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Disparity, diversity and body size changes of the Toarcian Spiriferinides (Brachiopoda, Lower Jurassic) in the westernmost Tethys

García Joral, Fernando[1], Baeza-Carratalá, José F.[2], Comas-Rengifo, María José[1], Goy, Antonio[1]

[1]Departamento de Geodinámica, Estratigrafía y Paleontología, Universidad Complutense de Madrid, 28040 Madrid, Spain
[2]Departamento de Ciencias de la Tierra y del Medio Ambiente, Universidad de Alicante, San Vicente del Raspeig, 03080 Alicante, Spain

Diszparitás, diverzitás és méretváltozás a toarci Spiriferinidáknál (alsó jura, Brachiopoda) a Tethys legnyugatabbi területein

Összefoglalás

Az Ibériai-masszívumot körülvevő spanyol és portugál medencék Spiriferinida-szukcessziója világviszonylatban is a csoport egyik legteljesebb és legjobban ismert fosszilis rekordját jelenti. Annak ellenére, hogy a csoporton belüli faji diverzitás alacsony, az Ibériai-masszívumot körülvevő medencékből a paleozoikum utáni fontosabb morfotípusok ismertek. Ilyen módon ezek az alakok közvetlenül a kora toarci tömeges kihalási esemény előtt „az elveszett Éden” utolsó képviselőinek tekinthetők. A brachiopodák morfológiai és testméretváltozásait a tömeges kihalás idejének megfeleltethető késő pliensbachi – kora toarci során a *Liospiriferina*-nemzetség réteg szerint gyűjtött maradványain vizsgáltuk. A cél a morfológiai változások vizsgálata volt az adott időszakra jellemző hipertermális esemény tükrében. A példányok az Ibériai-hegység két szelvényéből származnak. Az eredmények azt mutatják, hogy a csoport diverzitásának kezdeti hanyatlása és a korai méretcsökkenés a toarci elején bekövetkezett első komolyabb felmelegedési epizóddal állítható párhuzamba. A nemzetség utolsó képviselőinél megjelenő nagy méretű formák pedig feltehetően a tengervíz rövid ideig tartó, de erős lehűlésével kapcsolatosak. Ez a lehűlés két jelentős felmelegedési szakasz közé ékelődött, és ez lehetett a Spiriferinida-klád kihalásának kiváltó oka.

Tárgyszavak: brachiopoda, Spiriferinida, Liospiriferina*, jura, toarci, Tethys, Ibériai-masszívum*

Abstract

The fossil record of the Order Spiriferinida in the Toarcian basins surrounding the Iberian Massif (Spain and Portugal) is exposed as one of the most well-known, complete, and continuous worldwide. Despite the low specific diversity intrinsic to this group, the peri-Iberian basins include representatives of the main different morphological types recognized throughout the post-Paleozoic history of the group, representing the ultimate “Lost Eden” for this clade before its definitive demise in the Early Toarcian Mass Extinction Event (ETMEE). The changes in morphology and body size observed during the latest Pliensbachian–earliest Toarcian, corresponding to the Extinction interval of the ETMEE, are analyzed in specimens of the genus Liospiriferina carefully recorded bed by bed in two stratigraphical sections of the Iberian Range, in order to stablish their detailed relationship with the evolution of the seawater temperature during this hyperthermal event. This analysis has revealed an initial decrease in diversity and size coinciding with the first important warming episode at the beginning of the Toarcian, while the big sizes observed in the last representatives of this genus probably correspond with a short but intense event of seawater cooling, intercalated in the severe warming episode that most probably was the main triggering factor of the spiriferinide clade extinction.

Keywords: Brachiopoda, Spiriferinida, Liospiriferina, *Jurassic, Toarcian, Tethys, Iberian Massif*

Introduction

The Lower Jurassic spiriferinides (Order Spiriferinida Ivanova, 1972) together with the ultimate representatives of the Order Athyridida Boucot et al., 1964, constituted the only spire-bearing groups recorded in the Mesozoic in contrast with the extraordinary proliferation of these clades in the Paleozoic times. These orders became extinct coinciding with the last clade (or "fatal") extinction (*sensu* Vörös et al. 2019) in the evolutionary history of brachiopods, occurred in a timespan with critical perturbations in the environmental conditions of marine ecosystems, culminating ca. 183 Ma in the so-called Early Toarcian Mass Extinction Event (ETMEE). Remarkably, the extinction of the Paleozoic spire-bearing brachiopods also coincided with preceding events matching with the concept of "fatal extinctions" introduced by Vörös et al. (2019) to denote those episodes of synchronous extinction of high-grade taxa. It can therefore be stated that the last three fatal extinctions in the history of brachiopods especially affected the spire-bearing groups (Vörös et al. 2016, 2019), i.e., the Devonian crisis extinguishing Atrypida; the End-Permian extinction affecting Spiriferida; and the ETMEE where Spiriferinides and Athyridides became extinct (Vörös 2002; García Joral et al. 2011; Baeza-Carratalá et al. 2015, 2017; Vörös et al. 2016, 2019), excluding those from New Zealand attributed to *Spiriferina* by MacFarlan (2023), occurring in the Bifrons Zone, c.a. 1 Ma post-ETMEE. No other order of brachiopods became extinct since this last event.

On the other hand, another of the many inspired ideas put forward by Attila Vörös throughout his prolific career was to consider the Jurassic spiriferinides (along with the athyridides) as a "Dead Clade Walking" (*sensu* Jablonski 2002), alluding to their low diversity after surviving the severe end-Triassic extinction event and remaining in decline in the Early Jurassic (Vörös et al. 2016, 2019) up to their total extinction in the critical perturbation of the ETMEE. Thus, representatives of the Order Spiriferinida are profusely and widely recorded throughout the Western Tethys in the Early Jurassic but, despite their conspicuous occurrences, they have been arranged only in a very few long-established genera (e.g., Rousselle 1977; Manceñido 1981, 2004; Dulai 2003; Vörös et al. 2003; Carter & Gourvennec 2006; Comas-Rengifo et al. 2006; Vörös 2009; Mandl et al. 2010; He et al. 2015; Baeza-Carratalá et al. 2016c) denoting a relatively low supraspecific taxonomic diversity in contrast to their great abundance.

Likewise, another awe-inspiring concept put forward by Vörös was to consider the Western Tethys Ocean as the "Lost Eden" for brachiopods (Vörös 1993, 2005; Vörös et al. 2016) representing the most important refuge for this epibenthic biota during the different Mesozoic biotic crises, including that of the ETMEE in which the spire-bearing groups finally became extinct.

These three aforementioned concepts introduced and developed by Attila Vörös over the last decades have become a paradigm that supports outstanding interpretations on the palebiogeographic distribution and on the different adaptive strategies undertaken by different Jurassic brachiopod groups, especially around the ETMEE. In the framework of these precepts, the present work analyzes the changes and adaptations experienced by the last spiriferinides in the westernmost part of the Tethys Ocean during the Early Toarcian. The morphology and body size variations of representatives of this clade over time around ETMEE are quantified and their morphospaces are explored on the basis of the dataset derived from the marginal peri-Iberian platforms system, where spiriferinides have exposed the most complete record preceding their definitive extinction, postulating the sea-water temperature oscillations as a primary factor of environmental control just prior to the hyperthermal maximum recorded in the basal part of the Serpentinum Chronozone (García Joral et al. 2011; Gómez & Goy 2011; Caruthers et al. 2013; Danise et al. 2013; Baeza-Carratalá et al. 2015, 2017; Krencker et al. 2020, Ruebsam et al. 2020; Fernandez et al. 2021; Bucur & Reolid 2023), just coinciding with the spiriferinides global demise.

