

**Demise of the last two spire-bearing brachiopod orders (Spiriferinida and Athyridida)
at the Toarcian (Early Jurassic) extinction event**

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Abstract

Brachiopods were severely hit by several mass extinctions which fundamentally shaped their long evolutionary history. After the devastating end-Permian extinction, the fate of the four surviving orders differed significantly during the Triassic and Jurassic. Two orders, the rhynchonellids and terebratulids are extant today, whereas spiriferinids and athyridids, which possess spiral brachidia, suffered heavy losses at the end of the Triassic and became extinct in the Early Jurassic Toarcian event. Although the doom of the spire-bearing orders has been thought to be related to physiological traits, extinction selectivity across the end-Triassic and Toarcian event has not been rigorously assessed previously, and the reasons for their demise

at the later and lesser Toarcian event, rather than at the earlier and greater end-Triassic crisis remained unexplored. Using primarily the Paleobiology Database, we constructed diversity curves, estimated taxonomic rates, and assessed the temporal changes in geographic distribution of the two spire-bearing and two other orders in the Triassic-Jurassic interval. After shared trends and similar origination rates in the post-Permian recovery leading to a Late Triassic diversity maximum, the end-Triassic extinction was selective and preferentially eliminated the spire-bearers. In contrast to the rebound of rhynchonellids and terebratulids, spire-bearers failed to recover in the Early Jurassic, and their repeated selective extinction at the Toarcian event led to their final demise. The end-Triassic event also terminated the worldwide geographic distribution of spire-bearers, confining them to the Western Tethys, whereas the other groups were able to re-establish their cosmopolitan distribution. The morphologically diverse spire-bearers represent specialized adaptation, which further increased their extinction vulnerability compared to the other groups with conservative biconvex shell morphology. Another key difference is the physiological disadvantage of the fixed lophophore and passive feeding of spire-bearers, which became critical at times of increased environmental stress. The spire-bearing spiriferinids and athyridids were “dead clades walking” in the Early Jurassic and their disappearance in the Early Toarcian represents the last major, order-level extinction event for the brachiopods.

Keywords: diversity, Paleobiology Database, end-Triassic, mass extinction, paleobiogeographic distribution

1. Introduction

Brachiopods were severely affected by the end-Permian mass extinction and after that crisis they became subordinate in the shallow marine, level-bottom communities. In this habitat the group was largely replaced by the bivalves (Gould and Calloway, 1980; Thayer,

1985; Walsh, 1996), and brachiopods partially withdrew to the outer shelf environments or bathyal refugia (Sandy, 1995; Vörös, 2005). Five of the nine orders of articulate brachiopods (Subphylum Rhynchonelliformea) became extinct at the end-Permian event, whereas only one minor order (Thecideidina) originated afterwards in the Mesozoic (Curry and Brunton, 2007). The four surviving clades show a secondary peak of diversity in the Late Triassic but the worldwide end-Triassic and Toarcian extinction events imposed severe contractions in their taxic diversity (Hallam, 1990; 1996). The post-Permian diversity history of the four articulate brachiopod orders diverged significantly during and after these shared bottlenecks, a phenomenon analyzed in detail in this study.

The orders Rhynchonellida and Terebratulida diversified in the Jurassic and are still extant. On the other hand, the other two orders, Athyridida and Spiriferinida, were severely decimated by the end-Triassic crisis and became extinct in the Early Jurassic, during the second-order Toarcian extinction event, coincident with the Toarcian Oceanic Anoxic Event (T-OAE). The late-stage history of these groups thus exemplify the concept of “dead clade walking” (Jablonski, 2002), which denotes the survival of groups without recovery and refers to clades which survived mass extinctions but remained marginal or declined in their aftermath. The demise of the Athyridida and Spiriferinida was the last major, order-level extinction event within the phylum Brachiopoda.

The main shared anatomical and morphological feature of Athyridida and Spiriferinida was the possession of stiff, spiral brachidia which support the lophophore. These orders represented the last surviving spire-bearing clades, as the other spire-bearing brachiopods disappeared during the late Devonian crisis (Atrypida) or fell victim to the end-Permian extinction (Spiriferida). The spiral brachidia are in contrast to the shorter crura or loop of the Rhynchonellida and Terebratulida, respectively (Alvarez and Jia-yu, 2002; Carter and Johnson, 2006; Lee et al., 2006; Savage et al., 2002). The spire-bearers’ lophophore was fixed

at full length to the spiral brachidia, whereas the lophophore of the Rhynchonellida (spirolophore) and the Terebratulida (plectolophore) are only proximally supported by the crura and the loop, respectively (Fig. 1). The Athyridida and Spiriferinida were the last spire-bearing brachiopods and their decline and Early Jurassic extinction has long been thought to be related to the properties of the spiral brachidium, which supported a less flexible, therefore less effective lophophore (Ager, 1987). The inferred feeding mechanism of spire-bearing brachiopods was widely discussed by several authors (Rudwick, 1970; Vogel, 1975) and was recently studied by Manceñido and Gourvennec (2008), Shiino et al. (2009), and Shiino (2010).

The end-Triassic and the Toarcian extinction events, of paramount importance for the demise of spire-bearing brachiopods, share remarkable similarities. Both coincided with volcanism that led to the formation of large igneous provinces (LIPs), the Central Atlantic Magmatic Province and the Karroo-Ferrar Province, respectively (Pálffy and Kocsis, 2014; Burgess et al., 2015). Although details of both events are still debated, LIP volcanism is proposed to trigger similar environmental stressors and was suggested to be the common ultimate causal agent for many major and minor extinction events (Courillot and Renne, 2003; Bond and Wignall, 2014). The chain of interlinked environmental changes include short-term cooling followed by longer-term warming possibly culminating in super-greenhouse episodes (McElwain et al., 1999; Suan et al., 2010), changes in ocean circulation and development of widespread anoxia (Jenkyns, 2010), and acidification of the ocean (Greene et al., 2012; Hönsch et al., 2012). Despite the similar causation and processes in operation, the first-order end-Triassic and the second-order Toarcian extinction events are clearly of different magnitude (Alroy, 2014). Separated by ~19 m.y., the two consecutive crises pose intriguing questions with respect to the extinction of spire-bearing brachiopods. Their physiological traits and diversity histories, as well as similarities and differences of the

two events need to be analyzed in order to explain why and how the second and smaller, rather than the first and larger of the two events led to the final demise of the athyridids and spiriferinids.

Using the global dataset of the Paleobiology Database (PaleoDB, <http://paleobiodb.org/>, accessed via the FossilWorks gateway, <http://fossilworks.org/>), herein we (1) analyze the Early Mesozoic diversity trajectories of the articulate brachiopod (Rhynchonelliformea) orders with a focus on the spire-bearing clades; (2) reconstruct the trends in the morphological diversity of athyridids and spiriferinids, in contrast to the morphologically conservative terebratulids and rhynchonellids and use the observed trends to propose an explanation for the selective extinction processes; (3) assess the changes in paleogeographic distribution of the spire-bearing and the other brachiopod groups, and (4) evaluate the physiological advantage of active ciliate feeding of terebratulids and rhynchonellids in contrast to the assumed passive feeding of spire-bearing brachiopods.

For the analyses of taxonomic and morphological diversity, and the underlying evolutionary history of the four clades, we formulate and test the following three working hypotheses: (1) spire-bearing brachiopod orders were eradicated during the severe biotic crisis in the Toarcian stage, as these groups were significantly more affected by the environmental disturbance than terebratulids and rhynchonellids; (2) although the lophophore morphology has only minor influence on the origination pattern of brachiopods, it exerts significant influence on the probability of survival during environmental crises related to heat stress and/or anoxia; and (3) the disappearance of spire-bearing forms is at least partially attributable to their muted recovery after the end-Triassic mass extinction.

2. Data and methods

The Triassic and Early Jurassic brachiopod data coverage of PaleoDB has been assessed and complemented by data entry from additional references to approach comprehensiveness.

