Radiolarian biodiversity dynamics through the Triassic and Jurassic: implications for proximate causes of the end-Triassic mass extinction

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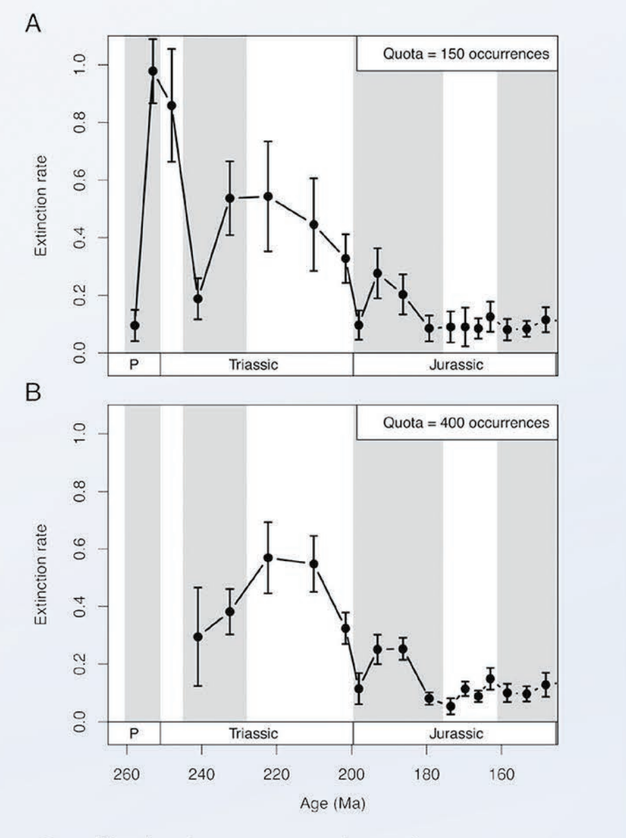
Introduction

The Late Triassic–Early Jurassic interval was a period of major changes in the Earth system, including the **end-Triassic extinction event** and several others of lesser magnitude. If **ocean acidification** was a dominant cause of the extinctions, radiolarians, as organisms with a siliceous test, may have been substantially less affected than organisms secreting calcium carbonate. On the basis of Sepkoski's (2002) compendium, Hautmann et al. (2008) have suggested that radiolarians were indeed only **marginally affected** by this crisis.

The rich fossil record of radiolarians is well-suited for global diversity analyses. However, the radiolarian range data of Sepkoski (2002) are rather outdated and some radiolarian workers maintain that the group was seriously hit by the end-Triassic event (Carter and Hori 2005). A recent sampling-standardized analysis of the radiolarian fossil record from the Late Permian to Late Jurassic concluded that although Rhaetian extinction rates were higher than in Sepkoski's compendium, there is no evidence for an end-Triassic mass extinction (Kiessling and Danelian 2011). Instead, the end-Triassic extinctions fall within the background of generally elevated Triassic extinction rates.

The Late Triassic–Early Jurassic interval includes **other, smaller** biotic and environmental events, whose characterization may be aided by studying radiolarian diversity patterns. Here we reassess radiolarian turnover rates from the Triassic to the earliest Cretaceous, using a finer, substage-level stratigraphic resolution in the Late Triassic–Early Jurassic (Carnian–Toarcian) interval and a novel taxonomic (origination and extinction) rate calculation method, the "gap-filler" equations (Alroy 2014).



Radiolarian extinction rates from Kiessling and Danelian, 2011.

Data

Radiolarian occurrence data of the Capitanian (Middle Permian) to Albian (mid-Cretaceous) interval were downloaded from the **Paleobiology Database** on December 16, 2013 and comprise 2144 fossil collections, each usually representing microfossils extracted from a single hand-sample. This data set is similar to the one used for a previous analysis (Kiessling and Danelian 2011) but has been supplemented by about 800 collections from more than 40 references.

