigraphically with respect to both conodont and ammonoid faunas (Kapoor, 1996; Orchard and Krystyn, 1998; Kozur, 2003; Korte and Kozur, 2005).

2.1.9. Mud, Spiti Valley, Himachal Pradesh, India

The Mud section was located on the southern margin of the Neo-Tethys Ocean (Fig. 1A). It was deposited in a carbonate ramp setting at water depths of ~50–70 m (Fig. 2A; Krystyn and Orchard, 1996; Krystyn et al., 2004, 2007). The section had been studied in detail and is a candidate for the GSSP of the Induan–Olenekian boundary (Krystyn et al., 2007; Orchard and Krystyn, 2007; Richoz et al., 2007). It comprises strata of Wuchiapingian and Griesbachian to lower Spathian age, with a prominent hiatus during the Changhsingian (Figs. 3 and 7; Krystyn and Orchard, 1996). The Wuchiapingian Kuling Group is ~11 m thick. The Lower Triassic strata (~16 m) consist of the *Otoceras* Beds, *Gyronites* Beds, *Flemingites* Beds, and *Parahedenstroemia* Beds in ascending order from the Griesbachian to the lower Spathian, and the Niti Limestone Member in the upper Spathian (Figs. 3 and 6; Krystyn et al., 2007).

2.1.10. Kap Stosch, East Greenland

The Kap Stosch section was deposited in a rift basin on the embayed northern margin of Pangea (Fig. 1A). The rapidly subsiding basin accumulated sediments at rates up to ~800 m Myr⁻¹ at water depths of ~100–300 m (Fig. 2A). The Upper Permian Foldvik Creek Formation consists of limestone and shale deposits from which the ammonoid *Cyclolobus* was recovered (Teichert and Kummel, 1976). The PTB

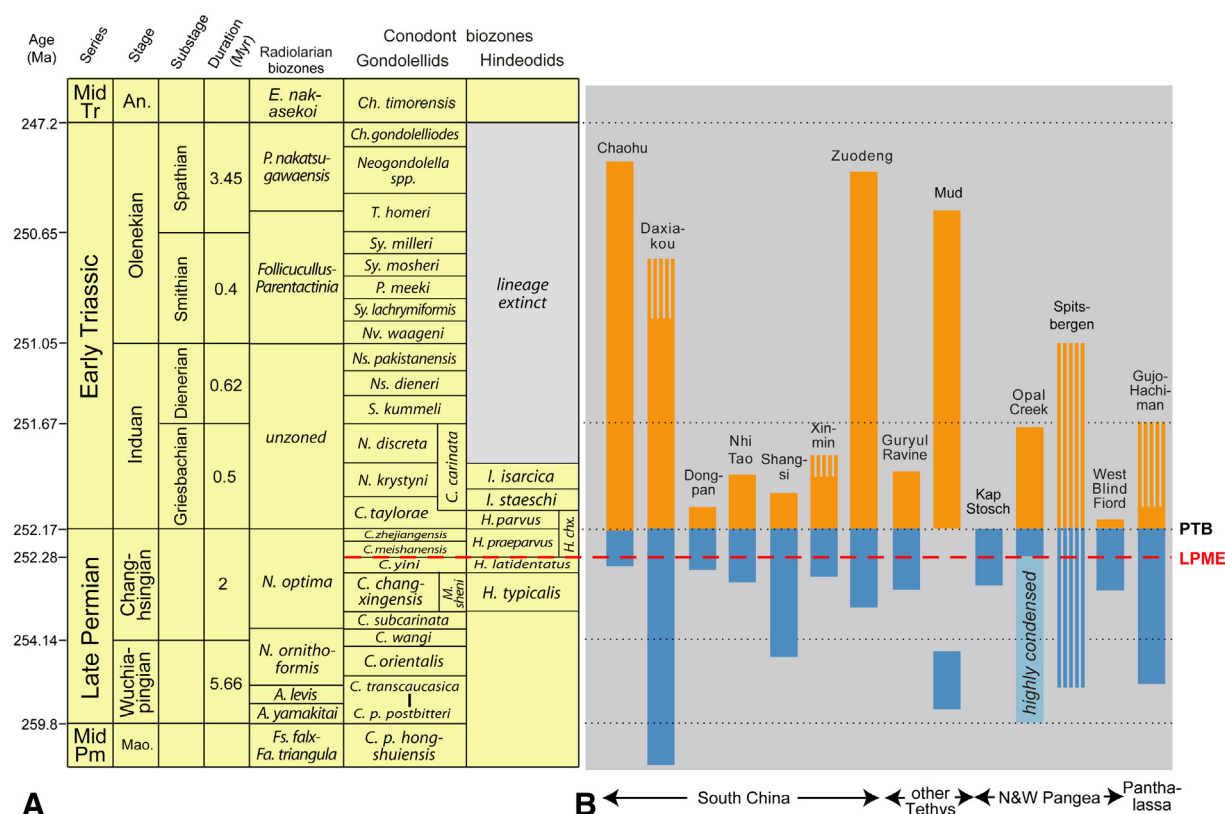


Fig. 3. (A) Timescale and biostratigraphic zonation for the Late Permian–Early Triassic (modified from Algeo et al. (2013); see text for more information). (B) Stratigraphic ranges of the study sections (vertical stripes indicate uncertain age ranges). Abbreviations: radiolarian genera: A. = Albaillella, E. = Eptingium, Fa. = Foremanhelena, Fs. = Follicucullus, N. = Neobaillella, P. = Parentactinia; conodont genera: C. = Clarkina, Ch. = Chiosella, H. = Hindeodus, I. = Isarcicella, M. = Mesogondolella, N. = Neoclarkina, Ns. = Neospathodus, Nv. = Novispathodus, P. = Paulella, S. = Sweetospathodus, Sy. = Scythogondolella, T. = Triassospathodus.

transition is marked by an abrupt shift to shales and sandstones of the Wordie Creek Formation (Teichert and Kummel, 1976; Stemmerik et al., 2001). Locally, the boundary coincides with a depositional hiatus overlain by a conglomerate containing fragments of fossil species that disappeared during the crisis (Teichert and Kummel, 1976). This area has been the subject of a number of recent chemostratigraphic studies (Hays et al., 2007, 2012; Nabbefeld et al., 2010). The present study interval consists of the Changhsingian stage, containing part of the *M. sheni* Zone (equal to the *C. changxingensis* Zone) (~5.3 m) and the *C. meishanensis* Zone (~5.7 m) (Figs. 3 and 7).

2.1.11. Opal Creek, Kananaskis Country, Western Canada

The Opal Creek section was deposited on the western margin of Pangea in a slope setting at water depths of ~200–500 m (Figs. 1A and 2A; Henderson, 1997). This section has been the subject of several biostratigraphic and chemostratigraphic studies (Henderson, 1997; Farley et al., 2005; Schoepfer et al., 2012, 2013). The Lower and Middle Permian are represented by the Johnston Canyon Formation and Ranger Canyon Formation, comprising cherts deposited in a productive continent-margin upwelling system (Schoepfer et al., 2012). The Upper Permian is represented by a thin (~1 m), highly condensed interval of chert and siltstone at the base of the Sulphur Mountain Formation assigned to the *M. sheni* and *C. hauschkei*–*C. meishanensis* zones of Changhsingian age. The Lower Triassic consists of ~42 m of organic-rich silty shales and siltstones of the Sulphur Mountain Formation assigned to the *H. parvus*–*C. taylorae* and *C. taylorae*–*C. cf. carinata* zones of Griesbachian age (Figs. 3 and 7; Schoepfer et al., 2012).

2.1.12. Spitsbergen, Svalbard, Norway

The Spitsbergen section was deposited on the northern margin of Pangea (Fig. 1A) in a ramp setting at water depths of ~100–300 m

(Fig. 2A). The ~90-m-thick Kap Starostin and ~93-m-thick Vardebukta formations represent the Upper Permian (Wuchiapingian–Changhsingian) and Lower Triassic (Griesbachian to lower Dinerian), respectively (Figs. 3 and 7; Buchan et al., 1965; Wignall et al., 1998).

2.1.13. West Blind Fiord, Arctic Canada

The West Blind Fiord section was deposited in the Sverdrup Basin, a craton-margin sag underlying the northern Canadian Arctic region (Fig. 1A; Embry and Beauchamp, 2008). This area has been the subject of a number of recent sequence stratigraphic and chemostratigraphic studies (Grasby and Beauchamp, 2008, 2009; Beauchamp et al., 2009; Grasby et al., 2011; Algeo et al., 2012). The section was deposited in a slope setting on the southeastern basin margin at water depths of ~100–300 m (Algeo et al., 2012). It consists of the uppermost 6 m of the upper Changhsingian Lindström Formation and the lowestmost 18 m of the uppermost Changhsingian–lower Griesbachian Blind Fiord Formation. Detailed conodont biostratigraphic studies have established the presence of the *M. sheni*, *C. hauschke* zones (equivalent to the upper part of *C. changxingensis* and *C. yini* zones at Meishan; Yin et al., 2001; Zhang et al., 2009a), and the *C. meishanensis* Zone in the Changhsingian, and the *H. parvus*–*C. taylorae* zones in the Griesbachian (Figs. 3 and 7; Algeo et al., 2012).

2.1.14. Gujo-Hachiman, Japan

The Gujo-Hachiman section was located in the central equatorial Panthalassic Ocean (Fig. 1A) and represents pelagic deep-ocean deposition at water depths of ~5000 m (Fig. 2A; Ando et al., 2001; Algeo et al., 2010, 2011b). The section comprises 6.9 m of green–gray ribbon chert of Late Permian age and 0.6 m of black shale of Early Triassic age (Algeo et al., 2010, 2011b). Radiolarian and conodont studies suggest that the Late Permian chert contains both the *Neoclarkina optima*–*Albaillella*

lauta Zone of Wuchiapingian age and the *A. angusta*–*A. flexa*, *A. triangularis*, *A. yaoi*, and *A. degradans* zones of Changhsingian age (Kuwahara and Yao, 2001; Yao et al., 2001; Xia et al., 2004). The Lower Triassic black shale largely lacks datable fossils but is thought to be of Griesbachian age (Figs. 3 and 7; Xia et al., 2004).

2.2. Provenance of organic matter

An important consideration in productivity studies is the source of organic matter in marine sediments. The bulk of TOC in marine sediments is commonly derived from marine phytoplankton although substantial fractions of terrestrially derived organic matter can be present in coastal areas (Hedges and Parker, 1976; Schowers and Angle, 1986; Gordon and Goñi, 2004). However, terrigenous influence may be minimal if fluvial inputs are limited (as in modern Narragansett Bay, Rhode Island; Gearing et al., 1984). Sediments deposited in deeper offshore areas (Calvert, 1987; Murray et al., 1994) and on isolated carbonate shelves and platforms (Lamb and Swart, 2008; Oehlert et al., 2012) tend to contain little organic matter of terrigenous origin. Another potential source of organics is recycled organic matter, ultimately of either marine or terrestrial origin, from subaerially weathered sedimentary rocks (Jiang et al., 2012; Johnston et al., 2012; Meyer et al., 2013). The flux of such material is roughly proportional to terrigenous sediment flux and, hence, also depends on fluvial influence.

The importance of possible terrigenous inputs to the 14 study sections can be inferred from various considerations, although it is not possible to strictly quantify such inputs. Paleogeographic factors argue against input of significant amounts of terrigenous debris to sections on the South China Craton: Zuodeng and Nih Tao were located on isolated carbonate platforms, and even the deep-ramp and basinal sections (Chaohu, Daxiakou, Dongpan, Shangsi, and Xinmin) are unlikely to have accumulated much terrigenous material owing to the small size of subaerially exposed landmasses on the periphery of the craton (Fig. 1B). These inferences are supported by petrographic, isotopic, and biomarker studies of these and correlative sections on the South China Craton (Kaiho et al., 2012; Sawada et al., 2012; Meyer et al., 2013; Luo et al., 2014; Saitoh et al., 2014).

Most of the non-Chinese sections in this study are likely to have accumulated some amount of terrigenous organic material owing to their locations on continental margins adjacent to large landmasses and their dominantly siliciclastic character. Petrographic analysis revealed relatively few organic macerals of terrigenous origin in the Mud and Guryul Ravine sections (J.C. Hower and T.J. Algeo, unpubl. data) and moderate quantities in the West Blind Fiord (Algeo et al., 2012) and Opal Creek (Schoepfer et al., 2013) sections. Large amounts of marine organic matter are present in sections from the northern and northwestern margins of Pangea, as shown by biomarker data (Hays et al., 2007; Algeo et al., 2012). Terrigenous inputs become increasingly important in the East Greenland–Spitsbergen–Norway region, where mixed marine–terrestrial organic matter assemblages are dominant (Fenton et al., 2007; Hermann et al., 2010; Nabbefeld et al., 2010; Hays et al., 2012). On the other hand, the abyssal Gujo-Hachiman section, located in the central Panthalassic Ocean (Fig. 1A), is unlikely to contain much terrigenous organic matter (Algeo et al., 2010, 2011b). The bulk of the organic matter in all sections is considered to be of marine origin. Further information regarding organic matter sources in the study sections is given in Algeo et al. (2013; their supplement, section 2.1).

2.3. Methods

2.3.1. Time scale and linear sedimentation rate

A plethora of recent biostratigraphic and radiometric studies have made possible development of a high-resolution timescale for the Permian–Triassic transition that was first published by Algeo et al. (2013) and was subsequently used in a slightly revised form in this

volume (Wei et al., in press; this study). The key stratigraphic tie-points are the Middle–Late Permian (259.8 Ma) and Wuchiapingian–Changhsingian boundaries (254.14 Ma; Gradstein et al., 2012), the LPME horizon (252.28 Ma) and PTB (252.17 Ma) (Shen et al., 2011), the Griesbachian–Dienerian boundary (interpolated at 251.67 Ma based partly on Wu et al. (2012)), and the Induan–Olenekian (251.05 Ma), Smithian–Spathian (250.65 Ma), and Early–Middle Triassic boundaries (247.2 Ma) (based on radiometric dating studies of Lehrmann et al. (2006); Ovtcharova et al. (2006); Galfetti et al. (2007)). These dates yield the stage and substage durations shown in Fig. 3 (see Algeo et al. (2013), for more details). Dates for individual conodont zones were obtained from a Milankovitch cyclostratigraphic analysis of the Daxiakou section (Wu et al., 2012) and the U–Pb dating of Meishan section (Shen et al., 2011), giving the following estimated zonal durations: *C. changxingensis* ~950 kyr, *C. meishanensis* ~110 kyr, *C. zhang* ~70 kyr, *C. iranica* ~60 kyr, *C. hauschkei* ~15 kyr, *C. meishanensis*–*H. praeparvus* ~120 kyr, *H. parvus* ~34 kyr, *I. staeschei*–*I. isarcica* ~24 kyr, and *N. discreta* ~66 kyr. The durations of the Griesbachian and Dienerian substages derived by Wu et al. (2012), i.e., 490 kyr and 670 kyr, respectively, are significantly different from those used by Algeo et al. (2013), i.e., 730 kyr and 270 kyr, respectively, necessitating some adjustments to the timescale of the latter. In this study, we used estimated durations of 260 kyr, 160 kyr, and 70 kyr for the *H. parvus*–*I. isarcica*, *N. krystyni*, and *N. discreta* zones, respectively. These estimates are based on a sum totaling to the inferred duration of the Griesbachian substage (490 kyr) and proportionate to the stratigraphic thicknesses represented by each biozone.

