Accepted Manuscript

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PII: S0031-0182(18)30464-4

DOI: doi:[10.1016/j.palaeo.2018.06.045](https://doi.org/10.1016/j.palaeo.2018.06.045)

Reference: PALAEO 8851

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 24 May 2018

Revised date: 29 June 2018

Accepted date: 29 June 2018

Please cite this article as: Fernando García Joral, José Francisco Baeza-Carratalá, Antonio Goy , Changes in brachiopod body size prior to the early Toarcian (Jurassic) mass extinction. *Palaeo* (2018), doi:[10.1016/j.palaeo.2018.06.045](https://doi.org/10.1016/j.palaeo.2018.06.045)

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Changes in brachiopod body size prior to the Early Toarcian (Jurassic) Mass Extinction

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Abstract

Herein we analyze the shell length as estimation of the body size of several brachiopod assemblages recorded into the extinction interval prior to the Early Toarcian Mass Extinction. They were collected from representative localities around the Iberian Massif (Spain and Portugal) presenting different paleoenvironmental conditions. The analysis performed has revealed two different trends of spatial and temporal changes in body size. (1) Mean size decreases in the assemblages following an anticlockwise pattern from Iberian to Lusitanian basins, in relation to the progressive environmental stress caused by shifts on terrigenous input and in depth. This diminution results from changes in the relative abundance of bigger or smaller species in each area rather than from miniaturization of the taxa. (2) Some new evolved or more resilient species show increasing sizes over time along the extinction interval. This increase affects both big spiriferinides in the Iberian Basin and small rhynchonellides and koninckinides in the Lusitanian Basin, and runs in parallel to the drop in diversity and the progressive warming of the sea water in this interval in all the localities. This increase in body size has been related to the changes in diversity that could have favored the access to resources for resilient or new evolved species. The observed patterns are comparable with those detected in the end-Permian Crisis, and might indicate a generalizable response to similar biotic crises.

Keywords: Biotic crises; Anoxic event; Spain; Portugal;

1. Introduction

In the Early Toarcian, an important Mass Extinction Event took place involving most of the marine benthic and nekto-planktic biota (Little and Benton, 1995; Gómez and Goy, 2011; Danise et al., 2013; Caruthers et al., 2014). Approximately 5% of the families were globally lost, suggesting a relatively minor crisis, but for the brachiopods this event represented one of the most severe extinction in their post-Paleozoic history. Two orders, Spiriferinida and Athyridida, became extinct and the Order Rhynchonellida underwent a notable renewal. Only the Order Terebratulida appears to remain quite unaffected (Vörös, 2002; García Joral et al., 2011; Baeza-Carratalá et al., 2015; Vörös et al., 2016). This loss of diversity can be globally detected in the Late Spinatum Chronozone of the Pliensbachian and in the Tenuicostatum Chronozone of the Toarcian, within the so-called "Extinction Interval", culminating in the early Serpentinum Chronozone with the "Extinction boundary" (García Joral et al., 2011; Baeza-Carratalá et al., 2017).

Estimation of changes in body size has been employed in numerous studies to investigate the response of brachiopods and other organisms to environmental stress situations associated with extinction events (Twitchett, 2006, 2007; He et al., 2007, 2010, 2015; Morten and Twitchett, 2009; Metcalfe et al., 2010; Posenato et al., 2014; Shi et al., 2016; Zhang et al., 2016, Wu et al., 2018). Specifically, miniaturization is the phenomenon frequently invoked in these studies.

On the Iberian Peninsula, numerous stratigraphical sections reveal a continuous record of brachiopods (chronostratigraphically well calibrated with ammonoids) close to the extinction boundary, enabling detailed study of diversity dynamics and faunal turnovers in the assemblages prior to and after the extinction event (García Joral and Goy, 2000, 2009; García Joral et al., 2011; Comas-Rengifo et al., 2013, 2015; Baeza-Carratalá et al., 2016, 2017). The present paper attempts to use this continuous and detailed record to put forward the changes in body size previous to the extinction in the brachiopod assemblages from the epicontinental basins surrounding the Iberian

Massif by the East, the North and the West, in which paleoenvironmental conditions range from well oxygenated and shallower habitats to oxygen depleted and deeper ones, thus testing the role played by the paleobathymetry, terrigenous input or the temperature as triggering factors causing the body size variation. The presence of several common taxa in such as different basins provides an exceptional scenario to better understand the adaptive responses to these biotic crises.