Genus-level occurrence data from the PaleoDB were downloaded on 16.02.2016 for the Capitanian (Middle Permian) to Valanginian (Early Cretaceous) interval and were resolved to the stratigraphic level of stages (Gradstein et al., 2012). The Early Jurassic part was further resolved to the level of substages, to better constrain the diversity trajectories in the critical, terminal part of the spire-bearers' evolutionary history. A single occurrence (Collection number 63775) of the genus *Spiriferina* in the Lower Temaikan (Aalenian) of New Zealand was omitted from the analysis due to stratigraphic correlation issues. The dataset (Appendix A) resolved at the stage level consists of 15,056 genus-level occurrences from 7,499 collections in the Triassic–Jurassic interval (Table 1). Age range data from the Treatise on Invertebrate Paleontology (Curry and Brunton, 2007) were used as a control and compared with the PaleoDB data. Geographical patterns of occurrences were analyzed using a 30×30° grid and the rotation files of Scotese (pers. comm. to the Paleobiology Database, 2001) which were implemented by J. Alroy (pers. comm.).

All statistics of diversity dynamics were calculated on the Triassic–Jurassic interval using stage-level resolution. Raw diversities were calculated with the range-through method (RT), subsampled richness values indicate the corrected sampled-in-bin (SIB) diversities rescaled with the three-timer sampling completeness (Alroy, 2009) to correct for the residual sampling error.

Taxonomic rates were computed using the equations for the per-capita rates of Foote (2000), as the relatively small sample sizes limit the applicability of the occurrence-based methods (Alroy, 2014). The time dimension was omitted from the turnover rate equation, to reflect magnitudes as if they happened instantaneously and to decrease the error otherwise introduced by time scale calibration uncertainties.

Both diversity and taxonomic rate estimates were also calculated with sampling standardization. The Shareholder Quorum Subsampling algorithm (Alroy, 2010) was utilized

to estimate the parameters at a given sampling level. The target quorum of 0.6 effectively represents the patterns emerging from a range of other settings. Other subsampling methods, e.g., classical rarefaction (Raup, 1975) were also tested and found to lead to the same general results.

To assess the selectivity of extinction and origination rates, we used the corrected Akaike Information Criterion (AICc) to distinguish whether the data at hand provide strong enough evidence to describe the extinction patterns when the data are subdivided into specific groups (e.g., Kiessling and Kocsis, 2015). Because the information theory-based approach cannot be used when the extinction rate equations are not applicable (i.e. at the final extinction of a taxon), binomial tests were used to assess the selective extinction risk of spire-bearing forms during the T-OAE. These tests calculate the probability of complete extinction of spire-bearing brachiopod genera (i.e., no surviving genus in the Aalenian, out of 6 genera extant in the Toarcian), given that their proportion of survival is predicted by the proportion of survival of other brachiopods.

In order to avoid spurious correlations emerging between two randomly changing variables, the method of generalized differencing (McKinney and Oyen, 1989) was applied to the correlation tests. All analyses were performed in the R environment (R Development Core Team, 2016).

3. Results

3.1. Brachiopod diversity

The raw generic diversity of the four brachiopod orders surviving the end-Permian show similar trajectories: the Triassic recovery reached a maximum in the Carnian and Norian, then the end-Triassic near-extinction was followed by secondary bloom in two phases in the Jurassic. The sampling standardized analysis reveals a gradual rebound of brachiopods after

the end-Permian extinction event (Fig. 2). The end-Triassic extinction severely hit the clade, thus diversity has a local minimum in the Hettangian, which is confirmed by the sampling standardization. The Jurassic blooms are attributable to the rhynchonellids and terebratulids, while the spire-bearing clades show only a subdued diversity increase in the Early Jurassic and vanish in the Toarcian (Figs. 3 and 4).

Range-through diversities of spire-bearing brachiopods were calculated using data from both the PaleoDB and the Treatise on Invertebrate Paleontology (Alvarez and Jia-yu, 2002; Savage et al., 2002; Carter and Johnson, 2006; Lee et al., 2006; Gourvennec and Carter, 2007). The resulting patterns closely parallel each other (Fig. 3), although some discrepancies are present. The differences most likely represent the combination of the effects produced by the omission of older monographs (e.g., Bittner, 1890; Bittner, 1900) that are not valid sources of occurrence data for PaleoDB and therefore are not included in the analysis, and the inclusion of much new information in the database. Curves of taxonomic rates also show a good resemblance.

3.2. Comparison of diversity dynamics

Different orders within the morphological groups show similar diversity history in the Triassic (Fig. 3). However, the diversity trajectories following the end-Triassic mass extinction are markedly different for the spire-bearing and the other orders (Fig. 5). The Triassic richness values are not significantly different, whereas the spire-bearing brachiopods have significantly lower diversities in the Jurassic than other types. Sampling standardization does not alter this pattern significantly.

Raw Spearman rank correlations are significant ($\rho = 0.81$, $p = 0.0218$) between origination rates of spire-bearing and other genera at the stage level. Although autocorrelation is not significant in the rate series, the generalized differencing was applied to confirm the previous pattern ($\rho = 0.82$, $p = 0.034$). Extinction rates were not correlated and selectivity

tests suggest that the combined spire-bearing brachiopod group suffered more severe extinctions in the Rhaetian stage (Fig. 6).

3.3. Failed recovery of the spire-bearing clades

The decreased importance of spire-bearing brachiopods in the Jurassic is also evident using other metrics. In addition to the lower number of overall occurrences in a stage, the median proportion of spire-bearing genera in individual collections decreased markedly after the Triassic-Jurassic boundary (Fig. 7, Wilcoxon signed-rank test, $p < 0.0001$). After the crisis, the overall geographic range of spire-bearing clades expressed by the number of occupied $30 \times 30^\circ$ paleogeographic cells decreased as well, and in the Jurassic it remained lower than the occupancy of other forms ($p < 0.042$). Due to the similar preservation potential of spire-bearing and non-spire-bearing brachiopods (which is confirmed by the not significantly different three-timer sampling completeness values in the overlapping parts of the time series) these likely translate to the difference in original abundance and overall geographic occupancy (Fig. 8). After the end-Triassic mass extinction the occurrences of Spiriferinida cluster in the western Tethys, whereas athyridids are confined to this region and never occurred outside of it (see Appendix B).

3.4. Extinction in the early Toarcian

Out of the 6 spire-bearing genera that cross the Pliensbachian-Toarcian boundary, none survives into the Aalenian stage, not even to the late Toarcian substage, i.e., after the T-OAE. This is significantly different from a predicted value on the basis of survivorship of the other clades (Rhynchonellida and Terebratulida), where 53 genera survived out of the 64 boundary-crossing taxa ($p < 0.0001$, Fig. 9). This range-based binomial test suggests that spire-bearing clades were more vulnerable to extinction during the Toarcian and this is confirmed by repeating the survivorship analysis with SIB counts ($p = 0.0253$). Carrying out this analysis at the substage-level yielded the same results for the Early Toarcian substage.

Similarly to the occurrence patterns described above, this is unlikely to be the result of different preservation potential of spire-bearing and other forms.

3.5. Temporal variation of spire-bearing morphotypes

During the long history of the subphylum Articulata (Rhynchonelliformea), various taxa have been morphologically adapted to different environments and life habits. This is especially true for the Paleozoic, when, besides the typical biconvex shells, a series of other forms were also common, including the flat, concavo-convex (leptaenoid), the laterally expanded (alate), and the strongly inaequivalve, almost conical (cyrtiniform) morphological types. These morphotypes commonly occurred among the spire-bearing orders (Athyridida and Spiriferinida) in the early Mesozoic, whereas the rhynchonellids and terebratulids maintained their conservative, biconvex shell form. The four morphotypes with their supposed environmental adaptation (Ager, 1967; Rudwick, 1970; Vörös, 2002; Baeza-Carratalá et al., 2016) are illustrated in Fig. 10.

In the Triassic, characterized by high diversity, different adaptive morphotypes were abundant in both spire-bearing orders (Fig. 11). After the end-Triassic extinction and diversity bottleneck, the alate (e.g., *Dispiriferina*) and cyrtiniform (e.g., *Cisnerospira*) morphotypes reappeared besides the conservative biconvex shells among the Spiriferinida, and these three morphotypes (represented by *Liospiriferina*, *Dispiriferina* and *Cisnerospira*) persisted up to the Early Toarcian. The order Athyridida was represented exclusively by the leptaenoid morphotype (Koninckinidae) in the Early Jurassic (Fig. 11).

