

# Evidence from ammonoids and conodonts for multiple Early Triassic mass extinctions

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**Ammonoids and conodonts, being characterized by exceptionally high background rates of origination and extinction, were vulnerable to global environmental crises, which characteristically intensified background rates of extinction. Thus, it is not surprising that these taxa suffered conspicuous mass extinctions at the times of three negative Early Triassic global carbon isotopic excursions that resembled those associated with the two preceding Permian mass extinctions. In keeping with their high rates of origination, both the ammonoids and conodonts rediversified dramatically between the Early Triassic crises. Other marine taxa, characterized by much lower intrinsic rates of origination, were held at low levels of diversity by the Early Triassic crises; because global mass extinctions affect all marine life, these taxa must have experienced relatively modest expansions and contractions that have yet to be discovered, because they do not stand out in the fossil record and because the stratigraphic ranges of these taxa, being of little value for temporal correlation, have not been thoroughly studied.**

carbon isotopes | Permian

The greatest mass extinction of the past half billion years occurred at the end of the Permian Period. A substantial biotic recovery was delayed until the end of the Early Triassic Epoch, which lasted  $\approx 6$  million years (My). After the destruction of coniferous vegetation, lycopod spore plants came to dominate the land (1), and total benthic marine diversity remained relatively low until the Middle Triassic time (2). This was an unusually long delay for biotic recovery after a mass extinction (3), and the Early Triassic has therefore often been viewed as an interval when global conditions remained hostile to life (4–6). Both the terminal Permian crisis and a lesser mass extinction at the end of the Middle Permian were accompanied by a sharp negative shift of stable carbon isotopes, as recorded in limestones and organic carbon in numerous marine and terrestrial strata (reviewed by Retallack et al., ref. 7). Three similar negative isotope spikes have been found in Early Triassic marine carbonate rocks (8). Similar excursions in paleosols (9) may correlate with them. In contrast, the carbon isotope curve for the Middle Triassic is quite stable after an initial positive shift (Fig. 1). The discovery of negative excursions in the Griesbachian, Smithian, and Spathian stages of the Early Triassic has led to the hypothesis that a succession of ecological crises similar to those of the Permian stifled recovery from the Permian crisis (9–12). Thus, intervals between crises might have been quite hospitable to life but too brief to permit substantial diversification by most taxa. The present paper confirms this hypothesis.

Rates of evolutionary radiation and background extinction for taxa tend to be positively correlated because these rates are governed by the same biological traits; furthermore, taxa that have high background rates of extinction tend to suffer preferentially in biological crises, during which background rates are multiplied (13). Taxa characterized by very high rates of evolutionary radiation and extinction might therefore be expected to display conspicuous patterns of expansion and decline during the Early Triassic. The two such marine taxa with well-studied Lower Triassic fossil records are the ammonoids and conodonts, and an analysis of their history indicates that they suffered mass

extinctions at the times of the negative carbon isotope shifts and rediversified markedly during the intervening intervals.

The extensive compilations of Tozer (14–16) are the basis for the following analysis. Tozer's assembly of Lower Triassic ammonoid occurrences (14–16), although somewhat dated, represents a large, global sample and has recently been used effectively to analyze patterns of ammonoid evolution after the terminal Permian mass extinction (17, 18). Orchard (19) has recently analyzed Lower Triassic conodont occurrences on a global scale with the remarkable resolution of  $\approx 100,000$  years.

## Results

Not surprisingly, the patterns of diversification and extinction of Early Triassic ammonoids and conodonts turn out to be remarkably similar (Fig. 1). Orchard (19) noted that each extinction interval for the conodonts was associated with a pronounced global negative carbon isotope excursion. In fact, in each case, heavy extinction began before the minimum isotopic value was reached (Fig. 1). The ammonoid extinction events were also temporally associated with these isotopic excursions, but the precise timing relative to the excursions is less clear. After the terminal Permian crisis, both the ammonoids and the conodonts experienced rapid recovery during the Griesbachian Age, followed by a major extinction. Taxonomic and stratigraphic uncertainties prevent a rigorous assessment of what clearly was a strong pulse of conodont extinction near the end of the Griesbachian: very few species of the two most diverse conodont families of this interval (the Neogondolellinae and Anchignathodontidae) survived into the Dienerian (19). Then, both the ammonoids and conodonts radiated rampantly during Dienerian and early Smithian time, and both suffered another mass extinction during the Smithian. For the conodonts, the Smithian crisis spanned  $\approx 1$  My, with only two species known to have persisted into the Spathian; similarly, only four ammonoid genera are known to have survived into the Spathian (Fig. 1). The Spathian radiation was slower than the Dienerian radiation for both taxa. Another mass extinction for the conodonts in late Spathian time spanned  $\approx 0.6$  My. The Smithian and Spathian declines for the ammonoids were presumably also protracted because, like the conodonts, the ammonoids did not radiate persistently throughout either interval: 27 ammonoid genera are known to have survived into the Smithian, yet a total of only 53 genera are recognized for this entire interval, and the corresponding numbers for the interval above the *Columbites* zone of the Spathian are 21 and 65 (Fig. 1).

