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

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

Ádám T. Kocsis, Wolfgang Kiessling, and József Pálfy

Abstract.—Within a ∼60-Myr interval in the Late Triassic to Early Jurassic, a major mass extinction took place at the end of Triassic, and several biotic and environmental events of lesser magnitude have been recognized. Climate warming, ocean acidification, and a biocalcification crisis figure prominently in scenarios for the end-Triassic event and have been also suggested for the early Toarcian. Radiolarians, as the most abundant silica-secreting marine microfossils of the time, provide a control group against marine calcareous taxa in testing selectivity and responses to changing environmental parameters. We analyzed the origination and extinction rates of radiolarians, using data from the Paleobiology Database and employing sampling standardization, the recently developed gap-filler equations and an improved stratigraphic resolution at the substage level. The major end-Triassic event is well-supported by a late Rhaetian peak in extinction rates. Because calcifying and siliceous organisms appear similarly affected, we consider global warming a more likely proximate trigger of the extinctions than ocean acidification. The previously reported smaller events of radiolarian turnover fail to register above background levels in our analyses. The apparent early Norian extinction peak is not significant compared to the long-term trajectory, and is probably a sampling artifact. The Toarcian Oceanic Anoxic Event, previously also thought to have caused a significant radiolarian turnover, did not significantly affect the group. Radiolarian diversity history appears unique and complexly forced, as its trajectory parallels major calcareous fossil groups at some events and deviates at others.

Ádám T. Kocsis and József Pálfy. MTA-MTM-ELTE Research Group for Paleontology and Department of Physical and Applied Geology, Eötvös University, Pázmány Péter sétány 1/C, Budapest, H-1117 Hungary. E-mail: adamkocsis@caesar.elte.hu, palfy@nhmus.hu
Wolfgang Kiessling. GeoZentrum Nordbayern, Universität Erlangen-Nürnberg, Loewenichstrae 28, D-91054 Erlangen, Germany. E-mail: wolfgang.kiessling@fau.de

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. Severe environmental changes led to the extinction of various marine organisms and reef crises. However, the causes and mechanisms remain controversial, and the geographical and temporal extents of these events are not adequately constrained.

Recent studies concerning the end-Triassic mass extinction demonstrated that extreme greenhouse warming and ocean acidification may have played a substantial role (McElwain et al. 1999; Hautmann et al. 2008; Kiessling and Simpson 2011; Steinthorsdottir et al. 2011; Greene et al. 2012; Hönisch et al. 2012). 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.

Large Databases vs. Section-based Studies.—Because of the focus on the potential mass extinction horizon, the best radiolarian-bearing localities (the Haida Gwaii [formerly Queen Charlotte Islands] in Canada and the Inuyama sections in Japan) are probably much better sampled at the Triassic/Jurassic boundary (TJB) than at other intervals. Although Carter and Hori (2005) stated that substantial turnover occurred at the TJB, this in itself cannot inform us about the relative magnitude of such a turnover compared to other events, possibly occurring at other stage boundaries. Continuous sections ranging through the TJB are very scarce and most of them lack the detail of lithological and paleontological evidence that properly document the short-term variations related to the environmental disturbance.

Renaudie and Lazarus (2013) argued that for applications of diversity analyses in paleoenvironmental reconstructions, data compilations such as the Paleobiology Database (PaleoDB) might not be useful, because the resolution of the time series is not fine enough. The average duration of time slices in our study is much longer than their preferred 100 Kyr, which cannot be attained at the TJB owing to the nature of the geologic record. A finer stratigraphic resolution could be achieved by computer-aided sequencing of events (Sadler 2004), but data from even the best studied fossil localities (such as Haida Gwaii) are compilations of partial sections, where most of the radiolarian-bearing samples are limestone nodules in fine-grained siliciclastic sedimentary rocks. Moreover, unbinned data are not suitable for sampling standardization.

Smaller Events.—The Late Triassic–Early Jurassic interval includes other, smaller biotic and environmental events, whose characterization may be aided by studying radiolarian diversity patterns. O'Dogherty (2010) claimed that radiolarians suffered significant extinctions in the Early Norian substage, which have not been quantitatively assessed before, nor have they been correlated to changes in any

environmental parameter. On the other hand, the much-studied early Toarcian Oceanic Anoxic Event (Jenkyns 2010) and the related second-order extinction is said to be manifested in elevated radiolarian turnover. Hori (1997) described a Toarcian radiolarian event from bedded cherts of Japan, but this has not been confirmed from elsewhere, and a distinct extinction peak is not evident at the stage level (Kiessling and Danelian 2011).

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). Extinction and origination rates of radiolarians are then compared with those of major calcareous marine invertebrate fossil groups, in order to test the ocean acidification hypothesis, which predicts that a biocalcification crisis preferentially affects marine calcifiers over silica-secreting organisms.

Data

Data Download and Taxonomic Revision.—Radiolarian occurrence data of the Capitanian (Middle Permian) to Albian (mid-Cretaceous) interval were downloaded from the PaleoDB 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. Genus occurrences marked as "aff." or "cf.", and those with quotation marks were excluded. For comparison, we have also downloaded occurrences of major benthic marine invertebrate groups with calcareous skeletons (bivalves, brachiopods, corals, calcareous sponges, gastropods).

Until recently, Mesozoic radiolarian data were not appropriate for turnover analysis because their taxonomy was unstandardized even at the genus level and the species concepts varied among taxonomists. To enhance the taxonomic robustness of the data set, we have entered taxonomic opinions from

recent monographs (Goričan et al. 2006; O'Dogherty et al. 2009a,b) to correct older occurrence entries automatically. We have also applied the same additional taxonomic corrections to the downloaded data that were performed in the previous study (Kiessling and Danelian 2011) (see Appendix).

Stratigraphic Resolution.—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.

We used the generally accepted substages for the Carnian to Toarcian stages (Gradstein et al. 2012) except for the short Hettangian stage. In addition, we subdivided the Rhaetian into two units, to assess the assumption that extinctions were concentrated near the TJB. Following Lucas (2002), we distinguished the *Paracochloceras amoenum* and *Choristoceras crickmayi* ammonite zones, which correspond to the *Proparvicingula moniliformis* and *Globolaxtorum tozeri* radiolarian zones suggested by Carter (1993), as the two subunits of the Rhaetian. On the other hand, to increase data density, we combined the Early Triassic stages and the middle and late Toarcian substages into one time slice each.

We excluded any occurrence data that could not be assigned to a single interval of our stage/substage timescale (Table 1). Although this loss of data is substantial in the substage-level part of the series, its effects on biodiversity dynamics are minor in this case (see Appendix) and there is no substantial change in the overall pattern of extinction rates at the stage level when compared with the results of Kiessling and Danelian (2011).