4. Discussion

Statistical analyses of diversity trajectories and taxic rates of spire-bearing vs. non-spire-bearing brachiopods confirm all of our initial working hypotheses. Accepting that the sampling measures do not indicate a difference in overall preservation potential, it is

demonstrated that the spire-bearing groups were indeed significantly more affected by both the end-Triassic and Early Toarcian environmental crises. Statistically, it is highly unlikely that inferior preservation potential is the reason for the selective disappearance from the record. The correlation and selectivity tests indicate that the extinction forcing of spire-bearing forms was different from other brachiopods.

Both spire-bearing orders reached their maximum Triassic diversity in the Carnian, and were only slightly surpassed by terebratulids and rhynchonellids in the Norian. Athyridida and Spiriferinida were severely affected by the end-Triassic crisis, and had a short and limited recovery before their final extinction in the Toarcian, providing an example of the concept “dead clade walking” of Jablonski (2002). The demise of the Athyridida and Spiriferinida was the last major, order-level extinction event within the phylum Brachiopoda.

At the superfamily level, the end-Triassic extinction had equal or stronger effects than the second, final extinction: two spiriferinid superfamilies (Spondylospiroidea and Thecospiroidea) and two major athyridid superfamilies (Retzioidea, Athyridoidea) went extinct at the Triassic-Jurassic boundary.

The Early Jurassic recovery of the two spire-bearing orders was similar in taxic diversity trajectories but very different in development of adaptive morphologies. Spiriferinids retained their morphological diversity, while athyridids were represented solely by the leptaeonoid morphotype in the Early Jurassic. Koninckinidae, the last group of the Athyridida, display an adaptive turnover: they left the various, mostly hard substrates for soft bottom habitats and migrated from the epicontinental Tethyan region to the epicontinental seas of Europe (Vörös, 2002; Baeza-Carratalá et al., 2015). Nevertheless, after the Triassic, this clade lost the adaptive morphological diversity, what may be considered as a herald of forthcoming extinction. However, not only the Athyridida but both spire-bearing clades were eradicated in the early Toarcian and this needs further explanation.

Morphological adaptation to various environments and substrates was manifold and contributed to the evolutionary success of brachiopods in the Paleozoic. However, the competition with bivalves was manifested in pre-emptive exclusion of brachiopods after each mass extinction (e.g., the end-Permian and the end-Triassic) (Walsh, 1996) and increased during the “Mesozoic marine revolution” (Vermeij, 1977). This competition needs to be considered as a factor in the slow and limited recovery of more specialized morphotypes of spire-bearing brachiopods from the end-Triassic event, and their final early Toarcian demise. The bivalves displaced mostly the infaunal and soft-bottom dwellers, i.e., the cyrtiniform, alate and leptaenoid forms, whereas the conservative, epifaunal Rhynchonellida and Terebratulida remained less affected by competition and survived owing to their less specialized morphology and broader environmental tolerance.

However, the biconvex shell and the epifaunal mode of life alone cannot fully explain the selective survival of rhynchonellids and terebratulids, because the same characters were also common to the Early Jurassic spiriferinids, even among their very last representatives in the early Toarcian, e.g., *Liospiriferina* (Comas-Rengifo et al., 2006; García Joral and Goy, 2000) and *Cisnerospira* (Manceñido, 2004; Baeza-Carratalá, 2013; Baeza-Carratalá et al., 2016). The selective extinction of spiriferinids, together with the other spire-bearing group, the athyridids, is best explained by their internal features: the spiral brachidia and the firmly attached lophophore.

Manceñido and Gourvennec (2008) gave an exhaustive review and evaluation of the decades-long research and debates by a great number of authors on the feeding current system of spire-bearing brachiopods, including the results of both early flume experiments and observations on fossil interactions with epi- and endobionts. Their tentative conclusion is that the extinct spiriferids and spiriferinids used their laterally tapering spiralia and the attached spirolophs as a kind of plankton net and took advantage of a passive flow system with a

median inhalant and two lateral exhalant sectors. The point of entry of the median inhalant sector was always situated at the ventral sulcus, whereas the outflows departed along the elongated lateral margins. This circulation pattern is opposite to all known feeding current systems of the present-day articulate brachiopods, where the outflow jet is always medially located.

The above model is convincingly supported by flume experiments by Shiino et al. (2009) and Shiino (2010). They used transparent models of Devonian spiriferides: *Paraspirifer*, a regular, biconvex form, and *Cyrtospirifer*, an alate form, both with ventral sulcus. The flow tests demonstrated that the continuous stream of the surrounding water generated a medial inflow current into the gaping shell models and wide zones of outflows along the lateral sides. Besides proving the previous model (Manceñido and Gourvennec, 2008), Shiino's (2010) experiments brought forward an important new element as they revealed the presence of an invariable spiral flow system inside the spiriferide models. This gyrating flow closely followed the laterally oriented spiral brachidium of the model specimens.

The above results allow the conclusion that the biconvex and ventrally sulcate spiriferids were adapted to continuous, low-velocity currents of the bottom water, where the passive gyrate flows carried the suspended food particles directly to the tentacles of the lophophore. This passive feeding mechanism is in contrast with the ciliary pump system of other articulate brachiopods. Modern rhynchonellids and terebratulids generate inflows through the lateral gape and jet-like anterior outflows, and they maintain this system by the activity of cilia aligned on the lophophore and also by active reorientation (Peck et al., 1997; Rudwick, 1970).

The passive feeding system of the biconvex, ventrally sulcate spire-bearing brachiopods was advantageous in stable, current-swept habitats, but, at the same time, it

323 resulted in environmental dependence. This dependence proved to be detrimental during the
324 unfavourable environmental conditions in times of biotic crises and resulted in partial or total
325 extinctions. The cyrtiniform genus *Cisnerospira*, adapted to semi-infaunal mode of life
326 (Baeza-Carratalá et al., 2016), also relied upon the changes in the hydrodynamic regime
327 because of the passive feeding by its fixed lophophore. Finally, all morphotypes of
328 spiriferinids became extinct at the time of the Toarcian anoxic event.

329 On the other hand, the ciliate active feeding of terebratulids and rhynchonellids
330 worked well in deeper or calmer seawaters, in refugia, e.g., in submarine crevices and
331 cavities, or even in intermittently oxygen-depleted environments. Such physiological
332 advantage of these orders helped them better cope with the environmental changes at the end
333 of the Triassic and in the early Toarcian, when the spire-bearing clades were more severely
334 affected and ultimately became extinct.

335 The end-Triassic and Toarcian bottlenecks in the taxic diversity of brachiopods
336 (Hallam, 1990; 1996) are mirrored by their spatial distribution (Fig. 8 and Appendices). In the
337 Late Triassic all four articulate orders had worldwide distribution. For the Hettangian, the
338 scatter of their occurrences became strongly reduced, with a focus in the western Tethys
339 (including the Gondwanan and Laurasian Seaways), and a similar spatial contraction is seen
340 in the Toarcian.

341 The distribution of the two spire-bearing orders even more clearly demonstrates this
342 spatial bottleneck effect. Their worldwide Late Triassic distribution shrunk to the western part
343 of the Tethys in the Hettangian. The athyridids (represented solely by the leptaenoid
344 koninckinids) remained restricted to the western end of the Tethys with a limited expansion to
345 the Laurasian Seaway, just before their extinction in the Early Toarcian. The spiriferinids
346 appear again in the eastern Panthalassa in the Sinemurian and Pliensbachian, but their last,
347 Toarcian occurrences seem confined again to the western parts of the Tethys (including the

Gondwanan epicontinental seas). On the other hand, the non-spire-bearing orders Rhynchonellida and Terebratulida regain their worldwide distribution in the rest of the Jurassic. This withdrawal of the “dead clades” to the western parts of the Tethys seems to support the idea that this part of the Mesozoic ocean was the most important refuge, a “lost Eden” for brachiopods (Vörös, 1993, 2005), probably due to the recoiling surface current system in the westerly closed ocean basin configuration of the Tethys.