The stratigraphic ranges of our 14 study sections vary considerably, some spanning most of the Upper Permian–Lower Triassic but others representing more limited intervals around the PTB (Fig. 3). We classified them into two groups as a function of section duration. One group represents stratigraphically long sections (Chaohu, Daxiakou, Dongpan, Shangsi, Mud, Xinmin, Zuodeng, Spitsbergen, Opal Creek, and Gujo-Hachiman), in which we focus on productivity variation at the level of stratigraphic stages or substages. The second group represents stratigraphically short sections that narrowly straddle the PTB, in which we focus on productivity variation at the level of individual conodont zones (Guryul Ravine, Kap Stosch, Nih Tao, and West Blind Fiord).

We calculated sedimentation rates and fluxes by stage and substage for the long sections and by conodont biozone for the short sections, when such zonation data were available. For the stratigraphic interval of interest, linear sedimentation rates (LSRs) were calculated as:

$$\text{LSR} = \text{thickness} / \text{duration} \quad (1)$$

where LSR is linear sedimentation rate in units of m Myr^{−1}. For the long sections that were evaluated at the stage/substage level, we found it convenient to consider the short interval between the LPME horizon and the PTB (~110 kyr; Shen et al., 2011) as part of the Early Triassic Griesbachian substage rather than as part of the Late Permian Changhsingian Stage. The reason is that the largest changes in sedimentation and marine productivity occurred at the LPME horizon, and assigning the post-crisis latest Permian beds to the Changhsingian would have biased flux calculations for that stage (cf. Algeo and Twitchett (2010); Algeo et al. (2013), who adopted the same convention). Thus, all durations and thicknesses for the Griesbachian began at the LPME horizon, not at the PTB.

2.3.2. Geochemical analyses

Study samples were analyzed in two different laboratories. Samples from some of the South China sections (Dongpan, Xinmin, and Shangsi) were analyzed at the China University of Geosciences (Wuhan). Major element abundances were determined by wave length-dispersive X-ray fluorescence (XRF) analysis of fused glass beads using a XRF-1800 in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan), and trace elements were

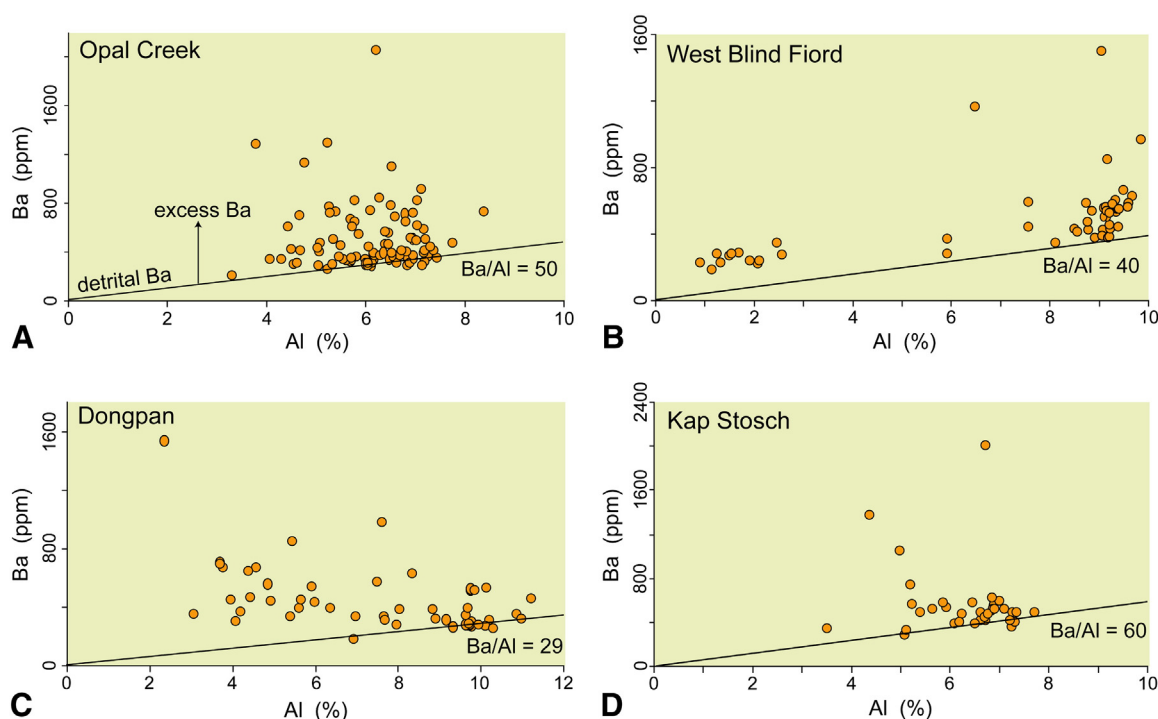


Fig. 4. Ba–Al crossplots for four study sections: (A) Opal Creek, (B) West Blind Fiord, (C) Dongpan, and (D) Kap Stosch. Ba–Al data for the other study sections is given in Table 1. Ba/Al ratios in A–D are in units of 10^{-4} (i.e., ppm/%).

measured using an Agilent 7500a inductively coupled plasma mass spectrometry (ICP-MS) at the State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences (Wuhan). The remaining study sections were analyzed at the University of Cincinnati, where major- and trace-element concentrations were determined by wavelength-dispersive Rigaku 3040 X-ray fluorescence (XRF) on pressed-powder mounts. For both labs, results were calibrated using USGS and internal standards (analyzed by XRAL Incorporated using XRF and INAA). Analytical precision based on replicate analyses was better than $\pm 2\%$ for major and minor elements and $\pm 5\%$ for trace elements, and detection limits were 1–2 ppm for most trace elements. TOC concentrations for all samples were measured using an Eltra 2000 C-S analyzer at the University of Cincinnati. Data quality was monitored via multiple analyses of USGS SDO-1 standard, yielding an analytical precision (2σ) of $\pm 2.5\%$ of the reported values for TOC.

2.3.3. Paleoproductivity proxy and flux calculations

Phosphorus speciation studies have shown that P can be present in multiple forms in marine sediments (Filippelli and Delaney, 1996; Schenau and De Lange, 2001; Schenau et al., 2005). However, all but the detrital P fraction are regarded as ‘reactive P’ that is ultimately derived from organic matter through recycling processes within the sediment (Schenau et al., 2005; Algeo and Ingall, 2007). Where determinations have been made, detrital P represents $<20\%$ of total P in both modern and ancient marine sediments (Algeo and Ingall, 2007). We therefore assume that total P is a good approximation of reactive P of organic origin (P_{org}) in the present study samples.

Ba is an element that commonly resides mainly in the detrital fraction of the sediment. Determining any authigenic Ba contribution requires estimating the amount of Ba present in the detrital fraction and subtracting this value from the total Ba concentration of the sample (Tribouillard et al., 2006). Al, which is generally of detrital origin and relatively immune to diagenetic remobilization, is commonly used to estimate the detrital fraction (Saito et al., 1992; Hetzel et al., 2011). We calculated the non-detrital or ‘excess’ fraction of total Ba as:

$$Ba_{xs} = Ba_{total} - Al \times (Ba/Al)_{detr} \quad (2)$$

where Ba_{total} , Ba_{xs} , and Al represent the total barium, excess barium, and aluminum concentrations, respectively, of a sample. We assumed excess Ba (Ba_{xs}) to be equivalent to biogenic Ba (Ba_{bio}), although it is possible that the former also includes Ba adsorbed onto other mineral components (e.g., Eagle et al., 2003). We estimated the detrital Ba/Al ratio of each study section ($(Ba/Al)_{detr}$) from Ba–Al crossplots (Fig. 4; Table 1; cf. Rutsch et al., 1995). This is superior to using a constant value based on, e.g., the composition of average shale (Taylor and McLennan, 1985; McLennan, 2001), because $(Ba/Al)_{detr}$ can vary spatially (cf. Reitz et al., 2004; Shen et al., 2012b). This approach is validated by our observation of systematic regional differences in $(Ba/Al)_{detr}$ in this study: 26 ± 6 for the South China region, 41 ± 1 in other Tethyan sections, 47 ± 8 in the N&W Pangean region, and 65 for the Panthalassic region (Fig. 4; Table 1). Only the Panthalassic region yielded a value similar to that for average shale (65), as represented by Post-Archean Australian Shale (PAAS, Taylor and McLennan, 1985).

In this contribution, the mass accumulation rates (MAR) of different proxies (TOC, P, and Ba_{bio}) were calculated to assess variations in paleomarine productivity (cf. Algeo et al., 2013), instead of just the

Table 1
Ratios of Ba to Al in study sections.

Section	Ba/Al ppm/%	Area
Chaohu	26	South China
Daxiakou	25	South China
Dongpan	29	South China
Nhi Tao	4	South China
Shangsi	25	South China
Xinmin	16	South China
Zuodeng	33	South China
Guryul Ravine	41	Other Tethys
Mud	40	Other Tethys
Kap Stosch	60	N&W Pangea
Opal Creek	50	N&W Pangea
Spitsbergen	40	N&W Pangea
West Blind Fiord	40	N&W Pangea
Gujo	65	Panthalassa

raw concentration data used in previous studies (e.g., Shen et al., 2014). In the following, we report MARs for TOC, P, and Ba_{bio} in the same units of flux per unit area (i.e., $mg\ cm^{-2}\ kyr^{-1}$) as we did in the associated contribution in this volume (Schoepfer et al., 2014). For each paleoproductivity proxy, we calculated its MAR as:

$$(X)AR = \text{Concentration}(X) \times LSR \times \rho \quad (3)$$

where X is the proxy of interest (TOC, P, or Ba_{bio}), LSR is linear sedimentation rate in unit of $m\ Myr^{-1}$, and ρ is sample bulk density, which for the sake of convenience was assumed to be $2.5\ g\ cm^{-3}$ for all samples. Note that LSR times ρ is equal to sediment bulk accumulation rate (BAR). The mass accumulation rates of TOC, P, and Ba_{bio} are abbreviated as OCAR, PAR, and BaAR, respectively. The densities of well-lithified, non-porous samples do not show a great range of variation, generally ca. $\pm 10\%$ (Schmoker, 1977), so the uncertainties introduced by this variable are limited (see Schoepfer et al. (2014), for further information).

Primary productivity estimates for the study units were calculated as:

$$PP18 = 1000 \times (10^{4.10} \times TOC) / BAR^{0.54} \quad (4)$$

$$PP21 = (10^{8.55} \times OCAR)^{0.43} \quad (5)$$

$$PP23 = (10^{3.46} \times PAR)^{1.14} \quad (6)$$

where the estimates of primary productivity (PP) are reported in the same units of flux per unit area (i.e., $mg\ cm^{-2}\ kyr^{-1}$) as used for the burial fluxes of productivity proxies in order to permit direct comparisons.

Eqs. (4)–(6) are empirical formulae for estimation of primary productivity in paleomarine systems based on Eqs. 18, 21, and 23 of Schoepfer et al. (2014). In that study, in-situ measurements of primary productivity in modern marine systems were compared with the burial fluxes of elemental productivity proxies (TOC, P, and Ba_{bio}) in order to establish quantitative relationships with applicability to paleomarine systems. The first of these formulae (Eq. (4)) is derived from the relationship of sediment bulk accumulation rate to organic carbon preservation factor, i.e., the fraction of primary production that is preserved in the sediment (Fig. 9A in Schoepfer et al., 2014). The inverse relationship of primary productivity to sediment bulk accumulation rate (BAR) might appear counter-intuitive, but it is accounted for via the effects of rapid sedimentation on organic carbon preservation: when BAR is high, the fraction of primary production that is preserved in the sediments as TOC increases, causing a relative reduction in productivity estimates. The latter two formulae (Eqs. (5) and (6)) are based on the relationships of primary productivity to OCAR and PAR in modern marine systems (Figs. 10A and 13A, respectively, in Schoepfer et al., 2014). As such, they are purely empirical and make no attempt to account for the effects of enhanced organic-matter preservation at high bulk accumulation rates. Rather, they represent the average relationship between primary productivity and elemental proxy fluxes in a wide range of marine environments spanning different redox settings, water depths, and styles of sedimentation.

3. Results

3.1. Linear sedimentation rates

Almost all study sections show an increase in linear sedimentation rates (LSR) from the Upper Permian to the Lower Triassic (Fig. 5; Tables 2 and 3). This increase is a global phenomenon, and there are no manifest differences among the different study regions except for a decline in the deep-ocean sections of the Panthalassic region (cf. Algeo and Twitchett, 2010). Among the long sections, LSRs tend to be low in

the Changhsingian (mostly $<20\ m\ Myr^{-1}$) and to increase at the Changhsingian–Griesbachian boundary (Fig. 5A; Table 2). For example, LSRs increase from 22 to 98 $m\ Myr^{-1}$ in the Spitsbergen section. However, some sections exhibit pronounced increases in LSRs at the Griesbachian–Dienerian substage boundary, as at Mud (from 1 to 7 $m\ Myr^{-1}$) and at Zuodeng (from 22 to 32 $m\ Myr^{-1}$). Other sections exhibit pronounced increases in LSRs at the Dienerian–Smithian substage boundary, as at Chaohu (from 21 to 131 $m\ Myr^{-1}$) and Daxiakou (from 30 to 56 $m\ Myr^{-1}$). For sections extending into the Spathian substage, LSRs tend to decline across the Smithian–Spathian boundary (cf. Zhang et al., 2014). Among the short sections, LSRs tend to increase from the C. yini Zone to the C. meishanensis Zone, as at West Blind Fiord (from 45 to 64 $m\ Myr^{-1}$) and at Guryul Ravine (from 15 to 22 $m\ Myr^{-1}$; Fig. 5B; Table 3). Increases in LSRs are also evident from the C. meishanensis Zone to the H. parvus–C. taylorae zones (i.e., the PTB), as at West Blind Fiord (from 45 to 86 $m\ Myr^{-1}$). These patterns are similar to previous reports regarding secular variation in LSRs through the Upper Permian and Lower Triassic (Algeo and Twitchett, 2010; Algeo et al., 2013).

