Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in Northern and Central Spain

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ABSTRACT

The Early Toarcian mass extinction event represented the most important Mesozoic and Cenozoic turnover of the population of brachiopods and severely affected other benthic fauna. Two main hypotheses have been proposed to explain the synchronous and global mass extinction: an oceanic anoxic event or a warming episode. To test both hypotheses, the dynamics of the brachiopod assemblages below and above the extinction boundary are analyzed and compared with the seawater paleotemperature variations, calculated from the $\delta^{18}O$ data recorded in belemnite rostra. Five sections from Northern and Central Spain, well dated with ammonites, have been selected for this study. The sections show no indication of sedimentary breaks and contain abundant brachiopods, which have been grouped into four assemblages. The changes observed in the brachiopod assemblages show a close correlation with the changes in the seawater paleotemperatures. The oldest assemblage (assemblage 1) coincides with a cooling interval recorded to have taken place in the latest Pliensbachian. Paleobiogeographical reconstruction shows that this assemblage was distributed at paleolatitudes between 30 and 45°N, with a preference for relatively cool waters. With the rise of temperatures that took place during the earliest Toarcian Tenuicostatum Zone, assemblage 1 was substituted by assemblage 2, which composed of different species of the same genera but considerably restricted to the warmer waters of lower paleolatitudes, between 28 and 35°N. Coinciding with the rapid and pronounced increase in seawater temperature, recorded at the Tenuicostatum–Serpentinum zonal boundary, all of these brachiopod species disappeared in the studied localities, marking clearly the extinction boundary. Predominant southward currents through the Laurasian Seaway precluded the possible migration of the brachiopods to cooler northern waters. The brachiopods' disappearance is independent from the oxygenation degree of the sea bottom, and therefore the rapid warming seems to be the most plausible cause of the mass extinction. After the extinction event, the recovery of the brachiopods was uneven. Subsequent to a brief pause, recovery was rapid in Central Spain and in other southern areas of Western Tethys, whereas in northern Spain and in the whole of Europe north of the French Central Massif, brachiopods did not recover until the Mid to Late Toarcian times.

*Keywords: Br*achiopods Mass extinction Paleoclimate Stable isotopes Early Toarcian

1. Introduction

One of the most important mass extinctions of the Mesozoic was recorded around the Tenuicostatum–Serpentinum zonal boundary (182.7 Ma, Ogg, 2004) of the Lower Toarcian (Lower Jurassic). This extinction event specially affected the benthic organisms, but nektonic groups also suffered significant crises (e.g. Hallam, 1986, 1987; Arias et al., 1992; Little and Benton, 1995; Aberhan and Fürsich, 1997; Harries and Little, 1999; García Joral and Goy, 2000; Pálfy and Smith, 2000; Vörös, 2002; Cecca and Macchioni, 2004; Zakharov et al., 2006; Gómez et al., 2008; Nikitenko, 2008; Gómez and Arias, 2010; Gómez and Goy, 2010).

Two different hypotheses have been proposed to explain this episode of massive loss of biodiversity. One hypothesis assumes that the main cause of the mass extinction is the global generalization of anoxic environments (e.g. Jenkyns, 1988; Bassoullet and Baudin, 1994; Nikitenko and Shurygin, 1994; Harries and Little, 1999; Pálfy and Smith, 2000; Jenkyns et al., 2002; Vörös, 2002; Aberhan and Baumiller, 2003; Mattioli et al., 2004, 2009; Tremolada et al., 2005; Wignall et al., 2005; Mailliot et al., 2008). This opinion is inferred from the deposition of organic-rich black-shale facies during Early Toarcian, as the result of a supposedly synchronous and global major Early Toarcian Oceanic Anoxic Event (ETOAE) (Jenkyns, 1985, 1988, 1999, 2003; Jenkyns and Clayton, 1986, 1997; Jenkyns et al., 1994, 2001, 2002; Jiménez et al., 1996; Mailliot et al., 2006). However, reappraisal of this hypothesis through high-resolution stratigraphy indicates that the ETOAE seems to be diachronous at the ammonite zone/subzone scale and only occasionally coincident with the mass extinction boundary (Wignall et al., 2005; Gómez et al., 2008; McArthur et al., 2008), and that

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deposition of significant black-shale facies, containing above 5 wt.% of total organic carbon (TOC), is restricted to some areas such as the Central European basin.

