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Testing the predation-diversification hypothesis for the Cambrian–Ordovician radiation

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Abstract. One of the commonest explanations for the evolutionary radiation of animals during the Cambrian and Ordovician periods (about 541 to 443 million years ago) is the predation hypothesis. According to this widely cited but untested idea, the first rise of predatory animals would have accelerated evolution, and so diversification, by increasing natural selection on preys and starting predator-prey coevolutionary arms races. This predation-diversification hypothesis is here tested for the first time for the Cambrian–Ordovician radiation, by comparing the pace of origination of marine invertebrates and the dynamics of the predator ratio in fossil communities, at the local scale and genus level, focusing on the open shelf habitat (reefs excluded). Overall, origination rates decreased whereas the median predator ratio first increased up to a maximum at the middle–late Cambrian and then decreased more or less gradually during the Ordovician. Time-series analysis, using data differencing and detrending, shows that there is no positive correlation between origination rate and synchronic predator ratio over the Cambrian and Ordovician. Thus, the results do not provide evidence of any acceleration of origination rate driven by the rise of predation. Predatory animals might have contributed to the start of the Cambrian–Ordovician radiation by promoting defensive exoskeletons and infaunal lifestyles, but the results suggest they did not facilitate diversification in any other way.

Key words: Cambrian explosion, macroevolution, paleoecology, Paleozoic, predator-prey ratio

Introduction

One of the key events in the evolution of life on Earth is the initial diversification and wide ecological expansion of biomineralized bilaterian animals shown in the fossil record over the Cambrian and Ordovician periods (about 551–443 million years ago). The Cambrian–Ordovician radiation represents the ultimate and seemingly irreversible change from the Precambrian world of microbial-dominated ecosystems to the Phanerozoic regime of animal-dominated communities. The radiation of skeletonized animals started at the end of the Ediacaran period (*Cloudina* assemblages) but especially at the beginning of the Cambrian ("small shelly fossils") (Kouchinsky *et al*., 2012), although the most basal animal clades might have diverged earlier, during the Cryogenian, according to molecular clocks (Erwin *et al*., 2011). Bilaterian animals diversified mainly at phylum level during the Cambrian and later at class, order and family levels during the Ordovician (Valentine, 1969; Webby, 2004). The initially broad anatomical and ecological diversification over the Cambrian was followed by Ordovician radiations within each big lineage. Although the main clades of biomineralized taxa appeared mainly during the early Cambrian (approximately 541 to 515 Ma, Kouchinsky *et al*., 2012), biodiversity curves using sampling standardization procedures show that the global number of genera gradually increased from the middle Cambrian up to the big mass extinction at the end of the Ordovician (Alroy *et al*., 2008), a pattern revealing approximately continuous evolutionary radiation over the lower Paleozoic.

There is no consensus on the trigger of the Cambrian–Ordovician radiation and especially of the diversification of the first skeletonized animals (Marshall, 2006). One of the many proposed hypotheses focuses on the first rise of predatory animals during the Cambrian and Ordovician. Macroscopic and anatomically complex predators were new and powerful agents of natural selection and they probably promoted coevolutionary arms races, thus accelerating evolution and facilitating diversification. In this way, predation could have driven this radiation event (Bengtson, 2002; Marshall, 2006; Leighton, 2011). The predation hypothesis is considered circular by Zhang *et* *al*. (2014), who argue that predator diversification is an effect, and not the cause, of the radiation. However, empirical evidence would be desirable to test the hypothesis. The scientific literature currently lacks any direct testing of the effects of predators on the early animal radiation, but some results indirectly suggest pros and cons:

Results indirectly supporting the predation hypothesis

a1. The oldest possible record of predation on a macroscopic organism, to date, coincides with the beginning of the radiation of skeletonized animals (borings in *Cloudina* shells, Bengtson and Zhao, 1992; Hua *et al*., 2003). Thus, predation could have been associated to the earliest diversification of skeletonized animals, although this is not a proof of a causal relationship.

a2. From the *Cloudina* assemblages onwards, the fossil record shows that skeletons were gradually more frequent in animals with increasingly energetic lifestyles, a trend which suggests increased predation pressure during the Cambrian radiation (Wood and Zhuravlev, 2012) and so a positive predation-diversification relationship.

a3. Predatory pressure might explain the origin of biomineralized exoskeletons as antipredatory defenses roughly at the beginning of the Cambrian (Evans, 1910; Vermeij, 1989), especially the polyphyletic skeletonization which resulted in the "small shelly faunas" (SSF) at the Nemakyt-Daldinian and Tommotian stages, at the base of the Phanerozoic, and its subsequent diversification during the early Cambrian (Kouchinsky *et al*., 2012). The widespread development of exoskeletons and infaunal lifestyles (the Verdun syndrome) at the beginning of the Cambrian suggests a general evolutionary response to increased predation (Dzik, 2005). However, exoskeletons may have not appeared first as antipredatory defenses (Vermeij, 1989; Cohen, 2004).