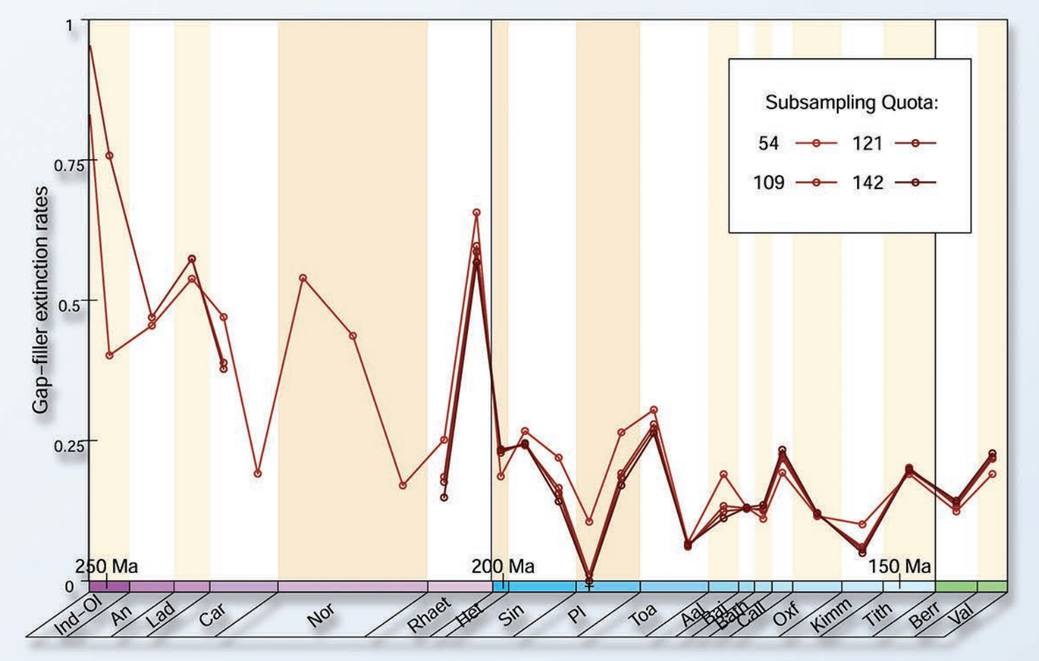
The default stratigraphic resolution of the PaleoDB is the geologic stage, also used in the analyses by Kiessling and Danelian (2011). To achieve a higher resolution in our focus interval, most of the 785 Late Triassic to Early Jurassic radiolarian **collections were assigned to substages**, on the basis of additional stratigraphic information gleaned from the original references. This resulted in a finer and more uniform stratigraphic resolution in terms of bin duration, with the average length of the time slices lowered from 6.4 to 5.1 Myr, and their standard deviation from 3.9 to 2.6 Myr.

Methods

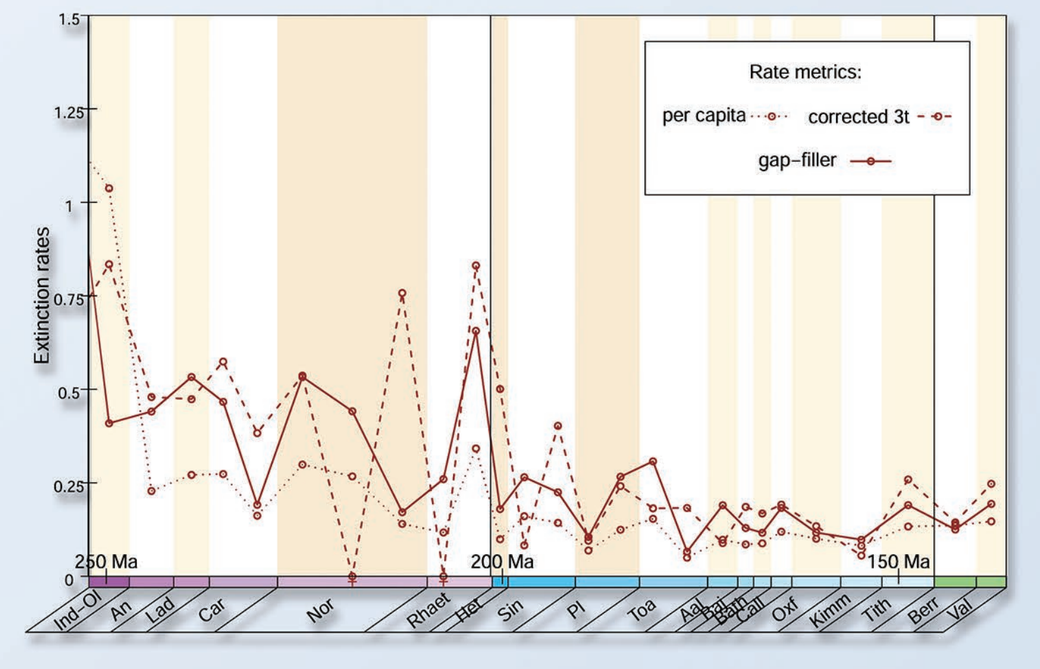
As occurrence-based data sets are becoming increasingly available and simple range-metrics cannot be corrected for heterogeneous sampling intensity, occurrence-based counting and standardization methods (Alroy 2010c, 2014) are increasingly being used to estimate fossil turnover rates. We chose to apply the modified three-timer metrics proposed by Alroy (2008, 2014), which are suited for sampling-standardization and avoid edge effects that usually create a backward smearing of extinction rates and forward smearing of origination rates. A recent modification of the three-timer metrics are the **gap-filler equations** (Alroy 2014). Because these require the three-timer sampling completeness (Alroy 2008) to be as even as possible (Alroy 2014), which is best accomplished by using **classical rarefaction** (CR; Raup 1975), an approach followed in this study. The genus richness was estimated by using the geometric means of genus counts in the individual subsampling trials with the applied target quota of 54 genus occurrences.

