

# Chapter 17

## Permian-Triassic Extinctions and Rediversifications

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### 17.1 Introduction

At the boundary between the Paleozoic and Mesozoic eras (~252 myr), the end-Permian mass extinction was the most devastating global-scale event ever recorded, resulting in the loss of more than 90% of marine species (Raup 1979) and the disappearance or severe reduction in diversity of typical Paleozoic organisms (e.g., trilobites, tabulate and rugose corals, brachiopods). The ecological recovery of the benthos is traditionally assumed to have spanned the entire Early Triassic (i.e. ~5 myr), thus strikingly contrasting with that of pelagic environments and their dwellers. Whether or not this difference is the result of a selective preservation bias against the benthos cannot be excluded. However, extreme diversity fluctuations of nekto-pelagic organisms (e.g., ammonoids and conodonts) during the entire Early Triassic indicate major environmental upheavals in the ocean in the wake of the end-Permian extinction(s). In support of markedly unstable Early Triassic times, several major events are known from the sedimentary, geochemical and palynological records (e.g., Payne et al. 2004, 2010; Galfetti et al. 2007a, b, c; Hermann et al. 2011, 2012; Sun et al. 2012; Grasby et al. 2013; Romano et al. 2013; Fig. 17.1a), suggesting profound global changes in climate, sea-level and oceanic geochemistry (e.g. anoxia, euxinia, acidification). The initial low resolution time frames of these recurrent environmental deterioration events after the Permian-Triassic boundary (PTB) crisis were therefore first lumped into a “delayed recovery” model which is still the standard in effect in some recent reviews (e.g., Chen and Benton 2012).

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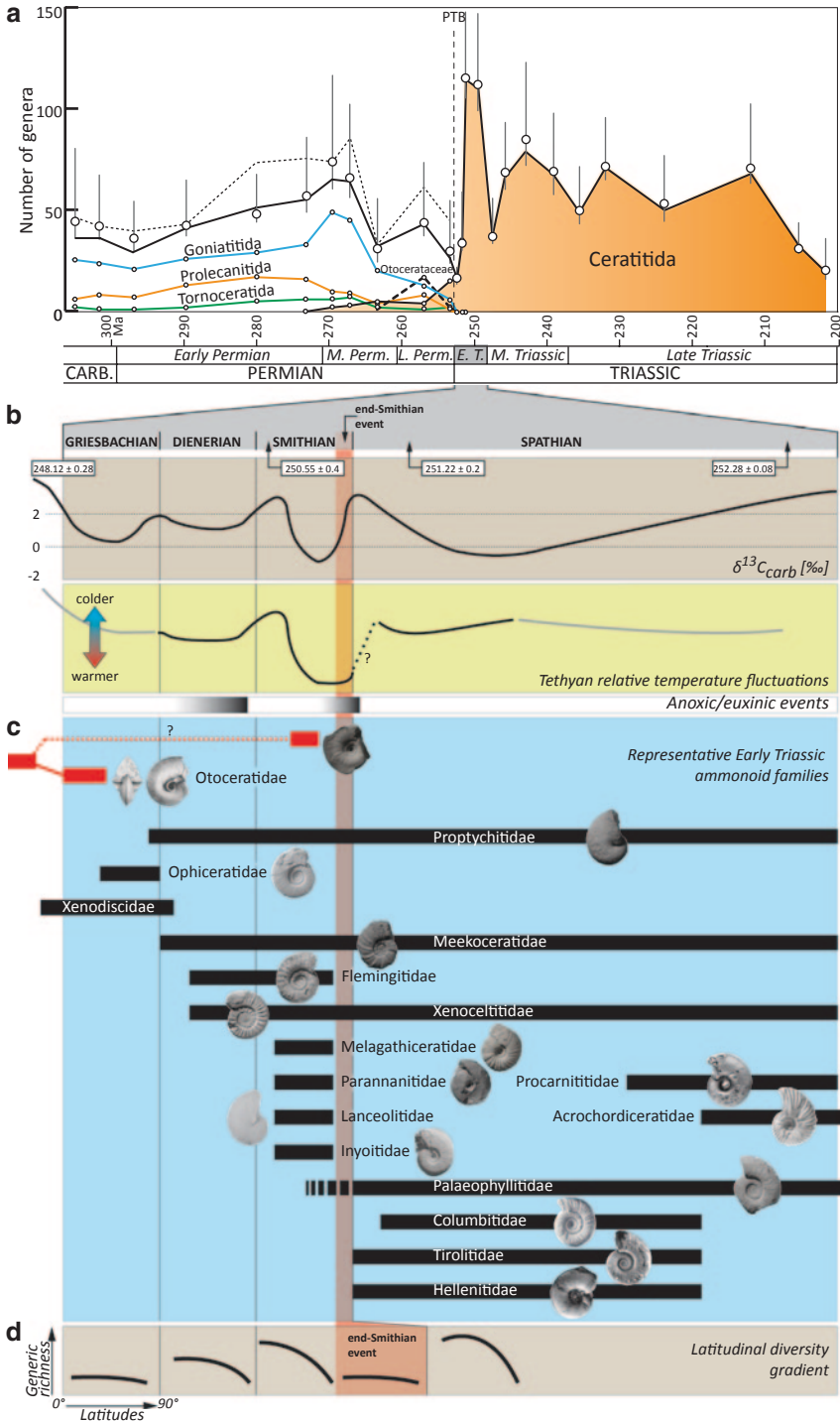
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Contrasting with this early view, recent analyses of nekto-pelagic taxa such as ammonoids and conodonts document an explosive Early Triassic rediversification (Orchard 2007; Brayard et al. 2009c). Indeed, although ammonoids were among the organisms most affected by the PTB mass extinction, Triassic ammonoids actually reached levels of diversity much higher than in the Permian less than  $\sim 1.5$  myr after the PT boundary (Brayard et al. 2009c). In this chapter, we provide a brief overview of the present state of our knowledge of the ammonoid record around the PTB crisis and during the recovery interval.