5. Conclusions

Our analyses of Triassic and Jurassic diversity trajectories, taxonomic rates, and geographic distribution patterns of the two extinct spire-bearing orders (Spiriferinida and Athyridida) and the two other, extant orders (Rhynchonellida and Terebratulida) led to the following conclusions.

The Triassic diversity trajectories of the four brachiopod orders are largely similar, their shared recovery after the end-Permian mass extinction led to a Late Triassic diversity peak in the Carnian-Norian. There is no systematic difference in the origination rates of spire-bearing and the other two orders, but the pattern of their extinction diverge significantly in the Rhaetian, attesting that the end-Triassic extinction was selective and more severely affected the spire-bearing orders. These groups were also more vulnerable during the Toarcian event which led to their final demise.

Not only did the end-Triassic extinction preferentially remove spire-bearing brachiopods, these groups also failed to recover from this crisis. Their failed recovery is manifest in the smaller number of occurrences, depauperate raw and standardized diversity, their lower proportion relative to rhynchonellids and terebratulids, and the areal contraction of their previously worldwide geographic distribution, confined to the western parts of the

Tethys in the Early Jurassic. Statistical analyses confirm that these patterns are genuine and cannot be ascribed to differences in preservation and sampling.

The spire-bearing athyridids and spiriferinids show more morphological variety in shell form, manifest in leptaenoid, alate and cyrtiniform shapes, compared to the exclusively conservative, biconvex-shelled rhynchonellids and terebratulids. The specialized forms were adapted to a narrower range of environmental parameters, making them vulnerable to stressors during the end-Triassic and Toarcian crises. In addition, there is a key physiological difference behind the selective extinction at times of complex effects of heat stress, anoxia, and altered ocean chemistry and circulation patterns. The passive feeding mechanism of spire-bearing brachiopods with fixed lophophores is less effective under adverse conditions than the ciliate active feeding of the more adaptable rhynchonellids and terebratulids.

Extinction forcing in spire-bearing brachiopods was a complex interplay of (i) physiological disadvantages of fixed lophophore anatomy and passive feeding at times of environmental crises, (ii) increased competition from bivalves in soft-substrate level-bottom habitats as the Mesozoic marine revolution unfolded, and (iii) their failed recovery after the first hit at the end-Triassic extinction, leading to their final demise at the Toarcian event. The Early Jurassic history of the spire-bearing orders provides an example of the “dead clade walking” phenomenon. The disappearance of the spiriferinids and athyridids in the Early Toarcian represents the last major, order-level extinction in the phylum Brachiopoda, one of the dominant elements of the Paleozoic evolutionary fauna.

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References

- Ager, D.V., 1967. Brachiopod palaeoecology. *Earth-Science Reviews* 3, 157-179.
- Ager, D.V., 1987. Why the rhynchonellid brachiopods survived and the spiriferids did not: a suggestion. *Palaeontology* 30, 853-857.
- Alroy, J., 2009. Speciation and extinction in the fossil record of North American Mammals. In: Butlin, R.K., Bridle, J.R., Schluter, D. (Eds.), *Speciation and Patterns of Diversity*. Cambridge University Press, New York, pp. 301-323.
- Alroy, J., 2010. The Shifting Balance of Diversity among Major Marine Animal Groups. *Science* 329, 1191-1194. doi: 10.1126/science.1189910
- Alroy, J., 2014. Accurate and precise estimates of origination and extinction rates. *Paleobiology* 40, 374-397. doi: 10.1666/13036
- Alvarez, F., Rong Jia-yu, 2002. Athyridida. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 4, Rhynchonelliformea (part)*. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 1475-1614.
- Baeza-Carratalá, J. F., 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 381-382, 76-91. doi: 10.1016/j.palaeo.2013.04.017
- Baeza-Carratala, J.F., Garcia Joral, F., Giannetti, A., Tent-Manclus, J.E., 2015. Evolution of the last koninckinids (Athyridida, Koninckinidae), a precursor signal of the Early Toarcian mass extinction event in the Western Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* 429, 41-56. doi: 10.1016/j.palaeo.2015.04.004
- Baeza-Carratalá, J.F., Manceñido, M.O., García Joral, F., 2016. *Cisnerospira* (Brachiopoda,

- Spiriferinida), an atypical Early Jurassic spire-bearer from the Subbetic Zone (SE Spain) and its significance. *Journal of Paleontology* (in press).
- Bittner, A., 1890. Brachiopoden der alpinen Trias. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt* 14, 1-325.
- Bittner, A., 1900. Brachiopoden aus der Trias des Bakonyerwaldes. In: *Resultate der wissenschaftlichen Erforschung des Balatonsees*, 1, Anhang: Palaeontologie der Umgebung des Balatonsees 2(1), 1-59.
- Bond, D.P.G., Wignall, P.B., 2014. Large igneous provinces and mass extinctions: An update. In: Keller, G., Kerr, A.C. (Eds.), *Volcanism, Impacts, and Mass Extinctions: Causes and Effects*. Geological Society of America Special Papers 505, pp. 29-55. doi: 10.1130/2014.2505(02)
- Burgess, S.D., Bowring, S.A., Fleming, T.H., Elliot, D.H., 2015. High-precision geochronology links the Ferrar large igneous province with early-Jurassic ocean anoxia and biotic crisis. *Earth and Planetary Science Letters* 415, 90-99. doi: 10.1016/j.epsl.2015.01.037
- Carter, J.L., Johnson, J.G., 2006. Spiriferinida. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 5, Rhynchonelliformea (part)*. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 1877-1890.
- Comas-Rengifo, M. J., Garcia-Joral, F., Goy, A., 2006. Spiriferinida (Brachiopoda) del Jurásico Inferior del NE y N de España: distribución y extinción durante el evento anóxico oceánico del Toarciense inferior. *Boletín de la Real Sociedad Española de Historia Natural* 101(1-4), 147-157.
- Courtillot, V., Renne, P.R., 2003. On the ages of flood basalt events. *Comptes Rendus Geoscience* 335, 113-140. doi: 10.1016/S1631-0713(03)00006-3

- Curry, G.B., Brunton, C.H.C., 2007. Stratigraphic distribution of brachiopods, In: Selden, P.A. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised)*, Volume 6, Supplement. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 2901-3081.
- Foote, M., 2000. Origination and Extinction Components of Taxonomic Diversity: General Problems. *Paleobiology* 26, 74-102. doi: 10.1666/0094-8373(2000)26[74:OAECOT]2.0.CO;2
- García Joral, F., Goy, A., 2000. Stratigraphic distribution of Toarcian brachiopods from the Iberian Range (Spain) and its relation to depositional sequences. *GeoResearch Forum* 6, 381-386.
- Gould, S.J., Calloway, C.B., 1980. Clams and brachiopods – ships that pass in the night. *Paleobiology* 6, 383-396.
- Gourvennec, R., Carter, J.L., 2007. Spiriferida and Spiriferinida. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised)*, Volume 6, Supplement. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 2772-2796.
- Gradstein, F.M., Ogg, J.G., Schmitz, M., 2012. *The Geologic Time Scale 2012*, 2-Volume Set. Elsevier Science & Technology Books, 1176 p.
- Greene, S.E., Martindale, R.C., Ritterbush, K.A., Bottjer, D.J., Corsetti, F.A., Berelson, W.M., 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. doi: 10.1016/j.earscirev.2012.03.009
- Hallam, A., 1990. The end-Triassic mass extinction event. *Geological Society of America Special Paper* 247, 577-583.
- Hallam, A., 1996. Recovery of the marine fauna in Europe after the end-Triassic and early