For comparison, we have also computed the taxonomic rates using Shareholder Quorum Subsampling (SQS; Alroy 2010a,b,c) with the targeted quorum of 0.6, and by-list occurrences weighted (OW) subsampling (Alroy et al. 2001), with the same quota as for CR.

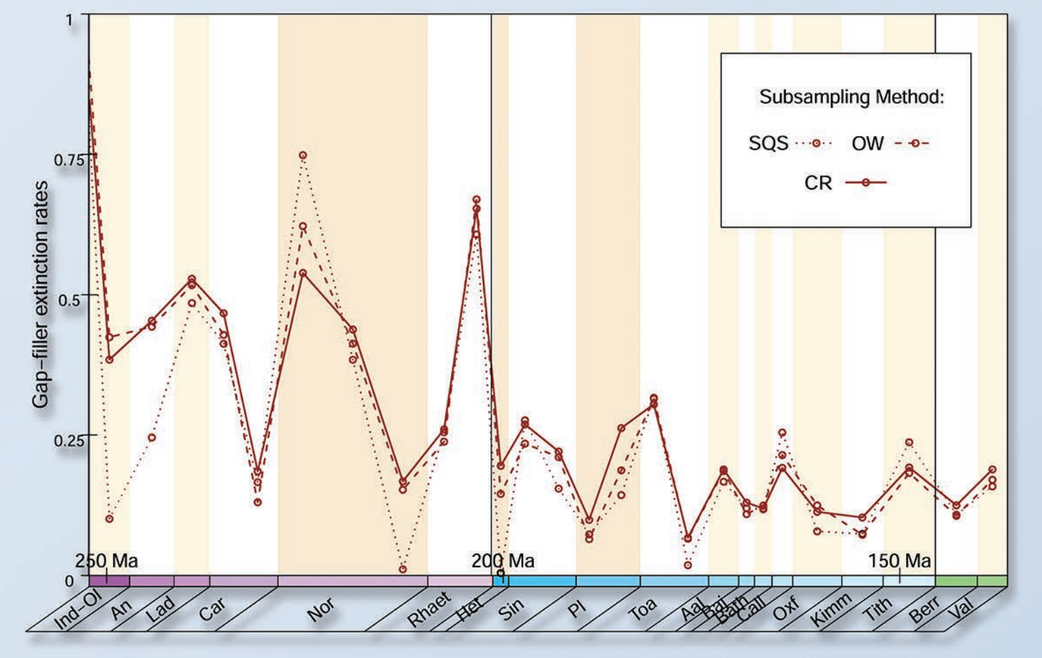
Subsampling and rate calculation



Radiolarian extinction rates with multiple subsampling quota employed with CR.