The other hypothesis links the mass extinction event to the outstanding Early Toarcian warming interval, which has been documented in many different areas of Western Europe such as the UK (Jenkyns et al., 1991; Sælen et al., 1996; McArthur et al., 2000; Jenkyns, 2003), Germany (Röhl et al., 2001; Schmid-Röhl et al., 2002), Spain (Rosales et al., 2003, 2004; Gómez et al., 2008; Gómez and Arias, 2010; Gómez and Goy, 2010), France (Dera et al., 2009), Bulgaria (Metodiev and Koleva-Rekalova, 2008), and that has also been recorded in North Siberia and in the Arctic (Zakharov et al., 2006). Synchronism between the mass extinction event and the recorded climate change supports that warming was the main cause of marine faunal extinction (Gómez et al., 2008; Gómez and Arias, 2010; Gómez and Goy, 2010). Among the benthic organisms, brachiopods are one of the groups that were more affected by this mass extinction, representing the most important turnover event recorded in this group during the Mesozoic and the Cenozoic eras (García Joral et al., 2000; Gahr, 2002; Vörös, 2002; Comas-Rengifo et al., 2006).

The variations in the brachiopod assemblages below and above the extinction boundary in two sections located in northern Spain (Asturias and the Basque–Cantabrian Basin) and in three sections located in central Spain (Iberian Range) are described (Fig. 1). In all the studied sections, the Lower Toarcian stratigraphical record is virtually continuous, with no significant sedimentary breaks; the brachiopods are abundant, represented by well known taxa from a systematic point of view, and quite similar from one locality to another.

The aim of this work is to show the changes in the diversity and taxonomical composition of the brachiopod assemblages before, during and after the extinction event and to compare the recorded changes with the synchronous climate change manifested in the seawater increment in temperature, inferred from the $\delta^{18}O$ values obtained from diagenetically screened calcite of belemnite rostra.

2. Materials and methods

The five sections have been studied bed by bed and those levels close to the extinction boundary were sampled more exhaustively to have a high resolution record of the present/absent taxa. Belemnites were prepared for isotopic studies in three of the studied sections. A total of 54 belemnite rostra were collected in the West Rodiles section, and 72 analyses of stable isotope were performed; 19 belemnites were collected and analyzed at the San Andres section and 50 belemnites were collected and analyzed at La Almunia section.

Belemnite rostra were selected to obtain the primary stable isotope signal of the Early Toarcian seawater. In order to test for any possible burial diagenetic alteration of the collected belemnites, the rostra were studied through polished samples and thick sections under the petrographic and the cathodoluminescence microscope. Only the potentially unaltered non-luminescent portions of the rostra were sampled using a microscope-mounted dental drill. Samples with insufficient space for sampling were rejected.

To be sure that only calcite was present in the samples, X-ray diffraction techniques were used in 30 belemnite samples. The stable isotope analyses were performed in the Michigan University (USA) and the Salamanca University (Spain) labs. Several samples were analyzed in both laboratories with acceptable repeatability. Isotope ratios are reported in per mil respect to the standard Peedee belemnite (PDB) in all samples. Analytical error was in most cases better than ± 0.1‰ on both carbon and oxygen.