Paleobiogeografic distribution of Jurassic spiriferinides

Jurassic spiriferinides have a worldwide distribution from the Hettangian to the early Toarcian, although most of their known records are comprised in the Western Tethys. In the Pliensbachian, a very high number of spiriferinide species have been described in basins belonging to different bioprovinces of this area (e.g., Alméras & Fauré 2000, Comas-Rengifo et al. 2006, Elmi et al. 2007, Vörös 2009, Baeza-Carratalá 2013, Benzaggagh 2023). However, they disappeared in the Toarcian in many basins of the Mediterranean Province, which typically includes more epioceanic areas than the Euro-Boreal one (cf. Vörös & Escarguel 2019). The westernmost part of the Tethys Ocean and its connection with the proto-Atlantic, together with the North-Gondwanan Paleomargin, seems to have represented a last refuge (the final relict of the "Lost Eden") for spiriferinides in the Early Toarcian (*Fig. 1A*).

As representatives of this ultimate refuge, the specimens herein analyzed derive from the Lower Jurassic peri-Iberian platforms system, constituted by different basins surrounding the Iberian Massif which, in paleogeographical and geotectonic terms, was operating as an isolated microplate during most of the Mesozoic times. The Jurassic peri-Iberian platforms system constituted, together with the Southern Betic unities (corresponding to the Alborán microplate margins) and the North-African margins, the westernmost marine environments and sub-environments of the Tethys Ocean. In the late Early Jurassic, the proto-Atlantic seaway connected this part of the Tethys with the Arctic and the Panthalassa via the Viking and the Hispanic Corridors (e.g., Poulton & Callomon 1977; Smith 1983; Manceñido 1990, 2002; Manceñido & Dagys 1992; Damborenea 2000; Bjerrum et al. 2001; Aberhan 2001; Sha 2002; García

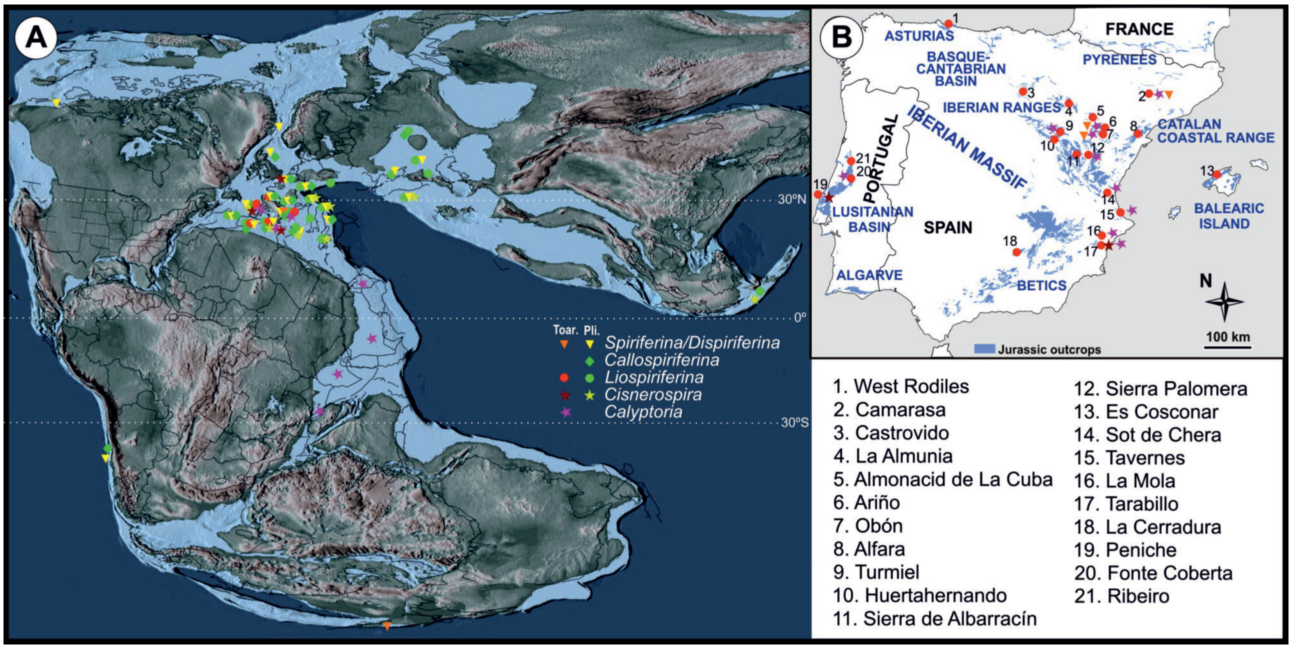

Figure 1. (A) Paleobiogeographic distribution of the Pliensbachian (greenish symbols) and Toarcian (reddish symbols) genera of spiriferinides. Data from the Paleobiology Database, consulted in December 2023, supplemented with data after Alméras & Fauré (2000), Alméras et al. (2007), Vörös (2009), Baeza-Carratalá (2008, 2013), and Benzaggagh (2023). Paleomap after Scotese (2013). (B) Toarcian spiriferinide genera recorded in selected localities from the peri-Iberian basins. Data sources after Comas-Rengifo (1982), Fernández-López et al. (1998), Comas-Rengifo et al. (1999, 2006, 2013, 2015, 2018a, 2018b), García Joral & Goy (2009), García Joral et al. (2011, 2022), Baeza-Carratalá et al. (2016a, 2016b, 2017, 2018). Symbols as in (A)

***1. ábra.** (A) A Spiriferinida-nemzetségek paleobiogeográfiai elterjedése. A pliensbachi előfordulások zöld színnel, a toarciak vörössel jelölve. Az adatokat a Paleobiology Database-ből 2023 decemberében töltöttük le, és kiegészítettük Alméras & Fauré (2000), Alméras et al. (2007), Vörös (2009), Baeza-Carratalá (2008, 2013) és Benzaggah (2023) adataival. A paleogeográfiai térkép Scotese (2013) nyomán készült. (B) Toarci Spiriferinida nemzetségek néhány lelőhelyen a Peri-Ibériai-medencében. Az adatok Comas-Rengifo (1982), Fernández-López és társai (1988), Comas-Rengifo és társai (1999, 2006, 2013, 2015, 2018a, 2018b), García Joral & Goy (2009), García Joral és társai (2011, 2022), Baeza-Carratalá és társai (2016a, 2016b, 2017, 2018) nyomán. Jelkulcs, mint az (A) ábrán*

Joral et al. 2011). The most relevant localities containing Early Toarcian spiriferinides in these basins have been indicated in the *figure 1B*.

Interestingly, the spiriferinide genera that settled in this area show a morphological disparity in accordance with that shown by the group throughout the Early Jurassic. In this sense, Vörös et al. (2016), taking into account the outline and global shape, differentiated three basic morphogroups among the Lower Jurassic spiriferinides: biconvex, winged, and cyrtiniform. On the other hand, Comas-Rengifo et al. (2006), bearing in mind the ribbing pattern of the shell, considered a different arrangement based on the record of this group derived from the northern and eastern peri-Iberian basins, discriminating the fully ribbed, smooth, and sparsely ribbed (including capillate) morphogroups. Combining both criteria, it can be deduced that all the four resulting morphogroups recorded throughout the Early Jurassic are also systematically represented during the Early Toarcian in the peri-Iberian basins (*Fig. 2*), i.e., *Cisnerospira* (smooth-cyrtiniform), *Spiriferina* (ribbed-winged), *Liospiriferina* (smooth-biconvex), and *Calyptoria* (capillate or scarcely ribbed-biconvex). In fact, this disparity is basically the same as that observed among spiriferinides in the Triassic, when the group expanded and filled the vacant eco- and morphospaces left after the disappearance of their Paleozoic relatives Spiriferides after the Permian–Triassic mass extinction (Guo et al. 2020).

