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Environmental determinants and ecologic selectivity of benthic faunas from nearshore to bathyal zones in the end-Permian mass extinction: Brachiopod evidence from South China

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ABSTRACT

In South China the Changhsingian brachiopods are extraordinarily abundant and diverse, comprising 447 species in 143 genera. They were widespread in nearshore, shallow sea, reef, carbonate platform, shelf basin, and bathyal zones. Brachiopod attachment modes were also highly diversified and include burrowing, body cementation, pedicle attaching on substratum, body spines anchoring on substratum, pedicle attaching on objects, and clasping spines anchoring on other objects. They suffered the species and genus extinction rates of 91.5% and 86%, respectively in the first episode of the end-Permian mass extinction and further species and genus extinction rates of 84.2% and 80.0%, respectively in the second crisis. For the Permian—Triassic (P–Tr) brachiopods, there were (1) selective extinction of the normal shallow marine dwellers relative to these inhabiting deep sea or marginal seas, and (2) among the normal shallow marine habitats, selective extinction of reef-dwellers relative to non-reef forms. Ecologically, the body-cementation forms suffered much higher extinction rates than other lifestyle elements. In contrast, both the burrowing and clasping spine-anchoring forms had much lower extinction rates than other lifestyle elements. Although the reef and bathyal dwellers partly survived the first extinction event, they migrated to other habitats to survive the crisis. The estimation of extinction rates based on the single-episode mass extinction pattern cannot reveal precisely the extinction severity of brachiopod faunas over the P–Tr transition. Brachiopod diversity changes support the two-stage mass extinction pattern near the P—Tr boundary.

1. Introduction

Brachiopods are numerically the most abundant invertebrates in the Permian oceans, but are also the second largest group of victims among the leading fossil groups that suffered the end-Permian mass extinction (Raup, 1979; Carlson, 1991; Erwin, 1993). Between the two major Permian mass extinctions, at the end-Guadalupian and end-Changhsingian, brachiopod faunas in South China are extraordinarily diverse and abundant (Chen et al., 2005a,c, 2006a). In particular, the Changhsingian brachiopod faunas are outstanding and comprise about 447 species in 143 genera (see below). They are much more abundant and diverse than any coeval faunas elsewhere in the world (Shen et al., 2000; Chen et al., 2005a). This extraordinary diversity is thought to have resulted from the heightened ecologic differentiation and diversified habitats in South China (Chen et al., 2006a).

Liao (1980a) was the first to establish two distinctive brachiopod biofacies for the Changhsingian: one characterized by the *Peltichia zigzag–Spinomarginifera alpha* fauna usually inhabiting shallow-water carbonate settings (mainly limestone); the other by the *Paryphella sulcatifera–Paracrurithyris pigmaea* fauna associated with "deep-water" siliceous mudstone. Later, Xu and Grant (1994) established numerous distinct assemblages from both siliciclastic and limestone lithofacies through the Wuchiapingian–Changhsingian. The Changhsingian siliciclastic lithofacies includes the nearshore terrigenous clastic facies and shelf basin facies successions (Liao, 1980a; Sheng et al., 1984). As such, their siliciclastic facies assemblages include admixed elements of both nearshore and shelf basin facies brachiopod associations (Xu and Grant, 1994).

It is of note, however, that the "deep-water" habitats in the above studies are usually represented by the Talung Formation, a siliceous shale or cherty limestone unit, confirmed to be deposited in the shelf basins between the carbonate platforms with water depth less than 200 m (Wang and Jin, 2000). More recently, the bathyal facies brachiopod faunas have been described from the Changhsingian of South China (He et al., 2005; Chen et al., 2006a, 2009a). Accordingly, the Changhsingian brachiopod faunas actually inhabited a wide range

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of environmental settings from the nearshore, siliceous shallow sea, carbonate platform, shelf basin, and bathyal zone. South China therefore provides a unique opportunity to assess environmental determinants and ecologic selectivity of brachiopods during the Permian–Triassic (P–Tr) mass extinction.

In South China, brachiopod extinction patterns across the Permian–Triassic boundary (PTB) have already been well documented in terms of biodiversity changes and taxonomic selectivity (Shen and Shi, 1996; Chen et al., 2002, 2005a; Rong and Shen, 2002; Shen et al., 2006). However, few studies (but see Chen et al., 2005a) have addressed environmental and ecologic selectivity of brachiopod faunas during this severe crisis, even though environmental determinants and ecologic selectivity have been increasingly emphasized in studies of other mass extinctions and, more generally, with respect to Phanerozoic global biodiversity dynamics (Rhodes and Thayer, 1991; Jablonski and Raup, 1995; Peters and Foote, 2002; Foote, 2006; Kiessling and Aberhan, 2007; Peters, 2008; Miller and Foote, 2009).