Methods

Rate Estimation.—Because traditional compilations (Sepkoski 2002) utilized first and last appearance data, the most widely used methods to assess originations and extinctions are based on stratigraphic ranges (i.e., Foote 2000). Foote's (2000) per capita, range-based estimates remained the "industry standard" in the calculation of origination and extinction rates. However, because 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 is the gap-filler equation (Alroy 2014). Rates are calculated from recorded occurrence data and use a four time-slice window, as do the corrected three-timer rates, but because of the different categorization of taxon counts, they are more robust for smaller data sets and lower sampling completeness values. The gap-filler extinction rates are calculated as

$$\mu = \log\left[(^2t_i + {}^p t_i)/(^3t_i + {}^p t_i + {}^u g_i)\right] \quad (1)$$

and the origination rates as

$$\lambda = \log\left[(^2t_{i+1} + {}^p t_i)/(^3t_i + {}^p t_i + {}^d g_i)\right], \quad (2)$$

where ^3t_i is the number of three-timer taxa that have occurrences in the focal bin as well as the time slice preceding and following it, ^2t_i is the number of two-timer taxa that have recorded occurrence in time slices i and $i-1$, and $^p t_i$ is the number of part-timers, the number of taxa that are not present in interval i, but occur in both the previous and following time slices. The novelty in these equations is the utilization of the gap-filler category, which in the case of extinctions ($^u g_i$) contains taxa that occur in time slices $i-1$, $i+2$ but are absent in bin $i+1$. In the case of originations, $^d g_i$ is the mirror image of $^u g_i$, containing the number of taxa present in time slice $i+1$ and $i-2$ but absent in $i-1$.

TABLE 1.   Timescale and summary table of the resolved data. The radiometric data for the Norian time slices were chosen to allow the substages to have equal durations. After filtering, 27,251 species-level and 16,975 genus-level occurrences of 540 genera from 1496 collections were available for analysis. The resolved data set is available online on the Dryad Digital Repository, along with a reference list of the primary data sources.

Time slice	Base (Ma)	Mean age (Ma)	Duration (Myr)	No. of collections	No. of occurrences (genera)	No. of occurrences (species)
Capitanian	265.8	263.1	5.4	30	146	241
Wuchiapingian	260.4	257.1	6.6	48	337	497
Changhsingian	253.8	253	1.6	193	1073	1521
Induan–Olenekian	252.2	249.65	5.1	26	109	133
Anisian	247.1	244.3	5.6	90	600	928
Ladinian	241.5	239.25	4.5	67	688	1110
L. Carnian	237	235.25	3.5	34	342	517
U. Carnian	233.5	230.95	5.1	16	121	237
L. Norian	228.4	225.25	6.3	37	610	1084
M. Norian	222.1	218.95	6.3	10	54	106
U. Norian	215.8	212.65	6.3	24	142	241
l. Rhaetian	209.5	207.45	4.1	42	616	968
u. Rhaetian	205.4	203.35	4.1	31	191	306
Hettangian	201.3	200.3	2	77	761	1079
L. Sinemurian	199.3	197.25	4.1	9	163	300
U. Sinemurian	195.2	193	4.4	42	583	914
L. Pliensbachian	190.8	189.15	3.3	69	696	1167
U. Pliensbachian	187.5	185.1	4.8	24	226	372
L. Toarcian	182.7	181	3.4	18	425	776
M.–U. Toarcian	179.3	176.7	5.2	44	293	496
Aalenian	174.1	172.2	3.8	29	384	815
Bajocian	170.3	169.3	2	69	712	1306
Bathonian	168.3	167.2	2.2	26	337	655
Callovian	166.1	164.8	2.6	40	489	758
Oxfordian	163.5	160.4	6.2	51	506	712
Kimmeridgian	157.3	154.7	5.2	38	443	697
Tithonian	152.1	148.8	6.6	133	2444	4313
Berriasian	145.5	142.85	5.3	45	1037	1609
Valanginian	140.2	138.3	3.8	47	775	1082
Hauterivian	136.4	133.2	6.4	23	640	877
Barremian	130	127.5	5	14	482	636
Aptian	125	118.5	13	12	209	279
Albian	112	105.8	12.4	38	341	519

Other rate metrics such as the per capita rates of Foote (2000) and the corrected three-timer rates of Alroy (2008) were also calculated for comparison, which allowed us to compare results obtained with three different taxonomic rate metrics. The performance of the gap-filler approach was deemed appropriate for this study, because it combines the advantages of occurrence-based methods with the wider applicability of range-based approaches.

The time series of extinction rates contains a substantial amount of noise due to the incomplete sampling of the fossil record. Because the three-timer method uses only a subset of the available data, in the case of smaller data sets, it amplifies the noise in the series which might result in negative rate

values when the binomial error is high (J. Alroy personal communication 2013). The gap-filler method utilizes more information resulting in less noise and fewer incidences of negative rate values.

Sampling Standardization.—The gap-filler equations 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. This low quota is necessary to achieve complete time series. An increase of the subsampling quota did only marginally

change the results in the less complete time series. We used a high number of 1500 iterations to ensure stability of the subsampled rates.

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.

Hypothesis Testing and Model Selection.—All correlation tests were performed using Spearman's rank-order correlation. Time-series data were first detrended by applying generalized differencing (McKinney and Oyen 1989; Kiessling 2005) to remove significant autocorrelations. The expanded set of rate calculation methods makes the comparison of different taxa difficult. We regard correlations as significant only when they are significant using both the per-capita and the gap-filler rates, thus we take into account both an occurrence- and a range-based method. Because the significance thresholds need to be adjusted in multiple comparisons, in such cases we applied a classical one-stage false discovery rate method (Pike 2011) to test the significance of the p-values.