Geological framework and chronostratigraphic record of spiriferinides around the Iberian paleomargins

In most of the peri-Iberian basins, the Lower Toarcian deposits are arranged in expanded stratigraphic sequences in which spiriferinides have been widely and profusely reported since the 18th century (e.g., Torrubia 1754; Deslongchamps 1863; Jiménez de Cisneros 1921, 1923; Dubar 1931; Delance 1969; Comas-Rengifo & Goy 1975; Rousselle 1977; Calzada 1979; Goy et al. 1984; Arias et al. 1992; Fernández-López et al. 1998; García Joral & Goy 2000, 2009; Gahr 2002; Comas-Rengifo et al. 2006, 2013, 2015; García Joral et al. 2011, 2022; Baeza-Carratalá 2011, 2013; Baeza-Carratalá et al. 2016a, 2016b, 2017, 2018). For the sake of consistency, the well-stablished record of spiriferinide taxa along the Tenuicostatum (Polymorphum)–Serpentinum chronozones in the peri-Iberian basins have been summarized in four regions on the basis of their paleobiogeographic situation and differences among depositional environments: i.e., those forming part of the East-Iberian Platforms System (*EIPS*: Iberian Range, Catalonian Coastal Range and the Balearic Basin); the *Northern-Cantabrian paleomargin* (Asturias and Basque-Cantabrian Basins); the *Atlantic paleomargin* (Lusitanian Basin); and the *South-Iberian paleomargin* (Subbetic-Alborán regions).

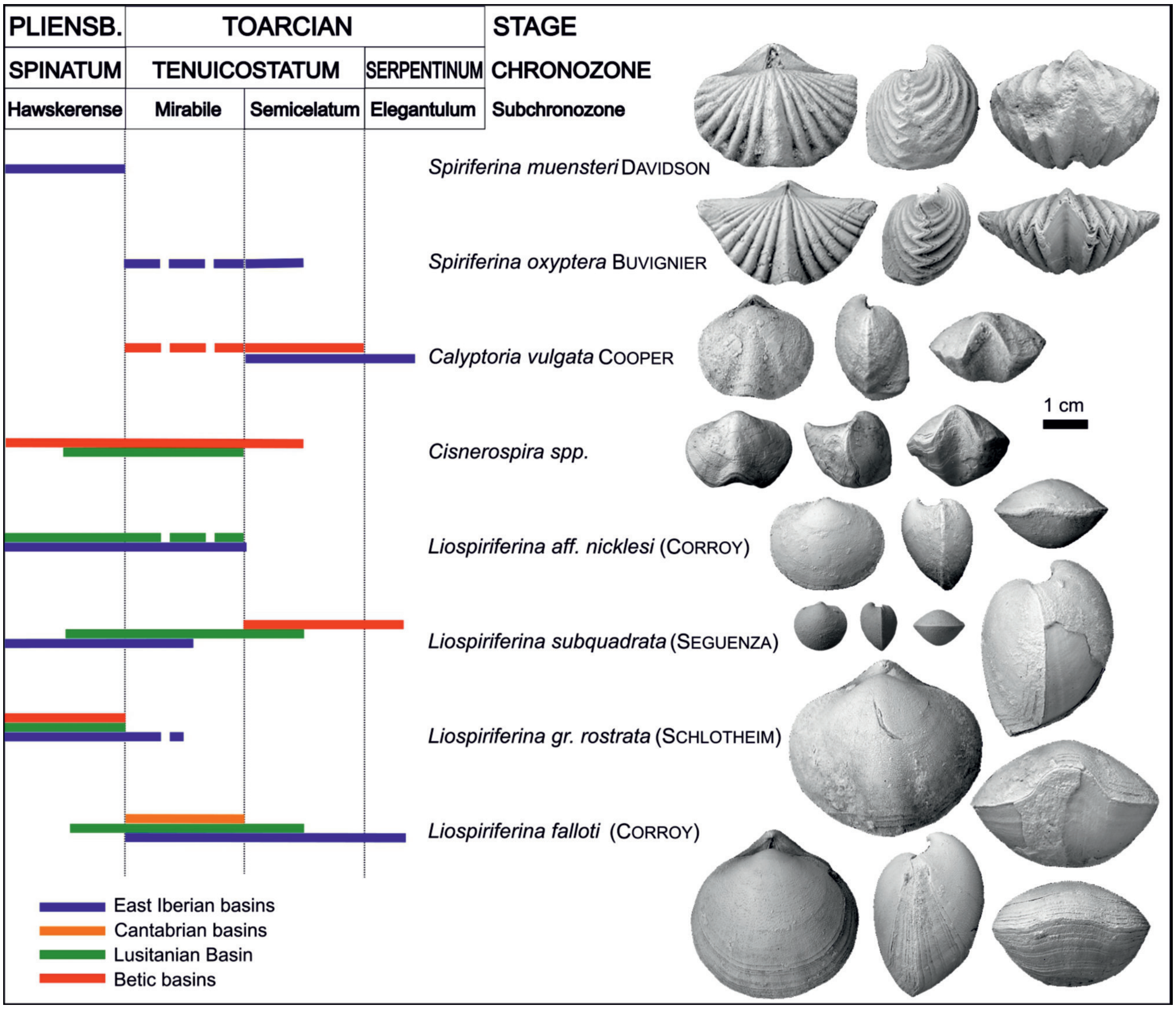

Figure 2. Chronostratigraphic distribution of the spiriferinides in the peri-Iberian basins. Photographs refigured from COMAS-RENGIFO et al. (2006) except for *L. subquadrata* (from COMAS-RENGIFO et al. 2013) and *Cisnerospira* spp. (from COMAS-RENGIFO et al. 2015)

2. ábra. *A Spiriferinidák időbeli elterjedése a peri-Ibériai-medencékben. Fotók: COMAS-RENGIFO et al. (2006) nyomán, kivéve* L. subquadrata *(COMAS-RENGIFO et al. 2013) és* Cisnerospira *spp. (COMAS-RENGIFO e al. 2015)*

The chronostratigraphical range of the main recorded taxa in the four established regions is shown in *Figure 2*.

EIPS – Representatives of Spiriferinida in this region are recorded in the Iberian Range within the Turmiel Fm., in a depositional environment representing a shallow epicontinental platform. These deposits consist of an alternation of well-bedded grey/yellowish marl and micritic mudstone beds arranged into deepening and shallowing-upwards sequences (GÓMEZ & GOY 2000). These marly facies are deposited overlying the red bioclastic grainstone-packstone beds of the Upper Pliensbachian-lowermost Toarcian Barahona Fm. where spiriferinides are recorded as well. In the Catalonian Coastal Range and Mallorca Island, spiriferinides are recorded in a lithostratigraphical framework comparable to that of the Iberian Range, in the last levels of the Barahona Fm. and the first levels of the El Caregol Mb. of the Sant Blai Fm. (FERNÁNDEZ-LÓPEZ et al. 1998), and in the Es Cosconar Fm. and the lower part of Gorg Blau Fm. (ROSALES et al. 2018, GARCÍA JORAL et al. 2022) respectively.

South-Iberian Paleomargin – In the easternmost Betic Range (East Spain) spiriferinides are recorded in the Pliensbachian–lowermost Toarcian sediments from the epioceanic External Subbetic area (BAEZA-CARRATALÁ 2013), which is characterized by pelagic seamount facies. Most of the taxa are recorded in the upper part of the Gavilán Fm. (late Pliensbachian), consisting of red crinoidal grainstone beds, and the marly levels of the Zegrí Fm. (uppermost Pliensbachian–lowermost Toarcian), consisting of marls and marly/sandy marlstone deposits. In the innermost part of the External Subbetic (La Cerradura, Jaen), the Zegrí Fm. was deposited in a deeper subsiding trough area with an expanded sedimentation and greater cumulative thickness (REOLID et al. 2014, BAEZA-CARRATALÁ et al. 2017). Lower Toarcian spiriferinides have been also recorded in the transitional areas of the Prebetic-Subbetic domains (La Mola, Alicante, E-Spain; Baeza-Carratalá et al. 2016b).