For the calculation of the Toarcian seawater temperatures recorded in the belemnite rostra, the Anderson and Arthur (1983) equation: $T(°C)=16.0-4.14\ (\delta_c-\delta_w)+0.13\ (\delta_c-\delta_w)^2$ has been used. In this equation $\delta_c=\delta^{18}O$ PDB is the composition of the sample, and $\delta_w=\delta^{18}O$ SMOW is the composition of ambient seawater. Normal values of marine salinity $S=34.3‰$ (Wright, 1987) and δ_w values of $-1‰$ for a non-glacial ocean water were used. To use the belemnite rostra as a proxy for paleotemperature calculation, it has been assumed that 1) the sampled non-luminescent biogenic calcite of the belemnite rostra collected in the Toarcian deposits of the three studied sections precipitated in equilibrium with the seawater, 2) biogenic calcite retains the primary isotopic composition of the seawater, and 3) sampling bias, vital effects, skeletal growth and belemnites migration are not mainly responsible for the obtained variations in the $\delta^{18}O$ values, and consequently that the obtained curve virtually only reflects changes in environmental parameters (Sælen et al., 1996; Rexfort and Mutterlose, 2009).

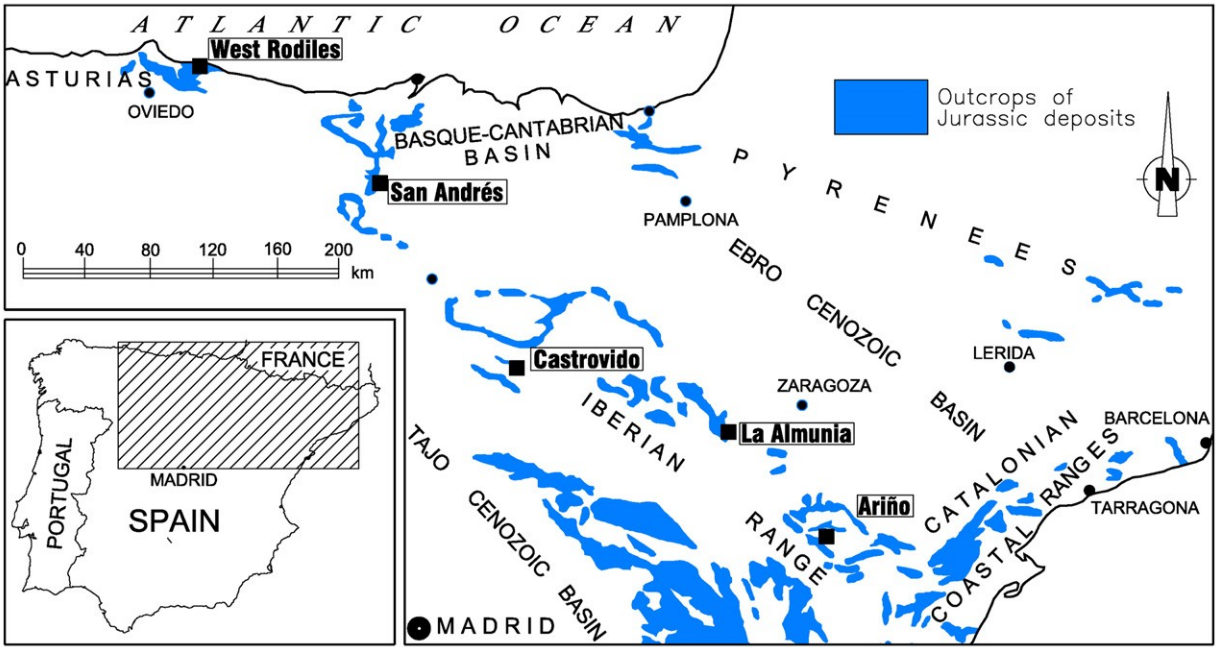


Fig. 1. Map showing the location of the studied sections. The study area constitutes a northeast–southwest transverse from the West Rodiles section in Asturias through the San Andrés section in the Basque–Cantabrian Basin and the Castrovido, La Almunia and Ariño sections in the Iberian Range.