Akaike weights calculated from the corrected Akaike Information Criterion (Burnham and Anderson 2002) were used to evaluate the relative support of turnover models and the robustness of order-specific extinction rate calculations for the selectivity tests (Kiessling and Simpson 2011). We used the lm and the nls2 R functions (from the stats and nls2 packages, respectively) to calculate the log-likelihoods of the various regression models of taxonomic rates. Selectivity of extinctions can be stated only if the model supporting individual extinction rates of the two groups in question (two-rate model) differs significantly from a one-rate model. The ratio of the weights expresses the relative likelihood of the evaluated models (Burnham and Anderson 2002), and we treated the evidence as strong enough to accept a model when the ratio of the weights exceeded 8 (Wagner et al. 2006). All analyses were performed using the R programming language and software environment (R Development Core Team 2013).
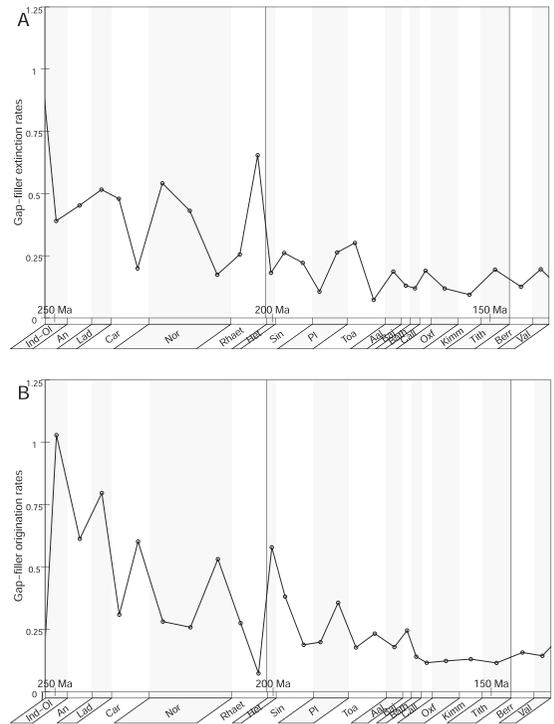
FIGURE 1. Sampling-standardized time series of radiolarian extinction (A) and origination (B) rates. Extinction rates assume a pulsed turnover, whereas equations for both pulsed and continuous turnover were applied to origination rates.

Results

Triassic–Jurassic Radiolarian Turnover Rates

Rate Changes through Time.—Kiessling and Danelian (2011) pointed out that the medians of the Triassic and Jurassic extinction rates (Fig. 1) differ significantly at the stage level, which is also true with our finer binning of the Triassic–Jurassic interval (Wilcoxon rank sum test: $W = 122$, $p = 7.46 \times 10^{-4}$). The finer stratigraphic resolution let us use more points for a correlation analysis, which revealed that extinction 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). We cannot distinguish between an exponential and linear decline, as the Akaike weights of these models are nearly the same (0.467 vs. 0.532).

Origination rates also declined over time (Fig. 1, Spearman's rank correlation with time
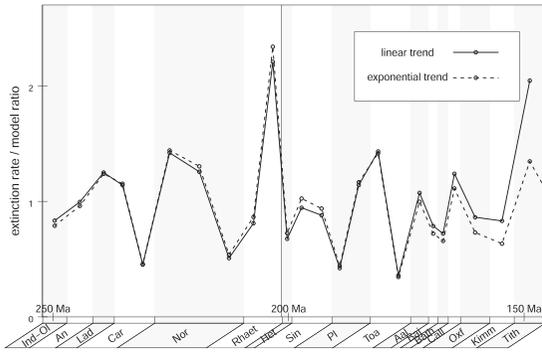
FIGURE 2. Detrended extinction rates from Figure 1A, assuming exponential and linear trends, respectively. Note the prominent late Rhaetian peak.

$\rho = 0.79$, $p = 4.794 \times 10^{-6}$ with the gap filler rates) and their overall trajectory is similar to that of extinctions, but Akaike weights support an exponential model better (0.925 vs. 0.075).

Magnitude of the End-Triassic Extinction.— The extinction rate of the late Rhaetian time slice is above the confidence interval of the point estimates of both the linear and the exponential regression (see Supplementary Materials), and it is over the 97.5% critical value of the detrended extinction rates (assuming normality, Shapiro-Wilk $W = 0.9183$, $p = 0.053$ detrended with a linear model), regardless of the function used to detrend the data (Fig. 2). Although it is possible that the late Rhaetian value is part of the log-normal distribution of detrended rates ($W = 0.9708$, $p = 0.6869$ with a linear function), similarly to the great Phanerozoic extinctions (Alroy 2008), the relative magnitude of this peak suggests that a significant extinction event occurred in the last time slice of the Triassic.

Extinction Selectivity at the Triassic/Jurassic Boundary.—Although a higher proportion of spumellarian (24%) than nassellarian genera (17%) have their last occurrences in the late Rhaetian, there is no statistical support for selective extinctions in the raw data, as a single rate model for the late Rhaetian is better supported (Akaike weights for the single and dual rate models: 0.73 and 0.27, respectively). Ecological selectivity could not be tested
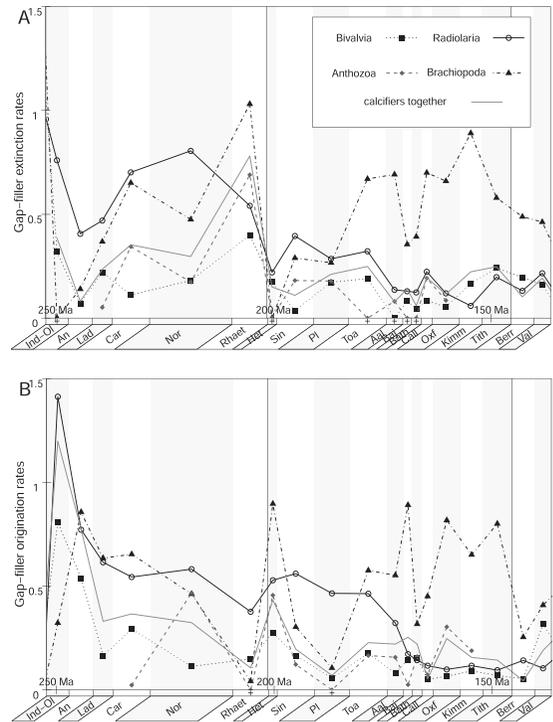
FIGURE 3. Comparison of stage-level radiolarian taxonomic rates with those of common macroinvertebrates. A, Extinction, B, Origination. All data sets were standardized using classical rarefaction to the maximum number of occurrences that still allowed retaining all time slices in the analyzed interval. The subsampling quotas were set as follows: 109 for radiolarians, 268 for bivalves, 28 for corals, 67 for brachiopods, and 505 for the bulk calcifier group. Justification of the use of different quotas for comparison of different taxonomic rates follows Kiessling et al. (2007). Cases of negative gap-filler rates were plotted as stochastically zero and are marked by plus signs below the horizontal axis.

because we know too little of Mesozoic radiolarian ecology.

Originations near the Triassic/Jurassic Boundary.—Although the drop in originations is not significant in the Late Triassic, the relatively lower rate values are noteworthy. The phenomenon that low origination rates of marine invertebrates characterized the interval preceding the end-Triassic biotic crisis is widely recognized (Bambach et al. 2004; Alroy 2008), and our results suggest that radiolarians show a similar pattern.

Comparison with Calcifying Organisms.—We used the same analytical toolkit to characterize the evolutionary trajectory of benthic calcifying macroinvertebrates (Fig. 3), and compare

TABLE 2. Spearman's rank correlations between interval mean ages and different stage-level taxonomic rates. Only radiolarian extinction rates decline significantly over the Triassic–Jurassic periods and the origination rates of radiolarians, bivalves and the bulk calcifier group show a declining pattern as well. Significant values were marked in bold, group names were only marked so when both rate calculation methods were significant.