Atlantic paleomargin – In the Lusitanian Basin, spiriferinides are found mainly in Toarcian sediments from the Rabaçal-Condeixa and the Peniche regions. They are recorded in the Coimbra area (Ribeiro and Fonte Coberta sections) in the São Gião Fm. (Comas-Rengifo et al. 2013) as whitish gray marly beds. In Peniche, occurred in the lower member of the Cabo Carvoeiro Fm. (Alméras et al. 1996, Comas-Rengifo et al. 2015). Both formations correspond to low-energy, distal homoclinal ramps, deeper to the west/northwest, typified by hemipelagic sequences and organic-matter-rich facies, where an alternation of marlstone and argillaceous limestone beds prevailed (Duarte 2007).

Northern-Cantabrian paleomargin – Toarcian spiriferinides have not yet been recorded in the Basque-Cantabrian Basin, and are scarce in Asturias, where they come from the Santa Mera Member of the Rodiles Fm., composed of rhythmic alternations of micritic and marly limestones with an episode punctually enriched in organic matter (black shales), interpreted as deposited on a hemipelagic carbonate ramp (García Joral & Goy 2009).

The lithostratigraphic differences and environmental scenarios among the different peri-Iberian basins influenced the characteristics of the spiriferinide record (*Fig. 2*). In the EIPS, which correspond to the best oxygenated areas, this record is more diverse and abundant. In the less oxygenated areas of the north and west of the Iberian Massif, the record basically consists of small specimens of *Liospiriferina*, together with few specimens of *Cisnerospira* and *Calyptoria* in the Lusitanian Basin. In the shallower epioceanic areas of the South-Iberian margin, such as the Subbetic Domain and the transitional zones to the more proximal areas, the record is also diversified throughout the Early Jurassic, similarly to that which took place in the EIPS, with standard-sized *Spiriferina, Callospiriferina, Dispiriferina, Liospiriferina*, and *Cisnerospira* as the main representative genera, but only *Cisnerospira* and *Calyptoria* persisted up to the uppermost Early Toarcian record, while the more restricted Betic troughs became deeper refuges, promoting the development of small *Liospiriferina* species and specimens just like those occurring in the Cantabrian and Lusitanian basins.

Evolutionary patterns of the last peri-Iberian spiriferinides

As previously stated, peri-Iberian spiriferinides preserve a remarkable morphological disparity in the Early Toarcian. Therefore, diversity dynamics in this group seems to have experienced significant changes, with a notable reduction if compared to the Pliensbachian diversity maximum (Comas-Rengifo et al. 2006).

The earliest important change took place concurring with the initial episode of the biotic crisis, which was considered by several previous authors as a multi-phase event (cf. Little 1996; Macchioni & Cecca 2002; Wignall & Bond 2008; Dera et al. 2010; Caruthers et al. 2013; Arias 2013; Baeza-Carratalá et al. 2015, 2017; Rita et al. 2016; Reolid et al. 2021). This earlier episode occurred at the beginning of the Tenuicostatum Chronozone, in a period of changes in long-term environmental conditions prior to the ETMEE boundary. In this first phase, while spiriferinides virtually disappeared in a great number of basins of the Mediterranean Bioprovince (Vörös 2005, Baeza-Carratalá 2013), in some peri-Iberian areas, as the EIPS, Pyrenees, or in the Northwestern African basins, spiriferinides still occurs, but their diversity decreased (cf. Comas-Rengifo et al. 2006). Simultaneously, in less oxygenated habitats, such as the Cantabrian and the Lusitanian basins, only some small-sized species thrived (Alméras et al. 1996; García Joral & Goy 2009; Comas-Rengifo et al. 2013, 2015).

The second phase of the biotic crisis is recorded in the last stratigraphic levels prior to the extinction boundary, in the uppermost Semicelatum Subchronozone and the first levels of the Elegantulum Subchronozone. The spiriferinides recorded in this interval (*Fig. 2*) correspond only to the biconvex *Liospiriferina*), considered as the most conservative and generalist morphotype (cf. Vörös et al. 2019), and *Calyptoria*, an immigrant who arrived just at this time from lower latitude areas (Baeza-Carratalá et al. 2018).

This decline in diversity follows the same global dynamics documented for all brachiopod clades in the Toarcian. In the Mediterranean Bioprovince, brachiopod diversity was not recovered until the Aalenian–Bajocian times (Vörös 2005, Vörös & Dulai 2007, Baeza-Carratalá 2013, Andrade et al. 2016). In the extinction interval some typical groups of this bioprovince show strategies to escape from unfavorable environmental conditions established in their homeland areas, moving towards deep refugia, such as the southernmost subsiding troughs in deeper-water settings of the Subbetic domain (Baeza-Carratalá et al. 2017), or migrating from the most intra-Tethyan areas up to some NW-European epicontinental seas (Vörös 2002, Baeza-Carratalá et al. 2015), where they found a suitable habitat to colonize. In other westernmost Tethys shallower regions (EIPS, Pyrenees, or several basins in the southern and western France), taxa of the NW-European Province persisted, although they underwent a remarkable renewal at species-level, entailing in some cases a size reduction stage (García Joral et al. 2011, Baeza-Carratalá et al. 2015, Piazza et al. 2020a).

Several of these new species survived up to the last stratigraphic levels prior to the extinction, when all the brachiopod species (and most of the genera) disappeared from the peri-Iberian basins and many other Western Tethys areas. Recovery and repopulation with new species, adapted to much warmer conditions (Ulmann et al. 2020), begun in several basins after a relatively short delay (cf. García Joral et al. 2011, Andrade et al. 2016).

Climate changes, and more specifically seawater temperature variations, were likely the most important triggering factors for these evolutionary patterns. Seawater temperature variations have been linked by Guo et al. (2020) to the diversity fluctuations among Triassic spiriferinides, so that major cooling events of seawater temperatures in the Anisian and Carnian seem to have facilitated the recovery of the spiriferinides and their radiation in the Triassic, and their noticeable diversification in the Late Pliensbachian coincides with another major cooling (icehouse) interval as well (Price 1999, Gómez et al. 2008, Gómez & Goy 2011, Rosales et al. 2018, Ruebsam et al. 2020). The brachiopod migration and dispersal movements observed at the Pliensbachian–Toarcian boundary can be correlated with the first warming pulse of the Early Toarcian Biotic crisis (Baeza-Carratalá et al. 2015, 2017), estimated to be approximately in 5 °C (Ruebsam et al. 2020, Fernandez et al. 2021) and can be interpreted as the probable response of most species to the geographic shift in their thermal optimum due to this global warming episode.

After a relative sea-water temperature cooling in the mid-Tenuicostatum Chronozone, a drastic rise of 10° C occurred concomitantly with the onset of the Early Toarcian Oceanic Anoxic Event near the Tenuicostatum–Serpentinum chronozones boundary (Ruebsam et al. 2020). The variation in the oxygen-isotope ratios ($\Delta^{18}O$) recorded in many basins of the Western Tethys corresponding with this severe warming episode shows the most negative excursion values in basins located at latitudes above 30°N, and the least negative (or even positive) values in lower latitude basins, such as the peri-Iberian and North African basins (Fernandez et al. 2021, Gambacorta et al. 2024). These variations should reflect not only temperature variations, but also a strong North–South salinity gradient, possibly due to the southward currents flow through the Viking Corridor of brackish waters derived from the Arctic (Bjerrum et al. 2001) and the progressive increase in runoff and fresh-water inputs to the epicontinental basins and sub-basins of northern Europe in correspondence with the general increase in temperature (Gambacorta et al. 2024). Thus, either because the water temperature was even higher in the areas located north of the peri-Iberian basins, or because they had too low levels of salinity or oxygen, the surviving spiriferinides (like the rest of the brachiopod species in these basins) did not manage to escape the hyperthermal event by moving to places further north.

