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Exploring the major depletions of conodont diversity during the Triassic

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In this paper, we show that the Triassic fossil record reflects just two great depletions of conodont diversity before the Rhaetian, which occurred in the Smithian (Olenekian, Early Triassic) and in the Julian (Carnian, Late Triassic). By exploring this context, our results highlighted that they respond to different origination–extinction dynamics. Thus, while the Smithian diversity depletion can be interpreted as a consequence of elevated extinction, the Julian diversity depletion was triggered by fluctuations in origination regime. This evidence suggests that, despite the role of extinction on diversity losses, conodonts suffered crucial changes on the origination regimes during the Late Triassic which triggered these events. Notwithstanding, our results indicate that the end-Triassic diversity depletion of conodonts was produced by background extinction levels in a context of lower origination. This suggests that several biological factors, rather than a unique, environmental and/or cyclic cause, could have influenced the evolutionary history of conodonts during the Triassic.

Keywords: diversity change; diversity depletion; origination regime; proportional extinction; Triassic conodonts

Introduction

The interaction of origination and extinction triggers diversity fluctuations through time. By definition, diversity is depleted when extinction is greater than origination, and conversely, diversity is increased when origination exceeds extinction. However, while extinction metrics have been extensively developed (see e.g. Cascales-Miñana et al. 2013 and references therein), less attention has been paid to the correct interpretation of diversity loss through changes in origination.

In 2004, Bambach et al. explored the role of origination levels in the major diversity depletions associated with the great five biotic crises registered from the marine fossil record, the so-called ‘Big Five’ taxonomic extinction events of past life. From this, it was demonstrated that when origination and extinction are considered together, only three of the ‘Big Five’ events (the end-Ordovician, end-Permian and end-Cretaceous crisis) appear to have been generated exclusively by elevated extinction, while the diversity depletions linked to the end-Devonian and end-Triassic extinctions are mainly generated by the suppression of origination levels (Bambach et al. 2004, figures 7 and 8). This evidence was used to argue that just three ‘true’ mass extinction events, and not five, affected the marine biota.

In a recent paper, Martínez-Pérez et al. (2014) re-evaluated the diversity dynamics of Triassic conodonts using a set of metrics that examines rates of evolution and diversity at a high-resolution temporal scale. From this, four important losses of diversity linked to high extinction

levels were documented in the following time intervals: Griesbachian (early Induan, Early Triassic), Smithian (early Olenekian, Early Triassic), Julian (early Carnian, Late Triassic) and Lacinian (early Norian, Late Triassic). But to date, it is unclear whether the main episodes of diversity depletion of Triassic conodonts are exclusively extinction driven, or if in contrast, changes in origination rates can provide an alternative explanation of the apparent diversity patterns.

Given this scenario, we explore the extinction pattern of Triassic conodonts as diversity depletions following the theoretical framework developed by Bambach et al. (2004). We aim to elucidate the role of origination levels in diversity changes associated with the main falls of diversity and to discern whether the major crises of Triassic conodont diversity are triggered only by extinction events or if, in contrast, fluctuations in origination levels can be considered a ‘cause’ of such crises as observed in two of the ‘Big Five’ extinction events.

Data

Raw data were extracted from the Plasencia et al. (2013) data-set, which was slightly modified by Martínez-Pérez et al. (2014). Data analysis was conducted mainly at the species level. However, a genus level analysis was also carried out to check whether this level follows the same trend as the species level concerning the significant falls. Thus, 327 conodont species belonging to 54 genera were considered. Absolute ages and time intervals were

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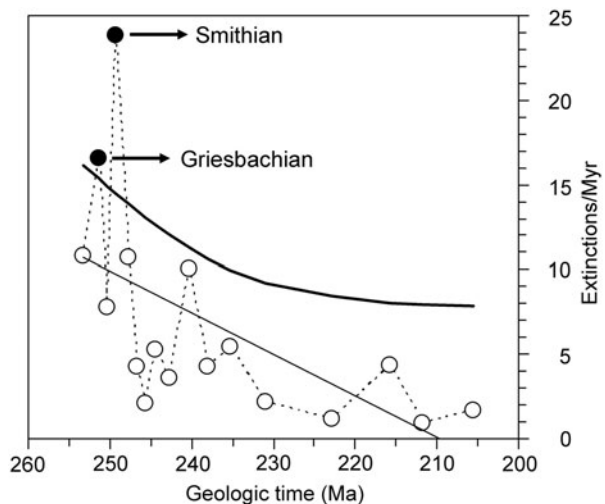