a4. Coinciding with the Cambrian–Ordovician radiation, the fossil record shows the apparition and diversification of predator clades: anomalocaridids (middle Cambrian onwards), predatory trilobites (mainly Ordovician), nautiloids (late Cambrian onwards), eurypterids (Ordovician), etc. (Bambach *et al*., 2007).

a5. The record of predation marks in fossil shells may show an increase in predation intensity during the early animal radiation. Huntley and Kowalewski (2007) compiled data of frequency of drillholes and repair scars in Phanerozoic marine shells with the aim of examining the relationship between diversity and predation intensity. Although they included 19 frequencies only for the early animal radiation (see their fig. 1; there are 2 frequencies from *Cloudina* at the end of the Ediacaran, 2 at the beginning of the Cambrian, 8 by the middle Cambrian, and 8 at the Late Ordovician), these few data may suggest an overall increase in predation intensity, but there is too much scatter to conclude anything with confidence.

a6. Predation is widely recognized as a cause of important changes in the fossil record of periods younger than the Ordovician. Most of these changes consist of the evolution of morphological antipredatory defenses or defensive lifestyles (Vermeij, 1977; Signor and Brett, 1984). Thus, predation could have played a similar role over the Cambrian and Ordovician.

Results indirectly against the predation hypothesis

b1. The fossil record of post-Cambrian times has not provided any general evidence that predator diversity increases prey diversity. Madin *et al*. (2006) report no relationship between the diversity of carnivores (genera relative to all taxa) and that of infaunal animals or mobile preys (genera relative to all prey taxa). However, this study cannot provide insight into the role of predators in the Cambrian–Ordovician radiation, because it focuses on carnivores from the Ordovician onwards (fig. 1A in Madin *et al*., 2006). Thus, it excludes the entire Cambrian and includes data from post-Ordovician times which adds noise to any conclusion which may apply to the Ordovician part of the radiation. The general conclusion that predators did not facilitate diversification could not be valid for the beginning of the Phanerozoic, when complex food webs first assembled and predator-prey coevolution started.

b2. Madin *et al.* (2006), using the Paleobiology Database (PBDB), show that predator diversity relative to all genera (sampled-in-bin) declined during the Ordovician, in spite of the great diversification event of this period. This counters the idea that predation intensity increased during the early animal radiation, as well as the dynamics of predator-prey ratios reported by Bambach (2002) based on the now outdated Sepkoski database. According to Bambach (2002), predator-prey ratios clearly increased during the Cambrian, but updated data are required to confirm this pattern.

b3. Before the Cambrian–Ordovician radiation, the oldest known animal communities (Ediacara biota, about 575–541 million years ago) show no evidence of macroscopic carnivores (Narbonne, 2005), but in spite of this their diversities fall within the usual range of modern ecological analogues (Clapham *et al*., 2003; Droser *et al*., 2006). This extreme diversity conservatism implies that predation did not drastically change community diversity since the earliest animal radiation. However, local diversities of the Ediacara biota usually match those of modern rather species-poor analogues, and therefore some diversity increase due to predation remains possible.

b4. Trilobite local diversity (alpha diversity) did not change substantially from the late Cambrian to the Late

Ordovician. Westrop and Adrain (1998) showed this for near-shore, shallow subtidal, carbonate buildups, and deep subtidal habitats. Intra-habitat species diversity remained essentially the same, in spite of the rise of nautiloids and other important predators over this interval (see the previous point a4). This suggests that local diversity did not respond to any predation increase during the Cambrian–Ordovician radiation. However, even the increase of predators is doubtful during the Ordovician (see point b2).

b5. The fossil record of crinoids demonstrates negative predation-diversification relationships are possible. They diversified after the removal of their predators in one of the Late Devonian extinction events, whereas crinoid diversification collapsed with the evolution of new predators in the Carboniferous (Sallan *et al*., 2011).

b6. There is experimental evidence that predation can slow down diversification, although the system is very different from marine invertebrate communities. Experiments in microbial microcosms show that predation delays diversification by reducing prey density and so weakening density-dependent natural selection (Meyer and Kassen, 2007).