- Toarcian mass extinctions. In: Hart, M.B. (Ed.), Biotic recovery from mass extinction events. Geological Society Special Publication No. 102, pp. 231-236.
- Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R., Kump, L., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer, D.L., Barker, S., Marchitto, T.M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L., Williams, B., 2012. The geological record of ocean acidification. *Science* 335, 1058-1063. doi: 10.1126/science.1208277
- Jablonski, D., 2002. Survival without recovery after mass extinctions. *Proceedings of the National Academy of Science USA* 99, 8139-8144.
- Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. *Geochemistry Geophysics Geosystems* 11(3), Q03004. doi: 10.1029/2009GC002788
- Kiessling, W., Kocsis, T.Á., 2015. Biodiversity dynamics and environmental occupancy of fossil azooxanthellate and zooxanthellate scleractinian corals. *Paleobiology* 41(3), 402-414. doi: 10.1017/pab.2015.6
- Lee, D.E., MacKinnon, D.I., Smirnova, T.N., Baker, P.G., Jin Yu-gan, Sun Dong-li, 2006. Terebratulida. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 5, Rhynchonelliformea (part)*. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 1965-2251.
- Manceñido, M.O., 2004. Las “espiriferinas” de Jurásico Inferior: una mirada retrospectiva a los estudios de Daniel Jiménez de Cisneros. *Geo-Temas* 7, 269-272.
- Manceñido, M.O., Gourvenec, R., 2008. A reappraisal of feeding current systems inferred for spire-bearing brachiopods. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 98, 345-356. doi: 10.1017/S1755691007078462
- McElwain, J.C., Beerling, D.J., Woodward, F.I., 1999. Fossil plants and global warming at

the Triassic-Jurassic Boundary. *Science* 285, 1386-1390. doi:
10.1126/science.285.5432.1386

McKinney, M.L., Oyen, C.W., 1989. Causation and nonrandomness in biological and geological time series; temperature as a proximal control of extinction and diversity. *PALAIOS* 4, 3-15. doi: 10.2307/3514729

Pálffy, J., Kocsis, T.Á., 2014. Volcanism of the Central Atlantic Magmatic Province as the trigger of environmental and biotic changes around the Triassic-Jurassic boundary. In: Keller G., Kerr, A.C. (Eds.), *Volcanism, Impacts and Mass Extinctions: Causes and Effects*. Geological Society of America Special Paper 505, pp. 245-261. doi: 10.1130/2014.2505(12)

Peck, L.S., Rhodes, M.C., Curry, G.B., Ansell, A.D., 1997. Physiology. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 1, Introduction*. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 213-242.

R Development Core Team. 2016. 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.

Rudwick, M.J.S., 1970. *Living and fossil brachiopods*. Hutchinson University Library, London, 199 p.

Sandy, M.R., 1995. Early Mesozoic (Late Triassic–Early Jurassic) Tethyan brachiopod biofacies: possible evolutionary intra-phylum niche replacement within the Brachiopoda. *Paleobiology* 21, 479-495.

Savage, N.M., Manceñido, M.O., Owen, E.F., Carlson, S.J., Grant, R.E., Dagys, A.S., Sun Dong-Li, 2002. Rhynchonellida. In: Kaesler, R.L. (Ed.), *Treatise on Invertebrate*

- Palaeontology. Part H, Brachiopoda (Revised), Volume 4, Rhynchonelliformea (part). Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. 1027-1376.
- Shiino, Y., 2010. Passive feeding in spiriferide brachiopods: an experimental approach using models of Devonian *Paraspirifer* and *Cyrtospirifer*. *Lethaia* 43, 223-231. doi: 10.1111/j.1502-3931.2009.00185.x
- Shiino, Y., Kuwazuru, O., Yoshikawa, N., 2009. Computational fluid dynamics simulations on a Devonian spiriferid *Paraspirifer bownockeri* (Brachiopoda): Generating mechanism of passive feeding flows. *Journal of Theoretical Biology* 259, 132-141. doi: 10.1016/j.jtbi.2009.02.018
- Suan, G., Mattioli, E., Pittet, B., Lecuyer, C., Sucheras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. *Earth and Planetary Science Letters* 290, 448-458. doi: 10.1016/j.epsl.2009.12.047
- Thayer, Ch.W., 1985. Brachiopods versus mussels: Competition, predation and palatability. *Science* 228, 1527-1528.
- Vermeij, G.J., 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology* 3, 245-258.
- Vogel, K., 1975. Das filter-feeding-System bei Spiriferida. *Lethaia* 8, 231-240.
- Vörös A., 1993. Jurassic microplate movements and brachiopod migrations in the western part of the Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology* 100, 125-145. doi: 10.1016/0031-0182(93)90037-J
- Vörös, A., 2002. Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda). *Lethaia* 35, 345-357. doi: 10.1111/j.1502-3931.2002.tb00093.x

Vörös, A., 2005. The smooth brachiopods of the Mediterranean Jurassic: Refugees or invaders? *Palaeogeography, Palaeoclimatology, Palaeoecology* 223, 222-242. doi: 10.1016/j.palaeo.2005.04.006

Walsh, J.A., 1996. No second chances? New perspectives on biotic interactions in post-Paleozoic brachiopod history. In: Copper, P., Jin, J. (Eds.), *Brachiopods*. Balkeema, Rotterdam, pp. 281-288.

Figure captions

Fig. 1. Comparison of lophophore anatomy of different articulate clades. A: fixed spirolophore of spire-bearing groups, here exemplified by Athyridida; B: free spirolophore of Rhynchonellida (heavy black lines: crura); C: free plectolophore of Terebratulida (heavy black lines: loop). After Rudwick (1970) and Peck et al. (1997).

Fig. 2. Diversity curves of brachiopod genera in the Triassic-Jurassic interval. Epochs are shaded. Raw diversity was calculated with the range-through method, subsampled richness estimates indicate sampled-in-bin diversity corrected with the three-timer sampling completeness as in Alroy (2010). The sampling standardization method was SQS with the shareholder quorum of 0.6.

Fig. 3. Raw range-through diversity curves of spire-bearing orders Athyridida and Spiriferinida in the Triassic-Jurassic interval from the Paleodb and the Treatise of Invertebrate Paleontology. Epochs are shaded. The two curves closely follow each other, although the diversity is commonly underestimated from the Paleodb compared with the Treatise data.

Fig. 4. Raw range-through diversity curves of brachiopod genera based on PaleoDB data in the orders Athyridida, Spiriferinida, Terebratulida and Rhynchonellida. Epochs are shaded. The spire-bearing orders (darker lines) have highly similar diversity trajectories, and both vanished by the end of the Early Jurassic.

Fig. 5. Raw and subsampled diversity curves and per-capita extinction and origination rates of spire-bearing and other brachiopod genera in the Triassic-Jurassic interval. Epochs are shaded. Triangles indicate intervals where the AICc model comparison indicates a two-rate model and selective extinctions. The target quorum for the shareholder quorum subsampling was 0.6. The estimates for richness were calculated using the range-through method for raw data and the corrected SIB method for subsampled data.

Fig. 6. Raw substage-level diversity curves and taxonomic rates of spire-bearing and other brachiopod genera; methods are the same as in Fig. 5 A, C and E. Epochs are shaded.

Fig. 7. Relative abundance and geographic occupancy shift of spire-bearing brachiopods at the Triassic-Jurassic boundary. A. The proportion of spire-bearing brachiopods in each alpha-level sampling unit (collection). B. The number of occupied 30×30° paleogeographic cells in a stage within the Triassic and Early Jurassic intervals. The single circle represents a value that is indicated to be an outlier (outside 1.5 times the interquartile range above the upper quartile).

Fig. 8. Occurrence patterns of brachiopods in the A: Norian and B: Pliensbachian age based on the data deposited in the PaleoDB. The geographic range of spire-bearing brachiopods

decreased after the Triassic-Jurassic boundary, compared to other forms. Polygons indicate convex hulls of occurrence in the projection. The asterisk indicates New Zealand occurrences of spire-bearing forms that are of uncertain stratigraphic positions.

Fig. 9. Selectivity of the Toarcian extinction event, based on the stage-level range data. Out of the 6 spire-bearing genera which cross the Pliensbachian-Toarcian boundary, none survives into the Aalenian. This proportion is significantly lower than that predicted by the survivorship of the other morphotypes, where 39 survived out of the 53 boundary-crossing genera. The plot was drawn using Monte Carlo simulations. The dashed line represents the proportion of trials required to reject the null hypothesis of non-selective extinctions at an alpha value of 0.05.