Figure 1. Evaluation of higher and background extinction levels of Triassic conodonts. Data analysis performed at sub-Age and species levels of resolution. The dashed line represents the total extinction rate (extinctions per Myr). The solid line represents the regression line of extinction points, while the bold line delimits the upper 99% confidence limit for that regression analysis. By taking this confidence limit as a criterion, the diagram shows two time units with higher extinction levels (black circles) in the Smithian and Griesbachian. Rarely preserved forms not included. See 'Methods' section for details.

extracted from The Geologic Time Scale 2012 (Gradstein et al. 2012). Data analysis was conducted at sub-Age level (see Ogg 2012, Table 25.3). In total, 18 time units from the Wuchiapingian (Lopingian, late Permian) to the Rhaetian (latest Triassic) were analysed.

Methods

First, to evaluate the fluctuation of diversity values through time, the proportional change in diversity was calculated by subtracting the number of taxa that crosses the bottom boundary from the number of taxa that crosses the top boundary of a given time unit, and dividing this value by the number of taxa at the start of the interval.

Afterwards, a confidence interval was added to evaluate the derived pattern of diversity changes. Bambach et al. (2004) established this interval considering the scenario described by the 'Big Five'. Raup and Sepkoski (1982) demonstrated that in the life history, there were five time intervals with higher extinction rates than the normal or background levels. Five great diversity depletions were linked with such intervals. Thus, Bambach et al. fixed a confidence interval to evaluate this pattern using the sixth largest diversity decrease of the marine fossil record to indicate the range that might be regarded as 'background' fluctuation in diversity (see Bambach et al. 2004, figure 2). We adopted here the same strategy.