	Per capita rates		Gap-filler rates	
	Spearman's ρ	*p*-value	Spearman's ρ	*p*-value
Extinctions				
Bivalves	0.3505	0.168	0.3015	0.239
Corals	**0.6964**	**0.0052**	0.2033	0.5053
Brachiopods	−0.0147	0.9585	**−0.5098**	**0.0386**
Calcifiers together	0.3775	0.136	0.3431	0.1776
Radiolarians	**0.8775**	**$<10^{-4}$**	**0.8554**	**$<10^{-4}$**
Originations				
Bivalves	**0. 9068**	**$<10^{-4}$**	**0.7353**	**0.0011**
Corals	**0.7428**	**0.0022**	−0.2033	0.5053
Brachiopods	0.4436	0.0761	−0.125	0.6322
Calcifiers together	**0.8308**	**$<10^{-4}$**	**0.6593**	**0.0050**
Radiolarians	**0.9485**	**$<10^{-4}$**	**0.9583**	**$<10^{-4}$**

it with that of radiolarians (for a detailed analysis of calcifiers, see Kiessling and Aberhan 2007 and Kiessling et al. 2007). 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 (Table 2), regardless of the rate metrics. Radiolarians are the only group for which extinction rates decline significantly over the Triassic–Jurassic interval.

Per capita rates tend to have better correlations than the gap-filler rates between the rates of different groups (Table 3), and extinction rates among taxa are better correlated than origination rates. Extinction rates of bivalves are correlated with those of both brachiopods and radiolarians. At the stage level, radiolarians have slightly lower extinction rates than the pooled calcifiers, but the evidence for differing values is not strong enough to support selectivity (0.32 is the Akaike weight for the single, 0.68 for the dual rate model).

Resolution-dependence of the Patterns.—The trajectory of stage-level extinction rates (Fig. 4) is very similar to that of Kiessling and Danelian (2011), although the latter was obtained using different metrics. The late Rhaetian is the time interval when the difference between the previous and our results are most pronounced. This is attributed to the enhanced stratigraphic resolution in our analysis.

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.

Pulsed vs. Continuous Turnover.—Alroy (2010c) characterized his occurrence-based rates as being "instantaneous," meaning that origination and extinction rates are independent from time slice durations. This is consistent with the simulations of Foote (2005), who proposed that turnover tends to be pulsed at the stage level of stratigraphic resolution. In our case, the independence of rate magnitudes from bin durations is supported by the lack of correlation between the gap-filler rates and the durations of the time slices (originations: Spearman's rank-order correlation ρ = 0.10, *p* = 0.5913; extinctions: ρ = −0.08, *p* = 0.6814). Normalizing the rate values with the time slice durations introduces artificial correlations between bin durations and both extinction (ρ = −0.47, *p* = 0.0096) and origination rates (ρ =

TABLE 3. Cross-correlation of turnover rates for well-sampled benthic macroinvertebrates and radiolarians based on generalized differencing. The upper right area of each part of the table reports correlation values; the bottom left reports the corresponding p-values. Values of pairwise correlations were marked as bold, if generalized differences of rates calculated with both types of methods yielded significant correlations.

	Bivalves	Corals	Brachiopods	Calcifiers	Radiolarians
Per capita extinction rates					
Bivalves	N/A	−0.04	0.53	**0.85**	**0.77**
Corals	0.8758	N/A	0.03	0.02	−0.10
Brachiopods	0.0090	0.9214	N/A	**0.69**	0.31
Calcifiers together	**$<10^{-4}$**	0.9410	**0.0003**	N/A	**0.75**
Radiolarians	**$<10^{-4}$**	0.6943	0.1495	**$<10^{-4}$**	N/A
Gap-filler extinction rates					
Bivalves	N/A	0.13	0.31	**0.83**	**0.48**
Corals	0.6706	N/A	0.4	0.55	0.81
Brachiopods	0.1481	0.1601	N/A	**0.60**	0.16
Calcifiers together	**$<10^{-4}$**	0.0459	**0.0029**	N/A	**0.50**
Radiolarians	**0.0241**	0.0012	0.4695	**0.0194**	N/A
Per capita origination rates					
Bivalves	N/A	0.13	0.70	**0.89**	0.51
Corals	0.6091	N/A	0.36	0.36	0.49
Brachiopods	$<10^{-4}$	0.1377	N/A	**0.81**	0.34
Calcifiers together	$<10^{-4}$	0.1401	$<10^{-4}$	N/A	0.58
Radiolarians	0.0136	0.0465	0.1033	0.0742	N/A
Gap-filler origination rates					
Bivalves	N/A	0.14	0.36	**0.81**	0.39
Corals	0.6158	N/A	0.58	0.47	−0.16
Brachiopods	0.0878	0.0362	N/A	**0.45**	−0.01
Calcifiers together	**$<10^{-4}$**	0.0938	**0.0310**	N/A	0.32
Radiolarians	0.0709	0.5911	0.9678	0.1508	N/A

−0.43, $p = 0.0202$), meaning that it is reasonable to assume that the pulsed model holds in the case of radiolarian turnover.

Subsampling Methods.—Applying different subsampling methods and increasing the subsampling quota led to only minor changes in the results (Fig. 5). In some cases the SQS
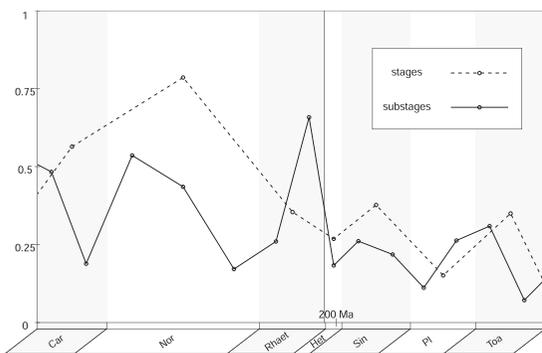
FIGURE 4. Comparison of extinction rates at stage- and substage-level stratigraphic resolution on the Late Triassic–Early Jurassic interval. Note the substantial differences in the Late Triassic. Subsampling quotas were set to 54 and 337 with the substage and the stage resolution rates, respectively. For the changes in the stage resolution rates due to changes in the subsampling quota, see the Supplementary Material.

extinction rates are negative, most likely due to the higher volatility of the three-timer sampling completeness, which is most even when the CR method is used (Alroy 2014).