## 17.2 Late Permian Events

Four major clades of Permian ammonoids (Goniatitida, Prolecanitida, Tornoceratitida and Ceratitida; Fig. 17.1a; e.g., Ruzhencev 1960; Glenister and Furnish 1981; Leonova 2002, 2011) are globally characterized by relatively slow and uncoupled origination and extinction dynamics (Brayard et al. 2009c). Goniatitida were the dominant group during the Early-Middle Permian interval (e.g., Ruzhencev 1960; Glenister and Furnish 1981; Leonova 2002, 2011). Following a diversity peak during the Middle Permian, all ammonoid groups show a protracted, two-step decline in diversity during the Late Permian (Capitanian and Changhsingian extinctions; Glenister and Furnish 1981; Stanley and Yang 1994; Zhou et al. 1996). The first extinction event in the Capitanian is now generally agreed to have been triggered by the eruption of the Emeishan flood basalts (Bond et al. 2010). Remarkably, Ceratitida did not follow this trend and flourished during the Wuchiapingian with the notable rapid diversification of the morphologically-singular Otocerataceae (Brayard et al. 2009c; Leonova 2002, 2011; Zakharov and Abnavi 2013). This time interval also corresponds to a marked restriction of global ammonoid morphological disparity (e.g., Saunders et al. 2008; Villier and Korn 2004; Leonova 2005). With blossoming Xenodiscidae and Pseudotiroplitidae, Ceratitida also largely embodied the taxonomic diversity of Changhsingian ammonoids. The PTB mass extinction was most probably triggered by eruption of the Siberian traps (Reichow et al. 2009; Svensen et al. 2009).