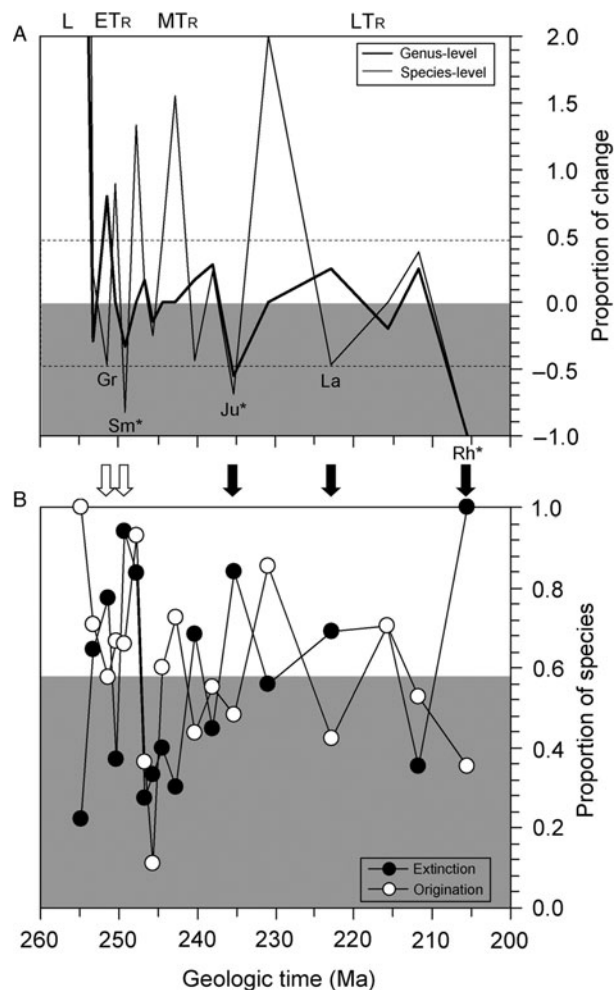


Figure 2. Analysis of the diversity depletions of Triassic conodonts. Data analysis performed at the sub-Age level of temporal resolution. (A) Proportion of gain or loss of conodont diversity. Data analysis conducted at genus and species levels. Bold line represents the proportional change of genus diversity. Solid line represents the proportional change of species diversity. The grey area indicates when the diversity (number of taxa) at the end of an interval is lower than at its beginning. The three major depletions of species diversity (decrease greater than 50%) are marked by an asterisk. Symmetrical dotted lines are drawn at -47% and $+47\%$ (based on the third largest diversity decrease before the extinction of the group) to indicate the range that might be regarded as 'background' fluctuations. Abbreviations: Gr, Griesbachian (early Induan, Early Triassic); Sm, Smithian (early Olenekian, Early Triassic); Ju, Julian (early Carnian, Late Triassic); La, Lacinian (early Norian, Late Triassic); Rh, Rhaetian (latest Triassic); L, Lopingian (late Permian); ETR, Early Triassic; MTR, Middle Triassic; LTR, Late Triassic. (B) Evaluation of the origination and extinction levels. Data analysis conducted at the species level. The grey area indicates when the proportional levels of origination or extinction are less than the total mean of origination and extinction for the Triassic (58% approx.). By taking this value as a reference, white arrows indicate great changes of diversity without diminished levels of origination. In contrast, black arrows indicate important changes of diversity with lower levels of origination. Black and white circles indicate extinction and origination proportions, respectively. See 'Methods' section for details.

Following the approach used by Raup and Sepkoski (1982), we explored the temporal distribution of the total extinction rate (see Cascales-Miñana et al. 2013, Table 1) by separating rates that cross the upper boundary of the 99% confidence interval of extinction pattern. The confidence interval of the pattern of diversity change was established in function of the diversity depletions linked to these extinction rates.

Subsequently, the proportional diversity change was compared with the origination and extinction levels. Such levels were evaluated using relative metrics of origination and extinctions per time unit (see Cascales-Miñana et al. 2013, Table 1).

Finally, we tested the ‘weight’ of origination and extinction levels (independent variables) on the proportion of diversity change (dependent variable) through a series of correlation analyses. Correlation was based on the Pearson (r), Spearman (r_s) and Kendall (s) coefficients. This combination was used for measuring the strength between variables and the correlation level of peaks and curves profiles, respectively (Fröbisch 2013). Raw data and data transformed using generalised differencing were employed to control false correlations resulting from overall trends between variables (see <http://www.graemetilloyd.com/methgd.html> for implementation; Benton et al. 2013). Three significance levels were used at 5%, 2.5% and 0.5% for comparison. Correlations were performed using the R statistical software (R Core Team 2013).

Results and discussion

The extinction pattern of conodonts during the Triassic is shown in Figure 1, together with the resulting regression line and its 99% confidence interval. Figure 1 shows just two time units with extinction levels significantly above the upper limit of the confidence interval. The maximum excursion corresponds to 23.9 extinctions per Myr registered in the Smithian (Olenekian, Early Triassic), while the second one corresponds to 16.6 extinctions per Myr registered in the Griesbachian (Induan, Early Triassic). In both cases, higher extinction levels were linked with two clear depletions of conodont diversity during the Early Triassic (Figure 2(A)). Following Bambach et al. (2004) criterion, this observation was used to establish the confidence interval of the diversity change pattern by using the third largest diversity depletion observed before the end-Triassic.

Figure 2(A) shows the proportional gain or loss in the number of species and genera during each Triassic sub-age. From this, we see that the two main crises of conodont diversity described by Martínez-Pérez et al. (2014) in the Smithian and the Julian (Carnian, Late Triassic), together with the largest extinction in the Rhaetian (latest Triassic), are the only intervals with more than a 50% proportional

loss of species diversity. We also see that the proportional change of genus diversity exhibits a similar pattern concerning the largest diversity decreases. However, by comparing the trajectories of the proportional change of diversity of both taxonomic levels, we also observe two interesting discrepancies at the Griesbachian (Induan, Early Triassic) and the Lacinian (Norian, Late Triassic), where it is possible to observe falls just from the pattern of diversity change at the species level. Interestingly, Stanley (2009) documented the major conodont extinction during the Early Triassic in the Griesbachian. We have also observed higher extinction levels in this time unit (Figure 1), together with clear diversity depletion at the species level (Figure 2(A)); however, during the Early Triassic, our results reflect the higher levels of diversity depletions in the Smithian.