Comparison of Different Rate Metrics.—The trajectories of the Late Triassic and Early Jurassic radiolarian extinction rates are similar when different metrics of taxonomic turnover are applied (Fig. 6). The gap-filler rate curve parallels the per capita rate curve closely, and although the gap-filler rate values are systematically higher, the two rate metrics correlate well ($\rho = 0.88$, $p = 5.98 \times 10^{-7}$ for extinctions and $\rho = 0.75$, $p = 4.44 \times 10^{-6}$ for originations). The corrected three-timer extinction rates correlate only moderately with the gap-filler extinction rates ($\rho = 0.53$, $p = 3.39 \times 10^{-3}$). The former are more volatile and produce negative rate values in the middle Norian and the early Rhaetian. The three-timer metric also yields pronounced extinction peaks in the late Norian and late Sinemurian time slices. 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.
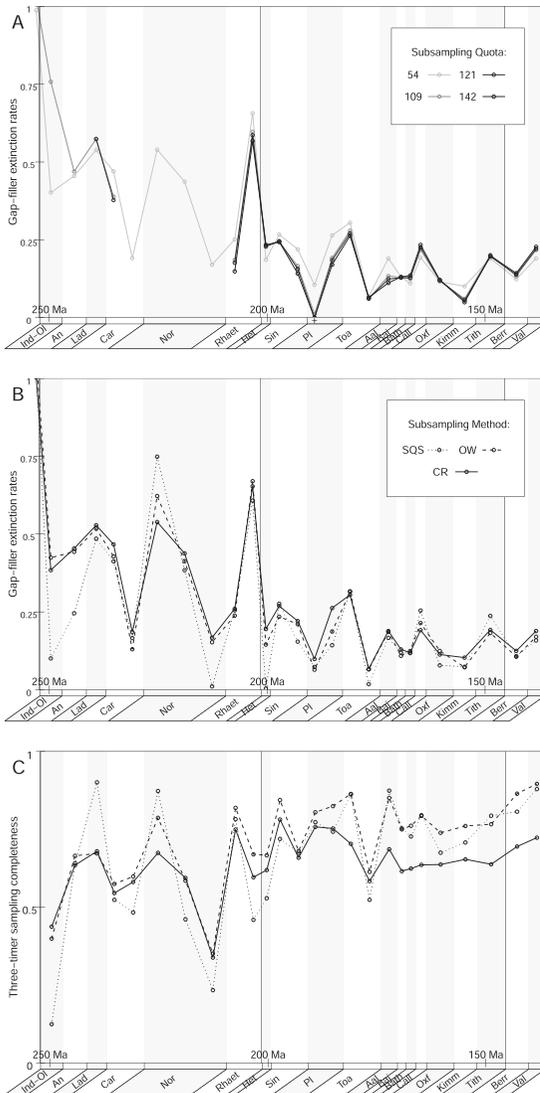
FIGURE 5. Time series of radiolarian extinction rates calculated with different subsampling quotas for classical rarefaction (A) and with different subsampling procedures applied to gap-filler rates (B), and to the corrected three-timer rates (C). The gradual increase of the subsampling quota systematically lowers the number of points in the time series related to that level of subsampling. Subsampling quota was 54 with both CR and OW; the shareholder quorum was set to 0.6 with SQS.

FIGURE 6. Time series of radiolarian extinction (A) and origination (B) rates, sampling standardized with classical rarefaction and calculated with different rate metrics. The occurrence-based methods produce systematically higher rates, and the corrected three-timer rates are the most volatile, producing strong peaks even where other methods do not show any. The subsampling quota was set to 54 occurrences.

The Effect of Unique Collections.—The raw extinction rates have a distinct peak in the Hettangian stage, which solely reflects the short-term survivor taxa from Haida Gwaii described by Longridge et al. (2007). Although they are assigned to the Hettangian on the basis of radiolarian biostratigraphy, the key samples (R1 from Section II of Kennecott Point, and R2 and R3 in Section III, Kunga Island) occur below the first appearance of psiloceratid ammonites, their faunal composition is mixed, and they clearly represent the transition between Triassic and Jurassic radiolarian faunas. Removal of these three samples (PaleoDB collection nos. 97,489, 97,493, 97,494) shifts the Hettangian extinction peak to the late Rhaetian, the probabilistic nature of the standardization reduces the effect of outliers. This accounts for the lowering of Rhaetian extinction rates on the stage-level plots (Fig. 4) as the subsampling quota increases.

Geographic Patterns.—To evaluate potential geographic biases we depicted the geographic coverage of radiolarian occurrence data (Fig. 7) and found this to be highly uneven in the Late Triassic and Early Jurassic, due to the scarcity of preserved geotectonic environ-

ments that are amenable to yielding well-preserved radiolarian assemblages. Collections from Haida Gwaii dominate this part of the record; more than half of the samples (53%) were collected from this area. The dominance of samples from Panthalassa decreases in the Middle Jurassic (Fig. 8) while Tethyan samples become more prominent. 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.

Extant and fossil radiolarians exhibit distinct provinciality (De Wever et al. 2001) and the Mesozoic is no exception (Kiessling 1999). In the Late Triassic–Early Jurassic this is reflected in the different zonal schemes established for the major outcrop areas where radiolarians occur (Carter et al. 2010). Nevertheless, the proportion of genera endemic to larger regions (such as the Supplee-Izee area
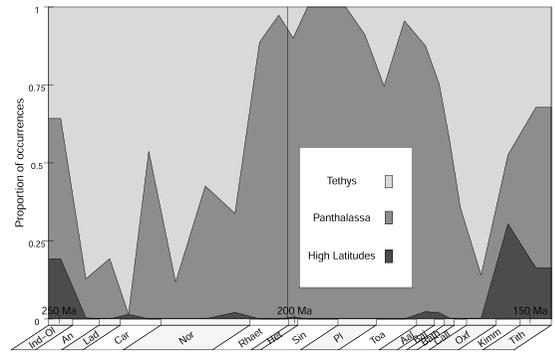
FIGURE 8. Proportions of occurrences from the main geographic regions of the Triassic–Jurassic interval. The latest Triassic–Early Jurassic interval is dominated by samples from the Panthalassa Ocean. A threshold of 50° absolute paleolatitude was set to separate high-latitude radiolarian occurrences.