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**Fig. 17.1** **a** Total ammonoid generic richness (*black bold line*: all ammonoids; *color lines*: major ammonoid groups; *Permian bold line*: data from Goniat.org; *Permian dotted line*: alternate data from the Ammon database (Korn and Ilg 2007); *Triassic bold line* modified after Brayard et al. (2009c) based on an updated database) and mean Chao2 estimate of the overall generic richness with its 95% Confidence Interval (large circles with vertical bars; see Brayard et al. 2015). PTB: Permian-Triassic boundary. E.T.: Early Triassic. Note that the end-Smithian ammonoid extinction event discussed in the text is not illustrated here due to its short time duration. **b** Chronostratigraphic subdivisions of the Early Triassic (radiometric ages by Ovtcharova et al. 2006; Galfetti et al. 2007b and Shen et al. 2011) with simplified trends of geochemical ( $\delta^{13}\text{C}_{\text{carb}}$ ; data from Galfetti et al. 2007b) and Tethyan relative temperature fluctuations during this period (data from Romano et al. 2013 [*black line*] and Sun et al. 2012 [*grey line*]). **c** Temporal distribution of some Early Triassic representative families (modified after Tozer 1981; Brayard et al. 2006, 2009c). Ammonoid illustrations from Brayard and Bucher (2008), Brayard et al. (2013) and Guex et al. (2010). **d** Simplified trend of the formation of a latitudinal diversity gradient during this period (modified after Brayard et al. 2006, 2007b, 2009b)

The Goniatitida and Tornoceratida completely disappeared with this event (Glenister and Furnish 1981; Tozer 1981; Leonova 2002, 2011) and apparently, only one Prolecanitida genus (*Episageceras*) survived the crisis (Kummel 1972; Tozer 1981; Dagens and Ermakova 1996; Leonova 2011; Zakharov and Abnavi 2013). Among the Ceratitida, only two main ammonoid clades survived across the PT boundary: the Otoceratidae and Xenodiscidae. *Otoceras* rapidly disappeared after the mass extinction, before the end of the Griesbachian. However, after a gap spanning the entire Dienerian, Otocerataceae probably had their final appearance with *Proharpoceras* in the Smithian (Brayard et al. 2007a). Thus, with very exceptions (*Episageceras*, *Otoceras*, *Proharpoceras*) and a still ambiguous case (Sagecerataceae) (e.g., Glenister and Furnish 1981; Tozer 1981; Becker and Kullman 1981; Brayard et al. 2007a; McGowan and Smith 2007), Triassic ammonoids are usually agreed to root into a single and morphologically very simple clade, the Xenodiscidae and are therefore interpreted as a monophyletic clade (Tozer 1981; Brayard et al. 2006; McGowan and Smith 2007). Following this hypothesis, all Mesozoic ammonoids are consequently derived from the xenodiscids, which went unscathed across the PTB mass extinction.

### 17.3 Early Triassic Events

Early Triassic times are commonly divided into four stages or substages of highly uneven duration (Griesbachian, Dienerian, Smithian and Spathian), which are very well defined by ammonoid zones and events (Fig. 17.1b; see Jenks et al. 2015 and Monnet et al. 2015). Based on ammonoids, the PTB is traditionally defined by the first occurrence of *Otoceras* (e.g., Tozer 1994, 2003; Dagens and Ermakova 1996; Zakharov 2002; Shevyrev 2006). Although knowledge of Griesbachian and Dienerian ammonoids is still limited, proptychitids and meekoceratids originated during the Dienerian. In their first steps, these Dienerian originations did not lead to any spectacular taxonomic diversification (e.g., Tozer 1974; Shevyrev 2001; Brühwiler et al. 2008; Ware et al. 2011; Fig. 17.1c). The beginning of the Smithian is defined by the origination of new families such as the highly speciose Flemingitidae and Kashmiritidae. Ammonoid richness first peaked during the middle Smithian through the evolution of extremely short-lived species (Brayard et al. 2009c; Brühwiler et al. 2010). The beginning of the Spathian witnessed an explosive radiation rooted in the latest Smithian *Xenoceltites*. Tirolitidae first quickly diverged from *Xenoceltites* and formed the basal group of from which the next radiation that began in the early Spathian and continued onward at a very high pace.

The tempo of recovery after the PTB mass extinction has recently been estimated thanks to new U-Pb radiometric ages allowing for more accurate and precise time calibrations (Ovtcharova et al. 2006; Galfetti et al. 2007b; Shen et al. 2011). The rediversification was explosive for some marine groups such as the ammonoids (Brayard et al. 2009c) and conodonts (Orchard 2007), spanning less than ~1.5 myr (Fig. 6.21a). Ammonoids reached levels of taxonomic richness in the Smithian that were already much higher than those of the Permian (see also Tozer 1981; Leonova 2002). Their recovery did not follow Sepkoski's (1978) classical logistic

diversification model, for which major assumptions are required about the carrying capacity of the environment, but it instead has been re-interpreted as a hierarchical model periodically interrupted by brief but significant extinction events (e.g., end-Smithian; Brayard et al. 2009c).