Hirsch (1994) compared conodont diversity with sea-level changes and found a stunning correlation. He demonstrated that higher peaks of conodont taxonomic diversity (i.e. Smithian, Spathian and Ladinian) showed a close relationship with marine transgression. By comparing the Hirsch (1994) patterns with our curves, we also see that the Spathian (end-Olenekian, Early Triassic) and the Longobardian (end-Ladinian, Late Triassic), although not the Smithian, show positive diversity change, suggesting a link between such diversity variations and the sea-level fluctuations. Following Hirsch’s viewpoint, we believe that environmental stress from sea-level changes and the accompanying changes in habitat, combined with trophic conditions, were enough to trigger survival tactics and origination followed by radiation. This scenario suggests that the variation of platform ecosystems could have induced, at least partially, the observed variation in the diversity of Triassic conodonts.

Bambach et al. (2004, figure 2) showed that all major biotic crises of marine realms were followed by a positive increase in diversity that crosses the upper limit of confidence interval. From this, it was shown that the combination of higher origination and lower extinction during the recovery phase after diversity depletion marks these intervals as times of unusually great proportional increase in diversity (Bambach et al. 2004, p. 527). Bambach et al. (2004) also postulated that the presence of higher origination rates after the major diversity depletions may reflect recovery from unusually low diversity and not just a problem of sampling. Accordingly, our results show that the higher increments of diversity change occur immediately after the significant depletions of conodont diversity (registered before the end-Triassic). Such a pattern is the characteristic of recovery phases. Our results also reveal that the single largest depletion without a significant recovery phase is detected before the final extinction of the group (see Lacinian negative peak from Figure 2(A)). This evidence is in concordance with Bambach et al. (2004) vision and would support biological

Table 1. Correlation analysis of raw and generalised–differenced (detrended) data.

Variables		Pearson		Spearman		Kendall	
Dependent	Independent	<i>r</i>	<i>p</i>	<i>r_s</i>	<i>p</i>	<i>t</i>	<i>p</i>
Raw data							
Diversity change	Extinction	−0.47	0.0485*	−0.66	0.0030***	−0.55	0.0016***
Diversity change	Origination	0.60	0.0082**	0.71	0.0009***	0.54	0.0019***
Detrended data							
Diversity change	Extinction	−0.43	0.0861	−0.48	0.0530	−0.35	0.0518
Diversity change	Origination	0.57	0.0171**	0.64	0.0064**	0.47	0.0079**

Notes: Data analysis conducted at the species level. Pearson (*r*), Spearman (*r_s*) and Kendall (*t*) correlation coefficients with their corresponding probability values of no-correlation are showed. Significant (**p* < 0.05), highly significant (***p* < 0.025) and very highly significant (***) (*p* < 0.005) correlations are indicated. See ‘Methods’ section for details.

explanations for the extinction rates during the Norian (see Tanner et al. 2004; Mazza et al. 2010).

As suggested by Chen and Benton (2012), Figure 2(A) can also be understood in the context of a long recovery period for the Triassic ecosystems. In fact, our results reveal three progressively higher positive peaks of diversity change in the Spathian (end-Early Triassic), Illyrian (end-Anisian, Middle Triassic) and Tuvolian (end-Carnian, Late Triassic) (Figure 2(A)). Different contexts can be inferred. Thus, for example, it is probable that large environmental fluctuations favoured the development of opportunistic/generalist species (r-selected) (with high rates of reproduction, many offspring and limited parental care, being able to adapt to a wide range of environmental circumstances and food sources), rather than specialist species (k-selected) (that can only thrive in a narrow range of environmental conditions or limited diet) (Chen and Benton 2012). In addition to the ecological conditions, conodonts show an important limitation in diversity towards the end-Triassic: just one family (Gondolellidae) survived the Lower/Middle Triassic boundary and, during the whole Triassic, it was subject to several important diversity crises (with the main ones being the Smithian/Spathian boundary and the late Carnian). Despite these circumstances, conodonts were able to replace most of the lost diversity throughout the Triassic. However, during the late Triassic, conodonts showed severe recovery difficulties, being able to develop only reduced and simpler forms that recall primitive morphologies (e.g. *Misikella* and *Parvigondolella*) (Dzik 1991; Hirsch 1994). This situation could be a consequence of the reduction of the gene pool of the group, considerably affecting the evolutionary plasticity of the clade and the chance of a long-term survival. Unfortunately, it is not possible to provide an in-depth investigation of such ideas here. The inference methods used are extremely valuable for describing the main events in conodont evolution and their consequences, but they do not speak about causes; however, as we have discussed, this new pattern (Figure 2(A)) suggests different scenarios to be tested in the future.