3.2. Concentrations of TOC, P, and Ba_{bio}

3.2.1. Sections from South China Craton

At Chaohu, both total organic carbon (TOC) and phosphorus (P) show a strong decrease at the LPME (from $0.48 \pm 0.65\%$ to $0.17 \pm 0.11\%$ for TOC, and from $497 \pm 634\ ppm$ to $368 \pm 108\ ppm$ for P from Changhsingian to Griesbachian) (Fig. 6; Supplementary Table 1). TOC remains generally low ($<0.5\%$) throughout the Lower Triassic, with only limited short-term increases (to $>1\%$) in the upper Smithian and lower Spathian. P concentrations are modest in the Griesbachian to mid-Smithian ($312 \pm 144\ ppm$) before declining abruptly to $86 \pm 100\ ppm$ in the upper Smithian and lower Spathian. The profiles of total Ba (Ba_{total}) and biogenic Ba (Ba_{bio}) are similar. Neither shows an obvious change from the Changhsingian ($337 \pm 387\ ppm$ and $171 \pm 394\ ppm$, respectively) to the Griesbachian ($349 \pm 772\ ppm$ and $214 \pm 750\ ppm$, respectively). The highest concentrations are found in the lower to mid-Smithian N. waageni Zone ($393 \pm 249\ ppm$ and $236 \pm 215\ ppm$, respectively) and sporadically in the lower Spathian T. homeri Zone (max values are 7057 ppm and 6860 ppm for total and biogenic Ba respectively). The Dienerian, upper Smithian, and much of the Spathian are characterized by near-zero concentrations of Ba_{total} and Ba_{bio} .

At Daxiakou, TOC exhibits low and uniform values from the Maokougian (late Guadalupian) to the late Changhsingian ($<0.5\%$), an increase in the uppermost Changhsingian ($2.29 \pm 1.71\%$), and a decrease in the Griesbachian ($0.22 \pm 0.14\%$) (Fig. 6; Supplementary Table 1). TOC concentrations remain relatively low during the Dienerian ($0.29 \pm 0.26\%$) and Smithian ($0.23 \pm 0.18\%$). P exhibits low and uniform values in the Maokougian through upper Changhsingian ($28 \pm 31\ ppm$) and a pronounced increase in the uppermost (post-LPME) Changhsingian ($633 \pm 296\ ppm$). P decreases somewhat in the Griesbachian ($183 \pm 144\ ppm$) before increasing again in the upper Griesbachian and Dienerian (max value up to 957 ppm). Ba concentrations are low ($<100\ ppm$) from the Maokougian to the upper Changhsingian but increase ($206 \pm 112\ ppm\ Ba_{total}$; $81 \pm 68\ ppm\ Ba_{bio}$) in the uppermost (post-LPME) Permian. These proxies decrease in the Griesbachian ($117 \pm 141\ ppm\ Ba_{total}$; $54 \pm 121\ ppm\ Ba_{bio}$) but increase again in the Dienerian and the lower Smithian ($174 \pm 167\ ppm\ Ba_{total}$; $78 \pm 126\ ppm\ Ba_{bio}$).

At Dongpan, TOC concentrations are generally low ($<0.2\%$) but nonetheless exhibit a slight decrease at the LPME event horizon ($0.11 \pm 0.05\%$ in the Changhsingian to the $0.09 \pm 0.03\%$ in the Griesbachian) (Fig. 6; Supplementary Table 1). P concentrations increase slightly from the upper Permian Changhsingian ($266 \pm 248\ ppm$) to the lower Triassic Griesbachian ($332 \pm 66\ ppm$). Ba concentrations decrease from the Changhsingian ($489 \pm 243\ ppm\ Ba_{total}$;

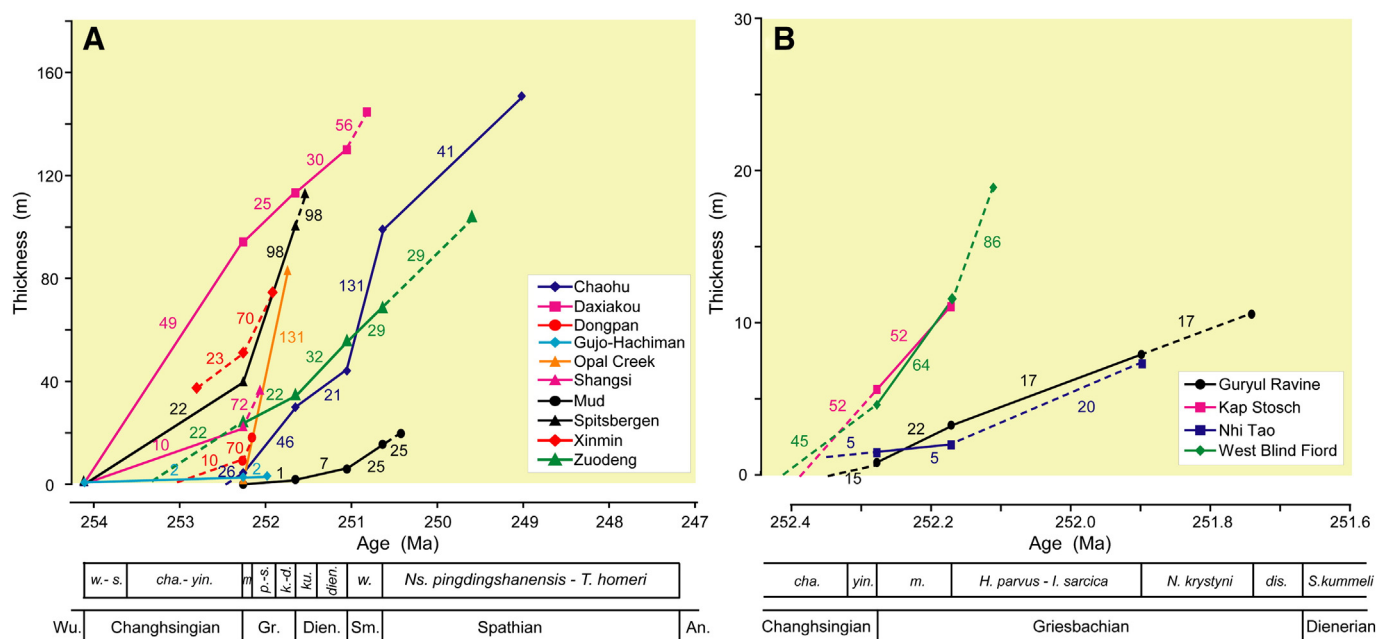


Fig. 5. Age-thickness models for (A) 10 long study sections spanning most or all of the Early Triassic, and (B) 4 short study sections bracketing the PTB. Sediment accumulation rates were calculated per Equation 1 and are given in units of m Myr^{-1} . Abbreviations: cha. = *C. changxingensis*, dien. = *Ns. dieneri*, dis. = *N. discreta*, k.-d. = *N. krystyni*–*N. discreta*, ku. = *S. kummeli*, m. = *C. meishanensis*, p.-s. = *H. parvus*–*I. staeschi*, w. = *Nv. waageni*, w.-s. = *C. wangi*–*C. subcarinata*, yin. = *C. yini*; An. = Anisian, Dien. = Dienerian, Gr. = Griesbachian, Sm. = Smithian, Wu. = Wuchiapingian. Other details as in Fig. 3. Unit thickness and LSR data are given in Tables 2 and 3.

292 ± 281 ppm Ba_{bio}) to the Griesbachian (326 ± 94 ppm Ba_{total} ; 62 ± 106 ppm Ba_{bio}).

At Nhi Tao, TOC concentrations decrease from $0.43 \pm 0.49\%$ in the *C. yini* Zone to $0.09 \pm 0.02\%$ in the *C. meishanensis* Zone and $0.08 \pm 0.02\%$ in the *H. parvus*–*I. sarcica* zones (Fig. 6; Supplementary Table 1). P concentrations are lower in the *C. yini* and *C. meishanensis* zones (15 ± 19 ppm and 28 ± 36 ppm, respectively) and somewhat higher in the *H. parvus*–*I. sarcica* zones (mean value is 102 ± 104 ppm). Ba concentrations decrease from the *C. yini* Zone (31 ± 31 ppm Ba_{total} ; 28 ± 32 ppm Ba_{bio}) to the *C. meishanensis* (22 ± 15 ppm Ba_{total} ; 19 ± 16 ppm Ba_{bio}) and *H. parvus*–*I. sarcica* zones (29 ± 18 ppm Ba_{total} ; 23 ± 19 ppm Ba_{bio}).

At Shangsi, TOC and P have similar profiles, with higher values in the Wuchiapingian ($6.98 \pm 4.29\%$ TOC; 1356 ± 1715 ppm P) and progressively lower values in the Changhsingian ($2.48 \pm 2.90\%$ TOC; 754 ± 1074 ppm P) and Griesbachian ($0.35 \pm 0.36\%$ TOC; 399 ± 115 ppm P) (Fig. 6; Supplementary Table 1). Ba concentrations are generally low and exhibit no obvious variation within the Wuchiapingian and Changhsingian (103 ± 68 ppm Ba_{total} ; 26 ± 19 ppm Ba_{bio}). However, Ba concentrations increase in the Griesbachian (231 ± 72 ppm Ba_{total} ; 79 ± 61 ppm Ba_{bio}).

At Xinmin, TOC decreases from the Changhsingian ($0.57 \pm 0.50\%$) to the Griesbachian ($0.27 \pm 0.07\%$), whereas P increases over the same stratigraphic interval (from 717 ± 487 ppm to 1231 ± 315 ppm) (Fig. 6; Supplementary Table 1). Ba concentrations increase modestly from the Changhsingian (175 ± 68 ppm Ba_{total} ; 65 ± 61 ppm Ba_{bio}) to the Griesbachian (261 ± 86 ppm Ba_{total} ; 136 ± 73 ppm Ba_{bio}).

At Zuodeng, TOC exhibits low values ($<0.2\%$) with little secular variation (Fig. 6; Supplementary Table 1). P concentrations are low (<50 ppm) from the Changhsingian through Dienerian but rise in the Smithian (108 ± 183 ppm) and Spathian (160 ± 168 ppm). Ba concentrations are uniformly low throughout the Changhsingian (<100 ppm) but episodically higher in the Griesbachian (86 ± 223 ppm Ba_{total} ; 64 ± 146 ppm Ba_{bio}), Smithian (79 ± 126 ppm Ba_{total} ; 30 ± 50 ppm Ba_{bio}), and Spathian (74 ± 146 ppm Ba_{total} ; 39 ± 110 ppm Ba_{bio}).

3.2.2. Sections from other regions

At Guryul Ravine, TOC concentrations are generally low ($<0.5\%$) and similar for the upper Permian ($0.17 \pm 0.12\%$) and lower Triassic ($0.20 \pm 0.05\%$) (Fig. 7; Supplementary Table 1). P exhibits moderate to high concentrations (2400 – 9500 ppm) throughout the section, with higher mean values in the *C. meishanensis* Zone (6288 ± 2424 ppm) compared to the *C. changxingensis* (4454 ± 1594 ppm) and *H. parvus*–*I. sarcica* zones (3506 ± 295 ppm). Ba concentrations show only minor differences between the *C. changxingensis* (297 ± 211 ppm Ba_{total} ; 121 ± 86 ppm Ba_{bio}) and *C. meishanensis* zones (370 ± 175 ppm Ba_{total} ; 65 ± 57 ppm Ba_{bio}) but a significant increase in the *H. parvus*–*I. sarcica* zones (577 ppm Ba_{total} ; 150 ± 27 ppm Ba_{bio}).

At Mud, TOC shows significantly fluctuating values, from 0.17% in min to 2.95% in max. High values were in the Wuchiapingian ($1.07 \pm 0.6\%$), Griesbachian ($1.24 \pm 0.97\%$), Dienerian ($1.08 \pm 0.62\%$) and the lower Smithian ($0.86 \pm 0.68\%$), followed by a decrease in the Spathian ($0.64 \pm 0.85\%$) (Fig. 7; Supplementary Table 1). P increases sharply from the Wuchiapingian (559 ± 1103 ppm) to the Griesbachian ($17,845 \pm 20,189$ ppm) with a secondary peak in the lower Smithian ($4598 \pm 11,554$ ppm). Low to moderate Ba concentrations in the Wuchiapingian (584 ± 118 ppm Ba_{total} ; 204 ± 95 ppm Ba_{bio}), Dienerian (674 ± 272 ppm Ba_{total} ; 290 ± 213 ppm Ba_{bio}), and Spathian (436 ± 237 ppm Ba_{total} ; 124 ± 147 ppm Ba_{bio}) alternate with high Ba concentrations in the Griesbachian (1809 ± 2884 ppm Ba_{total} ; 1327 ± 3019 ppm Ba_{bio}) and Smithian (1181 ± 2814 ppm Ba_{total} ; 852 ± 2764 ppm Ba_{bio}).

At Kap Stosch, TOC shows a large decrease from the *C. changxingensis* Zone ($4.36 \pm 2.16\%$) to the *C. meishanensis* Zone ($0.21 \pm 0.07\%$) (Fig. 7; Supplementary Table 1). The P profile shows mostly minor variation (almost range from 240 ppm to 320 ppm), although with local peaks in the upper *C. meishanensis* Zone (up to 2479 ppm). Ba concentrations decrease modestly from the *C. changxingensis* Zone (738 ± 502 ppm Ba_{total} ; 389 ± 511 ppm Ba_{bio}) to the *C. meishanensis* Zone (473 ± 80 ppm Ba_{total} ; 82 ± 68 ppm Ba_{bio}).

At Opal Creek, all productivity proxies show an increase from the Permian Changhsingian ($0.34 \pm 0.45\%$) to the Triassic Griesbachian

Table 2
Thicknesses and LSRs of long sections by stage/substage.

Boundary age	Duration	Method of LSR calculation	Chaochu		Donggan		Gujo		Opal Creel		Shangsi		Mud		Xinmin		Zuodeng		Spitsbergen	
			Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR	Thickness	LSR
Ma	Ma		m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma	m	m/Ma
Maokougian	259.80																			
Wuchiapingian	254.14																			
Changhsingian	252.28		4.82	26.37	8.20	10.00	3.40	1.88	0.60	11.00	9.00	10.22	10.50	1.13	7.90	22.70	22.00	21.89	41.00	21.51
Griesbachian	251.67		28.29	46.38	3.50	70.00	0.60	1.60	80.00	131.15	3.00	71.51	0.69	1.13	3.30	70.00	13.35	21.89	60.00	98.36
Dienerian	251.05		13.2	21.29									4.09	6.60			20	32.26	38.36	98.36
Smithian	250.65		52.39	130.97									9.92	24.80			11.5	28.75		
Spathian	247.20		55.00	40.81									1.32	24.80			42.05	28.75		

Footnotes:

Chaochu: some LSR (red values) from Algeo and Twitchett (2010).
Donggan: data from cyclostratigraphic analysis (Feng and Algeo, 2014).
Gujo-Hachiman: data from cyclostratigraphic analysis (Algeo et al., 2010, 2011b).
Xinmin: data from the average change of LSR (Algeo and Twitchett, 2010).
The other red values were assumed as the same values as their neighbors.

($1.34 \pm 0.64\%$) (Fig. 7; Supplementary Table 1). TOC peaks in the mid-Griesbachian (up to 3.03%). P has a similar trend to TOC throughout the section (mostly the Griesbachian) but shows a slight displacement of the higher values between them (the peaks of P are earlier than those of TOC). Ba concentrations are highest in the lower Griesbachian (712 ± 349 ppm Ba_{total} ; 411 ± 358 ppm Ba_{bio}), and lower in the Changhsingian (364 ± 188 ppm Ba_{total} ; 190 ± 128 ppm Ba_{bio}) and the upper Griesbachian (387 ± 119 ppm Ba_{total} ; 80 ± 112 ppm Ba_{bio}).