Fig. 10. Basic morphological types among the spire-bearing clades and their inferred environmental and substrate preferences. After Ager (1967), Rudwick (1970), Vörös (2002) and Baeza-Carratalá et al. (2016).

Fig. 11. Proportion of morphological types of spire-bearing genera during the Triassic-Jurassic interval. A. Spiriferinida, B. Athyridida. (Online version in color.)

615 **Highlights**

616 Four surviving brachiopod orders share Triassic recovery and diversity history

617 Toarcian demise of spire-bearing brachiopods follow selective end-Triassic extinction

618 Failed Early Jurassic recovery of spire-bearing orders made them “dead clade walking”

619 Specialized adaptation and restriction of geographic range also factors in extinction

620 Passive feeding by fixed lophophore prevented coping with environmental stress

621

Highlights

Four surviving brachiopod orders share Triassic recovery and diversity history

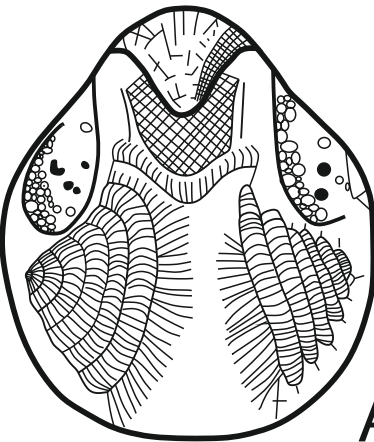
Toarcian demise of spire-bearing brachiopods follow selective end-Triassic extinction

Failed Early Jurassic recovery of spire-bearing orders made them “dead clade walking”

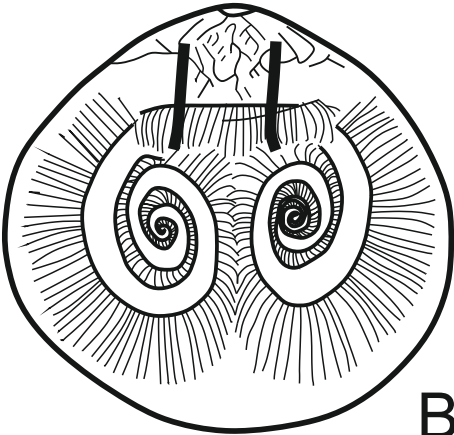
Specialized adaptation and restriction of geographic range also factors in extinction

Passive feeding by fixed lophophore prevented coping with environmental stress

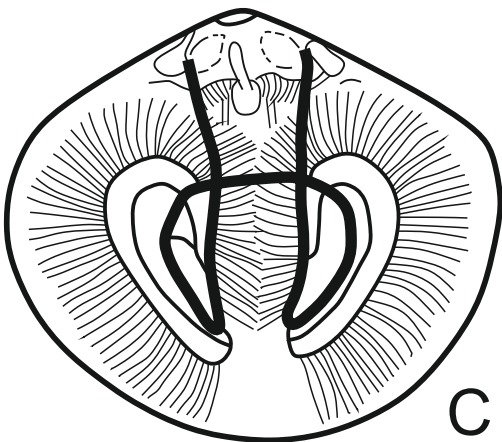
Figure



A



B



C

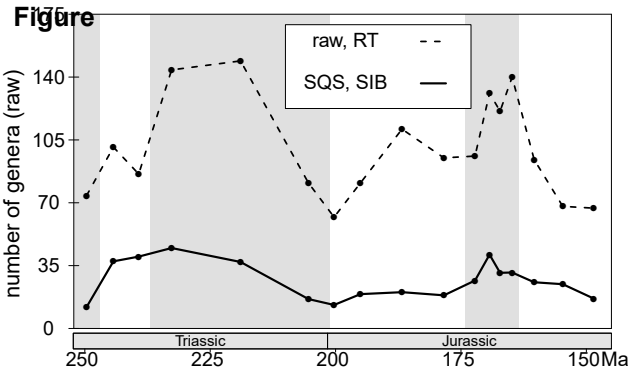


Fig 2. one column

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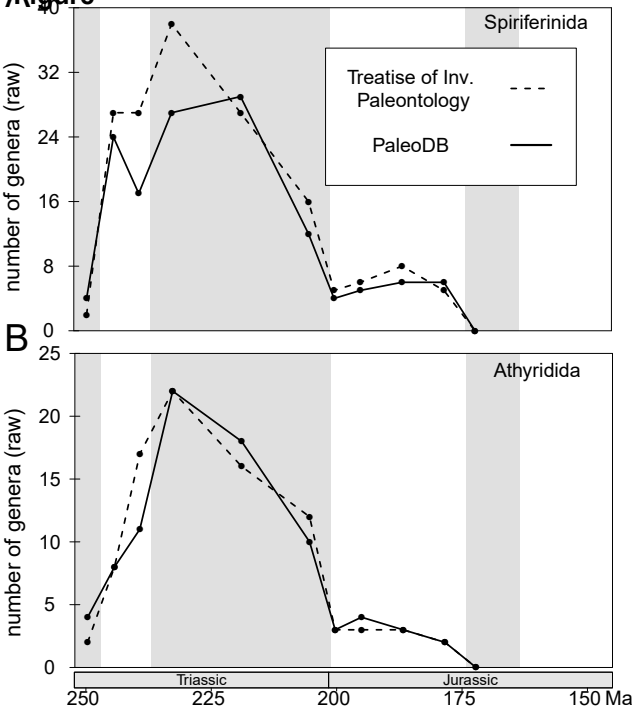


Fig 3. one column

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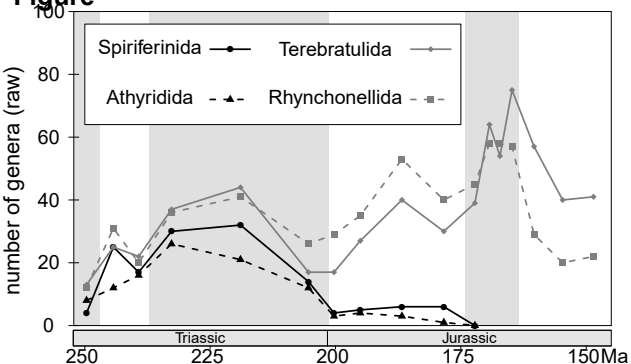