All the previous points do not support any conclusion about the predation-diversification hypothesis for the Cambrian–Ordovician radiation. The objective of the present work is to test whether the rise of predation accelerated animal diversification over the Cambrian and Ordovician. The originality and interest of this study is that it is the first one to test this popular hypothesis explicitly for the evolutionary radiation of animals at the beginning of the Phanerozoic.

Methods

In outline, the method consists of analyzing the correlation between the time series of origination rate vs. that of median predator rates in Cambrian and Ordovician fossil communities. These time series were obtained from the Paleobiology Database (PBDB). The statistical significance of the observed correlation was estimated using a permutation test. A significant positive correlation at $\alpha = 0.05$ was considered to support the predation-diversification hypothesis. Thus, this study will test the hypothesis that predation was positively associated to origination over the Cambrian–Ordovician radiation, but not the idea that these two factors originally triggered the "Cambrian explosion".

The dataset for this study was retrieved from the PBDB in September 2015; it consists of the record of global genera of marine invertebrates from open marine depositional environments, i.e., shallow and deep subtidal, off-shore, and slope/basin; reefs were excluded because they tend to be unusually diverse among marine environments and thus are not directly comparable with the other ones (Bambach, 1977). Data from unknown environments, form taxa, and ichnofossils were ruled out.

Predator ratios

The predator ratio in fossil communities of each time bin is here taken as a surrogate of the role of predation. Madin *et al.* (2006) demonstrated that the ratio of predatory genera relative to all genera correlates well to the relative number of occurrences of predatory taxa in fossil collections. Thus, the ratio can be taken as a proxy of predator abundance in fossil communities. Additionally, they showed that the ratios cannot be easily distorted by some major preservation biases. Therefore, in spite of the many conceivable sources of noise, the predator ratio seems to be a reasonable measurement of the role of predators in fossil communities. A higher ratio means a wider variety of predators for each prey type and thus, other things being equal, more predatory pressure—for example, more predation risk in different habitats for the same prey, or more predation risk in the same habitat due to different predatory techniques.

Before calculating the predator ratio of each time bin, data downloaded from the PBDB were sorted by diet (*diet1* field), then records with diets labeled as "*photoautotroph*" were ruled out in order to include in the ratio consumers only, repeated records of genera were deleted in each collection, and the predator ratio was calculated for collections with at least 10 genera with assigned diets. Then the median predator ratio was estimated for all the collections within each time bin. This is probably a better surrogate of predator pressure compared to the procedure by Madin *et al.* (2006) of pooling together all the genera sampled-in-bin. The reason is that different communities may tend to have the same predators but different preys, because Cambrian–Ordovician predators were mobile whereas many of their potential preys were sessile. In this situation, carnivore genera are expected to be a more constant component of each community compared to prey genera, and then pooling all carnivores sampled-in-bin would result in unrealistically low predator ratios compared to the real ones at the community scale. This problem is solved by focusing on the community scale.

The median provides a robust estimate of central tendency, and the use of communities as sampling units bypasses many of the sampling biases of the fossil record. Bambach (1977) adopted the same approach to study species richness in a classic contribution which should be consulted for the details of the advantages of this procedure. However, it could provide unrealistic images of epochal predator ratios if there are many communities with a distorted ratio (outliers). This potential problem was controlled by comparing the medians and their corresponding frequency histograms in order to confirm that they represent well the central trend. Error bands were calculated for each median by computing the median ratio upon the assumption that all genera without an assigned diet in each collection are carnivores (upper limit for the median) and the opposite (lower limit).

A possible source of bias in the median comes from the abundance of Konservat-Lagerstätten during the Cambrian. These fossil sites provide a much more accurate record of past animal communities because they include soft-bodied taxa. Unfortunately, there are too few Lagerstätten and they are too temporally restricted to compose a good sample over the entire Cambrian–Ordovician radiation. I examined the effect of Lagerstätten on predator ratio by looking for any difference in the median of the ratios from Lagerstätten compared to the median of their time bin. Lagerstätten were identified by the field of preservation of soft tissues in the collections retrieved from the PBDB. If a meaningful statistical difference was detected, then Lagerstätten were excluded from further analyses. Even in this case, the predator-prey ratios of Chengjiang and Burgess Shale were estimated for comparative purposes. I consulted the taxonomic list of both fossil sites in Dunne *et al.* (2008) at genus level.

Origination rates

Origination is the key process to focus on in order to understand the Cambrian–Ordovician radiation, because extinction did not contribute to increase diversification (that is, origination rate minus extinction rate) during this event. The reason is that the oldest faunas of the Phanerozoic suffered from *higher* mean extinction risk than younger faunas (Foote, 2003; Alroy, 2008).