At Spitsbergen, both TOC and P exhibit low values in the Wuchiapingian ($0.33 \pm 0.20\%$ TOC; 596 ± 709 ppm P) and Changhsingian ($0.41 \pm 0.13\%$ TOC; 325 ± 225 ppm P) and rising values in the Griesbachian ($0.40 \pm 0.33\%$ TOC; 807 ± 525 ppm P) (Fig. 7; Supplementary Table 1). Relative to the Griesbachian, the Dienerian exhibits a small decrease in TOC (to $0.17 \pm 0.03\%$) and a small increase in P (to 984 ± 265 ppm). Ba concentrations are low in the Wuchiapingian (166 ± 67 ppm Ba_{total} ; 100 ± 69 ppm Ba_{bio}) and Changhsingian (356 ± 153 ppm Ba_{total} ; 157 ± 182 ppm Ba_{bio}) except for a few samples. Mean Ba concentrations increase in the Griesbachian (420 ± 355 ppm Ba_{total} ; 190 ± 340 ppm Ba_{bio}) before decreasing again in the Dienerian (288 ± 48 ppm Ba_{total} ; 98 ± 49 ppm Ba_{bio}).

At West Blind Fiord, TOC concentrations are low and relatively uniform throughout the section, averaging $0.29 \pm 0.07\%$ in the *C. changxingensis* Zone and $0.36 \pm 0.08\%$ in the *H. parvus* Zone (Fig. 7; Supplementary Table 1). On the other hand, P concentrations decrease somewhat from the *C. changxingensis* Zone (676 ± 1193 ppm) to the *C. meishanensis* (432 ± 26 ppm) and *H. parvus* zones (460 ± 43 ppm). Ba_{total} concentrations are relatively invariant from the *C. changxingensis* Zone (473 ± 208 ppm) through the *H. parvus* Zone (467 ± 78 ppm), but Ba_{bio} decreases through the same stratigraphic interval (from 210 ± 145 ppm to 124 ± 91 ppm).

At Gujo-Hachiman, both TOC and P exhibit low values in the Wuchiapingian ($0.17 \pm 0.03\%$ TOC; 66 ± 31 ppm P) and Changhsingian ($0.22 \pm 0.08\%$ TOC; 169 ± 205 ppm P), followed by a pronounced increase in the Griesbachian ($1.24 \pm 0.49\%$ TOC; 555 ± 947 ppm P) (Fig. 7; Supplementary Table 1). Ba concentrations decrease slightly from the Wuchiapingian (567 ± 241 ppm Ba_{total} ; 500 ± 252 ppm Ba_{bio}) to the Changhsingian (481 ± 104 ppm Ba_{total} ; 406 ± 90 ppm Ba_{bio}). The Griesbachian is characterized by a modest increase in Ba_{total} (to 611 ± 80 ppm) and a modest decrease in Ba_{bio} (272 ± 110 ppm).

3.2.3. General patterns

TOC concentrations show considerable variation among the four study regions. In South China, mean TOC values are low in the Upper Permian ($<0.7\%$ except for Shangsi) and decrease further in the Lower Triassic (Fig. 8; Supplementary Table 1). In other Tethyan and N&W Pangean sections, mean TOC generally increases from the Changhsingian to the Griesbachian except for Spitsbergen, which exhibits a slight decrease (Fig. 8B; Supplementary Table 1). Mean TOC in the Panthalassic region increases sharply from the Changhsingian to the Griesbachian (Fig. 7; Supplementary Table 1).

P concentrations are generally low in South China sections (<600 ppm) except for Xinmin, where P concentrations are 700–1200 ppm (Figs. 6 and 8). Most South China sections exhibit a decreasing trend from the Changhsingian to the Griesbachian (Fig. 8D). The other regions examined in this study exhibit relatively higher P concentrations (400–1200 ppm) and generally show an increase from the Upper Permian into the Lower Triassic (Fig. 7). Within the Lower Triassic, higher mean P concentrations are associated with the Griesbachian and Smithian and lower concentrations with the Dienerian (Fig. 8D–F).

In most sections, the Ba_{total} and Ba_{bio} profiles show similar patterns (Figs. 6–7; Supplementary Table 1). Regionally, Ba_{bio} concentrations tend to be lower in the South China sections than elsewhere (Fig. 8G). Ba concentrations are distinctly lower (<200 ppm) in the shallow-water sections (e.g., Nhi Tao, Zuodeng) and higher (to 1200 ppm), although more variable, in the intermediate to deepwater sections (e.g., the mean values of Ba_{bio} is 1327 and 62 ppm in the Griesbachian

Table 3

Thicknesses and LSRs of short sections by conodont zone.

Conodont Zone	Duration Ma	Method of LSR calculation	Guryul		Kap Stosch		Nhi Tao		West Blind Fiord	
			Thickness m	LSR m/Ma	Thickness	LSR	Thickness	LSR	Thickness	LSR
<i>S. kummeli</i>	251.67									
<i>N. discreta</i>	251.74	0.07								
<i>krystyni</i>	251.90	0.16								
<i>H. parvus</i> – <i>Isarcica</i>	252.17	0.27								
<i>C. meishanensis</i>	252.28	0.11								
<i>C. yini</i>	252.32	0.04								
<i>C. changhsingian</i>										
		=thickness/duration	4.00	17.39			5.43	20.11	6.70	86.00
		=thickness/duration	4.55	16.85						
		=thickness/duration	2.45	22.27	5.70	51.82	0.50	4.55	7.00	63.64
		=thickness/duration	0.60	15.00	5.27	51.82	1.31	4.55	10.20	45.00
		=thickness/duration	7.20	15.00						

Footnote: West Blind Fiord: duration estimates taken from Algeo et al. (2012).

The other red values were assumed as the same values as their neighbors.

in Mud and Dongpan section respectively) (Fig. 8; Supplementary Table 1). Within the Lower Triassic, Ba concentrations tend to be higher for the Griesbachian and Smithian relative to the Dienerian, a pattern also observed for TOC and P (Fig. 8G–I).

3.3. Mass accumulation rates of TOC, P, and Ba_{bio}

In this section, the mass accumulation rates of TOC, P, and Ba_{bio} (i.e., OCAR, PAR, and BaAR, respectively) are reported in log units of $mg\ cm^{-2}\ kyr^{-1}$ (i.e., 2.0 represents $100\ mg\ cm^{-2}\ kyr^{-1}$) with values given as the mean plus/minus the standard deviation. Values of BaAR are for biogenic Ba rather than total Ba.

3.3.1. Sections from South China Craton

At Chaohu, the mass accumulation rates of all three proxies exhibit similar profiles. OCAR decreases slightly from the late Changhsingian (1.34 ± 0.32) through the Griesbachian (1.23 ± 0.23) to the Dienerian (0.96 ± 0.32) (Fig. 9). It then increases strongly in the mid-Smithian (1.83 ± 0.23) before declining modestly in the Spathian (1.41 ± 0.27). PAR increases from the Changhsingian (0.38 ± 0.30) to the Griesbachian (0.61 ± 0.13), before decreasing in the Dienerian (0.32 ± 0.11). It then rises sharply in the mid-Smithian (0.92 ± 0.36) before declining equally sharply in the Spathian (-0.36 ± 0.61). BaAR is generally low during the Changhsingian (-0.14 ± 0.34) and Induan (-0.09 ± 0.74) except for some peaks just below the LPME, in the mid-Griesbachian, and in the upper Dienerian. BaAR increases sharply in the Smithian (0.63 ± 0.53) before falling sharply in the Spathian (-0.18 ± 0.52).

At Daxiakou, OCAR is low and relatively uniform from the Maokougian to the upper Changhsingian (0.80 ± 0.43 ; Fig. 9). OCAR increases in the uppermost Changhsingian (2.24 ± 0.52 ; from ~7 m below the LPME; Fig. 8), decreases in the Griesbachian (1.08 ± 0.20), and then increases again in the Dienerian (1.22 ± 0.29) and Smithian (1.43 ± 0.24). PAR shows a similar pattern, with low values in the Maokougian and Wuchiapingian (-1.45 ± 0.47) and an increase in the Changhsingian (0.13 ± 0.71). PAR peaks in the uppermost Changhsingian (0.82 ± 0.23 ; from ~7 m below the LPME; Fig. 8), decreases in the Griesbachian (-0.07 ± 0.33), and then increases again in the Dienerian (0.28 ± 0.37) and Smithian (0.49 ± 0.36). BaAR is also low and relatively uniform from the Maokougian to the upper Changhsingian (-1.52 ± 0.68). BaAR increases in the uppermost Changhsingian (-0.08 ± 0.49), decreases in the Griesbachian (-0.76 ± 0.62), and then increases again in the Dienerian (-0.54 ± 0.54) and Smithian (-0.27 ± 0.56).

At Dongpan, OCAR, PAR, and BaAR are low throughout the section. OCAR shows an increase from the Changhsingian (0.38 ± 0.22) to the Griesbachian (1.18 ± 0.19) (Fig. 9). PAR also exhibits a significant increase (from -0.24 ± 0.18 in the Changhsingian to 0.76 ± 0.09 in the Griesbachian) at the LPME. BaAR shows a more limited increase

(from -0.23 ± 0.38 to 0.10 ± 0.61) from the Changhsingian to the Griesbachian.

At Nhi Tao, OCAR, PAR, and BaAR are low throughout the section (Fig. 9). OCAR decreases from the *C. yini* Zone (0.49 ± 0.39) to the *C. meishanensis* Zone (-0.02 ± 0.12) and then increases in the *H. parvus*–*C. taylorae* zones (0.61 ± 0.11). In contrast, PAR increases from the *C. yini* Zone (-2.04 ± 0.58) to the *C. meishanensis* Zone (-1.59 ± 0.42) and into the *H. parvus*–*C. taylorae* zones (-0.50 ± 0.47). BaAR is low (<-2.75) in the *C. yini* (-1.71 ± 0.51) and *C. meishanensis* zones (-1.83 ± 0.40) but increases slightly in the *H. parvus*–*C. taylorae* zones (-0.98 ± 0.39).

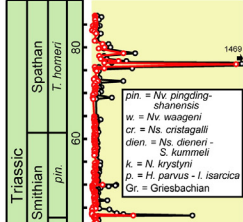
At Shangsi, OCAR and PAR have higher values in the Wuchiapingian (2.10 ± 0.46 and 0.28 ± 0.47 respectively), but decrease to the Changhsingian (1.46 ± 0.55 and 0.12 ± 0.39 respectively) (Fig. 9). OCAR and PAR increase within the Griesbachian (1.70 ± 0.23 and 0.83 ± 0.13 respectively) compared to the values in the Changhsingian. BaAR exhibits low and uniform values in the Wuchiapingian and Changhsingian (-1.27 ± 0.58 and -1.24 ± 0.59 respectively) and increases slightly in the Griesbachian (0.12 ± 0.23).

At Xinmin, OCAR is steady (near 1.5) throughout the section but exhibits some peaks (up to 2.24) in the lower part of section (equal to the lower part of the *C. yini* Zone) (Fig. 9). OCAR increases somewhat from the Changhsingian (1.40 ± 0.29) to the Griesbachian (1.65 ± 0.12). PAR exhibits an even larger increase from the Changhsingian (0.55 ± 0.26) to the Griesbachian (1.32 ± 0.14). BaAR is low and uniform in the Changhsingian (-0.70 ± 0.65) and then increases sharply in the Griesbachian (0.27 ± 0.41).

At Zuodeng, OCAR exhibits moderate and relatively uniform values through the Changhsingian (0.95 ± 0.12), Griesbachian (0.98 ± 0.23), Smithian (0.93 ± 0.14), and Spathian (0.86 ± 0.14), interrupted by a small positive anomaly in the Dienerian (1.08 ± 0.18) (Fig. 9). In contrast, PAR exhibits low values in the Changhsingian (-0.83 ± 0.32) and Griesbachian (-0.81 ± 0.31), followed by a small increase in the Dienerian (-0.58 ± 0.35) and Smithian (-0.43 ± 0.54), and a larger increase in the Spathian (-0.17 ± 0.50). BaAR shows a pattern that is similar to OCAR, with low and relatively uniform values in the Changhsingian (-0.74 ± 0.16), Griesbachian (-0.68 ± 0.29), Smithian (-0.74 ± 0.22), and Spathian (-0.78 ± 0.35), interrupted by a small positive anomaly in the Dienerian (-0.52 ± 0.26).

3.3.2. Sections from other regions

At Guryul Ravine, OCAR increases from the *C. changxingensis* Zone (0.71 ± 0.33) to the *H. parvus*–*C. taylorae* zones (1.06 ± 0.07), followed by a slight decrease in the *N. krystyni* Zone (0.98 ± 0.38) (Fig. 10). PAR exhibits an increase from the *C. changxingensis* Zone (1.19 ± 0.18) to the *C. meishanensis* Zone (1.51 ± 0.18), and a second increase from the *H. parvus*–*C. taylorae* zones (1.17 ± 0.04) to the *N. krystyni* Zone (1.47 ± 0.01). BaAR shows a pattern that is similar to OCAR, with an increase from the *C. changxingensis* (-0.49 ± 0.45) and *C. meishanensis*