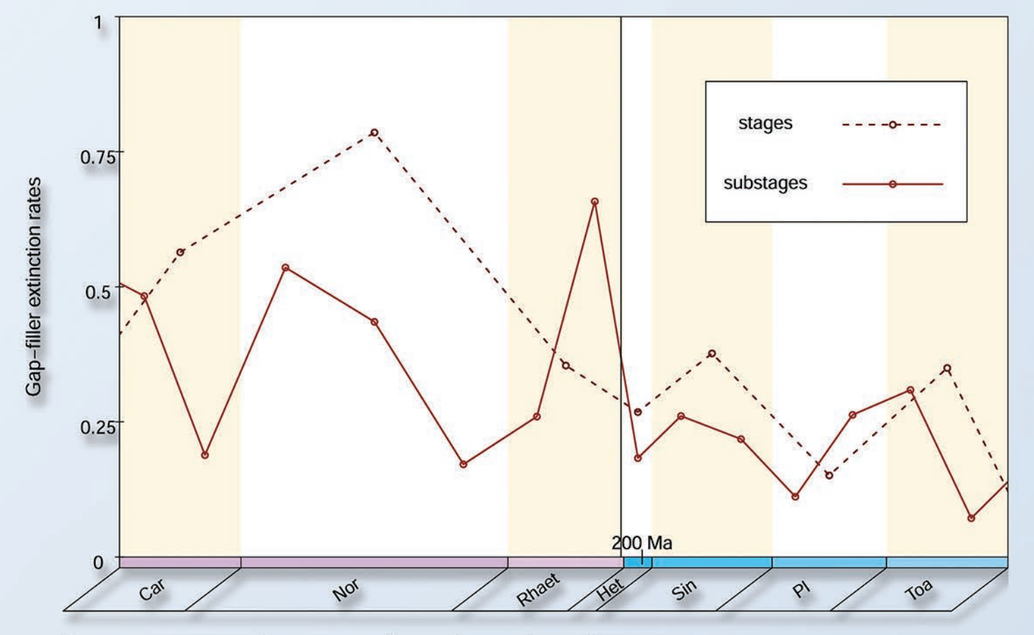


Radiolarian extinction rates calculated with multiple rate equations.



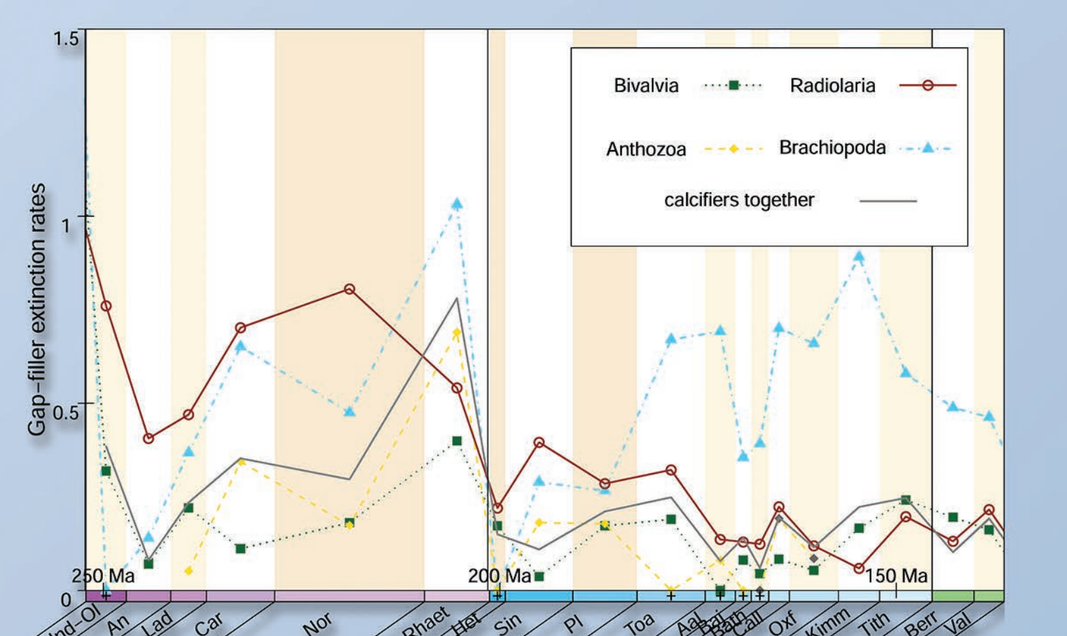
Radiolarian extinction rates calculated with multiple subsampling methods.