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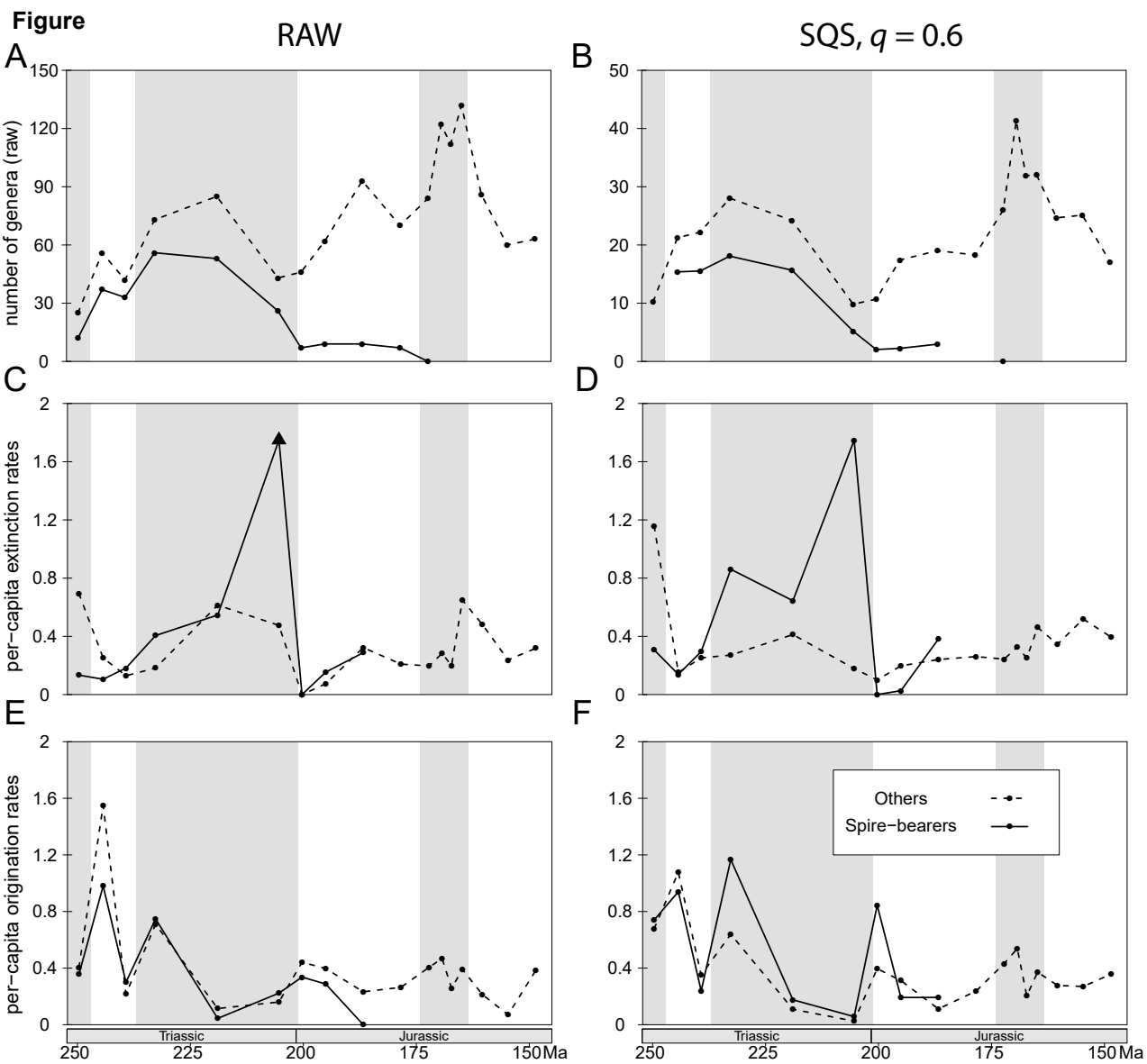


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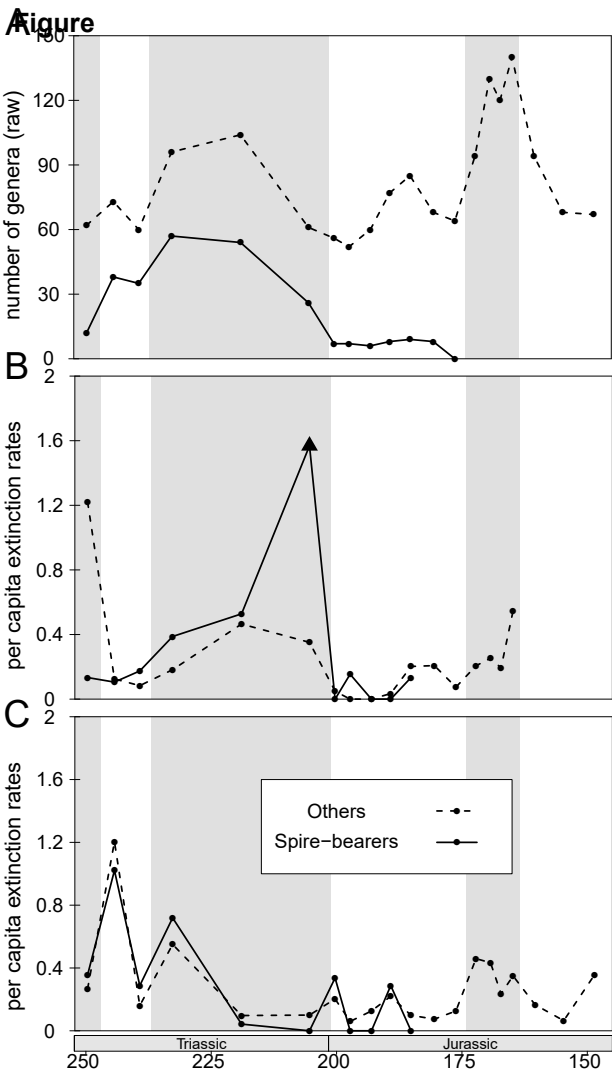


Fig 6. one column

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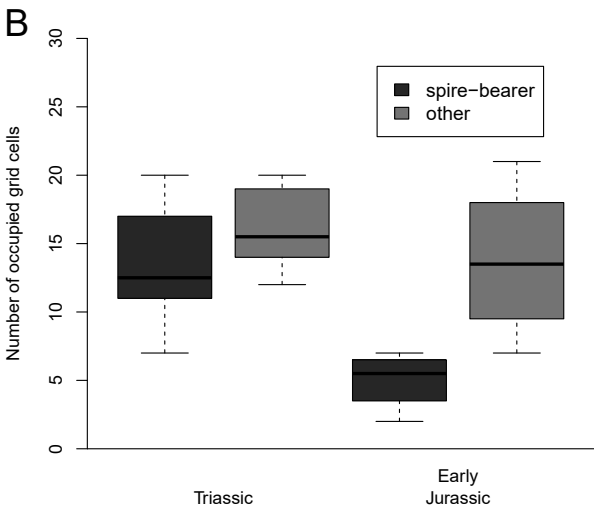
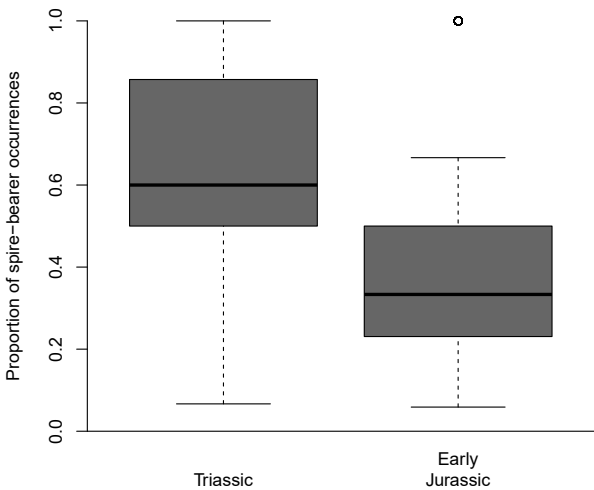
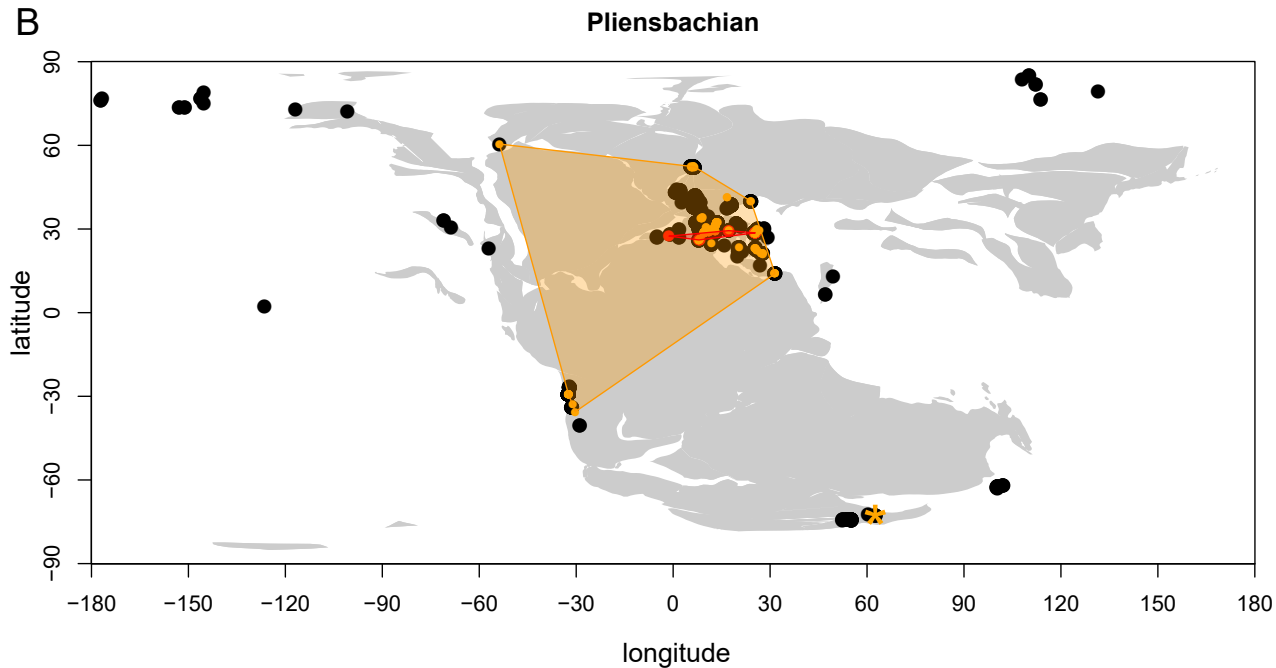
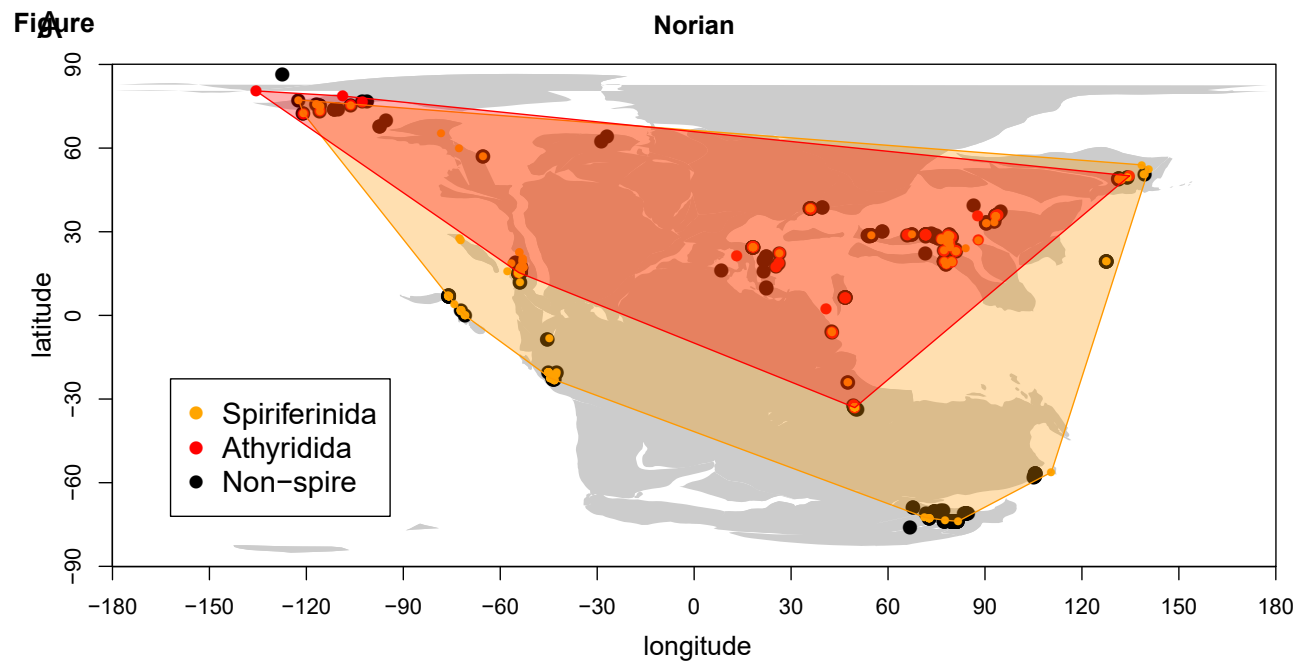