3. Stratigraphic sections

All the studied sections are expanded, with irrelevant or no indication of condensation or sedimentary discontinuities. From north to south, in the West Rodiles section at Asturias (Fig. 2), the Lower Toarcian deposits are composed of an alternation of limestone and marl corresponding to the Santa Mera Member of the Rodiles Formation (Valenzuela et al., 1986; García-Ramos et al., 1992), in which a thinly banded interval containing up to 3.2 wt.% TOC, marks the Tenuicostatum–Serpentinum zonal boundary. At the San Andres section (Fig. 2), located in the Basque–Cantabrian Basin, the Lower Toarcian deposits are represented by an alternation of limestone and marl corresponding to the Castillo Pedroso Formation (Quesada et al., 2005), with interbedded organic horizons (up to 1.5 wt.% TOC) below and above the Tenuicostatum–Serpentinum zonal boundary. In the Iberian Range sections (Figs. 2 and 3), the Lower Toarcian sediments are represented by an alternation of lime mudstone and marl corresponding to the Turmiel Formation (Goy et al., 1976; Gómez et al., 2003). No organic-rich facies were found and only one value above 1 wt.% TOC (1.2 wt.%), corresponding to the lower part of the Tenuicostatum Zone, was obtained from a single sample at La Almunia section. Chronostratigraphy obtained in the different areas has been adapted to the standard ammonite zones and subzones proposed by Dommergues et al. (1997), Elmi et al. (1997) and Page (2003).

4. Brachiopod assemblages

Significant differences in the brachiopod diversity have been observed among the sections located in northern Spain and the sections located in the Iberian Range of central Spain. The number of species represented in the northern Spain sections is significantly lower than the diversity found in the central Spain sections, probably reflecting different environmental conditions between both areas. In most cases shells are not recrystallized, and no significant differences in shell preservation are observed.

The twenty-two recognized species of brachiopods have been grouped into four assemblages, and their respective stratigraphical distribution has been represented in Figs. 2 and 3. These Lower Toarcian brachiopod assemblages, previously described by Goy et al. (1997) and García Joral and Goy (2000), are illustrated in Figs. 4 and 5.

Assemblage 1 is constituted of typical Pliensbachian taxa, which extend their stratigraphical distributions up to the lower part of the Tenuicostatum Zone of the Lower Toarcian. Assemblage 2 is mostly confined to the Tenuicostatum Zone, though some of its components can have their first appearance at the uppermost Spinatum Zone of the Upper Pliensbachian. The species included in assemblages 1 and 2 disappear around the Tenuicostatum–Serpentinum zonal boundary. Only locally some species of assemblage 2 can appear in the first bed of the Serpentinum Zone, but the possibility of local reworking with incorporation of some fossils from previous beds into the basal beds of the Serpentinum Zone cannot be dismissed. Consequently, the boundary between the Tenuicostatum and the Serpentinum zones marks the extinction boundary in all the studied sections, as in many other sections of Europe, Northern Africa and probably in North Siberia and the Arctic Region. Below this boundary, the uppermost Pliensbachian Spinatum Zone and the lowermost Toarcian Tenuicostatum Zone represent the extinction interval in the sense of Kauffman and Erwin (1995). Comparison of the age of this interval with other European sections indicates its synchronism (Hallam, 1987; Arias et al., 1992; Little and Benton, 1995; Aberhan and Fürsich, 1997; Goy et al., 1998; Harries and Little, 1999; García Joral and Goy;, 2000; Pálfy and Smith, 2000; Cecca and Macchioni, 2004; Zakharov et al., 2006; Gómez et al., 2008; Nikitenko, 2008; Gómez and Arias, 2010; Gómez and Goy, 2010). Assemblage 3 is constituted of just one species, *Soaresirhynchia bouchardi*, which first appears in the lower part of the Serpentinum Zone, just above the extinction boundary. Assemblage 4 appears at the Serpentinum Zone, starting in the last horizons containing *S. bouchardi*, and extends up to the Middle Toarcian Bifrons Zone. It is dominated by species of the genera *Homoeorhynchia* and *Telothyris*. Assemblages 3 and 4 clearly represent the repopulation interval, but this recovery is only recorded at the Lower Toarcian in the Iberian Range sections. These assemblages do not appear in the northern Spain sections, where no brachiopods are recorded below the Middle Toarcian. A similar delay in the recovery of the brachiopods after the extinction is observed in other regions of western Tethys (Fig. 6), so that assemblages 3 and 4 are present in warm areas from the Serpentinum Zone, whereas in many areas of Western Europe located north of the Massif Central in France, the recovery does not start until the Middle or Upper Toarcian (Ager, 1978; Tchoumatchenco, 1984; Georgescu, 1990; García Joral and Goy, 2009). Only occasional records of *Pseudogibbirhynchia jurensis* (Alméras et al., 1997) and *Neozeilleria lycetti* (Delance, 1974) have been cited in the Middle Toarcian Bifrons or Variabilis zones.