On the other hand, the results at species and genus levels are quite different. If we examine trajectories

defined by the profile of diversity change at both taxonomic levels (Figure 2(A)), they show that while the genus diversity is progressively reduced towards the mid-late Triassic, the positive increases of proportional diversity at the species level are even higher. This evidence can be interpreted under a scenario where the disparity is progressively reduced until reaching ‘saturation’ at the end-Norian, where no recovery phase is observed. The taxonomy of conodonts can provide numerical inflations of certain taxa as the result of over-active splitting. This problem is not simple to resolve, and reported statistics are mainly indicative of the general trend. However, important information can still be derived (see comments below).

The key element for exploring the great depletions of marine diversity was the observation that the Phanerozoic is divided into six stratigraphically coherent intervals (Cambrian and Early Ordovician, Middle Ordovician–Early Silurian, Middle Silurian–Early Carboniferous, Late Carboniferous and Permian, Triassic, Jurassic through Pleistocene) of alternating high and low extinction intensity (Bambach et al. 2004, see Table 1). Interestingly, the six time intervals do not match the standard stratigraphic scale, with a single exception, the Triassic Period. This scenario was used by Bambach et al. to calculate the mean proportion of origination and extinction for each of the longer time intervals to be used as a reference value. From this, it was possible to test the proportional influences of origination and extinction rates of a given time unit (e.g. the stages of higher extinction defined by Raup and Sepkoski (1982)) and establish that the end-Triassic mass extinction was not exclusively extinction driven. If we apply these principles to our context and scale, we observe the total mean proportion of species origination and extinction for the Triassic is 0.58 ± 0.06 (standard error mean) and 0.59 ± 0.05 , respectively. Using this average proportion of origination and extinction as the reference value (approximately 0.58 in both cases), two opposite scenarios are observed during the significant diversity depletions. During the Smithian diversity depletion, proportional extinction levels were at their highest (0.94), while origination was not markedly

higher ($0.66 > 0.58$). In this case, diversity loss can be ascribed to elevated extinction, and therefore, it represents a 'true' global extinction event *sensu* Bambach et al. (2004). In contrast, during the Julian diversity depletion, we see that extinction ($0.84 > 0.58$) and origination ($0.48 < 0.58$) levels are clearly higher and lower, respectively, than the average for its stratigraphic neighbourhood. In this second case, diversity loss is interpreted herein as a consequence of a high extinction in a context of suppressed origination. An identical context is observed during the final diversity depletion in the Rhaetian. Interestingly, despite the important extinction levels registered in the Griesbachian (Figure 2(B)), this time unit does not reflect deep diversity depletion, probably due to the lack of suppressed origination levels. Thus, our results show that (1) not all significant depletions of conodont diversity during the Triassic were driven entirely by elevated extinction and (2) it seems to be that the fluctuation of origination regimes triggered the magnitude of diversity depletions during the Late Triassic.

Supporting previous observations, correlation analysis revealed a strong relationship between the diversity changes and the origination values (see Table 1). Between both variables, the detrended data analysis showed, in all cases, high significance levels, independently of the correlation coefficient used. Notwithstanding, the corresponding raw data correlations showed the best fit of the analysis. In contrast, concerning extinction levels, results just provided significant correlation from raw data; however, the absence of significant values from detrended data does not support such correlation. Thus, these results suggest that extinction levels are less decisive than origination as explanatory variable to account for the changes of species diversity.

Conclusions

The results illustrate the existence of two great depletions of conodont diversity before the Rhaetian (latest Triassic): at the Smithian (Olenekian, Early Triassic) and at the Julian (Carnian, Late Triassic). Our results have also highlighted that these depletions result from different dynamic mechanisms. Thus, while the Smithian diversity depletion can be interpreted as a consequence of elevated extinction, the Julian diversity depletion was driven by fluctuations of the origination regime. This evidence suggests that independently of the role of extinction on diversity losses, Triassic conodonts suffered crucial changes on the origination regimes which triggered these events.

Thus, this study provides evidence that in conditions of suppressed origination, background extinction levels can

generate the largest diversity depletions, as observed in the end-Triassic diversity depletion of conodonts. This suggests that several biological factors, rather than a unique, external (so-called environmental) and/or cyclic cause, could have influenced the evolutionary history of conodonts during the Triassic.

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Note

1. These authors contributed equally to this work.

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