2. Materials and methods

The shell length of 903 specimens corresponding to four orders of rhynchonelliform brachiopods was measured. They derived from 7 localities considered representative of the Iberian, Basque-Cantabrian, Asturian, and Lusitanian basins (Fig. 1). The lithostratigraphy, chronostratigraphy and the distribution of the brachiopod species in each stratigraphical section are shown in García Joral et al. (2011) and Comas-Rengifo et al. (2013, 2015). The Asturian and Basque-Cantabrian basins, which are close to each other and present very similar facial development and faunal record, have been grouped together as “Cantabrian basins” for the analysis. All specimens were collected bed by bed together with ammonites and do not show evidences of taphonomic reelaboration. The biostratigraphical scheme proposed in each basin has been respected, but the presence in all sections of many common species of ammonites allows its correlation in most cases to the finest level of biohorizon. Even so, the subzone has been the preferred interval for the comparison, considering it the most appropriate for the correlation of the brachiopod assemblages, whose dispersal abilities do not allows for time correlation as finer as with ammonites. Statistical analyses have been performed and applied when enough data were available in each bed or subzone. Nevertheless, we have also used raw data to support some observations that have been considered informative although without a strict statistical value.

In previous research with similar objectives, different measures of body size have been proposed, depending on the group analyzed. In the present paper, shell length is used as appraisal of brachiopod body size, just as in Paknevilch (2009) and Peck and Harper (2010), as it is assumed to

be directly related to other variables, such as occupied volume or mass of living tissue (Peck et al., 1997). The values obtained can be found in the supplementary material to this paper. Data are treated using the PAST software package (Hammer et al., 2001).

3. Paleoenvironmental setting

The brachiopod assemblages analyzed were deposited in different environmental conditions depending on the basin. In the eastern Iberian Range the extinction interval is represented by rhythmic light-coloured marly-limestone sediments corresponding to the Turmiel Formation (Goy et al., 1976) which were deposited in a shallow and well oxygenated platform (Gómez and Goy, 2004, 2005). No organic-rich facies were found in this basin and only very scarce values above 1 wt.% TOC were obtained (Gómez and Goy, 2011).

In the North, the studied interval corresponds to the Castillo Pedroso Formation (Quesada et al., 2005). Sediments are darker; indicating poorly oxygenated sea bottoms and including an episode of black-shales in the upper part of the Semicelatum Subzone; in the Basque–Cantabrian Basin, TOC reach up to 1.5 wt% below and above the Tenuicostatum–Serpentinum zonal boundary, and 3.2 wt% TOC were obtained in this same interval in Asturias (García Joral et al., 2011), where the studied interval corresponds to the Rodiles Formation (Valenzuela et al., 1986).

In the Lusitanian Basin, the sediments were deposited in a carbonate ramp environment, deeper to the west, corresponding to the Lemede and Sao Gíao formations in the East (Fonte Coberta Section) and to the Lemede and Cabo Carvoeiro formations in Peniche (Duarte, 1998, 2007). Although in the Polymorphum Zone (Mediterranean equivalent to the Tenuicostatum Zone) TOC values are only around 1 wt.% (Hesselbo et al., 2007), sedimentation is highly argillaceous in the central and the external part of the ramp, where some turbiditic episodes can even be detected (Duarte, 1998, 2007).

Thus, an anticlockwise environmental gradient involving depth, oxygen content, and turbidity is perceived: the most favorable conditions for the establishment of steady brachiopod

communities were found in the East, in the Iberian Basin, and the least favorable ones in the external Lusitanian Basin.