The reduction of ammonoid and conodont diversity to very low levels at the end of the Griesbachian, Smithian, and Spathian and the subsequent appearance of new subtaxa must represent the kinds of biotic changes that long ago led to the recognition of these intervals as formal stages. The absence of heavy

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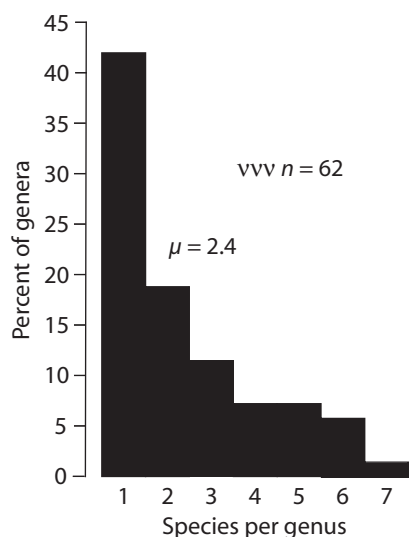


Fig. 2. Frequency distribution of numbers of species per genus for ammonoids of the post-Columbites interval of Early Triassic time (42).

radiation, the number of genera  $N_t$  at some previous time  $T$  can be obtained by first calculating exponential decrease from  $N$  at the rate ( $R$ ) at which the increase occurred:

$$N_t = Ne^{Rt}, \quad [1]$$

where  $t$  is negative, equaling  $-T$ . The number of genera that died out in the next interval of time will equal the extinction rate,  $E$ , times the number of lineages present:

$$ENe^{Rt}. \quad [2]$$

The total number of genera terminated since the start of a monophyletic radiation is then the summation for all past intervals:

$$EN \int_{-\infty}^0 e^{Rt} dt = EN/R \quad [3]$$

The total number of genera that the radiation produced is this number plus  $N$ , the number extant at the end of the radiation:

$$\tilde{N} = EN/R + N, \quad [4]$$

which yields  $E$ , and therefore  $O$ , because  $O = R + E$ .

The above formulation assumes monophyly, but the Dienerian radiation began with four genera (Fig. 1). Therefore, for the calculation,  $N$  (which equals 27) must be reduced to 6.75, and  $\tilde{N}$  (which equals 39) reduced to 9.8. The values of  $\tilde{N}$ ,  $N$ , and  $R$  for the ammonoids' radiation give  $E = 1.44 \text{ My}^{-1}$  and  $O = 4.62 \text{ My}^{-1}$ . Mean duration of genera ( $D = E^{-1}$ ) during the radiation, therefore, was 0.70 My. This result compares favorably with the estimate of  $\approx 0.5$  My for average species duration of Jurassic and Cretaceous ammonoids (22) because, as noted above,  $\approx 42\%$  of Early Triassic ammonoid genera contained only one recognized species (Fig. 2). Furthermore, "average" in Kennedy (22) is likely to have referred to modal or median, rather than mean, duration.

Rates noted above for conodont species extant during the Dienerian/Smithian radiation ( $O = 2.80 \text{ My}^{-1}$  and  $E = 1.12 \text{ My}^{-1}$ ) are of the same order of magnitude as rates calculated for ammonoid genera, with the somewhat higher  $O$  for ammonoids resulting in a higher  $R$ . Mean duration of conodont species is similar to that of ammonoid species and genera: 0.90 My for the

Dienerian/Smithian radiation (Fig. 1) and 0.80 My for the entire Dienerian-Smithian interval.

## Discussion

All rates ( $O$ ,  $E$ , and  $R$ ) for Early Triassic ammonoids and conodonts were much higher than those that characterize most other marine taxa ( $R \approx 0.06\text{--}0.4 \text{ My}^{-1}$ ,  $E \approx 0.04\text{--}0.33 \text{ My}^{-1}$ ,  $S \approx 0.1\text{--}0.74 \text{ My}^{-1}$ ) (13). Bivalve and gastropod mollusks are relatively abundant taxa in Early Triassic rocks. For extant genera and families of these taxa that have arisen at some time within the past 100 My and diversified more or less exponentially (with allowance for the terminal Cretaceous mass extinction for taxa that arose before it occurred), the mean rate of radiation has been only 0.076 per 1 My ( $t_2 = 9.1$  My). Thus, values of  $R$  for ammonoids in the Early Triassic were perhaps 20–40 times higher than typical values for radiating taxa of bivalves and gastropods. Triassic diversities also indicate this kind of disparity: a total of 132 ammonoid genera are recorded for the Early Triassic (14–16), and the large majority of these descended from the single genus *Xenodiscus* at the start of the epoch (14, 15). In contrast, 32 bivalve genera and 49 gastropod genera are recorded for the start of the Early Triassic, yet the generic numbers for these groups for the entire interval are only 63 and 67, respectively; the equivalent numbers for articulate brachiopods are 12 and 33 (23).