Origination was included in the analysis as three-timer (3T) origination rates. These rates consider two-timer taxa (that is, genera sampled in one interval and immediately before or after), three-timer taxa (genera sampled in one interval, immediately before, and after), and part-timers (genera sampled before and after one interval but not within it) to calculate sampling probabilities and turnover rates according to the equations provided by Alroy (2010), which are available as implements in the PBDB website. 3T origination and extinction rates are considered to be as unbiased as possible (nowadays) for estimating turnover rates from the fossil record when sample size is reasonably large (Alroy, 2010).

Time series analysis

The time series of predator ratios and origination rates cannot be directly analyzed because of problems of autocorrelation and temporal trends. Correlation analysis demands that consecutive data points of each variable must be statistically independent observations, but there are many genera present in consecutive time bins and this causes autocorrelation. The problem is potentially important because about 58% of the genera here considered have a lifespan of more than 10 Ma, which is approximately the duration of one time bin in the PBDB timescale. Furthermore, any temporal trend in both variables would make meaningless the measurements of central tendency and variability required by most statistical tests. These problems demand the use of time-series analysis to obtain any reliable statistical information from the dataset.

Following a standard procedure of time-series analysis, the variables were differenced (value of a time bin minus value of the previous one) in order to correct autocorrelation. As is usual when analyzing proportions, a logit transform [$\ln (p / (1 - p))$] was applied to predator ratios before differencing. In this way, the predator ratio (p), which is bounded to the range 0–1, becomes an unbounded variable like the 3T origination rate. After differencing, any trend in the variables was corrected by detrending them, that is, a regression model was fit to each time-series and then the residual value of each data point (observed minus predicted value) was extracted. This also reduces autocorrelation. Theory predicts any relationship between variables can be detected by examining these residuals (Wei, 1994). For detrending I used ordinary least-squares (OLS) regression with a range of linear and nonlinear models.

After detrending the differenced data, the residual origination rate was plotted against the corresponding residual predator ratio. The mutual relationship between both variables was explored by correlation analysis (Pearson correlation). The significance of the correlation coefficient was estimated with a permutation test (1,000 permutations). Lagged correlations were not analyzed because the predation-diversification hypothesis implies origination rate increases with synchronic predation pressure. A lagged correlation would make sense for examining the influence of predation on diversity, because diversity is the result of origination and so it requires some time to accumulate. However, here I am not focusing on diversity, but on the rate of production of diversity, and the predation-diversification hypothesis does not imply a delayed response of origination to predation pressure at geological timescales.

Since these correlation analyses require data as unbiased as possible, I examined how the detrended variables depend on sampling effort measured as the number of communities, or collections, necessary to obtain each

Table 1. Summary of the dataset. Available data do not allow the calculation of 3T origination rate for Cambrian 1, and its predator ratio (X) refers to the single community available with at least 10 genera with diets assigned in the PBDB (see the Results for details).

Time bin	Midpoint (Myr)	3T origination rate	Collections for origination rate	Communities with estimated predator ratio	Median predator ratio
Ordovician 5	446.6	0.52	898	104	0.05
Ordovician 4	455.2	1.23	2342	407	0.08
Ordovician 3	463.4	1.06	439	78	0.2
Ordovician 2	472.3	1.36	971	104	0.29
Ordovician 1	483.5	2.3	719	57	0.27
Cambrian 4	494.6	2.31	1223	164	0.33
Cambrian 3	507	1.94	783	79	0.3
Cambrian 2	521.5	4.33	444	32	0.25
Cambrian 1	536	–	16	1	0*

data point. Any significant dependence was corrected by the extraction of new residuals from the best fit regression model (OLS regression) chosen among a range of linear and nonlinear options; then these second residuals were analyzed in the correlation test instead of the first residuals. Statistical analyses were carried out using Statgraphics 5.1.

Results

The dataset of marine invertebrates from Cambrian–Ordovician open shelf environments retrieved from the PBDB contains 7,835 collections containing occurrences of 47,207 consumer genera with an assigned diet out of 49,372 genera recorded without repeats within all the collections (Kiessling *et al*., 2015). The predator ratio was estimated for 1,026 communities containing at least 10 genera with diets. The dataset together with the list of references from the PBDB is available as Supporting Online Material at http://www.bioone.org/toc/jpal/20/4. A data summary appears in Table 1.