Resolution-dependence

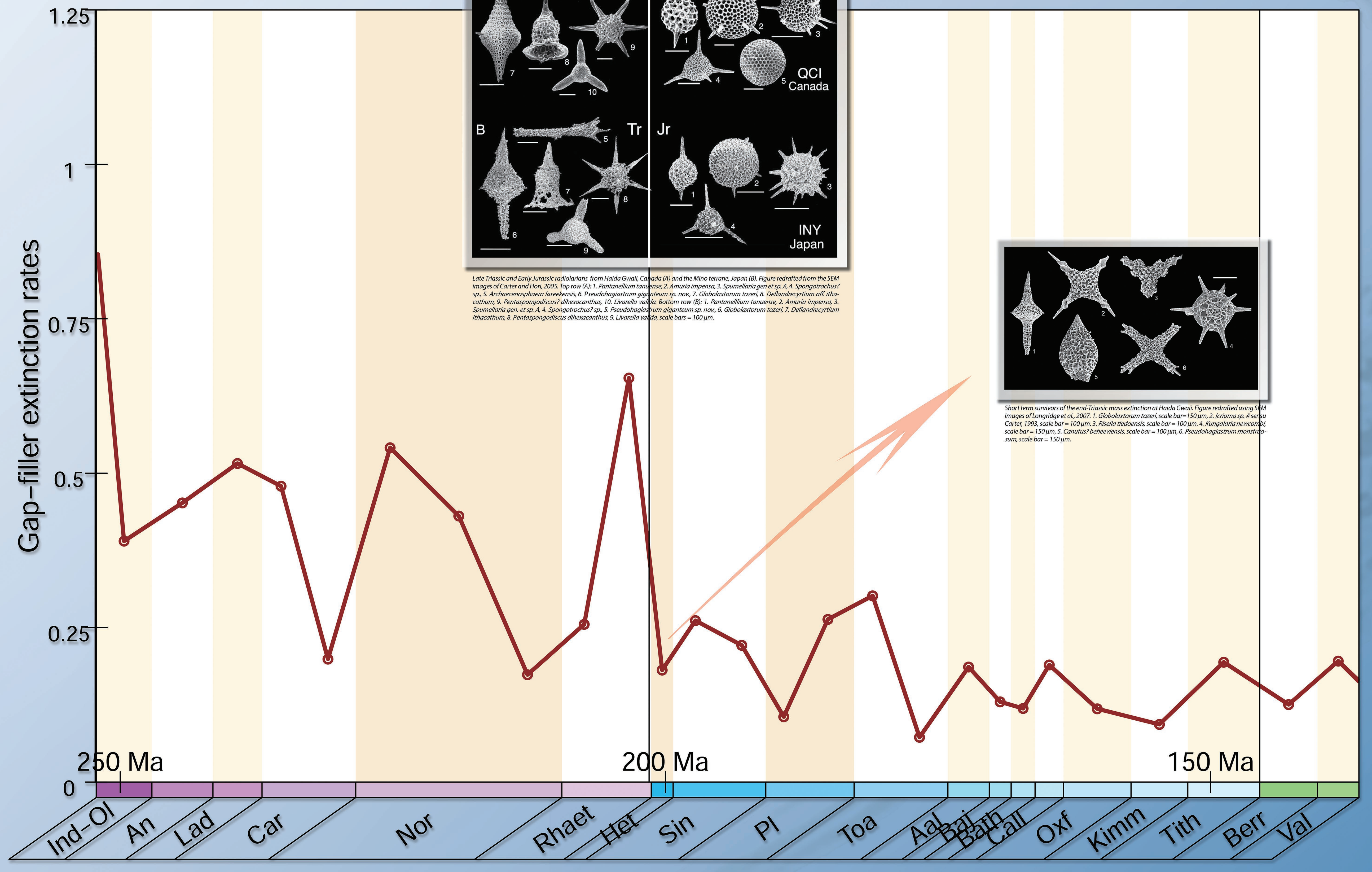


Stage vs. substage level extinction rates.

Comparison with benthic calcifiers



Radiolarian extinction rates compared with those of benthic calcifiers.



Radiolarian extinction rates. note the late Rhaetina spike.

Late Triassic and Early Jurassic radiolarians from Haida Gwaii, Canada (A) and the Mino terrane, Japan (B). Figure redrafted from the SEM images of Carter and Hori, 2005. Top row (A): 1. Pantanellium tanuense, 2. Amuria impensa, 3. Spumellaria gen et sp. A, 4. Spongotrochus? sp., 5. Archaecenosphaera laseekensis, 6. Pseudohagiastrum giganteum sp. nov., 7. Globolaxtorum tozeri, 8. Deflandrecyrtium aff. ithacathum, 9. Pentaspongodiscus? dihexacanthus, 10. Livarella valida. Bottom row (B): 1. Pantanelllium tanuense, 2. Amuria impensa, 3. Spumellaria gen. et sp. A, 4. Spongotrochus? sp., 5. Pseudohagiastrum giganteum sp. nov., 6. Globolaxtorum tozeri, 7. Deflandrecyrtium ithacathum, 8. Pentaspongodiscus dihexacanthus, 9. Livarella valida, scale bars = 100 μm.