in Oregon) does not exceed 25% in the Early Jurassic. Moreover, the number of endemic genera in each area is correlated with the number of collections and occurrences ($\rho =$ 0.61, p-value $= 6.6 \times 10^{-3}$ and $\rho = 0.78$, p-value $= 1.147 \times 10^{-4}$ respectively), suggesting that the apparent Early Jurassic provinciality is at least partially a sampling artifact, demonstrating the failure to sample cosmopolitan genera at localities with poorer preservation.
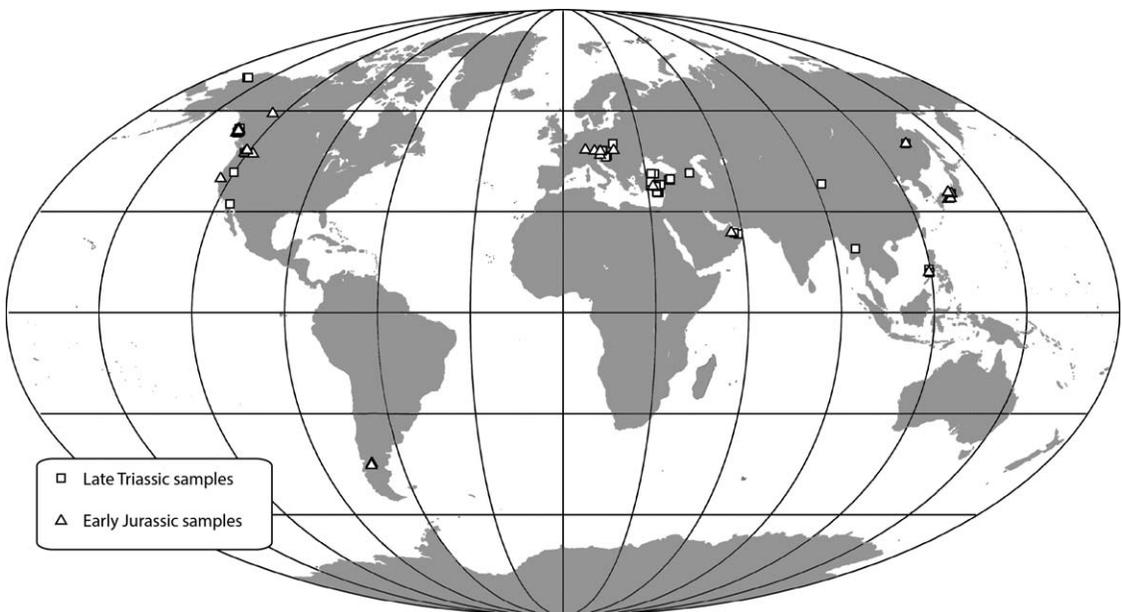
FIGURE 7. Geographic distribution of Late Triassic (squares) and Early Jurassic (triangles) radiolarian samples from the PaleoDB collections.

Discussion

Triassic/Jurassic Mass Extinction.—The distinct radiolarian extinction peak in the late Rhaetian partially revises the previously established views (Kiessling and Danelian 2011). The reason for this difference is by and large in the different temporal resolution. The end-Triassic mass extinction for radiolarians becomes apparent only at a substage level. The end-Triassic extinction rates of radiolarians were still substantially smaller than the end-Permian ones and there was no similar taxonomic restructuring at the ordinal level (De Wever et al. 2006).

Several lines of evidence suggest that the radiolarian extinction pulse in the late Rhaetian coincided with the devastating mass extinction of benthic organisms (Kiessling and Aberhan 2007; Kiessling et al. 2007), carbon cycle perturbations (Ruhl and Kürschner 2011), and the eruption peaks of the Central Atlantic Magmatic Province (Pálfy 2003). An abrupt increase of pCO$_2$ (McElwain et al. 1999; Beerling and Berner 2002) is thought to have promoted ocean acidification, which is proposed to be one of the proximate causes of extinction of marine calcifiers (Hautmann et al. 2008; Greene et al. 2012).

Although advances have been made in the last decade on long-term culturing experiments of radiolarians (Matsuoka 2007), our knowledge is still limited about their biology, including shell secretion and physiological reactions to changes of seawater chemistry. We believe that changes in seawater pH are unlikely to have seriously hindered the silica secretion ability of radiolarians. Other organisms, such as siliceous sponges and diatoms, produce biogenic silica in specialized membrane-bound compartments in which they control silica secretion with pH regulation (Coradin and Lopez 2003). Using PDMPO, an acidophoric fluorescent compound, Ogane (2009) demonstrated that similar silica deposition vesicles also exist in extant radiolarian species such as *Rhizosphaera trigonacantha* and *Spirocyrtis scalaris*. Seawater chemistry does not interfere directly with the skeleton forming process because the vesicles are enclosed in an organic matrix. The capability to regulate pH, and create such acidic conditions within isolated compartments suggests well developed physiological buffering abilities that would make radiolarians highly resistant to external pH changes, similarly to diatoms (Li et al. 2012; Tatters et al. 2013).

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 not directly affected by changes in seawater chemistry, the populations of other organisms upon which radiolarians preyed might have collapsed. Although the calcareous phytoplankton, which were obviously prone to suffer from acidification, were not widely distributed yet (Bown et al. 2004), the physiological buffering capacity of other phytoplankton groups with less-developed cellular structures was potentially much lower. 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).

Global Warming.—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. The mean longevity of *Spongaster tetras tetras* in controlled environments decreased markedly when temperature was raised (Anderson et al. 1989). The measured mean longevity of 23 days at 27.5°C dropped to 2 days at 33°C, coupled with a reduction of growth rate above 31°C. No individuals survived above 36°C. Similarly, rapid decreases in mean and maximum longevity were observed with cultures of *Didymocyrtis tetrathalmus* at temperatures of 31°C or higher (Anderson et al. 1990). Similar

patterns were observed in experiments with cultures of *Dictyornyne truncatum*; skeletal growth and survival were remarkably suppressed at temperatures above 32°C (Matsuoka and Anderson 1992).

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).

Smaller Events.—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. Because there is no evidence for any environmental disturbance that could have triggered significant extinctions, we conclude that the early Norian extinction peak observed in the raw data (Fig. 7) 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, at the boundary of the *Parahsuum simplum* and *Hexasaturnalis hexagonus* assemblage zones (corresponding to the lower/ middle Toarcian boundary; Carter et al. 2010), also appears to be a sampling artifact. Although global warming was substantial in this interval (Bailey et al. 2003), the Toarcian extinctions are largely attributed to oceanic anoxia (Aberhan and Baumiller 2003), which might explain the limited response of radiolarians. Some radiolarian taxa are thought to have been associated with dysoxic environments in the Cretaceous (Erbacher and Thurow 1997), but anoxia itself might have had only a minor effect on the group, as radiolarians attain maximum abundance and diversity in the surface layer of today's ocean, and there is no reason to assume that this has changed over time.

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.

Conclusions

The analysis of evolutionary trajectories of radiolarians reveals some similarities but also intriguing differences from those of the more commonly analyzed calcareous benthic organisms. A feature shared with all benthic macroinvertebrates is the end-Triassic extinction pulse. Consequently, a biocalcification crisis alone cannot fully account for the marine mass extinction, but other factors, such as extreme warming, must have been important drivers of radiolarian extinctions. In the Late Triassic–Early Jurassic interval, radiolarians responded differently to other environmental perturbations. Notably, global changes in climate and ocean chemistry during the Toarcian Oceanic Anoxic Event had only minor effects on radiolarian origination and extinction rates.