The time bin Cambrian 1 yields no 3T origination rate because it is the start of the PBDB timescale and a previous interval is necessary to calculate this 3T rate. I tried to estimate the 3T ratio by hand by including genera from the last 10 Ma of the Ediacaran, following the records of the PBDB, but not a single three-timer genus was found, that is, no genus ranges from the terminal Ediacaran to Cambrian 2 in the database. Thus, the ratio cannot be calculated. This problem, together with the lack of communities where the predator ratio can be estimated (a single one, with ratio = 0), forced me to rule out Cambrian 1 from the analysis. Therefore, the "Cambrian explosion", that is, the rapid buildup of diversity of bilaterian *phyla* about 541–515 Ma (Kouchinsky *et al*., 2012) will be represented in this study as the time bin Cambrian 2 (530–513 Ma). Anyway, this implies including most of the results of the "explosion," since 16 out of 26 skeletal clades at *phylum* to class level first appeared over Cambrian 2, according to the chronology compiled by Kouchinsky *et al.* (2012).

Figure 1 shows the frequency histograms of predator ratios for each time bin. The modal interval for the predator ratio is always the lowest one (0.00 to 0.20) except for Cambrian 2 and Cambrian 3, whose modal class is the second (0.20 to 0.40). Since all the histograms are rather monotonous patterns (decreasing or bell-shaped curves), the medians provide a meaningful summary of their shapes. Figure 2A shows the time-series of the medians together with the error bands. Error bands widen towards the earliest Cambrian due to the increasing uncertainty about the diets of problematic taxa exclusive of the Cambrian explosion. The medians follow a well defined pattern: overall, the time series resemble a bell whose uppermost part is placed at the end of the Cambrian. Even the error bands suggest the same pattern. Figure 2D displays the decrease of origination rates during the Cambrian–Ordovician radiation. It shows the monotonically decreasing trend which has been previously noticed in many works.

The taxonomic lists from Dunne *et al.* (2008) yield a predator ratio of 0.44 for Chengjiang (Cambrian 2) and 0.32 for the Burgess Shale. The value from Chengjiang is higher than the median of Cambrian 2, but that from the Burgess Shale is very close to its corresponding median (Figure 1). Among the collections with a calcu-