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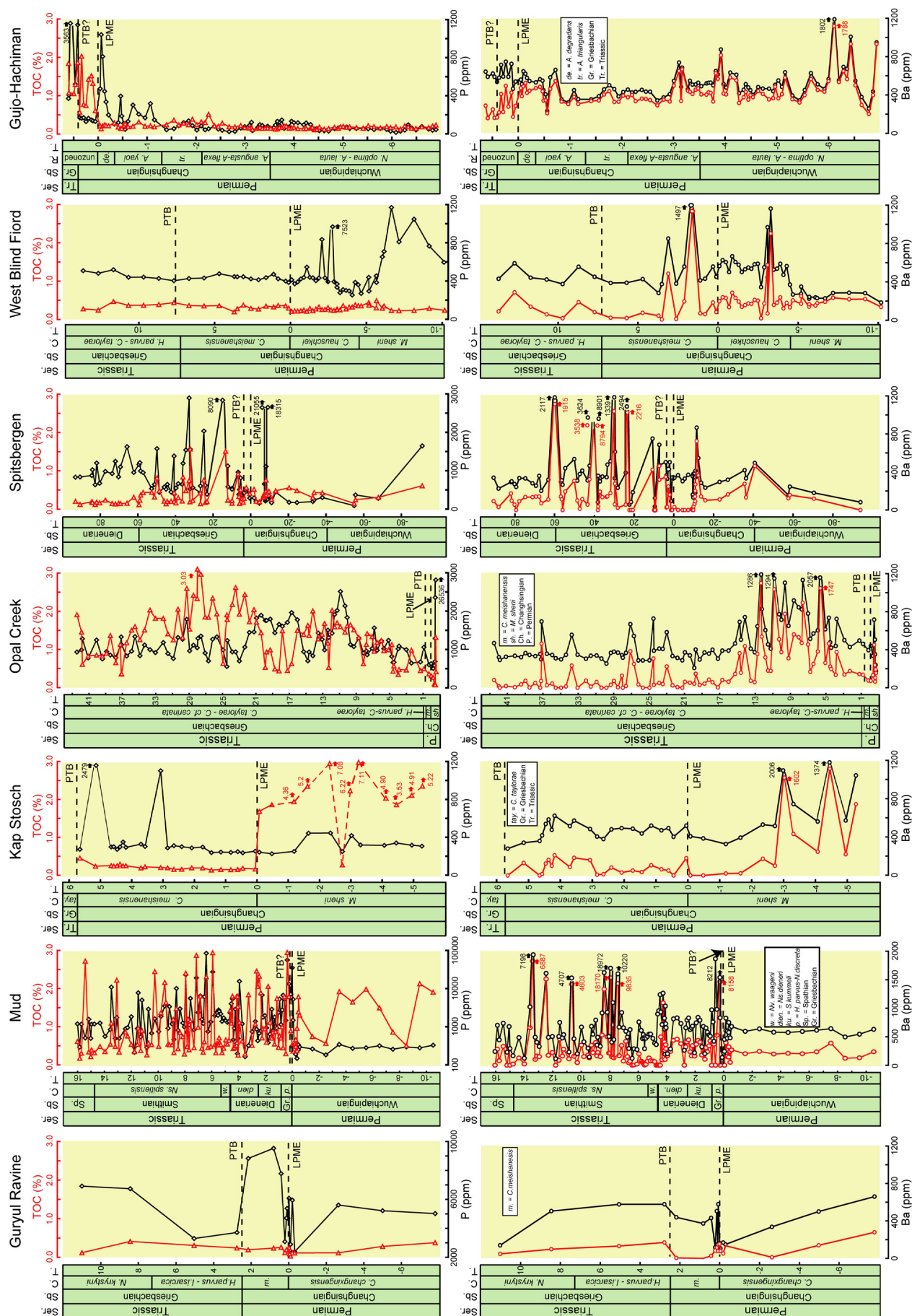


Fig. 7. Paleoproductivity proxies for the non-Chinese study sections. Other details as in Fig. 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

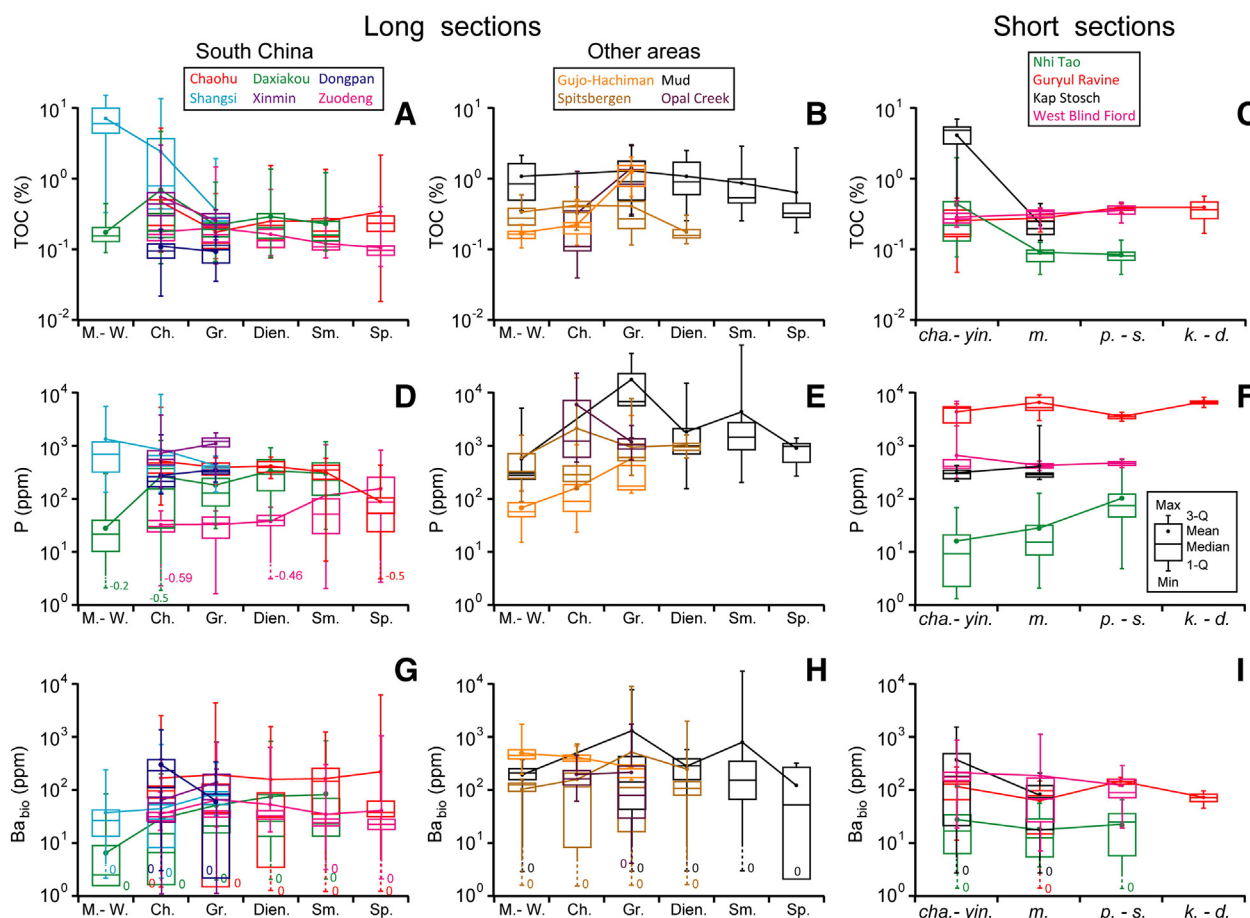


Fig. 8. Mean concentrations of TOC (A, B, and C), P (D, E, and F), and biogenic barium (Ba_{bic}) (G, H, and I) for both long sections (left and middle columns) and short sections (right column). Concentrations of all proxies are in log units. Ch. = Changhsingian, M.-W. = Maokougian–Wuchiapingian, Sp. = Spathian. Other details as in Figs. 3 and 5. Data given in Supplementary Table 1.

zones (-0.57 ± 0.57) to the *H. parvus*–*C. taylorae* zones (-0.20 ± 0.08), followed by a decrease in the *N. krystyni* Zone (-0.53 ± 0.22).

At Mud, OCAR is low in the Wuchiapingian (0.40 ± 0.27) and Griesbachian (0.42 ± 0.37) but increases sharply during the Dienerian (1.18 ± 0.26) and Smithian (1.63 ± 0.28) before declining slightly in the Spathian (1.41 ± 0.37) (Fig. 10). PAR shows a strong increase from the Wuchiapingian (-1.04 ± 0.34) to the Griesbachian (0.45 ± 0.53) and a second strong increase from the Dienerian (0.29 ± 0.43) to the Smithian (1.07 ± 0.49), followed by a modest decline in the Spathian (0.71 ± 0.26). BaAR is low through the Wuchiapingian (-1.25 ± 0.20) and Griesbachian (-0.89 ± 0.77), rises to a maximum in the Dienerian (-0.35 ± 0.36), and then declines somewhat in the Smithian (-0.04 ± 0.79 ; n.b., local peaks within the Smithian) and Spathian (-0.08 ± 0.51).

At Kap Stosch, OCAR is high in the *C. changxingensis* Zone (2.65 ± 0.40) and declines modestly in the *C. meishanensis* Zone (1.42 ± 0.12) (Fig. 10). PAR is generally high but, in contrast to TOC, shows no change from the *C. changxingensis* Zone (0.61 ± 0.10) to the *C. meishanensis* Zone (0.63 ± 0.24). BaAR exhibits high and fluctuating values in the *C. changxingensis* Zone (0.45 ± 0.65), followed by a decrease in the *C. meishanensis* Zone (-0.06 ± 0.42).

At Opal Creek, all three productivity proxies exhibit a huge increase from the Upper Permian to the Lower Triassic, from 0.74 ± 0.45 to 2.58 ± 0.25 for OCAR, from 0.77 ± 0.68 to 1.57 ± 0.14 for PAR, and from -0.36 ± 0.27 to 0.54 ± 0.61 for BaAR (Fig. 10). The increase for OCAR is about twice as large (in log units) as for PAR and BaAR.

At Spitsbergen, OCAR shows moderately high values in the Wuchiapingian (1.19 ± 0.25) and Changhsingian (1.32 ± 0.14), followed by a sharp rise in the Griesbachian (1.90 ± 0.28) and a modest

decline in the Dienerian (1.62 ± 0.11) (Fig. 10). PAR also shows a sharp rise from the Wuchiapingian (0.28 ± 0.52) and Changhsingian (0.36 ± 0.59) to the Griesbachian (1.25 ± 0.29) but, in contrast to OCAR, PAR continues to rise into the Dienerian (1.37 ± 0.11). On the other hand, BaAR shows a pattern that closely mirrors variation in OCAR, with intermediate values in the Wuchiapingian (-0.15 ± 0.07) and Changhsingian (-0.13 ± 0.46), a sharp rise in the Griesbachian (0.63 ± 0.63), and a modest decline in the Dienerian (0.48 ± 0.41).

At West Blind Fiord, OCAR increases somewhat from the *C. changhsingensis* Zone (1.50 ± 0.09) to the *H. parvus*–*C. taylorae* zones (1.88 ± 0.10) (Fig. 10). PAR also shows a moderate increase over the same stratigraphic interval (from 0.73 ± 0.26 to 0.99 ± 0.04).

BaAR is largely unchanged between the *C. changxingensis* Zone (0.31 ± 0.25) and *H. parvus*–*C. taylorae* zones (0.30 ± 0.38), although it declines modestly in the *C. meishanensis* Zone just above the LPME (0.05 ± 0.62).

At Gujo-Hachiman, OCAR is low and relatively uniform during the Wuchiapingian (-0.12 ± 0.08) and Changhsingian (-0.01 ± 0.14) but exhibits a sharp rise within the Griesbachian (0.66 ± 0.19) (Fig. 10). PAR exhibits a similar pattern, with an increase from the Wuchiapingian (-1.55 ± 0.21) and Changhsingian (-1.29 ± 0.39) to the Griesbachian (-0.94 ± 0.44). In contrast, BaAR exhibits a decline from the Wuchiapingian (-0.66 ± 0.16) and Changhsingian (-0.73 ± 0.09) to the Griesbachian (-0.99 ± 0.17).

3.3.3. General patterns

OCAR generally shows an increase from the uppermost Permian (Changhsingian) to the lowermost Triassic (Griesbachian) (Fig. 11A–B; Supplementary Table 1). In many sections, this increase continues

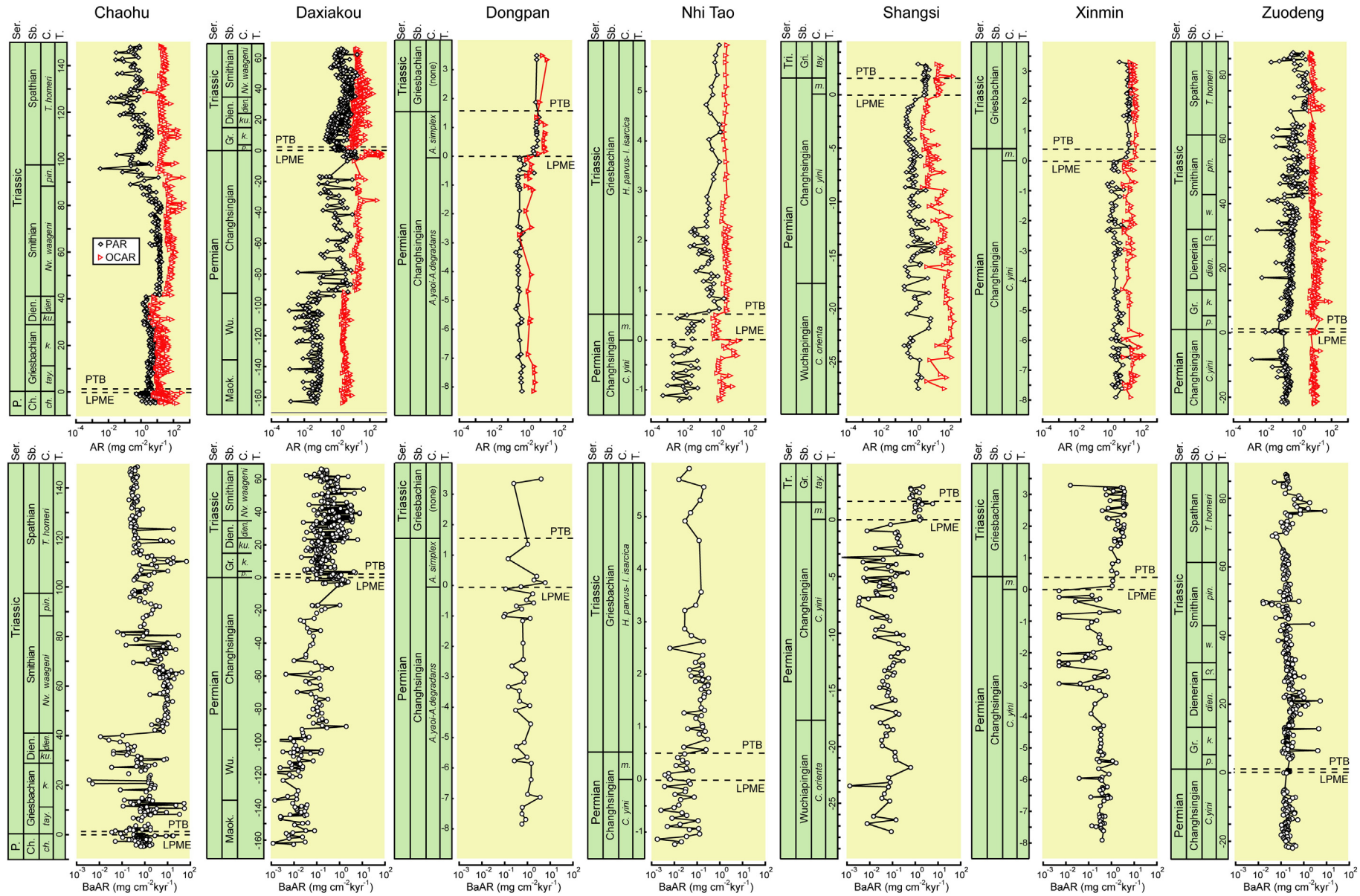


Fig. 9. Accumulation rates of paleoproductivity proxies for the South China study sections: TOC (red curves) and P (black curves) in upper row and BaAR in lower row. OCAR, PAR, and BaAR are the mass accumulation rates of organic carbon, phosphorus, and biogenic barium, respectively. Other details as in Figs. 3 and 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