Our study underlines the importance of increased stratigraphic resolution in database analyses, and the adequate performance of the new gap-filler method for calculating taxonomic metrics from medium-sized data sets. The different patterns of taxonomic turnover revealed through the increase of temporal resolution calls for more detailed studies about the effects this may impose in other focal groups and time intervals.

Acknowledgments

Literature Cited

Aberhan, M., and T. K. Baumiller. 2003. Selective extinction among Early Jurassic bivalves: a consequence of anoxia. Geology 31:1077–1080.

Alroy, J. 2008. Dynamics of origination and extinction in the marine fossil record. Proceedings of the National Academy of Sciences USA 105:11,536–11,542.

———. 2010a. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. Palaeontology 53:1211–1235.

———. 2010b. The shifting balance of diversity among major marine animal groups. Science 329:1191–1194.

———. 2010c. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. In J. Alroy and G. Hunt, eds. Quantitative methods in paleobiology. Paleontological Society Papers 14:55–80.

———. 2014. Accurate and precise estimates of origination and extinction rates. Paleobiology 40:374–397.

Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivanyi, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. J. Sepkoski, M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Sciences USA 98:6261–6266.

Anderson, O. R., P. Bennett, and M. Bryan. 1989. Experimental and observational studies of radiolarian physiological ecology. 3. Effects of temperature, salinity and light intensity on the growth and survival of Spongaster tetras tetras maintained in laboratory culture. Marine Micropaleontology 14:275–282.

Anderson, O. R., M. Bryan, and P. Bennett. 1990. Experimental and observational studies of radiolarian physiological ecology. 4. Factors determining the distribution and survival of Didymocyrtis tetrathalamus tetrathalamus with implications for paleoecological interpretations. Marine Micropaleontology 16:155–167.

Bailey, T. R., Y. Rosenthal, J. M. McArthur, B. van de Schootbrugge, and M. F. Thrilwall. 2003. Paleoceanographic changes of the Late Pliensbachian–Early Toarcian interval: a possible link to the genesis of an Oceanic Anoxic Event. Earth and Planetary Science Letters 212:302–320.

Bambach, R. K., A. H. Knoll, and S. C. Wang. 2004. Origination, extinction, and mass depletions of marine diversity. Paleobiology 30:522–542.

Beerling, D. J., and R. A. Berner. 2002. Biogeochemical constraints on the Triassic-Jurassic boundary carbon cycle event. Global Biogeochemical Cycles 16. doi: 10.1029/2001GB001637.

Bown, P., J. Lees, and J. Young. 2004. Calcareous nannoplankton evolution and diversity through time. Pp. 481–508 in H. Thierstein, and J. Young, eds. Coccolithophores. Springer, Berlin.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer, New York.

Carter, E. S. 1993. Biochronology and paleontology of uppermost Triassic (Rhaetian) radiolarians, Queen Charlotte Islands, British Columbia, Canada. Mémoires de Géologie (Lausanne) 11:1–175.

Carter, E. S., and R. S. Hori. 2005. Global correlation of the radiolarian faunal change across the Triassic–Jurassic boundary. Canadian Journal of Earth Sciences 42:777–790.

Carter, E. S., Š. Goričan, J. Guex, L. O'Dogherty, P. De Wever, P. Dumitrica, R. S. Hori, A. Matsuoka, and P. A. Whalen. 2010. Global radiolarian zonation for the Pliensbachian, Toarcian and Aalenian. Palaeogeography, Palaeoclimatology, Palaeoecology 297:401–419.

Coradin, T., and P. J. Lopez. 2003. Biogenic silica patterning: simple chemistry or subtle biology. ChemBioChem 3:1–9.

De Wever, P., P. Dumitrica, J. P. Caulet, and M. Caridroit. 2001. Radiolarians in the sedimentary record. Gordon and Breach, Amsterdam.

De Wever, P., L. O'Dogherty, and Š. Goričan. 2006. The plankton turnover at the Permo-Triassic boundary, emphasis on radiolarians. Eclogae Geolocicae Helvetiae 99(Supp. 1):S49–S62.

Erbacher, J., and J. Thurow. 1997. Influence of oceanic anoxic events on the evolution of mid-Cretaceous radiolaria in the North Atlantic and western Tethys. Marine Micropaleontology 30(1–3):139–158.

Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. In D. H. Erwin and Scott L. Wing, eds. Deep time: Paleobiology's perspective. Paleobiology 26(Suppl. to No. 4):74–102.

———. 2005. Pulsed origination and extinction in the marine realm. Paleobiology 31:6–20.

Goričan, Š., E. S. Carter, P. Dumitrica, P. A. Whalen, R. S. Hori, P. De Wever, L. O'Dogherty, A. Matsuoka, and J. Guex. 2006. Catalogue and systematics of Pliensbachian, Toarcian and Aalenian radiolarian genera and species. Založba ZRC, Ljubljana.

Gradstein, F. M., J. G. Ogg, M. Schmitz, and G. M. Ogg. 2012. The geologic time scale 2012. Elsevier, Boston.

Greene, S. E., R. C. Martindale, K. A. Ritterbush, D. J. Bottjer, F. A. Corsetti, and W. M. Berelson. 2012. Recognising ocean acidification in deep time: an evaluation of the evidence for acidification across the Triassic-Jurassic boundary. Earth-Science Reviews 113:72–93.

Hautmann, M., M. J. Benton, and A. Tomašových. 2008. Catastrophic ocean acidification at the Triassic-Jurassic boundary. Neues Jahrbuch für Geologie und Paläontologie 249:119–127.

Hori, R. S. 1997. The Toarcian radiolarian event in bedded cherts from southwestern Japan. Marine Micropaleontology 30:159–169.

Hönisch, B., A. Ridgwell, D. N. Schmidt, E. Thomas, S. J. Gibbs, A. Sluijs, R. Zeebe, L. Kump, R. C. Martindale, S. E. Greene, W. Kiessling, J. Ries, J. C. Zachos, D. L. Royer, S. Barker, T. M. J. Marchitto, R. Moyer, C. Pelejero, P. Ziveri, G. L. Foster, and B. Williams. 2012. The geological record of ocean acidification. Science 335:1058–1063.

Jenkyns, H. C. 2010. Geochemistry of oceanic anoxic events. Geochemistry, Geophysics, Geosystems 11(3):Q03004. doi: 10.1029/2009GC002788.

Kiessling, W. 1999. Late Jurassic radiolarians from the Antarctic Peninsula. Micropaleontology 45(Suppl. 1):1–96.

———. 2005. Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs. Nature 433:410–413.

Kiessling, W., and M. Aberhan. 2007. Environmental determinants of marine benthic biodiversity dynamics through Triassic–Jurassic time. Paleobiology 33:414–434.