Short term survivors of the end-Triassic mass extinction at Haida Gwaii. Figure redrafted using SEM images of Longridge et al., 2007. 1. Globolaxtorum tozeri, scale bar=150 μm, 2. Icrioma sp. A sensu Carter, 1993, scale bar = 100 μm. 3. Risella tledoensis, scale bar = 100 μm. 4. Kungalaria newcombi, scale bar = 150 μm, 5. Canutus? beheeviensis, scale bar = 100 μm, 6. Pseudohagiastrum monstruosum, scale bar = 150 μm.

Results

The finer stratigraphic resolution revealed that e**xtinction rates declined significantly** over time in the Triassic–Jurassic interval (Spearman's rank correlation $\rho = 0.67$, $p = 4.186 \times 10^{-4}$ between the gap-filler rates and mean time slice ages). **Origination rates also declined** over time (Spearman's rank correlation with time $\rho = 0.79$, $p = 4.794 \times 10^{-6}$ with the gap filler rates) and their overall trajectory is similar to that of extinctions.

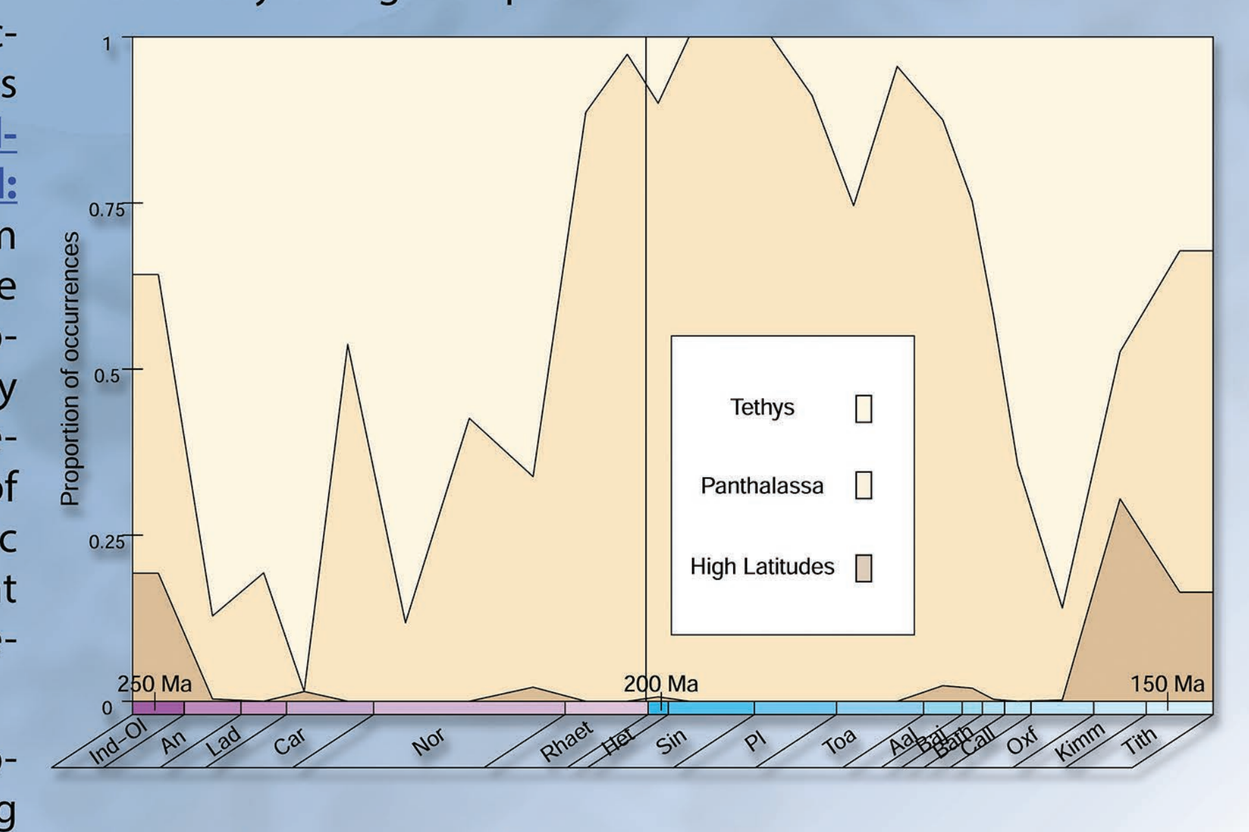
The extinction rate of the late **Rhaetian slice is over the 97.5% critical value** of the detrended extinction rates (see the published study), regardless of the function used to detrend the data. Although the drop in originations is not significant in the Late Triassic, the relatively lower rate values are noteworthy. There is no statistical support for selective extinctions in the raw data.