Dramatic evolutionary recoveries by ammonoids and conodonts between the Early Triassic mass extinctions suggest that although the ocean became increasingly stratified during the Late Permian and remained in this state during the Early Triassic (24), marine taxa in general were not held back by persistently hostile environmental conditions. Rather, as hypothesized previously (9–12, 25), mass extinctions were so frequent that most taxa were unable to recover markedly until the end of the epoch, and their losses in the three mass extinctions were also too light to have stood out in the fossil record. This appears to be true for common Early Triassic benthic taxa, such as bivalves, gastropods, and brachiopods, all of which are characterized by much lower characteristics of rates of diversification and extinction than ammonoids and conodonts (23). Nonetheless, these taxa must have suffered modest losses in the three Early Triassic mass extinctions because all other marine mass extinctions have struck all taxa living in the ocean, albeit to differing degrees. The temporal ranges of the Early Triassic genera and species of bivalves, gastropods, and brachiopods have never been evaluated carefully because of their limited value for stratigraphic correlation; these ranges warrant detailed study.

Ecological changes in local faunas of the Early Triassic actually reflect modest recoveries by benthos between times of crisis. A substantial increase in species richness of faunas in well-oxygenated, shallow marine habitats during the Griesbachian time suggests that anoxia at greater depths has led to underestimation of the rediversification by benthos after the terminal Permian mass extinction (26, 27). Trace fossil faunas also indicate a substantial diversification of burrowing taxa during the Dienerian and Spathian (26, 28). In addition, gymnosperm floras reclaimed the land at the start of Spathian time (11).

Both the ammonoids and conodonts appear to have been mobile carnivores, and like most carnivores, they were probably selective in their diets. It is possible, however, that many ammonoids were microphagous (29). The modern genus *Conus* is a highly selective carnivorous gastropod, with many species focusing on a single species of prey (30). The rate of radiation of *Conus* during the late Cenozoic has been remarkably high compared with rates for gastropod grazers and bivalve suspension and deposit feeders, all of which are relatively unselective in their food consumption. Small populations of the latter taxa that constitute new species have little chance of expanding their

populations and are likely to suffer rapid extinction because they have the same generalized feeding habits as their congeners. However, an incipient species of *Conus*, when focusing on a prey species unexploited by its congeners, is likely to undergo a population explosion and survive (31). It is reasonable to attribute, in large part, the very high rates of speciation of the predatory ammonoids and conodonts to this same kind of trophic specialization. Specialized reproductive behavior in these groups, readily leading to reproductive isolation via minor changes, may also have contributed to their high speciation rates; specialized behavior also rendered ammonoid and conodont species vulnerable to environmental change and, presumably, therefore contributed to their high rates of extinction (13, 32).

The factors most often hypothesized to have produced the two large negative isotope excursions of the Permian are: destruction of primary producers and oxidation of their organic carbon, which is isotopically light; a reduced rate of burial of organic carbon; and release of bacterially generated methane hydrates from the sea floor as a result of global warming (reviewed by Berner in ref. 33). Other suggested causes are a shift from algae and cyanobacteria to sulfur bacteria as the dominant photosyn-

thesizers in the ocean (34) and release of large volumes of isotopically light carbon as the magmas that produced the massive Siberian Traps rose burned their way through the world's largest coal deposit (35). In fact, any of the five isotopic excursions considered here may have had more than one agent, perhaps as a result of positive feedback. Climatic warming at the time of the terminal Permian crisis (36) may have played a dominant role in the extinctions. Also hypothesized as agents are poisonous emissions of CO<sub>2</sub> (37) or H<sub>2</sub>S (38) from the deep sea, extensive oceanic anoxia (39), and a sharp decline in atmospheric pO<sub>2</sub> as atmospheric pCO<sub>2</sub> rose (40, 41). Whatever disrupted the biosphere in the latter part of the Permian and early in the Triassic, the association of the repeated isotopic excursions with mass extinctions indicates that these excursions represent significant changes in the global carbon cycle. Explanation of these changes may shed light on the causes or consequences of the associated biotic crises.

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