Fig 7. one Column



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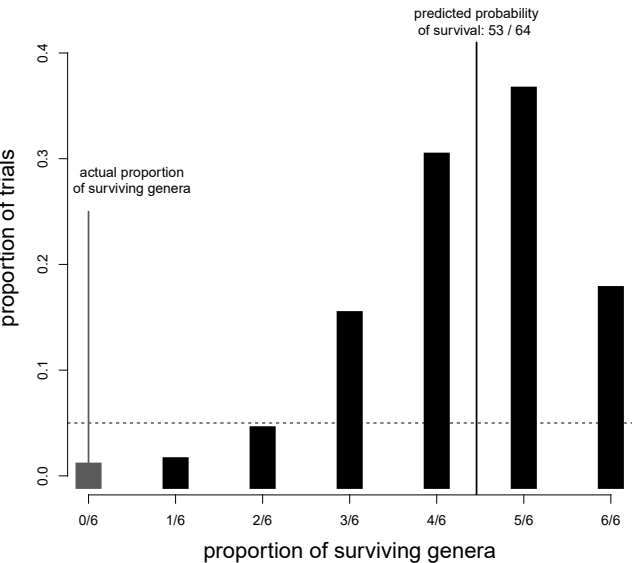


Fig 9. one column

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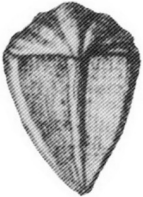
			
<i>biconvex</i>	<i>leptaenoid</i>	<i>alate</i>	<i>cyrtiniform</i>
conservative	adapted	adapted	adapted
Attached by pedicle, hard bottom	Free lying, soft bottom	Free lying, soft bottom	Infaunal, or free-lying, hard, or soft bottom

Fig 10. one column

Figure

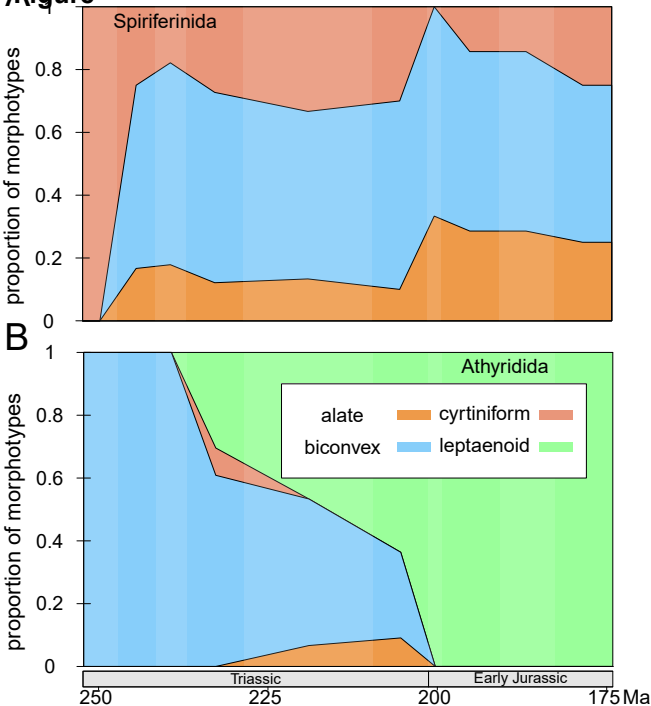


Fig 11. one column

Table 1. Time scale and occurrence data of brachiopods from the study interval. Genus level occurrence counts are reported.

<i>interval</i>	<i>bottom (Ma)</i>	<i>top (Ma)</i>	<i>collections</i>	<i>spire-bearer occurrences</i>	<i>other brachiopod occurrences</i>
E-Triassic	252.2	247.1	407	32	539
Anisian	247.1	241.5	477	580	696
Ladinian	241.5	237	346	121	424
Carnian	237	228.4	337	304	460
Norian	228.4	209.5	390	272	395
Rhaetian	209.5	201.3	441	194	600
Hettangian	201.3	199.3	126	16	231
Sinemurian	199.3	190.8	314	96	591
Pliensbachian	190.8	182.7	1128	246	2421
Toarcian	182.7	174.1	1091	161	1796
Aalenian	174.1	170.3	293	0	504
Bajocian	170.3	168.3	435	0	960
Bathonian	168.3	166.1	449	0	1051
Callovian	166.1	163.5	528	0	1199
Oxfordian	163.5	157.3	290	0	610
Kimmeridgian	157.3	152.1	140	0	204
Tithonian	152.1	145	207	0	353