We used the same analytical toolkit to characterize the evolutionary trajectory of benthic calcifying macroinvertebrates. Because a substage stratigraphic resolution could not be achieved for the great majority of macroinvertebrate occurrences we compare rates at the stage level. Taxonomic **rates of radiolarians are higher than those of benthic calcifiers,** among which bivalves exhibit the lowest turnover rates. The overall trajectories of origination rates of calcifiers are similar to those of radiolarians, but only bivalves exhibit a similar decline over time and radiolarians are the only group for which extinction rates decline significantly over the Triassic–Jurassic interval.

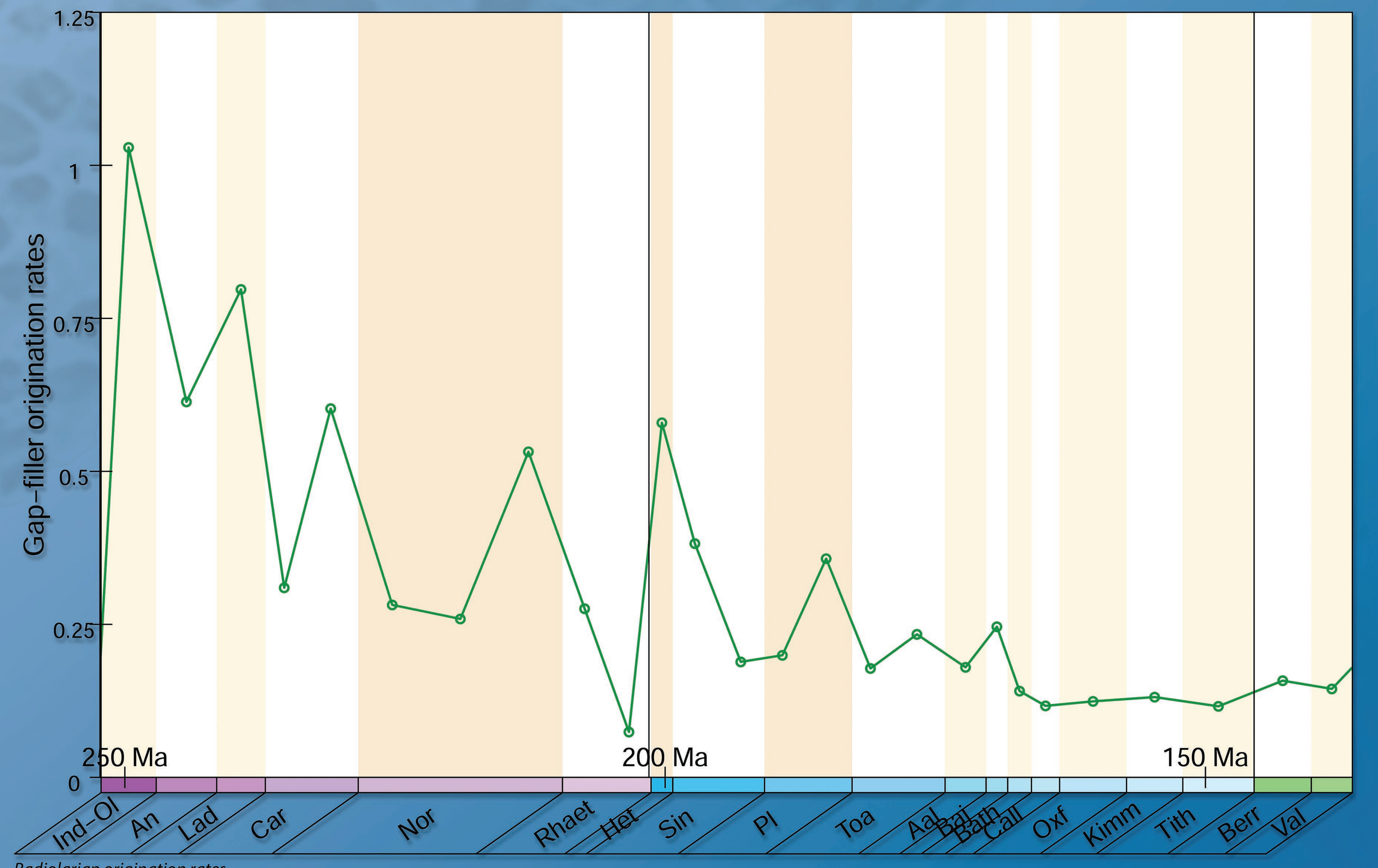
The end-Triassic mass extinction of radiolarians becomes **evident only with an analysis at the substage level:** even though the long-term trends did not change, the short-term pattern at the substage resolution is remarkably different from that at stage level. The apparent variability of the substage-level taxonomic rates suggests that significant turnover might have happened within the stages.