Morphology, size changes and seawater temperature in the Toarcian *Liospiriferina* from the Iberian Basin

Analyzing the body-size changes in the brachiopods recognized in the Extinction interval prior to the ETMEE from the peri-Iberian basins, García Joral et al. (2018) found two crossing trends involving not only latitudinal and temporal gradients but also environmental factors. On one hand, a diminishing tendency in the brachiopods body size is noticed from shallower and well-oxygenated regions to the muddy and oxygen-depleted bottoms, in line with what was observed in the Western Tethys as a whole in the first phase of the biotic crisis. On the other hand, an increasing-size trend over time is revealed in some species in all the peri-Iberian basins. The first tendency affected the taxonomic composition of the assemblages, so that the larger species are recorded to the east of the Iberian Massif whereas the smaller ones occurred in the northern and western peri-Iberian platforms.

The increasing-size trend over time is related to within-species changes affecting the intraspecific size of individuals throughout the extinction interval. This increase is revealed in the most profusely recorded taxa and it is independent of their standard size, affecting both the large spiriferinides in the most favorable habitats prevailing in the Iberian Basin and the small rhynchonellides and koninckinides in more adverse conditions from the Cantabrian and Lusitanian basins (García Joral et al. 2018).

Regarding this size increasing trend, experienced, among others, by the last representatives of the genus *Liospiriferina* in the Iberian Range, it seems to be inconsistent with the customary global postulation expecting an inverse relationship between size and temperature in numerous organism groups, the so-called “Bergmann’s Rule” or the temperature-size rule (TSR). According to this “rule” ectotherm organisms acquire the mature ontogenetic conditions at smaller adult body size in warmer conditions (Atkinson 1994), although compliance with this rule is not so evident in the case of brachiopods (cf. Peck & Harper 2010).

In this way, Piazza et al. (2020a, 2020b) carried out a comprehensive analysis on the bivalve and brachiopod body size variation from a single lower Toarcian locality of the Iberian Basin, concluding that a decreasing-size pattern of benthic communities was linked to the increasing of the sea-water temperatures during the extinction interval, admitting a more manifest relationship when analyzed in bivalves and less statistically evidenced in brachiopods. These authors also remarked that the key factor of size reduction was a decrease in the occurrence and abundance of larger species rather than a within-species change in size. In the case of brachiopods, this trend is supported by the presence of *Soaresirhynchia bouchardi*, which is an opportunistic taxon that colonized the basin from deeper and warmer waters after the ETMEE (cf. Baeza-Carratalá et al. 2017, Ulmann et al. 2020). However, in other areas, such as the Lusitanian Basin, *S. bouchardi* shows larger size than those brachiopods occurring prior to the extinction boundary (cf. Comas-Rengifo et al. 2013, 2015; Piazza et al. 2019). Excluding *S. bouchardi,* the coupling of brachiopod size changes with the increasing of sea-water temperatures is not statiscally significant along the Tenuicostatum Zone (Piazza et al. 2020a).

In order to better understand the effect of the sea-water temperature in the brachiopod body sizes, a more detailed comparative analysis has been now performed taking into account not only the changes in body size, but also morphological patterns and morphospace occupation recorded in the Iberian Basin among the spiriferinide representatives assigned to the genus *Liospiriferina*, which represents the only of the four genera with a certified continuous record in the peri-Iberian paleomargins during the uppermost Pliensbachian – lower Toarcian interval. Simultaneously, these changes are interrelated with the paleotemperature pattern derived from the sea-water temperature curves estimated by the different authors for this basin.

A total number of 345 specimens of *Liospiriferina* Rousselle, 1977 were included in the analysis, all of them collected and studied bed-by-bed in the Almonacid de la Cuba (after Comas-Rengifo et al. 2010) and the Ariño localities (after Goy et al. 1998, García Joral et al. 2011), spanning the uppermost Pliensbachian – lower Toarcian deposits throughout the Hawskerense, Mirabile, and Semicelatum subzones. The extensive record of spiriferinides in the Semicelatum Subzone, that probably represents a longer time interval that of the Mirabile subzone, have been divided in two parts (lower and upper part of the Subzone) for a more detailed analysis. All specimens analyzed are deposited at the Department of Geodynamics, Stratigraphy and Paleontology (Universidad Complutense de Madrid, Spain; DPUCM). With the purpose of analyzing the morphologic variability and the size changes over time, the main biometric parameters suggested by Manceñido (1981) for the characterization of the spiriferinides were directly measured on the 252 complete available specimens (*Fig. 3*): total length (L), width (W), thickness (T), dorsal valve length (Ldv), distance from the apex to the maximum width of the shell (Wm), height of the cardinal area (Ha), width of the dorsal median fold (Wf), and maximum height of the fold in the anterior commissure (Hf). Subsequently, Principal Component Analysis (PCA) was conducted as exploratory method for variable reduction (Hammer & Harper 2006) using a correlation matrix instead of variance-covariance, considering that there is a great difference in the width of the range of values between some variables and others. The correlation matrix is more appropriate when the ranges of values are different because it standardizes the data so that all variables contribute equally to the analysis These analyses and successive statistical explorations were carried out by means of the PAST 3.22 software package (Hammer et al. 2001). The labelling of the specimens studied at each stratigraphic level and their measurements are included as supplementary material. Correlation of size, diversity, and disparity changes with seawater paleotemperatures are based on temperature curves published by different authors. The ammonoid chronostratigraphic zonal scheme is based on the standard zones proposed by Elmi et al. (1997), and Page (2003) for the Tethys Realm.

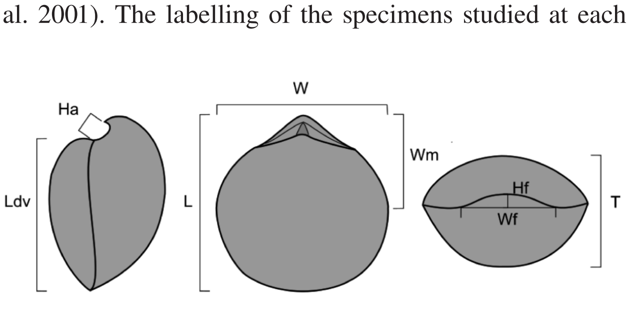

Figure 3. Main biometric parameters measured on *Liospiriferina* specimens from Almonacid de la Cuba and Ariño localities: L: total length; W: width; T: thickness; Ldv: length of the dorsal valve; Wm: length from the apex to the maximum width; Ha: Height of the cardinal area; Hf: height of the dorsal anterior fold; Wf: width of the dorsal anterior fold

3. ábra. *Az Almonacid de la Cuba és az Ariño lelőhelyekről származó* Liospiriferina*-példányokon mért fontosabb méretek. L: teljes hosszúság; W: szélesség; T: vastagság; Ldv: a dorzális teknő hossza; Wm: a csúcstól a legnagyobb szélességig mért távolság; Ha: a cardinális terület magassága; Hf: a dorzális anterior kiemelkedés magassága; Wf: a dorzális anterior kiemelkedés szélessége*

By correlating all the main biometric parameters using a correlation matrix (*Table I*), it can be deduced that all of them are closely related ($p < 0.05$). The lowest correlation values are observed for the height of the cardinal area (Ha) and the height of the dorsal median fold (Hf), these revealed as the most independent parameters, and consequently being responsible for the greatest shape variations non-aligned with the body-size.