4. Results

The species used in the analysis correspond to the Assemblage 1 described by García Joral and Goy (2000) for the Iberian Basin, which mainly consists of lower Toarcian species but including taxa, particularly at a generic level, which range from the Pliensbachian (*Liospiriferina*, *Gibbirhynchia*, *Quadratrhyndia*, *Lobothyris*, *Zeilleria*, *Aulacothyris*), thus covering the entire Extinction Interval. At more detailed level, two subsets can be differentiated in this assemblage (García Joral et al., 2011): the first one consists of species originated in the Late Pliensbachian which present a wide geographic distribution (*Liospiriferina alpina*, *Lobothyris edwardsi*, *Aulacothyris resupinata*) while the second one includes species taxonomically close to the previous ones, but evidencing a more endemic nature (*Liospiriferina falloti*, *Calyptraria vulgata*, *Dispiriferina? oxyptera*, *Quadratrhyndia attenuata*, *Gibbirhynchia cantabrica*, *Lobothyris arcta*, *Zeilleria culeiformis*, *Aulacothyris iberica*). Some of these last species are almost exclusively distributed in the Semicelatum Subzone. The same assemblage has been recorded in the Cantabrian basins, although showing much lesser diversity (García Joral and Goy, 2009; García Joral et al., 2011). In the Lusitanian Basin, Comas-Rengifo et al. (2013, 2015) identified also two assemblages of equivalent age (assemblages 2 and 3 in Comas-Rengifo et al., 2015) sharing some common species with the Iberian and Cantabrian basins, together with several endemic or more restricted taxa (*Liospiriferina subquadrata*, *Cirpa fallax*, *Nannirhynchia pygmaea*, *Pseudokingena deslongchampsii*, and *Koninckella liasina*), most of them constituting the so-called “*Koninckella* Fauna” (Alméras et al., 1989, Vörös, 2002).

The specimens belonging to all these assemblages, recorded from the Hawskerense-Elisa to the Elegantulum subzones have been measured for the analysis. The Order Rhynchonellida is the best represented in the samples, with several species in most localities. Spiriferinida and

Terebratulida orders are scarcer, especially in the Cantabrian basins while Athyridida, represented by the Family Koninckinidae, was only found in the Lusitanian Basin.

Estimating size at order level, overall smaller sizes are observed in the Lusitanian Basin compared to those from the Iberian Basin (Fig. 2). In the Cantabrian basins only rhynchonellides could be considered, due to the scarcity of the other groups, and these seem to be also smaller than in the Iberian Basin, but larger than in the Lusitanian Basin. An ANOVA analysis has been computed to test whether these apparent differences are statistically significant (Table 1). The analysis shows that the differences in size between basins are significant in rhynchonellides and probably in spiriferinides, though the scarce number of specimens of this last order in the Paltum/Mirabile Subzone implies too different variances to perform comparisons. Nevertheless, the Welch F test (applicable in the case of unequal variances) gives a very low value of p , indicating that the difference in size must be significant. As stated previously, the terebratulides are the less affected group in this extinction event, and the analysis do not allow considering significant size changes.

When species level is considered (Fig. 2), in all cases size reduction is the result of changes in the relative abundance in each basin of bigger or smaller species (Fig. 3A). Thus, brachiopods from the basins on the northern and western sides of the Iberian Massif are not smaller specimens of the same species found in the eastern side, but rather standard specimens of small-sized species. In the case of the rhynchonellides, in the Iberian Basin the large *Quadratrhynchia attenuata* and the small *Gibbirhynchia cantabrica* show similar abundance, whereas the latter species is much more abundant in the northern Cantabrian Basins. In the western Lusitanian Basin, the even smaller *Nannirhynchia pygmaea* predominates.

The same is applicable for the spiriferinides. In the Iberian Basin, the large-sized species *Liospiriferina falloti* predominates, whereas in Portugal the prevailing spiriferinides are the minute *Liospiriferina subquadrata* and *Liospiriferina* confer *falloti*, the morphological counterpart of the large *L. falloti* from the East, but only half its size.