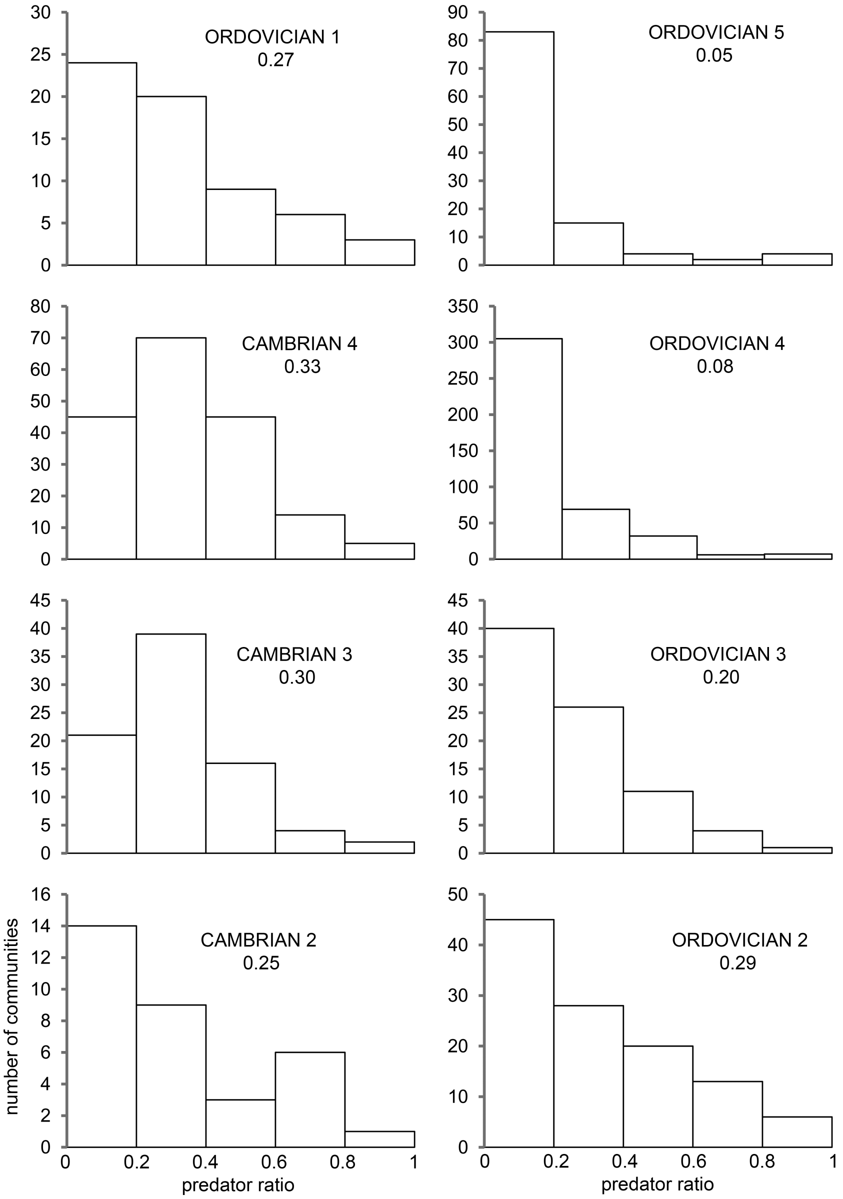

Figure 1. Frequency histograms of the predator ratio over the Cambrian and Ordovician. The median is shown in each time bin.

lated predator ratio, there are 32 Lagerstätten which are distributed in the time bins Cambrian 2 (*n* = 2), Cambrian 3 (*n* = 27), Cambrian 4 (*n* = 1), Ordovician 1 (*n* = 1), and Ordovician 3 (*n* = 1). Thus, a reasonable statistical comparison is possible only for Cambrian 3. The median in this case is 0.30, which matches exactly the median obtained for all the collections considered from Cambrian 3. Since no difference at all is observed, the Lagerstätten were included in the analysis. This decision is reinforced by the fact that the predator ratios from the Lagerstätten of the dataset follow broadly the same pattern of the time-series of Figure 2A: initial rise up to a peak in Cambrian 4, and then a decrease over the Ordovician—the values are 0.29 and 0.30 in Cambrian 2, 0.58 in Cambrian 4, 0.31 in Ordovician 1, and 0.22 in Ordovician 3.

The variables show moderate to low autocorrelation at one time lag, the coefficients of autocorrelation being 0.56 for logit-predator ratio and 0.21 for 3T origination rate. The differenced time-series are shown in Figure 2D, E. These time-series were detrended using the equations of Table 2 (the regressions lines are shown in Figure 2B,

Table 2. Regression equations used for detrending the time series data. The independent variable of each model is age in million years of the upper midpoint of each time interval, according to Table 1.

Variable	Regression equation	R^2	p-value
predator ratio (logit-transformed)	$y = 0.0171x - 8.385$	0.634	0.032
3T origination rate (raw data)	$y = -0.0170x + 7.4957$	0.155	0.382