The global first-order trend in increasing ammonoid diversity was accompanied by a progressive change from cosmopolitan to latitudinally-restricted distribution during the Early Triassic with the formation of a clear latitudinal diversity gradient during most of the Smithian and Spathian sub-stages (Fig. 17.1d; Brayard et al. 2006, 2015). Marked intertropical faunal exchanges across the Tethys and Panthalassa are obvious at that time with the occurrence of identical ammonoids on opposite sides of Panthalassa, illustrating latitudinally-restricted faunal exchanges during the Smithian (Brayard et al. 2007b, 2009a, b, 2013; Jenks et al. 2010), and the Spathian (Galfetti et al. 2007b; Guex et al. 2010; Monnet et al. 2013).

The global recovery trend was not a continuous process. It was interrupted at least once during a brief episode of ammonoid cosmopolitanism combined with a marked extinction event during the end-Smithian (e.g., Tozer 1982; Dagys 1988; Brayard et al. 2006). This extinction event was the most important one within the entire Triassic and its intensity compares with that of the PTB extinction. Only four species-poor families (the xenoceltitids and the sageceratids, but also virtually the palaeophyllitids and the proptychitids) survived the late Smithian extinction.

Similarly, conodonts reached their highest Triassic generic diversity during the middle Smithian, but only a very few species went through the end-Smithian crisis. On land, floras underwent a drastic ecological turnover with a middle Smithian spore peak comparable to the end-Permian one, followed by an early gymnosperm recovery during the late Smithian (Hermann et al. 2011). An abrupt, global change from hygrophytic to xerophytic associations characterizes the Smithian-Spathian boundary (Galfetti et al. 2007c; Hermann et al. 2011). The global carbon isotope record also reached a marked negative peak during the middle Smithian, followed by an abrupt positive shift in the late Smithian (e.g., Payne et al. 2004; Galfetti et al. 2007b). In the Tethys, the oxygen isotope record from biogenic phosphate tends to track the carbon isotope record and indicates a temperature drop of ca. 7.5 °C close to the Smithian-Spathian boundary (Romano et al. 2013).

It is well known by ammonoid workers (e.g., Kummel and Steele 1962) that the Early Triassic ammonoid radiation is represented by numerous homeomorphic taxa. Trends in morphological disparity and richness were especially decoupled during the Griesbachian and Dienerian with persisting low disparity values in the Dienerian whereas richness shows a weak increase (McGowan 2004, 2005; Brosse et al. 2013). The first disparity peak occurred early in the Smithian (Brosse et al. 2013). The end-Smithian extinction had obvious consequences with a marked contraction of the previously occupied morphospace. The Spathian corresponds to a second disparity peak with a morphospace analogous to the early-middle Smithian. However, Spathian superfamilies occupied more restricted portions of the morphospace (Brosse et al. 2013).

Ammonoid recovery during the Early Triassic therefore appears as the combined outcome of (i) the classical rapid refilling of a vacated ecospace after the mass extinction, and (ii) the successive extinction events and recurrent stressful

environmental conditions that may have enhanced their high turnover rates. Most likely explanations for the end-Smithian extinction call upon the combined consequences of the concentration of carbon dioxide of volcanic origin (e.g., Galfetti et al. 2007b) and sea-level changes. Whatever the precise cause(s), it had a deep impact on the biotic rediversification, especially for ammonoids, conodonts and plant ecological assemblages as well. We cannot exclude the possibility that a few other Early Triassic biotic events are still hidden due to the insufficient knowledge of intervals such as the Griesbachian and Dienerian. However, significant results and new questions on the Early Triassic recovery will certainly arise from further studies of ammonoids and their spectacular evolutionary rebounds, which are hardly reconcilable with the alleged persistence of globally devastated ecosystems.

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