The Order Terebratulida, less affected by the environmental changes, shows also a species-related size decrease from the Iberian to the Lusitanian basins. While the record of the large-sized *Lobothyris arcta* / *edwardsi* group is conspicuous in the Iberian Range, in Portugal this group is very scarce, and the minute and strange *Pseudokingena deslongchampsii* appears.

The fourth order, the athyridides, is only recorded in the Lusitanian Basin in the extinction interval. Nevertheless, when studying the evolution of the entire group (the Family Koninckinidae), a similar pattern to that of the other orders can be inferred. Mediterranean koninckinids in the Pliensbachian are relatively larger, and exhibit an adaptive turnover close to the Spinatum–Tenuicostatum chronozone boundary (Baeza-Carratalá et al., 2015). This turnover entailed the evolution of a new Euro-Boreal species (*Koninckella liasina*), smaller than their Pliensbachian Mediterranean relatives and seemingly adapted to less oxygenated and more argillaceous environments.

Thus, a decreasing gradient of brachiopod body size can be deduced, from favorable to less favorable environmental conditions, expressed as differences in the taxonomic composition of the assemblages which contains larger species on the platforms east of the Iberian Massif and smaller species north and west of it.

On the other hand, another size variation trend can be interpreted from the data represented in the Figure 2. An increase in size over time is detected within the extinction interval. This is deduced more clearly in the jitter plot, in which a number of species seems to present bigger sizes in the Semicelatum Subzone than in the Paltum/Mirabile one. This trend is better enlightened if the maximum size recorded per subzone and species are represented. Figure 3B shows the data of maximum size per subzone when more than 10 individuals have been recorded in at least two consecutive subzones. There are only five species that fulfill these requirements, corresponding to the most abundant taxa in each basin, showing all of them, except for *Q. attenuata*, a linear size increasing with time. The dynamics of the body-size of the prevailing species in each basin in the

Paltum/Mirabile and in the Semicelatum subzones is also analyzed (Fig. 4), showing all of them a statistically coherent increasing in size (table 2) as well.

Increasing in size can be also inferred from the maximum size measured in each bed of the different sections (Fig. 5). In Ariño, which can be considered as representative locality of the Iberian Range record, *L. falloti* is the dominant species in the Semicelatum Subzone, and its maximum size is recorded in the higher levels. In this same locality one can observe that the also abundant terebratulide *L. arcta* does not show this tendency to increase in size. In the Cantabrian Basins, represented by the San Andrés section, only *G. cantabrica* can be compared, showing the same tendency to increase in size as previously inferred at the subzone level. In the Lusitanian Basin, two small species (*N. pygmaea* and *K. liasina*) dominate the assemblages of the Semicelatum Subzone in the Peniche and Fonte Coberta sections, showing the same trend towards an increase in size over time. The largest specimens of these minute species are always recorded in the upper part of the Semicelatum Subzone.

5. Discussion

The results of our analysis show a clear spatial decreasing in size between the Iberian and the Cantabrian and Lusitanian basins, which are a probable consequence of the differences in the paleoenvironmental conditions in these areas, less favorable to the north and west than to the east of the Iberian Massif. Some previous authors have considered the “*Koninckella* Fauna” recorded in the Lusitanian Basin as a peculiar environmental-controlled assemblage adapted to deep troughs (Alméras et al., 1989, Alméras and Elmi, 1993). However, in our opinion, the adaptation resides precisely in its small size, since these micromorphic species, such as *N. pygmaea* or *K. liasina* derive from standard-sized species of the same genera present in the Pliensbachian of nearby basins in which environmental conditions are different (Baeza-Carratalá et al., 2015). Therefore, it is the same pattern observed contemporarily in other genera such as *Gibbirhynchia*, *Liospiriferina* or *Lobothyris*, which have not been considered as “peculiar”. Alméras et al. (1989) compiled as

members of the *Koninckella*-fauna a number of species belonging to very different lineages whose only common characteristic is the minute size. As indicated by Baeza-Carratalá et al. (2015), some species like *K. liasina* are present in muddy or oxygen-depleted bottoms because these species became adapted by miniaturization to these environments, discarding that koninckinids were a group initially adapted to these conditions. It seems clear that small size is a generalized response to environmental stress, not to a particular environment.