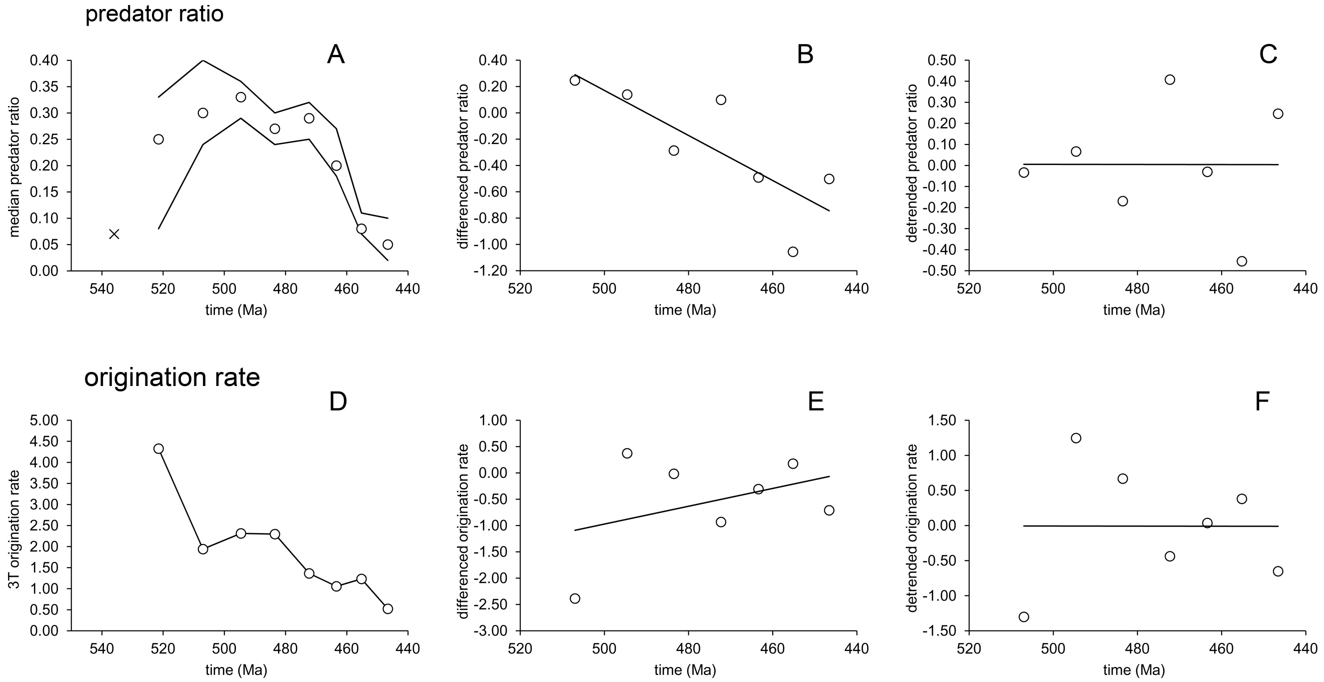

Figure 2. Time-series of predator ratio and origination rate during the Cambrian and Ordovician. **A**, Raw predator ratio (medians). The lines are absolute error limits obtained by assuming genera of unknown diet are all carnivores (upper line) and the opposite (lower line). The data point of Cambrian 1 (×) is included for comparison; it was calculated by pooling together all genera sampled-in-bin, a procedure that makes it not directly comparable to the other points. **B**, Differenced logit-transformed predator ratio, with regression line (Table 2). **C**, Detrended logit-predator ratio after differencing, with regression line showing no trend. **D**, Raw 3T origination rate. **E**, Differenced 3T origination rate, with regression line (Table 2). **F**, Detrended origination rate after differencing, with regression line showing no trend.

E). The residuals do not show any trend over time (Figure 2C, F), and so they are adequate for statistical analyses. They do not seem to depend on sampling effort, since each regression line in Figure 3 explains less than 7% data variance with a slope far from statistical significance ($R^2 < 0.07$, $p > 0.57$).

The final relationship observed between predation and origination is shown in Figure 4. The correlation obtained is −0.346, that is, negative instead of positive as the hypothesis predicts. It is clearly not significant, with a p-value of 0.773 in the permutation test. The type-II error (β) cannot be calculated because, if we assume the observed correlation is the expected value of the alternative hypothesis, then it would be opposite to the alternative hypothesis here considered (namely, that the correlation is positive). This situation implies no theoretical risk of a false negative. Overall, this statistical analysis does not support the predation hypothesis, and the negative correlation even suggests that predation may have contributed to *slow down* the Cambrian–Ordovician radiation.

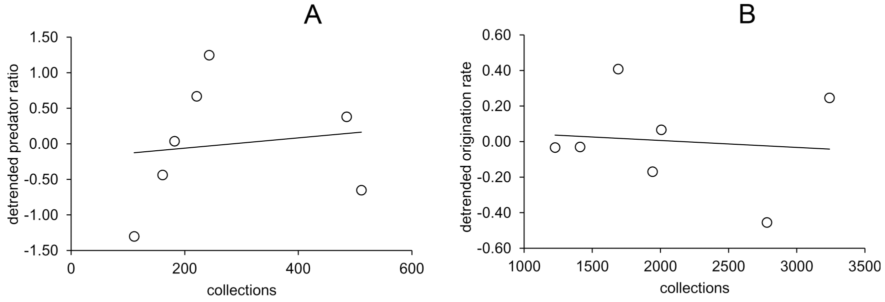

Figure 3. Relationship between sampling effort and detrended origination rate and logit-predator ratio.

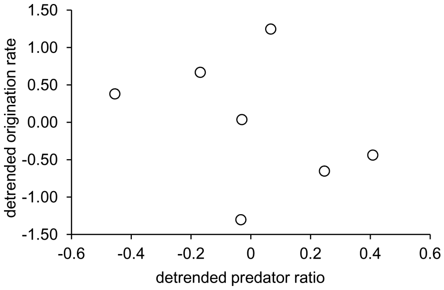

Figure 4. Scatterplot of the final data points of the correlation analysis.

Discussion

The results extend to the Cambrian–Ordovician radiation the lack of correlation between predation and origination noticed by Madin *et al.* (2006) for the post-Cambrian record. Thus, the main conclusion of the present study is qualitatively the same in spite of the fact that Madin *et al.* (2006) calculated predator ratios by pooling together all the genera within a time bin, instead of considering data for single communities like the present study does—this last procedure is probably a better surrogate of predator pressure (see the Methods section).