The PCA plot (*Fig. 4*) also reveals that morphospaces occupation varied over time, mainly along the PC2 axis. The specimens recorded in the uppermost Pliensbachian (Hawskerense Subzone of the Spinatum Zone) occupied a much greater range along this axis than those recorded in the Tenuicostatum Zone (Mirabile and Semicelatum subzones) from the lowermost Toarcian. This wide-range variability in the PC2 scores corresponds to the great morphological variability observed among spiriferinides from the Late Pliensbachian of the Iberian Range, that have led to the taxonomic determination of several species assigned to the genus *Liospiriferina*, such as *L. rostrata* (Schlotheim), *L. terebratuloides* (Seguenza), *L. hartmani* (Zieten), *L. falloti* (Corroy) and some other taxa (cf. Comas-Rengifo et al. 2006) which have been grouped as *Liospiriferina* gr. *rostrata* in the *Figure 2*.

However, the morphological variability of the *Liospiriferina* specimens from the Mirabile and Semicelatum subzones is considerably lower than in the Hawskerense Subzone, as indicated by the reduction in the morphospaces occupied in the PCA plot, so that, in our opinion, all these specimens can be assigned to a single species, *L. falloti*, which corresponds to a simplified morphology, less folded and with the cardinal area less curved, among the *L. rostrata* group. The decrease in variability is concurring in the Mirabile Subzone and in the lower part of the Semicelatum Subzone with a significant reduction in size of the individuals, indicated by the contraction of the PC1 scores. This miniaturization has been related in the Iberian Basin to the first episode of the ETMEE, that as previously explained, consists of the replacement of some species of brachiopods by other smaller ones within the same genus (e.g. *Lobothyris*, *Aulacothyris*, *Quadratirhynchia*, *Gibbirhynchia*), also involving the genus *Liospiriferina* (cf. García Joral & Goy 2000, García Joral et al. 2011). On the other hand, while the variation in the morphological variability between the specimens of the two Toarcian subzones can be interpreted as scarce from the wide-ranging PC2 scores, the size of the specimens (estimated, given the rounded style of the shells, as the volume of an ellipsoid whose three axes correspond to the main dimensions of the shell: length, width and thickness, as proposed by Guo et al, 2022) changed noticeably,

Table I. Below, colored: Linear correlation coefficient (*r*) between the measured dimensions. Above: *p* (uncorrected) values of normality. In red boxes *r* values lower than 0.5; in orange boxes *r* values between 0.5 and 0.7. All *p* values are lower than 0.05. Biometric abbreviations as in *Figure 3*

I. táblázat. *Alul, színesben: a mért értékek közötti lineáris korrelációs együttható (*r*). Fent:* p *(nem korrigált) normalitás értékek. Piros dobozokban a 0,5-nél alacsonyabb* r *értékek; narancssárga dobozokban a 0,5 és 0,7 közötti* r *értékek. Minden* p*-érték 0,05-nél alacsonyabb*

	W	**L**	**T**	**Ha**	**Ldv**	**Wm**	**Hf**	**Wf**
W		4.62E-100	2,3213E-85	3,6902E-28	3,0854E-95	2,05E-63	5,7695E-25	4,1407E-67
L	0.91422		3.9224E-88	7.741E-25	1.5811E-127	2.2496E-78	5.5253E-21	7.2435E-76
T	0.88588	0.8919		9.7245E-17	2.5313E-81	2.1232E-65	1.7226E-30	7.9129E-49
Ha	0.62002	0.5881	0.4916		1.4863E-18	5.651E-15	5.9645E-07	2.4674E-22
Ldv	0.90584	0.94919	0.87646	0.51608		1.1784E-69	9.2537E-17	1.2457E-65
Wm	0.82325	0.86905	0.83023	0.46578	0.8442		5.2912E-12	2.2602E-47
Hf	0.58939	0.54603	0.64043	0.30833	0.4919	0.41666		3.0369E-20
Wf	0.83601	0.86238	0.7607	0.56146	0.83103	0.75316	0.53722	

decreasing in the Mirabile Subzone and in the lower part of the Semicelatum Subzone and increasing in the upper part of the Semicelatum Subzone (*Fig. 5*).

Thus, the restriction of the morphological variability detected in the *Liospiriferina* individuals from the morphospace occupation resulting in the PCA analysis (*Fig. 4*), as well as the size decreasing episode identified in the Mirabile Subzone (*Fig. 5*), can be related to the first stages of the Early Toarcian Biotic Crisis. However, size-changes pattern in the rest of the Tenuicostatum Zone probably needs a further interpretation.

Regarding the sea-water paleotemperatures, a number of previous authors have profusely studied their oscillations in this timespan through different methods and techniques, both globally and regionally in the peri-Iberian platforms system (Bailey et al. 2003; Rosales et al. 2004, 2018; McElwain et al. 2005; Gómez et al. 2008; Comas-Rengifo et al. 2010; Gómez & Goy 2011; Danise et al. 2019; Piazza et al. 2019, 2020a; Ruebsam et al. 2019, 2020; Fernandez et al. 2021). Most of these works were based on the changes in the O^{16}/O^{18} isotopic ratio analyzed in belemnites rostra, and bivalves or brachiopods shells. Recently, the oscillation curve presented by Ruebsam et al. (2020), based on the TEX86 paleotemperature proxy (Schouten et al. 2004) provides a

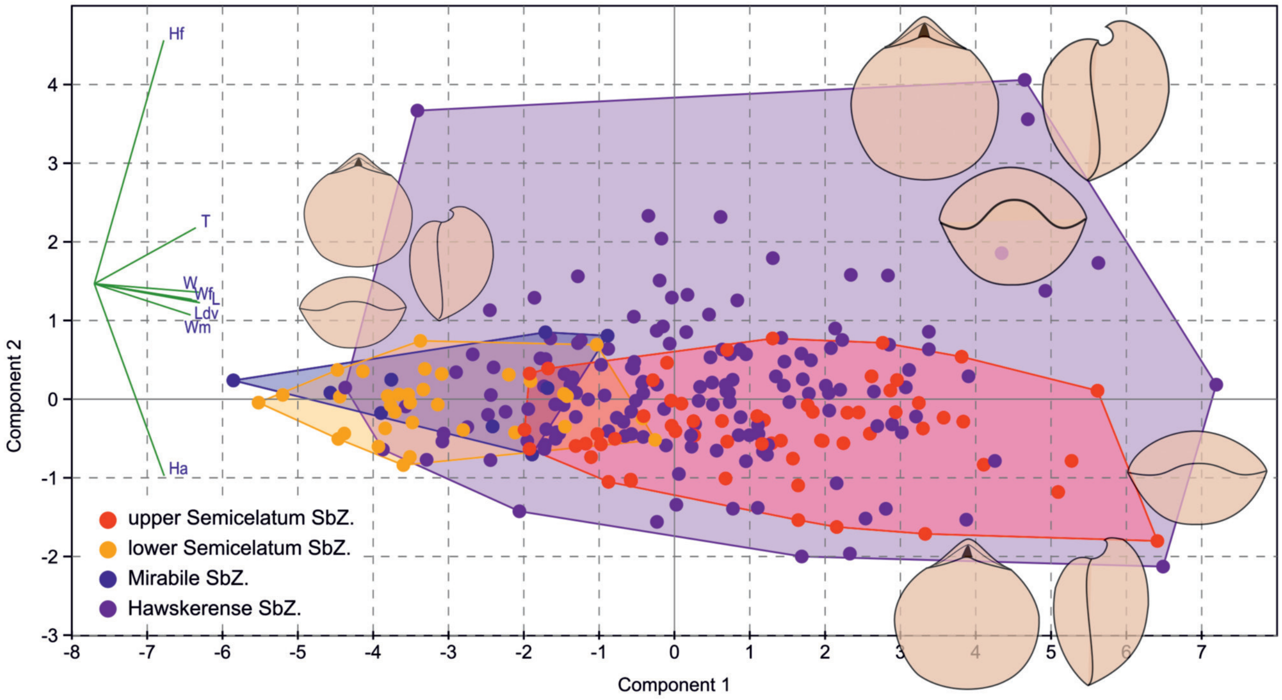

Figure 4. Morphometric scatter diagram of the analyzed representatives of *Liospiriferina* from the Iberian Basin, showing the morphospaces defined by the first two axes of the Principal Component Analysis (PCA). Clusters take into account the distribution over time. Dimensional vectors have been plotted to show the main discriminating factors