Kiessling, W., and T. Danelian. 2011. Trajectories of Late Permian–Jurassic radiolarian extinction rates: no evidence for an end-Triassic mass extinction. Fossil Record 14:95–101.

Kiessling, W., and C. Simpson. 2011. On the potential for ocean acidification to be a general cause of ancient reef crises. Global Change Biology 17:56–67.

Kiessling, W., M. Aberhan, B. Brenneis, and P. J. Wagner. 2007. Extinction trajectories of benthic organisms across the Triassic-Jurassic boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 224:201–222.

Li, W., K. Gao, and J. Beardall. 2012. Interactive effects of ocean acidification and nitrogen-limitation on the diatom Phaeodacty-

lum tricornutum. PLoS ONE 7(12):e51590. doi: 10.1371/journal.pone.0051590.

Longridge, L. M., E. S. Carter, P. L. Smith, and H. W. Tipper. 2007. Early Hettangian ammonites and radiolarians from the Queen Charlotte Islands, British Columbia and their bearing on the definition of the Triassic-Jurassic boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 244:142–169.

Lucas, S. G. 2002. Introduction. Pp. 1–16 *in* S. G. Lucas, ed. The Triassic timescale. Geological Society, London.

Matsuoka, A. 2007. Living radiolarian feeding mechanisms: new light on past marine ecosystems. Swiss Journal of Geosciences 100:273–279.

Matsuoka, A., and O. R. Anderson. 1992. Experimental and observational studies of radiolarian physiological ecology. 5. Temperature and salinity tolerance of *Dictyocoryne truncatum.* Marine Micropaleontology 19:299–313.

McElwain, J. C., D. J. Beerling, and F. I. Woodward. 1999. Fossil plants and global warming at the Triassic-Jurassic boundary. Science 285:1386–1390.

McKinney, M. L., and C. W. Oyen. 1989. Causation and nonrandomness in biological and geological time series; temperature as a proximal control of extinction and diversity. Palaios 4:3–15.

O'Dogherty, L., E. S. Carter, P. Dumitrica, Š. Goričan, P. De Wever, A. Hungerbühler, A. N. Bandini, and A. Takemura. 2009a. Catalogue of Mesozoic radiolarian genera, Part 1. Triassic. Geodiversitas 31:213–270.

O'Dogherty, L., E. S. Carter, P. Dumitrica, Š. Goričan, P. De Wever, A. N. Bandini, P. O. Baumgartner, and A. Matsuoka. 2009b. Catalogue of Mesozoic radiolarian genera, Part 2. Jurassic–Cretaceous. Geodiversitas 31:271–356.

O'Dogherty, L., E. S. Carter, Š. Goričan, and P. Dumitrica. 2010. Triassic radiolarian biostratigraphy. Pp. 163–200 *in* S. G. Lucas, ed. The Triassic timescale. Geological Society, London.

Ogane, K., A. Tuji, N. Suzuki, T. Kurihara, and A. Matsuoka. 2009. First application of PDMPO to examine silicification in polycystine Radiolaria. Plankton and Benthos Research 4:89–94.

Pálfy, J. 2003. Volcanism of the Central Atlantic Magmatic Province as a potential driving force in the end-Triassic mass extinction. American Geophysical Union, Geophysical Monograph Series 136:255–267.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Pike, N. 2011. Using false discovery rates for multiple comparisons in ecology and evolution. Methods in Ecology and Evolution 2:278–282.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology 1:333–342.

Renaudie, J., and D. B. Lazarus. 2013. On the accuracy of paleodiversity reconstructions: a case study in Antarctic Neogene radiolarians. Paleobiology 39:491–509.

Ruhl, M., and W. M. Kürschner. 2011. Multiple phases of carbon cycle disturbance from large igneous province formation at the Triassic-Jurassic transition. Geology 39:431–434.

Sadler, P. M. 2004. Quantitative biostratigraphy—achieving finer resolution in global correlation. Annual Review of Earth and Planetary Sciences 32:187–213.

Sepkoski, J. J. J. 2002. A compendium of fossil marine animal genera. Bulletins of American Paleontology 363:1–560.

Steinthorsdottir, M., A. J. Jeram, and J. C. McElwain. 2011. Extremely elevated CO_2 concentrations at the Triassic/Jurassic boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 308:418–432.

Tatters, A. O., M. Y. Roleda, A. Schnetzer, F. Fu, C. L. Hurd, P. W. Boyd, D. A. Caron, A. A. Y. Lie, L. J. Hoffmann, and D. A. Hutchins. 2013. Short- and long-term conditioning of a temperate marine diatom community to acidification and warming. Philosophical Transactions of the Royal Society of London B 368. doi: 10.1098/rstb.2012.0437.

Appendix

Although radiolarian taxonomy in the Paleobiology Database is good compared to some other groups (e.g., ammonites), the downloaded data were not free of genus-level taxonomic errors. However, after the revision of about 130 of the 625 genus entries, the subsampled turnover rates did not change substantially (Fig. A1).

We ignored the occurrences that could not be stratigraphically resolved at the stage level, which accounts for the lower number of occurrences in our data set compared to that of Kiessling and Danelian (2011), as they chose to assign those occurrences

FIGURE A1. Time series of radiolarian extinction rates demonstrating the effects of additional taxonomic corrections of the downloaded data when we used substage-level stratigraphic resolution in the Carnian–Toarcian interval. The gap-filler origination (A) and extinction (B) rates were calculated from data sets with classical rarefaction applied, the targeted subsampling quota was 109.

FIGURE A2. Radiolarian extinction rates demonstrating the effects of data reduction due to the substage resolution in the Late Triassic–Early Jurassic interval. The resolvable collections were compiled, and the taxonomic rates were calculated at the same stratigraphic resolution. Gap-filler origination and extinction rates were calculated by applying classical rarefaction; the quota was 109. Bootstrap results report the averages of 1000 resampling trials; the error bars denote the 95% percent confidence interval of the resampling distributions.

randomly. Also, not all radiolarian occurrences in the Late Triassic–Early Jurassic could be binned at the substage level of stratigraphic resolution. In this interval, 625 collections (11,105 occurrences) were resolved at the stage level, of which 477 collections (8563 occurrences) were assigned to a substage. Because this data loss is substantial, the stage-level rates were compared with rates that were calculated from substage-level data with collections reassigned to form a stage-level series again. After the omission of about 150 collections (24%), the subsampled results barely changed. We have also conducted by-collection resampling of the data to estimate the values and deviations of the taxonomic rates at a subsample size that corresponds to the number of collections that can be resolved to substages (Fig. A2). The taxonomic rates calculated from the resolvable data set have slightly higher values in the Norian than implied from a random reduction of the data. This suggests that both originating and disappearing genera tend to be somewhat overrepresented in the Norian part of the finer-resolution time series, but this should have no biasing effects on the results.