The environmental explanation of the observed spatial pattern of size decrease is then similar to that inferred by previous authors analyzing the dynamics of body-size changes on brachiopods at the end-Permian mass extinction in South China (He et al., 2007, 2017; Shi et al., 2016; Zhang et al., 2016; Wu et al., 2018). In these works, small sizes have been related to depth and environmental deterioration.

But, what environmental parameters drove the increase in body size in time, deduced from our analysis? In this sense, the most evident factor might be temperature. Seawater temperatures from the isotopic data of $\delta^{18}\text{O}$ adapted from Gómez and Goy (2011) show a progressive increase across the extinction interval in the studied basins (Fig. 6). Indeed, this progressive warming likely constituted the main triggering factor of the Extinction Event, culminating in the early Serpentinus Chronozone with an episode of sudden warming which was lethal for many organisms (García Joral et al., 2011; Gómez and Goy, 2011). The relationship between body size and seawater temperature has been invoked in extant brachiopods (cf. Paknevič, 2009), but for most authors this relationship is uncertain (Zezina, 2008; Peck and Harper, 2010), whereas size changes are more often associated both in extant and fossil brachiopods with food supply (Perez-Huerta and Sheldon, 2006) or food availability (Peck and Harper, 2010; Zhang et al., 2016).

It can be alternatively supposed that, for most species, environmental stress would have led to extinction or to substitution by smaller species, but the most resilient species or those better adapted to the changing environmental conditions could have taken advantage of the low level of competition to increase in size. He et al. (2010) described a similar situation and assumed the same

interpretation in the end-Permian crisis from South China, where two extinction-resistant species show a size increase after the other brachiopods disappeared.

Moreover, Zhang et al. (2016) have shown that in the unfavorable environmental conditions previous to the Permian-Triassic collapse, some newly evolved species, seemingly better adapted to the situation, do not suffer miniaturization as the previously existent species do. Similarly, in the upper Semicelatum Subzone of the Iberian Range two spiriferinide species of standard size appear for the first time: *Dispiriferina? oxyptera* and *Calyptoria vulgata*. The last one shows an important dispersal episode without significant changes in size from the Arab-Madagascan area to the Western Tethys, interpreted as driven by the notable warming taking place at this time that implies similar temperatures in both regions (Baeza-Carratalá et al., 2018).

Analogous situation has been recently deduced in La Cerradura section, a deep pelagic refuge from the South-Iberian palaeomargin. In this section, two new species have been recorded in the uppermost levels deposited just prior to the global extinction boundary (a koninckinide and a rhynchonellide) that are bigger than any other representative of these groups in the Semicelatum or Elegantulum Subzones (Baeza-Carratalá et al., 2017).

Thus, similarly to what has been observed in the end-Permian crisis, the reduction in size in the case of the Early Toarcian must have been related with the induced paleoenvironmental stress for this time, while the tendency to stabilize or increase in size of several resilient or new evolved species in the upper part of the extinction interval was probably related to the lack of competition for feeding resources or to the decrease in predation pressure.

Harries and Knorr (2009) discussed a similar effect for abyssal assemblages, where low food resources combined with reduced predation pressure could have caused changes in body size similar to those resulting from the "Island Rule" (Van Valen, 1973; Lomolino et al., 2010): large species that reduce their size, and small species that increase it, in response to the relative scarcity of resources in the first case and the reduction or lack of predators or competitors in the second one.

In this case, the brachiopods, small and with low food requirements, would have taken advantage of the diversity losses.