5. Paleogeography and paleobiogeographical distribution of the brachiopod assemblages

5.1. Paleogeographical setting

During the Late Pliensbachian–Early Toarcian, central Iberia was located at a latitude of about 30–35°N (Osete et al., 2000, 2010), constituting a system of platforms that were distributed around the Iberian Massif. This platform system was connected eastward with the Neotethys Ocean, to the north with the Arctic, through the so-called "Viking Straits" (Poulton and Callomon, 1977; Callomon, 1979) or "Laurasian Seaway" (Bjerrum et al., 2001), and to the West with South America through the Hispanic Corridor, probably intermittently open since the Sinemurian/Pliensbachian (Smith, 1983; Damborenea, 2000; Aberhan, 2001; Sha, 2002) (Fig. 6a and b). Modeling of the paleoceanographical conditions through the Laurasian Seaway indicate the presence of predominant southward currents along this passage (Bjerrum et al., 2001), which has also been supported by the distribution of the ostracods at that time (Arias, 2006, 2007), by the Koninckinid brachiopods (Vörös, 2002) and by the neodymium isotopes (Dera et al., 2009).

In regions of Western Europe located north of the Iberian Massif, an euxinic basin, mostly due to the stagnation of stratified water masses, gave rise to the deposition of well developed black-shale facies where values higher than 5 wt.% TOC are common (Sælen et al., 2000; Röhl et al., 2001; van Breuguel et al., 2006; McArthur, et al., 2008). To the south of this area, scattered intervals commonly containing below 5 wt.% TOC, have been found in many other places (e.g. Southern France, Spain, Portugal, Italy, and Northern Morocco). In Argentina, only two samples having TOC values slightly above 5 wt.
% TOC have been reported from the boundary beds between the Tenuicostatum and Hoelderi Zones in the Neuquén Basin (Al-Suwaidi et al., 2010), indicating the presence of local, ephemeral and/or diachronous restriction conditions. For the Early Toarcian euxinic sea of NW Europe, the term regional anoxic event, (RAE) has been proposed by McArthur et al. (2008) to substitute the concept of oceanic anoxic event (OAE) proposed by Jenkyns (1988).

5.2. Paleobiogeographical distribution of the brachiopod assemblages

Plotting the distribution of the brachiopod assemblages referred to in this paper on the paleogeographical map of Europe and northern Africa (Fig. 6) shows that these assemblages are present in a wide area.

Assemblage 1 shows a clear relationship with the taxa found in other neighboring platforms such as in the UK, Germany, France, Portugal and northern Africa, the so-called "European" province (cf.