Previously, most studies addressing brachiopod extinction across the PTB in South China (Shen and Shi, 1996; Rong and Shen, 2002; Shen et al., 2006) considered the P–Tr mass extinction as an abrupt, single-episode event, as documented by Jin et al. (2000) from the Meishan section, South China. However, there is growing evidence that the P–Tr crisis actually includes two episodes, calibrated to the bases of Bed 25 and Bed 28, respectively at the Meishan section, South China (Xie et al., 2005; Yin et al., 2007; Chen et al., 2009b,c; Song et al., 2009). The former event is equivalent to the P–Tr mass extinction recognized by Jin et al. (2000) and was named the first/or main episode, while the latter is termed the second episode of the end-Permian crisis (Xie et al., 2005; Yin et al., 2007). These two events are distinguished from one another based on the conodonts *Neogondolella meishanensis*, *Hindeodus changxingensis*, *H. parvus*, and *Isarcicella staescheri* Zones (Jiang et al., 2007), although the strata interval may have been of very short depositional duration (Chen et al., 2009b; Fig. 1). Between these two events, brachiopods are fairly common worldwide (Chen et al., 2005a) and were later termed the survival faunas 1–2 (Chen and McNamara, 2006; Chen et al., 2006b). The brachiopod extinction patterns following these two extinction scenarios (Fig. 1) are evaluated herein.

Ecologically, most brachiopods were sessile benthic organisms (Rudwick, 1970). Their interaction with the substratum therefore had the great ecologic importance and this may be reflected in many major features of morphology and adaptation to varying environments (Rudwick, 1970). Thus, this study evaluates environmental determinants and ecologic selectivity of brachiopod extinction through this critical interval based on comparisons of extinction rates in habitats ranging from the nearshore through bathyal zone.

2. Materials and methods

Species-level brachiopod data have been based on critical reviews of the published data from both primary and summary literature sources and, where possible, supplemented with first-hand materials. A new reef facies fauna from the uppermost Changhsingian of the Fuyao area of Dongluo County, Guangxi Province, South China (Chen et al., in preparation) is also taken into account in the quantitative analysis. A recent update of the 32 marine Late Permian sections in South China (Liao, 1979, 1980a,b, 1982, 1983, 1984, 1987; Zhan in Hou et al., 1979; Zhao et al., 1981; Liao and Meng, 1986; Yang et al., 1987; Ding et al., 1989; Wang and Jin, 1991; He and Shen, 1991; Shen and He, 1991, 1994; Shen et al., 1992, 2004; Zeng, 1993; Zeng et al., 1995,

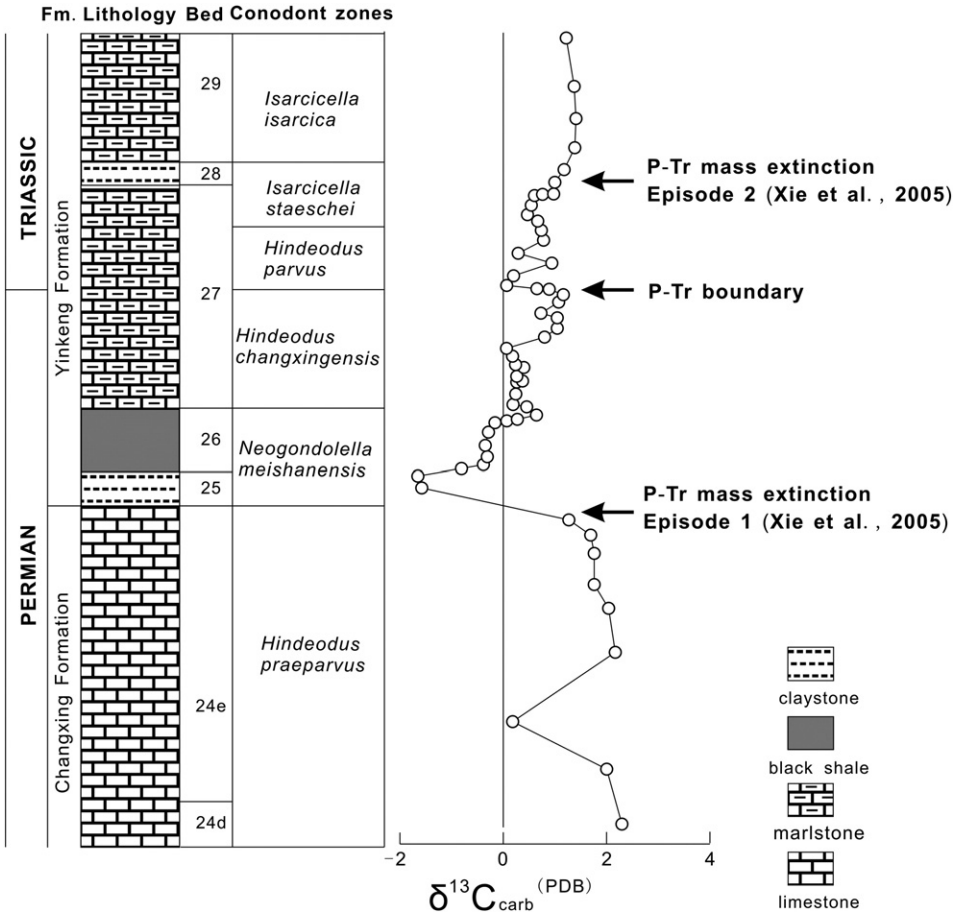

Fig. 1. Permian–Triassic (P–Tr) boundary and mass extinction horizons recorded at the Meishan section, Changxing county, Zhejiang Province South China (after Chen et al., 2009a). P–Tr boundary was placed at the middle part of Bed 27 (Yin et al., 2007); conodont zones follow Jiang et al. (2007); carbon isotope curve follows Jin et al. (2000).