The increase in size is observed in all the three regions studied, but with different intensity. In order to test a possible warming-controlled pattern in body size, the changes of seawater temperature and the diversity dynamics of brachiopod species have been plotted in parallel (Fig. 6). Temperature shifts and decrease in diversity are similar in all basins along the Paltum / Mirabile Subzone. However, in the Semicelatum Subzone there is a clear difference in the changes in diversity. In the Iberian Basin, where environmental conditions were still tolerable, the number of species does not show a significant drop in diversity, while in the Cantabrian and Lusitanian basins the reduction of diversity was more progressive, leading even to the early extinction in the Cantabrian basins coinciding with "black shales" deposits, generally indicative of anoxic conditions (see Section 3). It is precisely in the Iberian Basin where the largest species are found, new standard-sized spiriferinides appear, the terebratulides have a more extensive record, and the increase in size in the Semicelatum Subzone is more remarkable. Perhaps the Iberian Basin has worked as "temporary refuge" for several taxa at this time. Whether the possible existence of this refuge contributes or is the cause of the increase in size is difficult to determine, but this potential scenario does not contradict the proposed hypothesis linking the increase in size to the decrease in diversity. This relationship has been clearly observed in all the basins, standing out in the populations of *G. cantabrica* of the Cantabrian basins, where the environmental deterioration is evident.

The possible existence of some refuges in the Iberian Basin or in the Betics (Baeza-Carratalá et al., 2017) suggest that the deterioration of environmental conditions referred to poorly oxygenated bottoms, scarce food availability, or the increase of terrigenous inputs or deeper habitats do not seem to have enough strength to cause the extinction of so many brachiopods. It was necessary an additional triggering factor such as the super-warming episode occurred in the

Elegantulum Subchronozone, too severe and unbearable for the brachiopod fauna in all the peri-Iberian epicontinental seas as well as in the westernmost Tethyan Ocean as a whole.

Vörös et al. (2016) have considered spiriferinides and athyridides as “dead clades walking” in the Early Jurassic, as they failed to recover after the extinction of the Triassic-Jurassic boundary and their diversity remains much reduced until its definitive extinction at this moment. Carrying this metaphor a little further, it could be said that the last resilient representatives of these “dead clades walking” took a last splendid dinner just before its execution.

6. Conclusions:

Two crossing gradients of changing body size have been observed in the brachiopod assemblages from the Early Toarcian extinction interval of the peri-Iberian basins: one of reduction in body size, from the shallow and well oxygenated areas to oxygen-depleted and argillaceous bottoms, and another of size increasing over time in some species in all the basins. The former affected the taxonomic composition of the assemblages, with larger species to the East and smaller ones to the north and west of the Iberian Massif, whereas the latter manifested itself inside the species affecting the size of the individuals throughout the extinction interval. This increase is shown by the most abundant species and is independent from their standard size, affecting both big spiriferinides in the more favorable conditions on the Iberian Basin and small rhynchonellides and koninckinides in the less favorable habitats in the Cantabrian and Lusitanian basins. The decrease in size can be explained as a response to the environmental stress associated with deeper and more turbid bottoms; while species that were more resilient or better adapted to the degraded environmental conditions increased in size probably as a response to the decline in diversity, which allowed access to more resources. The observed trends show a remarkable parallelism with those detected in the end-Permian crisis, which suggests a standard pattern in the biotic responses of brachiopods to anoxic episodes; something that, in turn, can help improve our forecasts in relation to the ecological effects of processes such as the current global warming of the oceans.

Acknowledgments

This research is a contribution to the IGCP-655 Toarcian Oceanic Anoxic Event: Impact on marine carbon cycle and ecosystems, and was supported by projects CGL2015-66604-R (MINECO, Government of Spain), and to Research Groups PBM-910431 (Complutense University of Madrid) and VIGROB-167 (University of Alicante). We wish to thank M.J. Comas-Rengifo, L.V. Duarte and F.F. Félix for their collaboration in the sampling and study of the Portuguese sections. We also gratefully thank the EIC Thomas Algeo as well Attila Vörös and another anonymous reviewer for their constructive comments.