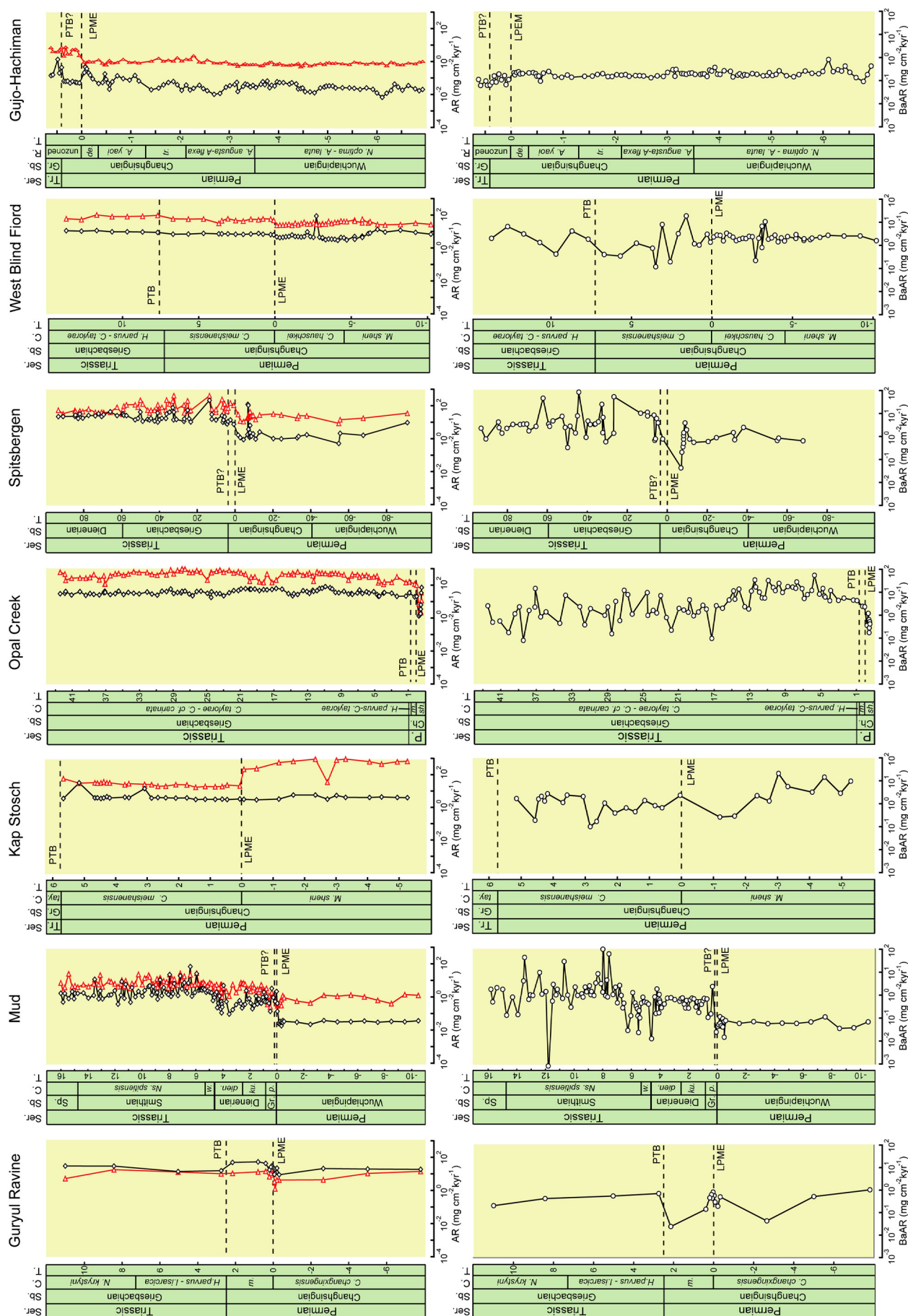


Fig. 10. Accumulation rates of paleoproductivity proxies for the non-Chinese study sections. Other details as in Figs. 6 and 9. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

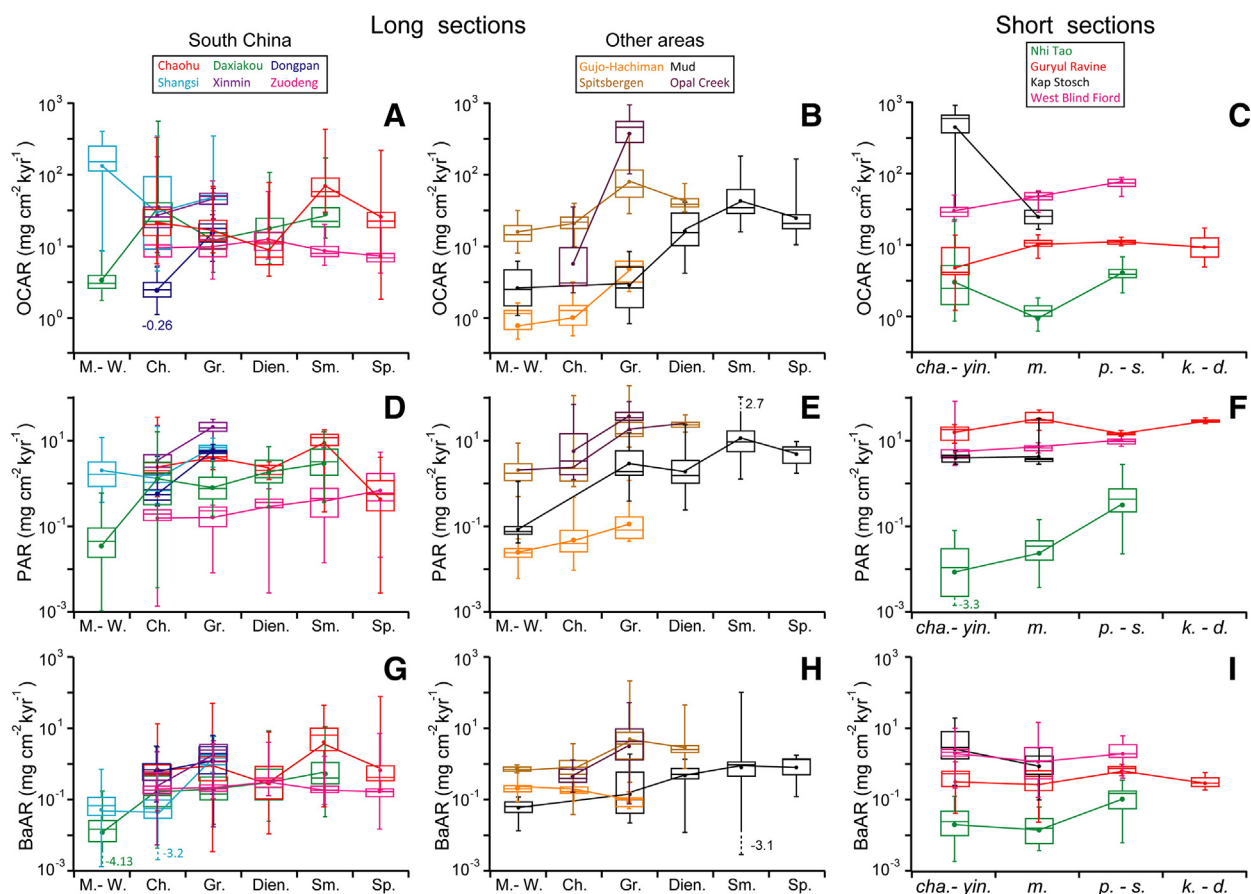


Fig. 11. Mean mass accumulation rates of TOC (A–C), P (D–F), and Ba_{Bio} (G–I) for long sections (left and middle columns) and short sections (right column). Other details as in Fig. 8.

through the Smithian, although the Dienerian may exhibit somewhat lower values than the preceding (Griesbachian) and following (Smithian) substages. OCAR generally declines somewhat in the Spathian relative to the rest of the Lower Triassic, although values often remain higher than for the Changhsingian. In the short sections, OCAR typically shows a large increase from the *C. yini* and *C. meishanensis* zones to the *H. parvus* Zone, except for Kap Stosch and Nih Tao (Fig. 11C). The four study regions do not show any obvious pattern of variation specific to an individual region.

PAR generally shows an increase from the uppermost Permian (Changhsingian) to the lowermost Triassic (Griesbachian) (Fig. 11D–E; Supplementary Table 1). In many sections, this increase continues through the Smithian, e.g., at Daxiakou, Zuodeng, and Spitsbergen. PAR generally declines somewhat in the Spathian relative to the rest of the Lower Triassic, although values often remain higher than for the Changhsingian. In the short sections, PAR typically shows a large increase from the *C. yini* and *C. meishanensis* zones to the *H. parvus* Zone (Fig. 11F). The four study regions do not show any obvious pattern of variation specific to an individual region.

BaAR generally shows an increase from the uppermost Permian (Changhsingian) to the lowermost Triassic (Griesbachian), with the exception of Gujo-Hachiman (Fig. 11G–H; Supplementary Table 1). In many sections, this increase continues into the Dienerian and Smithian. BaAR generally declines somewhat in the Spathian relative to the rest of the Lower Triassic, although values often remain higher than for the Changhsingian. In the short sections, BaAR typically shows a large increase from the *C. meishanensis* Zone to the *H. parvus* Zone (Fig. 11I). The four study regions do not show any obvious pattern of variation specific to an individual region.

High positive correlations between OCAR, PAR, and BaAR ($r^2 = 0.55$, 0.30, and 0.35 for OCAR–PAR, OCAR–BaAR, and PAR–BaAR, respectively;

Fig. 12 A–C) suggest that the accumulation rates of all productivity proxies were controlled by a common parameter, i.e., the sinking flux of organic matter, which we tentatively infer to reflect primary productivity rates in the surface watermass. However, all three proxies also show a strong relationship to sediment bulk accumulation rate (BAR), with r^2 values of 0.52, 0.44, and 0.30, respectively (Fig. 12D–F). The strength of these relationships suggests that BAR was an important control on productivity proxy fluxes (cf. Tyson, 2005; Schoepfer et al., 2014).

3.4. Paleoproductivity estimates

The transfer functions used to estimate paleoproductivity (Eqs. (4)–(6)) yield productivity values similar to those for modern marine environments, i.e., between 10³ and 10⁵ mg cm⁻² kyr⁻¹ (Longhurst et al., 1995). A large majority of the productivity estimates of both PP18 (Eq. (4)) and PP21 (Eq. (5)) fall within this range, although some higher values are seen, particularly at Shangsi, Spiti, and Gujo-Hachiman (Fig. 13A–F). On the other hand, PP23 (Eq. (6)) generated a wider range of productivity estimates, from <10¹ mg cm⁻² kyr⁻¹ for some intervals at Nih Tao, Daxiakou, and Zuodeng, to >10⁶ mg cm⁻² kyr⁻¹ for some intervals at Spitsbergen, West Blind Fiord, and Spiti (Fig. 13G–I). Because P is susceptible to diagenetic concentration or loss to a greater degree than organic carbon, we regard the productivity estimates based on organic carbon (i.e., PP18 and PP21) as more reliable.

Productivity estimates based on TOC, OCAR, and PAR (Eqs. (4)–(6)) follow the patterns of secular and geographic variation exhibited by the underlying proxy concentrations and fluxes. Variations in PP18 are similar to that in TOC and OCAR in most sections (Figs. 8 and 13A–C). A decreasing trend from the Changhsingian to the Griesbachian is evident in all of the South China sections as well as some sections from other areas (e.g., Spitsbergen). In the short sections, a decreasing trend is apparent

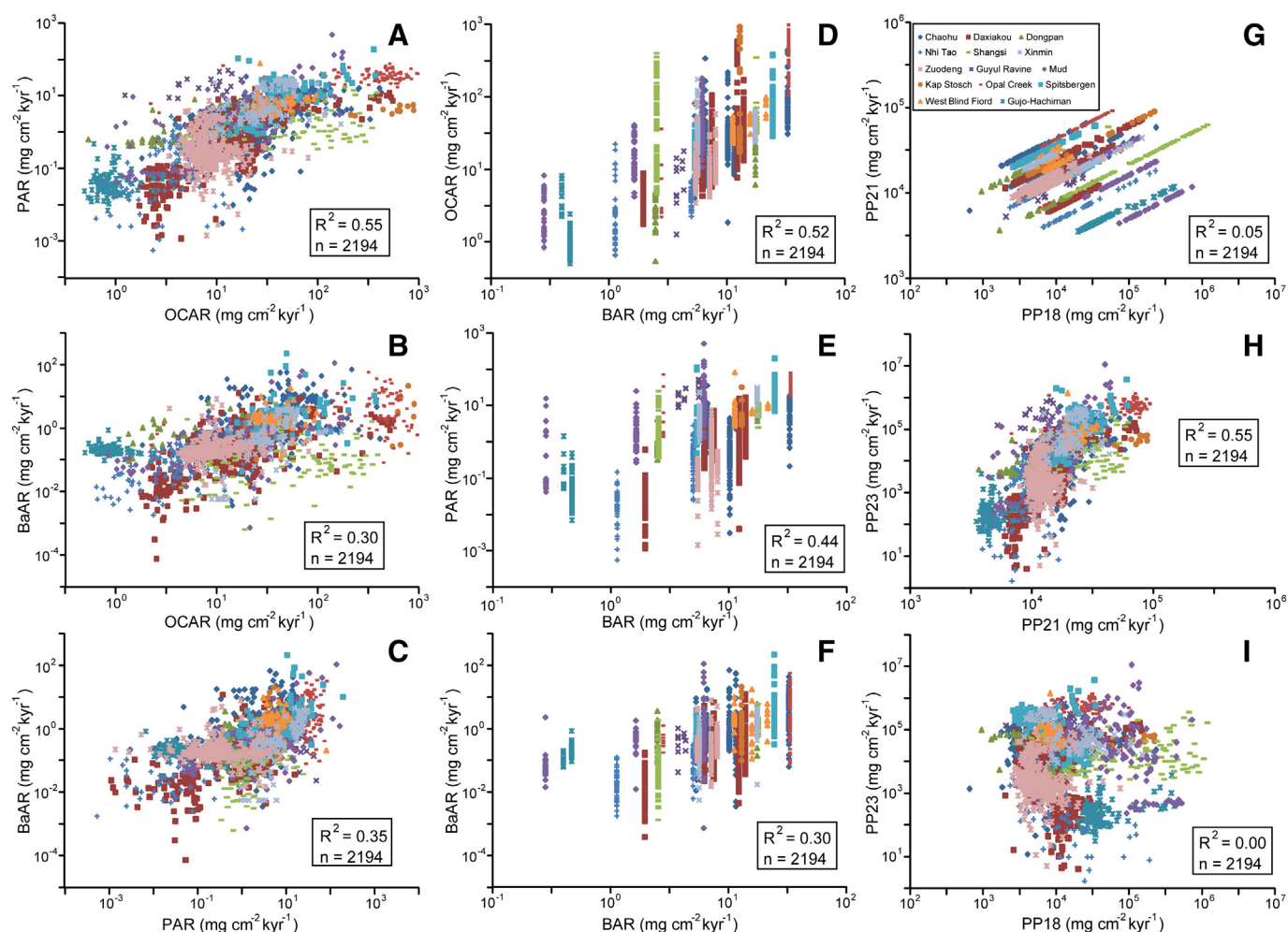


Fig. 12. Crossplots of BAR versus (A) OCAR, (B) PAR, and (C) BaAR. Primary productivity by Equation 18 (PP18) to PP21 (D), PP18–23 (E), and PP21–PP23 (F), PP18, PP21, PP23 were calculated per Eqs. (4), (5), and (6), respectively.

from the *C. yini* Zone to the *C. meishanensis* Zone. PP21 shows an increase from the Changhsingian to the Griesbachian in most study sections of all regions, although Daxiakou is an exception (Fig. 13D–E). PP21 also exhibits high values in the Smithian of many of the long sections (Fig. 11A–B). PP21 shows no obvious variations in the short sections from the *C. yini* Zone to the *C. meishanensis* Zone (Fig. 13F). PP23 exhibits a trend similar to that of PAR (Fig. 11D–F). Both increase from the Changhsingian to the Griesbachian in most long sections, with Daxiakou again being an exception (Fig. 13G–H). PP23 also yields an increase from the *C. yini* Zone to the *C. meishanensis* Zone in the short sections (Fig. 13I).