The shortcomings of the method and data here considered recommend caution when interpreting the results. Of course, correlation is not causation, and the lack of correlation does not imply lack of relationship—confusion factors may exist and remain uncorrected, although they are not easy to see in this case. But the inevitable limitations we face when analyzing the fossil record rule out any experiment to test causal relationships, and so all we can do is to test the association between variables. Caution is also recommended by the paucity of data, but it cannot be overlooked that the seven data points shown in Figure 4 have been obtained using 53,913 occurrences of genera for 3T origination rates and 19,801 for predator ratios. Similarly, the nonrandom signals observed in the raw time-series (Figure 2A, D) suggest that their main patterns have been retrieved even using the few available time bins. In spite of these empirical constraints, here a positive correlation was predicted and the data yielded *the opposite*. As far as this analysis can go, this result suggests no relationship existed between predation pressure and diversification during the Cambrian–Ordovician radiation. Thus, the effect of predators over this key episode in the history of life on Earth does not seem to have been different than their effect on diversification over the remaining of the Phanerozoic (Madin *et al.*, 2006).

However, this interpretation does not imply that predators did not have any evolutionary impact at the beginning of the Cambrian radiation. Predatory pressure probably favored the origin of exoskeletons and other defenses (Evans, 1910; Vermeij, 1989; Bengtson, 2002; Dzik, 2005; Wood, 2011). In this way, predators could have contributed to the very start of the Cambrian–Ordovician radiation because in many phyla the skeleton acts as a highly versatile anatomical scaffold which allows many variations and this would facilitate evolutionary divergence even without any direct effect of predators on diversification. This hypothetical indirect effect of predators on the "Cambrian explosion" will deserve further analysis in a future work (under preparation).

The negative correlation coefficient here obtained suggests predators may have impeded the Cambrian–Ordovician radiation, a possibility which fits with certain fossil and experimental evidence—see the points b5 and b6 in the Introduction. We need to pay more attention to this kind of options before repeating again the *leitmotiv* that predators probably facilitated the "Cambrian explosion".

The assignment of the diets of many bizarre animals from the early Cambrian is especially difficult due to the lack of modern counterparts, the fragmentary or problematic nature of their fossils, or both. Thus, caution is recommended especially when interpreting the low predator ratio from the time bin Cambrian 2. However, we can expect a relatively low ratio at the beginning of the Cambrian, because the ratio increased later but there is no convincing record of carnivore taxa in the Ediacara biota (Narbonne, 2005). The most parsimonious option for the start of the Cambrian is the mean of these two situations, that is, a low predator ratio. Thus, the time-series of Figure 2A probably represents the main pattern of predator ratio during the Cambrian in spite of the uncertainty about Cambrian 2 and Cambrian 1.

The predator ratio may have decreased during the Ordovician due to a taxonomic artifact, if diversification increased the species-genus ratio so that a high predator ratio at the species level was masked as a low ratio at genus level because many predator species belonged to the same genera. I think this possibility is unlikely, since diversification happened mainly at the order and family levels during the Ordovician, but not within genera (Valentine, 1969; Webby, 2004). However, if I am wrong, then an increase in species-genus ratios should also hold for preys and thus the predator ratio would be compensated.

An important source of noise in the predator ratio may come from taxonomic bias in the collections. Animal clades accumulated during the lower Paleozoic, and so more taxa-specific studies become possible in the Ordovician. Therefore, more fossil collections are expected to deal with a single taxonomic group in this period. This will bias the calculation of predator ratios. For example, in the PBDB there may be many fossil collections from studies focusing on Ordovician brachiopods only, thus excluding nautiloids and other predators. The exclusion of predators from the published fossil collections may be the cause of the low predator ratios obtained for the Ordovician. However, this is an unlikely option according to the shape of the histograms of median predator ratios (Figure 1). If Ordovician collections had high taxonomic bias, then there would be many collections focusing on typical carnivore groups (mainly nautiloids, and trilobites of the Order Phacopida), which would produce a peak at the highest predator ratios. The rarest ratios in the histograms would be at the middle values, because these values would represent collections obtained without the taxonomic bias (which, by assumption, would be rampant). In summary, a bimodal histogram would result with a peak at the lowest (preys) and highest (carnivores) ratios. This is clearly not the case in any of the Ordovician histograms (Figure 1). Taxonomic bias may be present, but it is unlikely to be responsible for the general shape of the histograms, and so for the medians here analyzed. These arguments suggest the results obtained in the present study are not fatally distorted by taxonomic bias in the fossil collections.

The debate about the possible explanations for the Cambrian radiation would benefit from the kind of empirical approach here adopted, since sometimes this field suffers from the risk of becoming a pool of untested but likely hypotheses, ideas which are widely considered as reasonable explanations in theory but which are never subject to confirmation using data. However, many of the hypotheses about the Cambrian–Ordovician radiation can be tested with an adequate approach, as this work exemplifies for predation, and so there is no reason to maintain the explanations of this event in the realm of informed speculation.

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