4. ábra. *Az Ibériai-medencéből származó* Liospiriferina*-példányok morfometriai szórásdiagramja; a morphospace-t a főkomponens-analízis első két tengelye határozza meg. A klaszterek az időbeliséget érzékeltetik. A dimenziós vektorok a fő megkülönböztető faktorokat mutatják*

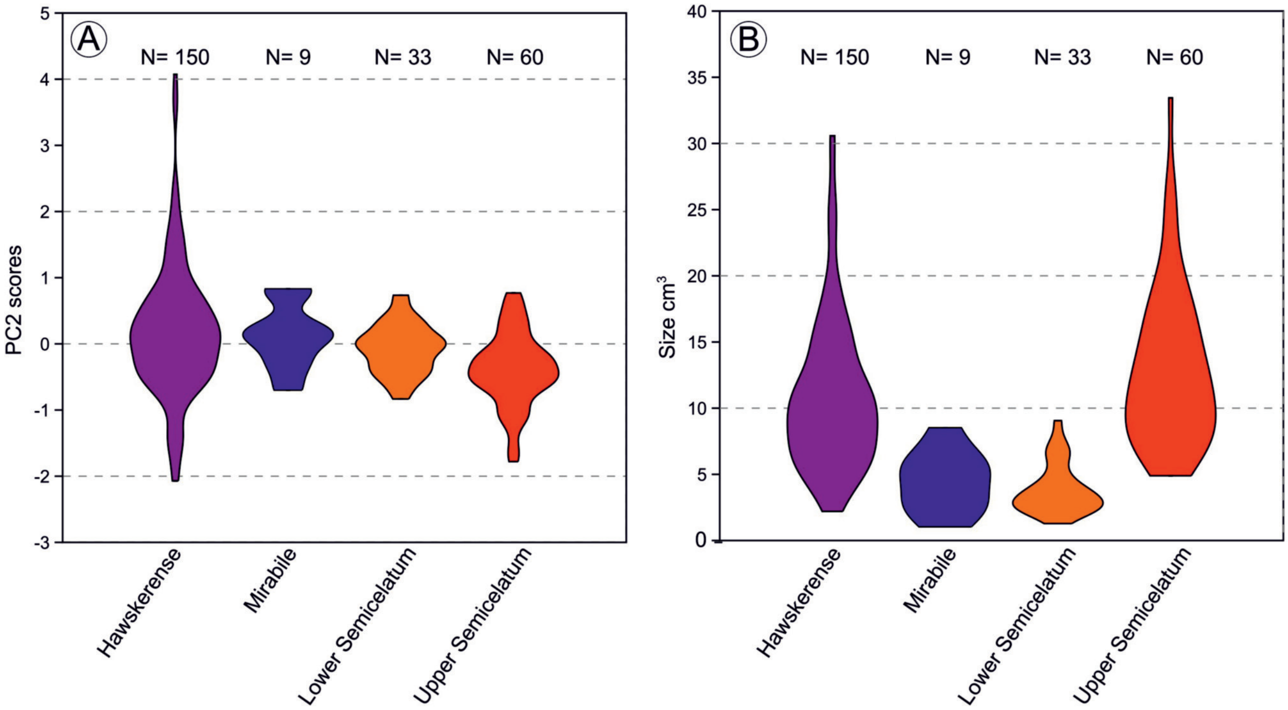

Figure 5. Spindle diagrams of the PCA2 scores (A) and size (B) (estimated volume in cm^3) of the measured specimens of *Liospiriferina* in the studied time intervals. Width of the spindles correspond to the proportion of individuals of each interval of values within the same temporal interval

5. ábra. *Az adott időszakban vizsgált* Liospiriferina*-példányok főkomponens-analízisének dobozdiagramja. A: méreteloszlás; B: becsült térfogat* cm^3*-ben. A dobozok szélessége arányos az egyes értékintervallumokban szereplő egyedek számával*

different perspective and seems to be useful to explain generalized climate change episodes at a regional scale.

To further refine the comparison between size and temperature in the studied *Liospiriferina*, their changes in body size have been confronted in the *Figure 6* with the most detailed temperature curves obtained in the Iberian Range and the SST (Sea Surface Temperature) curve calculated by Ruebsam et al. (2020), which is considered to reflect the annual mean temperature in the upper mixed layer of the ocean on a regional scale. Despite the differences in the temperature data revealed in these studies, and although in the case of the Almonacid de la Cuba stratigraphic section the data do not reach the upper part of the Semicelatum Subzone, a general paleotemperature pattern can be extracted for the Iberian Basin. It seems that, after the important warming episode occurred in the lowermost early Toarcian, fluctuation of cooling and warming periods took place at the time corresponding to the upper part of the Mirabile Subzone and the lower part of the Semicelatum Subzone, followed by a hyperwarming event in the uppermost part of this last Subzone, which may have been of 10 to 15 °C until the end of the Elegantulum Subzone (cf. Gómez & Goy 2011). In La Almunia section, where the more detailed curve was obtained, this severe warming episode is disrupted by a short cooling event coinciding with the Tenuicostatum–Serpentinum zones boundary, which is also recorded in other peri-Iberian and North-European basins (Gómez & Goy 2011, fig. 11) and in the SST curve calculated by Ruebsam et al. (2020).

The significant seawater warming occurred at the beginning of the Mirabile Subzone can be reasonably linked to the decrease in size in the studied *Liospiriferina* representatives (*Fig. 6*). The subsequent significant change in size is an increase recorded in the upper part of the Semicelatum Subzone, which is also observed in other brachiopod genera (cf. Baeza-Carratalá et al. 2017, García Joral et al. 2018). This increase can be correlated with the cooling pulse that has been inferred for this time in the sections of the Iberian Basin shown in *Figure 6*. The SST curve of Ruesbam et al. (2020) does not differentiate the two subzones of the Tenuicostatum Zone, but it also indicates an important cooling phase within this zone that possibly coincides in age with that deduced for the Iberian Basin. After this relative cooling, the second and most severe phase of the hyperthermal event took place. The rapid initial warming is correlated in the Ariño section with a notable decrease in size in the last layer belonging to this subzone, immediately followed by an even more notable increase in size in the overlying level already belonging to the Elegantulum Subzone of the Serpentinum Zone, that coincides with the sudden cooling previously commented. These biggest *Liospiriferina* individuals, together with the standard-sized *Calyptoria* recorded in the same levels in Ariño and in some other localities of the peri-Iberian basins, are the last known representatives of the spiriferinides in the Western Tethys.