The three productivity estimates derived in this study exhibit varying degrees of correspondence. Positive covariation between PP18 and PP21 (Fig. 12G) reflects the presence of OCAR in the numerator of each equation. PP21 and PP23, in which primary productivity is estimated from proxy accumulation rates, show a positive and approximately linear relationship (Fig. 12H), although it is unclear if primary productivity rates or bulk sediment accumulation rates are the underlying control on this correlation. Weak to non-existent covariation between PP18 and PP23 (Fig. 12I) indicates that differences in preservation between organic carbon and phosphorus, as well as the different handling of preservational effects associated with BAR in Eqs. (4) and (6), are sufficiently large as to mask any relationship between these productivity proxies. Indeed, strong correlations of OCAR, PAR, and BaAR with bulk accumulation rates (BAR) suggest that bulk sediment flux may have been a major control on the burial fluxes of productivity proxies (Fig. 12D–F; cf. Tyson, 2005). High values of BAR served to enhance

the preservation of sedimentary organic matter by rapidly removing it from the surface zone of aerobic degradation (Hedges et al., 1988; Canfield, 1994; Tyson, 2005; Schoepfer et al., 2014).

4. Discussion

4.1. Sediment flux changes during the Permian–Triassic transition

Sedimentation rates in shallow-marine settings appear to have increased substantially from the late Permian to the earliest Triassic as a consequence of environmental changes related to the LPME. Average shallow-marine sediment fluxes were estimated to have increased by $\sim 7\times$ at the LPME (Algeo and Twitchett, 2010), a value that was subsequently revised to $\sim 4\times$ based on timescale changes (Algeo et al., 2013). In this study, LSRs are observed to have increased from the Changhsingian to the Griesbachian in most sections, followed by a second increase during the Smithian (Fig. 5). For many sections, LSRs are somewhat lower in the Dienerian relative to the Griesbachian and Smithian, although still elevated relative to the pre-LPME interval. A larger and more universal decline in LSRs is recorded in the Spathian (Fig. 5).

The most important trigger of sedimentation rate changes during the PTB crisis was the eruption of the Siberian Traps Large Igneous Province (LIP). This magmatic system, which produced $\sim 2.5\text{--}3.0 \times 10^6 \text{ km}^3$ of flood basalt lavas (Fedorenko et al., 1996; Reichow et al., 2009), also released large quantities of greenhouse gases such as CO_2 and CH_4 (Wignall, 2001; Shen et al., 2012a) as well as SO_2 that was hydrolyzed

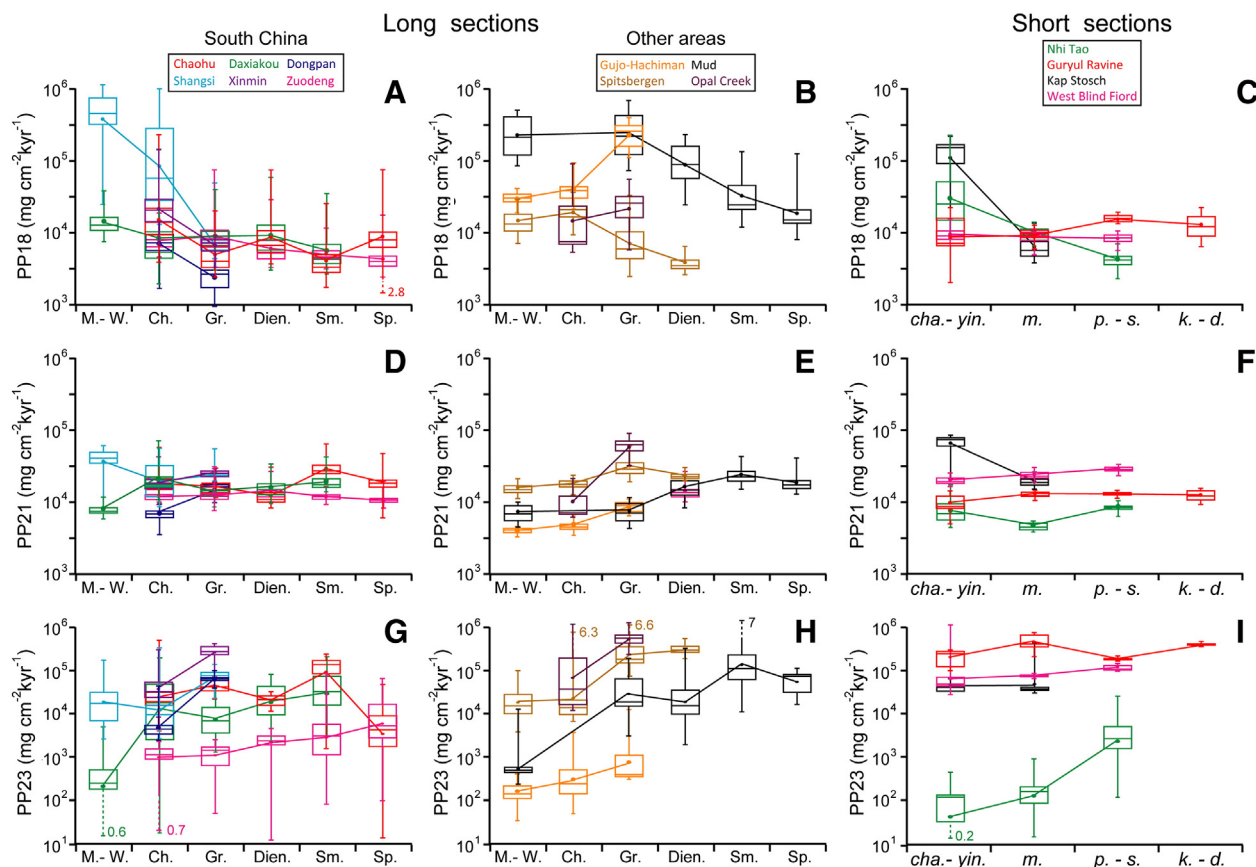


Fig. 13. Primary productivity for long sections (left and middle columns) and short sections (right column). Other details as in Figs. 8 and 11.

to acid rain (Black et al., 2014). The greenhouse gases led to strong climatic warming (Joachimski et al., 2012; Sun et al., 2012; Romano et al., 2013), and all emissions contributed to intensified subaerial chemical weathering (Algeo et al., 2011a) and the loss of terrestrial vegetation (Looy et al., 1999, 2001). Landscape denudation further contributed to erosion rates owing to the loss of the stabilizing influence of vegetation (Algeo et al., 2011a). Markedly elevated sedimentation rates persisted from the latest Changhsingian through the Smithian, an interval of ~1.7 Myr, possibly representing the duration of large-scale magmatic activity of the Siberian Traps LIP. If so, then the relatively higher sedimentation rates of the Griesbachian and Smithian relative to the Dienerian (Fig. 5) may indicate that there were two main phases of magmatism, each lasting ~0.5 Myr and separated by a ~0.7-Myr-long epoch of reduced activity.

Elevated terrestrial sediment fluxes can have many effects on the marine environment, including (1) increased dissolved inorganic nutrients, (2) enrichment with particulate organic matter, (3) increased turbidity, and (4) increased sedimentation (Hay, 1998; Fabricius, 2005). These effects, in turn, create stresses for marine organisms: (1) changes in productivity, especially increased productivity related to eutrophication of surface waters, (2) decreased dissolved oxygen levels, (3) reduced light levels owing to increased turbidity, and (4) sediment smothering of benthic organisms (Fabricius and Wolanski, 2000). These stresses result in higher energy costs to remove sediment particles, slower growth, more limited reproductive activity and larval recruitment, osmoregulatory difficulties, and increased susceptibility to disease. Persistently high sedimentation rates from the latest Changhsingian through the Smithian may have been a factor in the delayed recovery of marine ecosystems during the Early Triassic (Algeo and Twitchett, 2010).

4.2. Primary productivity changes during the Permian–Triassic transition

Changes in marine primary productivity in conjunction with the end-Permian biocrisis remain a matter of contention. Based on carbon isotopes, TOC, and other geochemical data, decreased productivity has been inferred either globally (Rampino and Caldeira, 2005) or regionally within the Tethys Ocean (Algeo et al., 2013). On the other hand, increased productivity following the crisis has been inferred for many non-Tethyan sections (Kakuwa, 1996; Suzuki et al., 1998; Algeo et al., 2013) and some Tethyan sections (Meyer et al., 2011). Paired $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{34}\text{S}_{\text{sulf}}$ analyses can provide an assessment of secular variation in the global burial fluxes of organic carbon and pyrite (Luo et al., 2010; Song et al., 2014), which are likely to be related to marine productivity fluctuations. If so, then the Early Triassic was characterized by large swings in marine primary productivity, with a major decrease during and immediately following the LPME and a subsequent major increase in the Early Triassic (Song et al., 2014). However, such global assessments can obscure local variation that is best captured through an analysis of sedimentary fluxes within individual sections (e.g., Algeo et al., 2010, 2012, 2013).

The present study sections exhibit pronounced secular variation in marine primary productivity, as proxied by OCAR, PAR, and BaAR, although with some local deviations from the general trend. Productivity fluxes tend to be largest in the Griesbachian and Smithian and relatively smaller in the Dienerian and Spathian, although fluxes for all of the Early Triassic substages are higher than those for the latest Permian Changhsingian stage (Fig. 11). The immediate cause of secular variation in productivity appears to be generally higher sediment fluxes during the Griesbachian and Smithian (see Section 4.1), which may have both stimulated marine productivity through higher nutrient fluxes and

enhanced organic carbon preservation through higher sediment bulk accumulation rates. The ultimate cause of such secular variation is likely to lie in changes in the frequency or intensity of environmental perturbations, presumably linked to eruptions of the Siberian Traps Large Igneous Province (Reichow et al., 2009; Korte et al., 2010).

The present study sections also exhibit some pronounced patterns of regional variation in marine primary productivity. Among the long sections, those from the South China Craton exhibit large decreases in OCAR from the Changhsingian to the Griesbachian (Fig. 11A), whereas those from other areas globally exhibit increases in OCAR during that interval (Fig. 11B). Algeo et al. (2013) interpreted this pattern as a collapse of marine primary productivity across the South China Craton during the earliest Triassic. An alternative possibility is that a shift in dominance from eukaryotic algae to bacterioplankton intensified recycling of organic matter in the ocean-surface layer, resulting in a drastic reduction in the export flux of organic carbon (cf. D'Hondt et al., 1998; Sigman and Hain, 2012; Luo et al., 2014). This pattern needs to be evaluated further in light of mixed trends for the short sections from the South China Craton, in which OCAR may either decrease or increase from the *C. yini* Zone to the *C. meishanensis* Zone (Fig. 11C). Both PAR and BaAR show mixed changes from the Changhsingian to the Griesbachian in the South China region (Fig. 11D–E), suggesting possibly complex patterns of paleoproductivity variation.

Some of the regional variation in paleoproductivity estimates is likely related to paleogeographic factors, i.e., ocean circulation patterns and localized areas of upwelling. Sections located at subtropical and higher latitudes along the northwestern and northern margins of Pangaea, such as Opal Creek, West Blind Fiord, Kap Stosch, and Spitsbergen, show some of the highest values, with PP21 productivity estimates of $10^{4.5}$ – 10^5 mg cm^{−2} kyr^{−1}. This region of the Permian–Triassic ocean has been interpreted as representing a productive coastal upwelling system on the basis of circulation models (Winguth and Maier-Reimer, 2005) and sedimentological characteristics (Beauchamp and Baud, 2002; Schoepfer et al., 2012, 2013). Satellite-based productivity estimates from modern subtropical upwelling systems and the high-latitude ocean show a similar range of values, with average productivity value of $10^{4.4}$ mg cm^{−2} kyr^{−1} for the Chile–Peru coast, $10^{4.6}$ mg cm^{−2} kyr^{−1} for the coastal California Current, $10^{4.5}$ mg cm^{−2} kyr^{−1} for the Benguela Current, and $10^{4.7}$ mg cm^{−2} kyr^{−1} for the Arctic Atlantic (Longhurst et al., 1995).

The nutrient and productivity dynamics of the Tethys Ocean have been controversial, with some models inferring that it acted as a high-productivity “nutrient trap” (Meyer and Kump, 2008) and other models inferring low productivity (Winguth and Winguth, 2012). The latter view is favored by its abundant and diverse, carbonate-producing benthic fauna, which are consistent with low-turbidity and oligotrophic conditions (Brasier, 1995). Among the study sections, carbonate-dominated Tethyan locales such as Nhi Tao and Daxiakou yield the lowest PP21 productivity estimates ($<10^4$ mg cm^{−2} kyr^{−1}). These values are lower than those found in modern regions of abundant coral growth in the Caribbean and Indo-Pacific, which generally yield productivity values of $10^{4.3}$ – $10^{4.5}$ mg cm^{−2} kyr^{−1} (Longhurst et al., 1995). The comparatively lower values of Early Triassic Tethyan sections may reflect genuinely lower productivity rates as a result of environmental stresses, or higher rates of recycling of organic matter in the ocean-surface layer as a consequence of dominance of bacterioplankton (cf. D'Hondt et al., 1998; Sigman and Hain, 2012; Luo et al., 2014).

The pelagic open-ocean section of Gujo-Hachiman exhibits the lowest productivity estimates, with PP21 values of $\sim 10^{3.6}$ mg cm^{−2} kyr^{−1}. These values are substantially lower than the Longhurst et al. (1995) estimate for the modern equatorial Pacific Ocean ($10^{4.0}$ mg cm^{−2} kyr^{−1}). The lower values may have resulted from genuinely lower productivity rates, perhaps as a consequence of fixed-N limitation in Early Triassic oceans (Kidder and Worsley, 2010; Takahashi et al., 2014). Expansion of oceanic oxygen-minimum zones due to widespread anoxia during the Early Triassic (Algeo et al., 2010, 2011b; Brenneke et al., 2011;

Winguth and Winguth, 2012) is likely to have resulted in intensified water-column denitrification, as evidenced by shifts toward higher $\delta^{15}\text{N}$ values in upwelling regions (e.g., Algeo et al., 2012) and lower $\delta^{15}\text{N}$ values in areas of enhanced cyanobacterial N fixation (e.g., Luo et al., 2011).