Applying different subsampling methods and increasing the subsampling quota led to only **minor changes** in the results. The unique extinction peak in the late Rhaetian is independent of the rate metric applied, as all three methods exhibit a distinct extinction peak in this time slice.

To evaluate potential geographic biases we depicted the **geographic coverage** of radiolarian occurrence data (and found this to be **highly uneven** in the Late Triassic and Early Jurassic, due to the scarcity of preserved geotectonic environments that are amenable to yielding well-preserved radiolarian assemblages. Although spatial coverage is limited before and after the TJB, **abrupt changes** in the proportions of covered regions **did not create artifactual extinctions** (for example, in the late Norian or the Oxfordian), suggesting that the lower representation of these regions does not interfere substantially with the extinction pattern observed at the TJB, but rather indicates the presence of genera with wide geographic ranges.



Geographic coverage of Triassic-Jurassic radiolarian occurrences.



Radiolarian origination rates.

Discussion

The **distinct radiolarian extinction peak in the late Rhaetian** partially revises the previously established views (Kiessling and Danelian 2011). Several lines of evidence suggest that the radiolarian extinction pulse in the late Rhaetian coincided with the devastating mass extinction of benthic organisms, carbon cycle perturbations, and the eruption peaks of the Central Atlantic Magmatic Province. An abrupt increase of pCO_2 is thought to have promoted ocean acidification, which is proposed to be one of the proximate causes of extinction of marine calcifiers.

The recognition that radiolarians were affected by the end-Triassic event **does not necessarily disprove** the potential role of **ocean acidification** in the extinction scenario. Even if **radiolarian biomineralization** was most likely not directly affected by changes in seawater chemistry, the populations of other organisms upon which radiolarians preyed might have collapsed. The **scarcity of prey** could create a bottleneck, selecting for those taxa that could survive due to their inferred photosynthetic symbionts, which are present in several groups of extant radiolarians (Matsuoka 2007).

Multiple lines of evidence suggest that **global warming** was the primary trigger mechanism of the end-Triassic extinctions (Kiessling and Aberhan 2007; Kiessling and Simpson 2011). Relatively little information is available on the effects of elevated seawater temperature on living radiolarians. Experimental evidence suggests that although they achieve their highest diversity in tropical surface waters, and although some radiolarians more common in colder waters proliferate when introduced into warmer environments, even these forms are **extremely intolerant** of higher temperatures.

Even if early Mesozoic radiolarians had different temperature tolerances, the consequences of global warming would involve substantial poleward migrations and community changes leading to novel biotic interactions and detrimental effects via altered nutrient supply and **increased stratification** of upper part of the water column (Parmesan 2006).

Although O'Dogherty et al. (2010) reported that radiolarians suffered elevated extinction in the **early Norian**, which primarily affected multicyrtid nassellarians, in our sampling-standardized analyses the early Norian extinction rate remains within the range of background values therefore we conclude that the early Norian extinction peak observed in the raw data is probably an artifact related to the poor sampling of the other Norian time slices. Similarly, the allegedly drastic turnover, described by Hori (1997) as the **Toarcian Radiolarian Event**, also appears to be a **sampling artifact**.

In comparison with benthic calcifiers, evolutionary forcing affecting radiolarians in their planktonic habitat appears significantly **different**. The good radiolarian data across the TJB largely come from the Panthalassa ocean (Japan and Wrangellia), whereas the benthic animal diversity dynamics are largely based on Tethyan shelf deposits. These settings presumably differed in several aspects such as $CaCO_3$ saturation state and nutrient regimes. Nevertheless the end-Triassic extinction event affected radiolarians and benthic calcifiers similarly, suggesting a **common extrinsic cause**, most likely the extreme global warming.

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