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FIGURE CAPTIONS

Figure 1: A: Location of the Upper Pliensbachian-lower Toarcian studied outcrops in the peri-Iberian Jurassic platform system. B: Paleogeographic map of the Early Toarcian with the location of the studied basins. Adapted after Andrade et al. (2016), Damborenea (2002) and Baeza-Carratalá et al. (2016)

Figure 2: Above, Box-plots of the size distributions according to subzones and basins of the studied specimens, separated by orders. Box includes data between the 25-75 percent quartiles. The median is shown with a horizontal line inside the box. Below, the same distributions of sizes with specification of the size values obtained for each species and figures of the most representative taxa. IBER= Iberian Basin; CANT= Asturias and Basque-Cantabrian basins; LUSI= Lusitanian Basin; PALT= Paltum Subzone; SEMI= Semicelatum Subzone; MIRA= Mirabile Subzone. The measures used to design the graphs can be consulted in the supplementary data to this article.

Figure 3: A) Relative abundance in number of recorded specimens of the studied species in each basin and subzone. B) Maximum size recorded per subzone and basin of the species represented for more than 10 individuals in two or more successive subzones. Abbreviations as in Figure 2, plus HAWS: Hawskerense Subzone.

Figure 4: Box-Plots of the sizes in the Paltum/Mirabile and Semicelatum subzones of the more abundant species in each basin: *Liospiriferina falloti* in the Iberian Basin, *Gibbirhynchia cantabrica* in the Cantabrian basins, and *Nannirhynchia pygmaea* in the Lusitanian Basin. Abbreviations as in figure 2. The measures used to perform the graphs can be consulted in the supplementary data to this article.

Figure 5: Maximum size per layer of the most abundant species in three stratigraphic sections representative of the areas studied (Ariño: Iberian Range; San Andrés: Cantabrian basins; Fonte Coberta: Lusitanian Basin). Stratigraphic logs after García Joral et al. (2011) and Comas-Rengifo et al. (2013).

Figure 6: Variation in the seawater temperature and in the diversity dynamics taking into account the quantitative absolute species abundance data for each interval and basin analyzed. Temperature data from δO^{18} isotopic analysis are adapted from Gómez and Goy (2011).

Table 2: One-way ANOVA of the data shown in Figure 4: $p < 0.05 \Rightarrow$ different mean in each subzone

	<i>L. falloti</i> Iberian Basin	<i>G. cantabrica</i> Cantabrian basins	<i>N. pygmaea</i> Lusitanian Basin
Test for equal means	0.017	0.001	0.039
Levene's test for homogeneity of variance (from means)	0.219	0.024	0.942
Levene's test for homogeneity of variance (from medians)	0.233	0.024	0.068
Welch F test in the case of unequal variances	0.007	< 0.001	0,033

Table 1: One-way ANOVA of the data shown in Figure 2: $p < 0.05 \Rightarrow$ different mean in each basin

	PALTUM/MIRABILE			SEMICELATUM		
	RHYNCH.	SPIRIF.	TEREBR.	RHYNCH.	SPIRIF.	TEREBR.
Test for equal means	< 0.001	< 0.001	0.043	< 0.001	< 0.001	< 0.001
Levene's test for homogeneity of variance (from means)	< 0.001	0.087	0.011	< 0.001	< 0.001	0.064
Levene's test for homogeneity of variance (from medians)	< 0.001	0.082	0.190	< 0.001	< 0.001	0.118
Welch F test in the case of unequal variances	< 0.001	< 0.001	0.166	< 0.001	< 0.001	< 0.001

Highlights:

1. Two crossing trends of spatial and temporal changes in body size are observed.
2. Size decreases in relation to the progressive environmental stress.
3. Some species show increasing sizes over time throughout the extinction interval.
4. The size increase affects both big and small species
5. This increase has been related to changes in diversity that would favor access to resources.

Figure 1

RHYNCHONELLIDA

Quadratorhynchia attenuata

Cirpa fallax

Gibbirhynchia cantabrica

Nannirhynchia pygmaea

others

1 cm

SPIRIFERINIDA

Liospiriferina falloti

L. cf. falloti

L. subquadrata

Calyptoria vulgata

Dispiriferina? oxyptera

others

TEREBRATULIDA

Lobothyris arcta

L. edwardsii

Zeilleria quadrifida

Z. culeiformis

Pseudokingena deslongchampsii

Figure 2

Figure 3

L. falloti

G. cantabrica

N. pygmaea

Figure 4

Figure 5

Figure 6