4.3. Influence of redox conditions on organic matter preservation

Redox conditions can exert a significant influence on the preservation of organic matter (Pedersen and Calvert, 1990; Canfield, 1994; Tyson, 2005). An increase in the burial flux of organic carbon can potentially be due to intensification of reducing conditions in bottom waters, slowing the rate of organic matter decay, in the absence of any productivity changes. However, enhanced anoxia and increased productivity commonly develop jointly owing to a positive feedback: higher productivity increases the sinking flux of organic matter, thus favoring reducing conditions at depth, and intensified anoxia results in a greater diffusive flux of P out of the sediment, enhancing marine productivity in surface waters (Murphy et al., 2000; Algeo and Ingall, 2007). Separating changes in productivity from changes in organic matter preservation due to enhanced anoxia is notoriously difficult (Pedersen and Calvert, 1990), although an assessment potentially can be made where sedimentation rate information is available (Canfield, 1994; Tyson, 2005; Schoepfer et al., 2014).

Evaluating the influence of redox conditions on organic matter preservation in the study units requires assessment of redox proxies for each section and their relationship to the productivity proxies employed here. We used three redox proxies based on elemental ratios for this purpose: U/Th, DOP_T, and C_{org}:P. U is normalized to Th because both are heavy elements (Atomic number = 92 and 90, respectively), and Th is relatively insoluble and immobile in the diagenetic environment. Seawater U is taken up by sediments under suboxic to anoxic conditions (Zheng et al., 2002; Morford et al., 2009), resulting in enrichment relative to Th (Wignall and Meyers, 1988). The upper continental crust has an average U/Th ratio of 0.27 (McLennan, 2001), so significantly higher ratios in marine sediments are an indication of authigenic U enrichment. DOP_T is an estimate of the degree of pyritization of a sample based on total Fe rather than total reactive Fe content. It is calculated as pyrite Fe/total Fe, with values ranging between 0 (most oxidizing) and 1.0 (most reducing) (Algeo et al., 2008b, their Supplemental Information). DOP_T values are not exactly equivalent to those for true DOP (Raiswell et al., 1988), and DOP_T can be considerably lower than DOP for a given redox condition, especially in carbonate facies. C_{org}:P ratios in marine sediments correlate significantly with benthic redox conditions (Algeo and Ingall, 2007). Given an initial C_{org}:P ratio of 106:1 (i.e., the Redfield ratio of marine algae), the relative amounts of organic C and Pin marine sediments change during early diagenesis, with low ($<50:1$), intermediate ($\sim 50:1$ – $200:1$), and high ($>200:1$) values indicative of oxic, suboxic, and anoxic conditions, respectively.

Redox proxy data are indicative of mainly oxic to suboxic conditions at all locales during the Permian–Triassic transition, as shown by the median values of U/Th, DOP_T, and C_{org}:P for each section (Table 4). The most reducing conditions are shown by Shangsi and Zuodeng, the only sections with median U/Th >1.0 and median DOP_T >0.20 . However, the reliability of U/Th and DOP_T as paleoredox indicators in carbonate facies is uncertain, and the C_{org}:P ratios of these sections are $<100:1$, suggesting no more than suboxic conditions on average. None of the mainly siliciclastic sections from outside the South China Craton show elevated median values for any of the redox proxies. The 84th percentile values (i.e., one standard deviation above the median) suggest that several sections experienced intermittently anoxic conditions, including Daxiakou, Nhi Tao, Shangsi, and Zuodeng in the South China area as well as Kap Stosch in East Greenland. Thus, the South China Craton appears to have been more prone to anoxia than other areas globally. No relationship of redox conditions to water depth is apparent for the South China Craton, however, as Daxiakou and Shangsi are deepwater

Table 4
Redox proxies and correlations with productivity proxies.

Section	n	Redox proxies				Correlation coefficients				
		U/Th		DOP _T		Corg:P		r(OCAR–U/Th)	r(OCAR–DOP _T)	r(OCAR–Corg:P)
		Median	16th–84th	Median	16th–84th	Median	16th–84th			
Chaoju	428	0.39	(0.18–1.29)	0.03	(0.01–0.51)	19	(9–107)	0.00	–0.02	–0.03
Daxiakou	489	0.86	(0.23–3.82)	0.09	(0.02–0.36)	38	(13–209)	–0.05	0.32	–0.05
Dongpan	53	0.20	(0.17–0.25)	0.01	(0.01–0.01)	9	(5–14)	–0.09	–0.48	–0.02
Nhi Tao	93	0.63	(0.23–1.35)	0.04	(0.01–0.09)	64	(17–456)	–0.12	–0.08	0.56
Shangsi	125	3.20	(0.35–12.34)	0.36	(0.06–0.63)	37	(17–256)	0.16	0.48	0.64
Xinmin	138	0.50	(0.28–0.73)	0.01	(0.00–0.02)	7	(3–19)	0.34	–0.22	0.61
Zuodeng	343	1.74	(0.53–4.53)	0.26	(0.06–0.62)	83	(20–205)	0.08	0.11	0.08
Guryul Ravine	19	0.44	(0.13–6.11)	0.01	(0.00–0.02)	1	(0.5–1.7)	0.67	–0.16	0.63
Spiti	135	0.32	(0.15–0.97)	0.05	(0.01–0.10)	14	(5–64)	0.52	0.23	–0.14
Kap Stosch	34	0.30	(0.09–2.16)	0.20	(0.02–0.33)	21	(15–396)	0.88	0.71	0.97
Opal Creek	99	0.37	(0.17–0.57)	0.31	(0.16–0.54)	27	(12–49)	–0.02	–0.32	0.83
Spitsbergen	81	0.25	(0.12–0.45)	0.16	(0.06–0.29)	9	(4–27)	–0.05	–0.04	–0.12
West Blind Fiord	56	0.18	(0.09–0.34)	0.04	(0.01–0.17)	18	(11–25)	–0.04	0.85	0.46
Gujo–Hachiman	99	0.40	(0.00–0.79)	0.02	(0.01–0.16)	67	(32–145)	0.45	0.72	0.43

sections whereas Nhi Tao and Zuodeng are shallow-water sections (Algeo et al., 2013; Song et al., 2013).

The redox proxy data for the 14 study sections show variable relationships to the productivity proxies employed in this study. Positive covariation of redox and productivity proxies is common for the mainly siliciclastic sections outside of South China but rare for the mainly carbonate sections from the South China Craton (see correlation coefficients, Table 4). Given that redox conditions were weighted toward somewhat more reducing conditions on average for the South China sections, the prevalence of positive correlations between redox and productivity proxies among the non-Chinese sections is not a strong indicator of enhanced preservation of organic matter as a result of anoxia. Rather, this relationship may reflect the fact that, in siliciclastic sediments, most organic matter is associated with finer grain size (i.e., clay minerals), and finer grain size almost invariably correlates with anoxia in the early diagenetic environment owing to (1) presence of more organic matter to consume dissolved oxygen, and (2) lower sediment permeability, reducing diffusive resupply of dissolved oxygen (Kennedy et al., 2002; Rothman and Forney, 2007). Although a comprehensive analysis of redox–productivity relationships in the 14 study sections is beyond the scope of the present contribution, the data presented in Table 4 are sufficient to demonstrate that there is no general control of productivity proxies by benthic redox conditions.

4.4. Relationship of productivity changes to plankton community composition

Changes in marine productivity are closely linked to changes in the composition of the marine plankton community during the Early Triassic. Eukaryotic algae declined sharply and were partially replaced by prokaryotic photoautotrophs following the LPME (Knoll et al., 2007; Payne and van de Schootbrugge, 2007). The development of widespread suboxic to anoxic conditions in the global ocean (Algeo et al., 2010; Brenneke et al., 2011; Winguth and Winguth, 2012) fostered the proliferation of green sulfur bacteria (Chlorobiaceae) and N-fixing diazotrophic cyanobacteria. Green sulfur bacteria are obligate anaerobes that typically live in the deeper part of the photic zone (Summons and Powell, 1987). Their widespread occurrence in uppermost Changhsingian and Griesbachian strata of both shallow (e.g., ~30 to 60-m-deep Meishan section; Grice et al., 2005; Cao et al., 2009) and intermediate to deep sections (e.g., Hays et al., 2007, 2012; Algeo et al., 2012) indicates a pronounced expansion and shallowing of oceanic oxygen–minimum zones following the end-Permian crisis (Feng and Algeo, 2014). Diazotrophic cyanobacteria are N-fixing prokaryotes that proliferate under conditions of N limitation of plankton productivity, whose presence can be recognized using the 2-methylhopanoid index

(Summons et al., 1999). Expansion of oceanic oxygen–minimum zones resulted in a loss of fixed N in seawater through denitrification, favoring diazotrophs (Anbar and Knoll, 2002; Schoepfer et al., 2012, 2013), the prevalence of which during the Early Triassic has been documented in many sections (Grice et al., 2005; Xie et al., 2005, 2007; Hays et al., 2007, 2012; Algeo et al., 2012).

Increased temperatures during the Early Triassic may have been an additional factor favoring the proliferation of cyanobacteria. Cyanobacteria tend to dominate phytoplankton assemblages at higher temperatures due to physiological factors, e.g., more rapid growth and wider enzymatic temperature tolerances (Davis et al., 2009; O'Neil et al., 2012). Cyanobacterial blooms are commonly harmful to marine ecosystems because of (1) production of toxins, and (2) depletion of dissolved oxygen in the water column during decay of the large mass of organic matter produced by algal blooms (Paerl et al., 2011; O'Neil et al., 2012). In contrast, eukaryotic algae and animals are severely stressed at high temperatures. For example, many ostracods decline at 30–35 °C and do not survive at temperatures >40 °C (Khudairi and Ruber, 1974). Corals are even more temperature-sensitive, with 90% mortality after three hours at 29 °C in laboratory experiments (Nozawa and Harrison, 2007). Recent oxygen–isotope studies have inferred that tropical sea-surface temperatures were mostly >35 °C during the first two million years of the Early Triassic (Sun et al., 2012; Romano et al., 2013), which would have favored cyanobacteria over higher organisms.

Spatially variable changes in the composition of Early Triassic plankton communities may account for apparent regional variation in marine productivity. In the South China region, there is abundant evidence for a proliferation of prokaryotic disaster taxa, including green-sulfur bacteria, cyanobacteria, short-spined acritarchs, and various chemoautotrophs (Grice et al., 2005; Xie et al., 2005, 2007, 2010; Shen et al., 2013a; Luo et al., 2014; Wu et al., 2014). Dominance of bacterioplankton results in increased recycling of organic matter within the ocean surface layer and a strong reduction in the export flux of organic carbon (cf. D'Hondt et al., 1998; Sigman and Hain, 2012; Luo et al., 2014). Export of organic matter may also have been limited by a major reduction in zooplankton abundance, resulting in more limited production of fecal pellets (Algeo et al., 2010; Feng and Algeo, 2014). These factors can potentially account for the substantial reduction in productivity across the PTB reported for the South China region (Algeo et al., 2013). The abrupt decreases of TOC and OCAR coincided with the appearance of cyanobacterial mats (microbialites) across the South China Craton at the base of the *C. meishanensis* Zone (Wang et al., 2005; Xie et al., 2010). Microbialites are relatively more abundant in the Tethyan region than elsewhere globally during the Early Triassic (Kershaw et al., 2007, 2012).

4.5. Relationship of productivity changes to the end-Permian biocrisis and Early Triassic recovery

The ultimate trigger for marine productivity changes during the Permian–Triassic transition is thought to have been the eruption of the Siberian Traps Large Igneous Province (Payne and Kump, 2007; Reichow et al., 2009; Korte et al., 2010). Emission of greenhouse gases (e.g., volcanic CO₂ and volcanogenic CH₄; Retallack and Jahren, 2008; Svensen et al., 2009; Zi et al., 2013) resulted in extreme climate warming during the latest Permian and Early Triassic (Joachimski et al., 2012; Sun et al., 2012; Romano et al., 2013). Warming would have increased water-column stratification and reduced the vigor of ocean circulation, contributing to oceanic anoxia (Algeo et al., 2011a; Song et al., 2013, 2014). The effect of these processes on marine productivity is not entirely clear, however, and may have been spatially variable. At a global scale, warming and stagnated ocean circulations are likely to have resulted in lower marine productivity owing to reduced upwelling of nutrient-rich intermediate waters. However, climate warming and intensified terrestrial erosion are also likely to have increased the flux of river-borne nutrients to epicontinental seas and continental shelves, at least locally resulting in a stimulation of marine productivity (Algeo and Twitchett, 2010; Algeo et al., 2011a). The harmful effects of these changes on marine organisms include reduced feeding activity, growth rate, body size, and reproductive success (Algeo and Twitchett, 2010).

Changes in marine productivity and plankton community composition may have also contributed to the delayed recovery of marine ecosystems during the Early Triassic (Bottjer et al., 2008; Chen and Benton, 2012). In many of the present study sections, LSRs and MARs show peak values during both the Griesbachian and Smithian substages of the Early Triassic (cf. Wei et al., in press). This pattern suggests that the disturbances that triggered higher sediment fluxes and marine productivity rates persisted, albeit with varying intensity, through at least the first ~2 Myr of the Early Triassic. The slow tempo of recovery likely resulted from continued but intermittent environmental stresses during this interval (Retallack et al., 2011; Wei et al., in press). Indeed, some biotic groups show multiple episodes of recovery and extinction during the Early Triassic (e.g., Brayard et al., 2009; Stanley, 2009), demonstrating the episodicity of the environmental stresses that slowed the overall recovery of marine ecosystems. The availability of nutrients in the ocean-surface layer, the composition of marine plankton communities, and the rates of marine productivity are likely to have fluctuated in concert with these environmental perturbations.

5. Conclusions

Based on analysis of rates of sediment accumulation and marine primary productivity from 14 Permian–Triassic boundary sections with a wide global distribution, we conclude that: (1) Sedimentation rates were generally elevated from the latest Permian through the Smithian substage of the Early Triassic due to increased chemical and physical weathering of unstable land surfaces, extreme climate warming, and acidic precipitation; (2) in most regions, primary productivity increased from the late Changhsingian to the Griesbachian and again during the Smithian; (3) the increase in the burial fluxes of productivity proxies (TOC, P, and Ba_{bio}) during the Early Triassic was due to a combination of elevated nutrient fluxes owing to intensified chemical weathering and enhanced organic matter preservation owing to intensified physical weathering and increased sediment fluxes from land areas; (4) the South China region shows an atypical pattern of lower productivity in the Griesbachian, due either to a 'productivity crash' or to enhanced recycling of organic matter in the ocean-surface layer as a consequence of a shift in dominance from eukaryotic algae to bacterioplankton; and (5) generally elevated productivity contributed to widespread and intense oceanic anoxia during the Early Triassic, which was a likely factor

in the ~2 to 5-Myr delay in the recovery of marine ecosystems following the end-Permian biocrisis.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.earscirev.2014.11.002>.

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