Therefore, the tendency to increase in size in certain resilient species of brachiopods exposed in our previous work (García Joral et al. 2018), analyzed at Sub-chronozone level, can now be qualified with the more detailed analysis carried out in this work in light of the more accurate

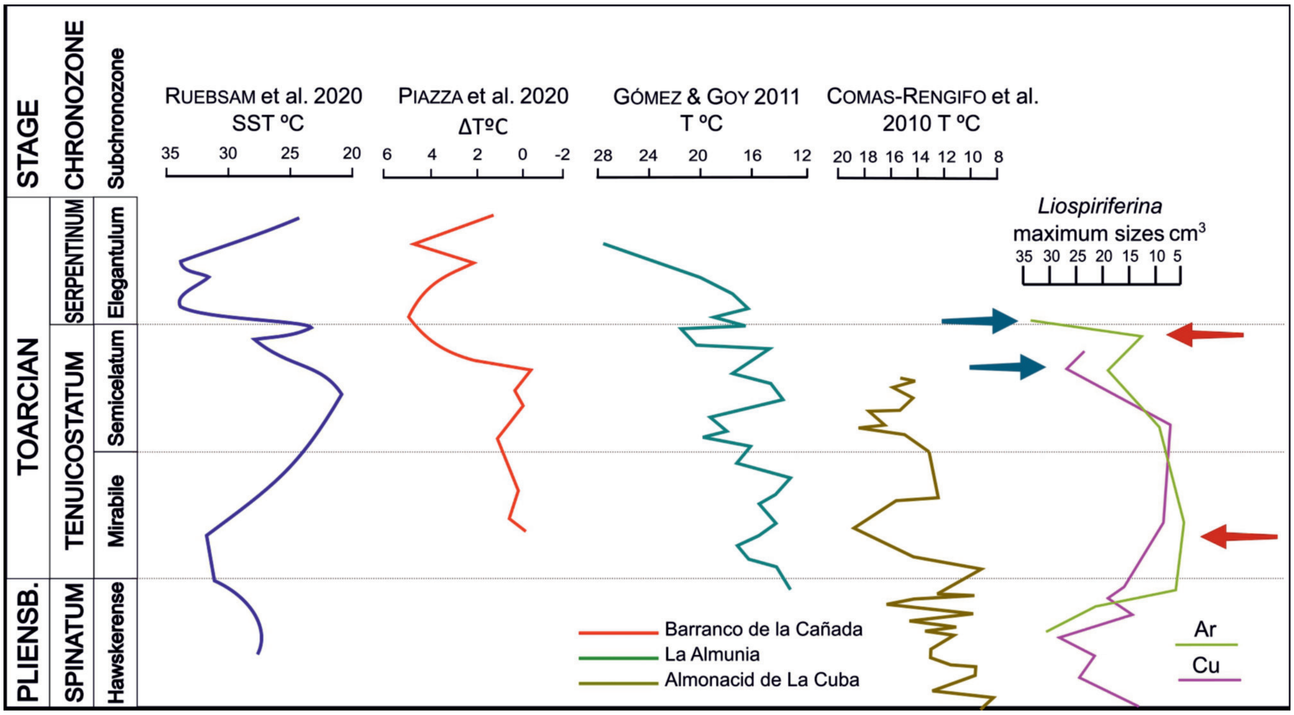

Figure 6. Temperature curves for the extinction interval of the Early Toarcian Biotic Crisis compared with the maximum sizes of the *Liospiriferina* specimens measured in the studied sections. More explanations in the text. Ar: Ariño section; Cu: Almonacid de La Cuba Section

6. ábra. *A kora toarci biotikus krízis idejére eső hőmérsékleti görbék és a* Liospiriferina*-példányok maximális méreteinek összehasonlítása. További magyarázatok a szövegben. Ar: Ariño-szelvény; Cu: Almonacid de La Cuba-szelvény*

temperature and body size data achieved from the Iberian basin. The big size in the *Liospiriferina* specimens – as well as in other representatives of several species – reached in the upper Semicelatum Subzone, could correspond to the cooling episode prior to the maximum hyperthermal event, whereas the even larger size of the last spiriferinides could represent the last heyday of the scarce survivors to the rapid onset of the seawater warming, taking advantage of the short cooling episode around the zonal boundary.

Finally, the severe warming that took place at the beginning of the Serpentinum Chronozone, when the sea-water temperature increased very noticeably (Hu et al. 2020, Ruebsam et al. 2020) seems to have been unbearable for these resilient species.

The Early Toarcian Hyperthermal Event has been related to the widespread occurrence of black shales in many basins around the globe, evidencing a global anoxic event (the so-called Early Toarcian Anoxic Event or "Jenkyns Event"). Anoxia has been recurrently invoked to explain the extinction of the last spire-bearer brachiopods in the Early Toarcian (Vörös 2002). As exposed by Ager (1987) and Vörös et al. (2016), the passive feeding mechanism of spire-bearing brachiopods with fixed lophophores becomes less effective under adverse conditions of oxygenation than the ciliate active feeding of the more adaptable rhynchonellides and terebratulides, and this could have been a factor influencing the extinction of spiriferinids and the survival of the other orders. However, there are no evidence of anoxic environments in most of the peri-Iberian basins, precluding this interpretation in this region (Gómez et al. 2008, García Joral et al. 2011, Gómez & Goy 2011, Piazza et al. 2020b). The severe warming is the most feasible cause of the clade or "fatal extinction" (*sensu* Vörös et al. 2019) that brachiopod fauna experienced at this time, an extinction that is among the most important in the post-Paleozoic history of this phylum and represents, as previously mentioned, the disappearance of the Order Spiriferinida (García Joral et al. 2011; Vörös et al. 2016, 2019). The survival, for a short time, of spiriferinides in the cold seawater habitats of the high latitudes from New Zealand is also consistent with this postulate. As can be seen in *Figure 1A*, the few Pliensbachian spiriferinide records known outside the Western Tethys region are mainly representatives of the "ribbed/winged" morphotype, arranged into the genus *Spiriferina*, which have been considered as the best adapted to the high latitude environments (cf. Guo et al. 2020 and references therein). This is the same morphotype of the last recorded spiriferinides in the New Zealand region (cf. MacFarlan 2023).

Subordinately to the present analysis, it can be also corroborated that brachiopods were unmistakably more sensitive to the sea-water temperature increase (at least in the post-Paleozoic times) than other groups of benthic epibiota, such as bivalves; this is clearly manifested in the different intensity of extinction if both groups are compared in the Early Toarcian (Piazza et al. 2019, 2020a, 2020b).

Conclusions

The significant environmental changes that occurred in the early Toarcian biotic crisis seriously affected the brachiopod fauna, especially to the Order Spiriferinida, whose diversity was previously quite restricted to the point of having been considered as a "Dead Clade Walking". In the lowermost Toarcian, the earlier phase of this crisis entailed a first significant seawater warming episode, leading to the greatly constricted paleobiogeographic distribution of this clade, being limited to the westernmost corner of the Tethys Ocean, in contact with the "Viking" and the "Hispanic" corridors. In this area, the spiriferinides preserved a morphological disparity like that revealed throughout the entire Early Jurassic, although represented by very few species. Furthermore, these species suffered a generalized reduction in size, more noticeable in the more oxygen-starved areas. In the second phase of this ecological crisis, occurred at the basal Serpentinum Chronozone, a new and even more intense warming episode could not be overcome by the few spiriferinide species remaining in this region, thus representing the "fatal extinction" of the Order Spiriferinida.

The abundant and continuous record of spiriferinides in the basins surrounding the Iberian Massif, in Spain and Portugal, allows us to study in detail the changes experienced by the group during this crisis. The analysis of morphology and size changes in individuals of the best represented genus (*Liospiriferina*) in the Iberian Basin, where their record is the most abundant and continuous, reveals a drastic decrease in both features as a consequence of the first marine warming phase, while the only resilient inhabitant species of the genus (*L. falloti*), maintained or even increased their size until the last moment. These size changes may be related to the more or less intense water temperature fluctuations, so that the last big sizes observed are possibly an ultimate response to a short cooling event, intercalated within the very intense warming that is very probably the main cause responsible for the extinction of the spiriferinide clade, together with paleogeographic conditions preventing escape to colder waters environments.

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