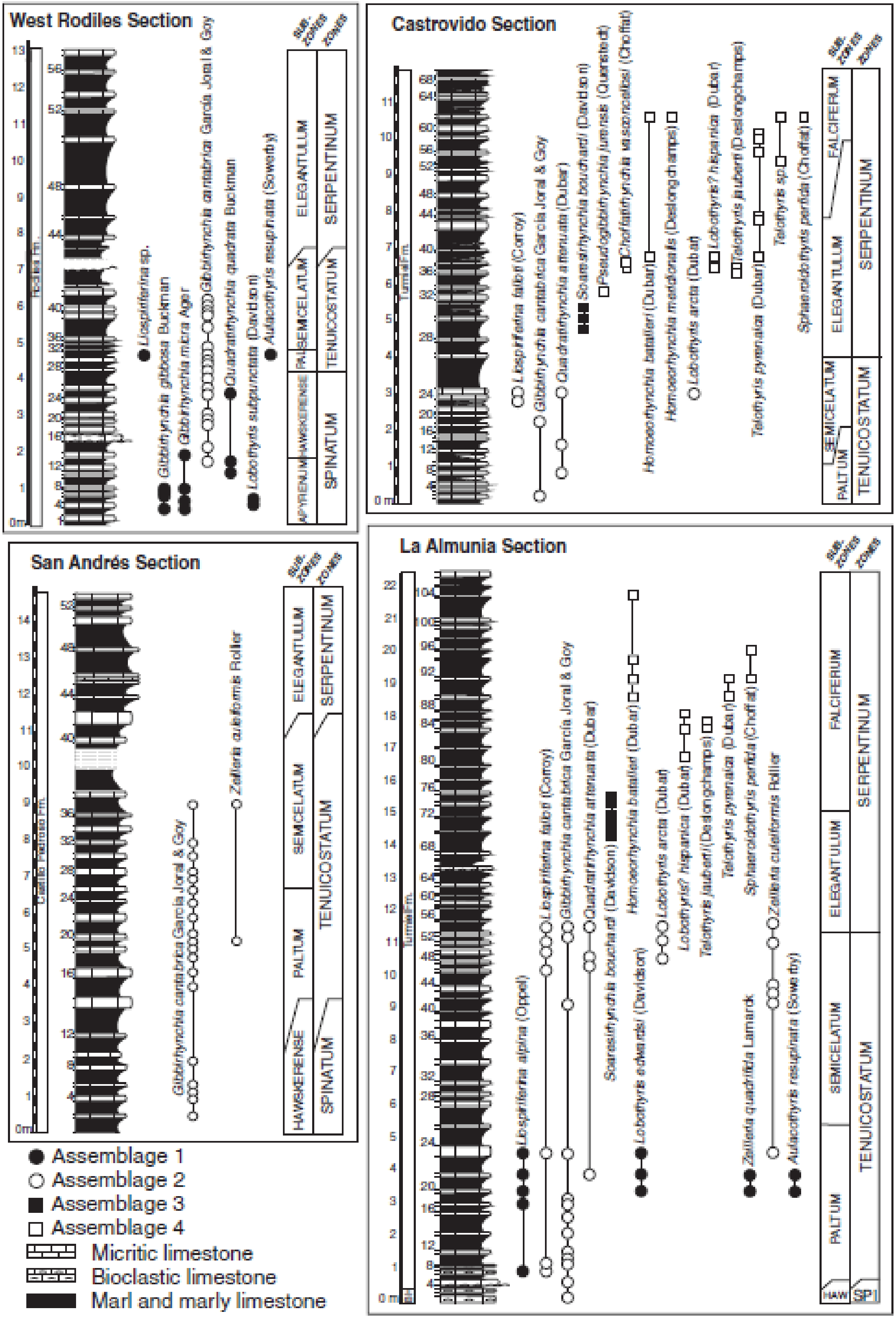


Fig. 2. Distribution of the species and assemblages of brachiopods in the West Rodiles, San Andrés, Castrovido and La Almunia sections. Ammonites-based biochronostratigraphy in the West Rodiles section after Gómez et al., (2008), García Joral and Goy (2009), in the San Andrés section modified after Goy et al. (1994), in the Castrovido section modified after Comas-Rengifo et al. (1988), and in the La Almunia section after Goy and Martínez (1990), Goy et al. (1996), Gómez et al. (2008).

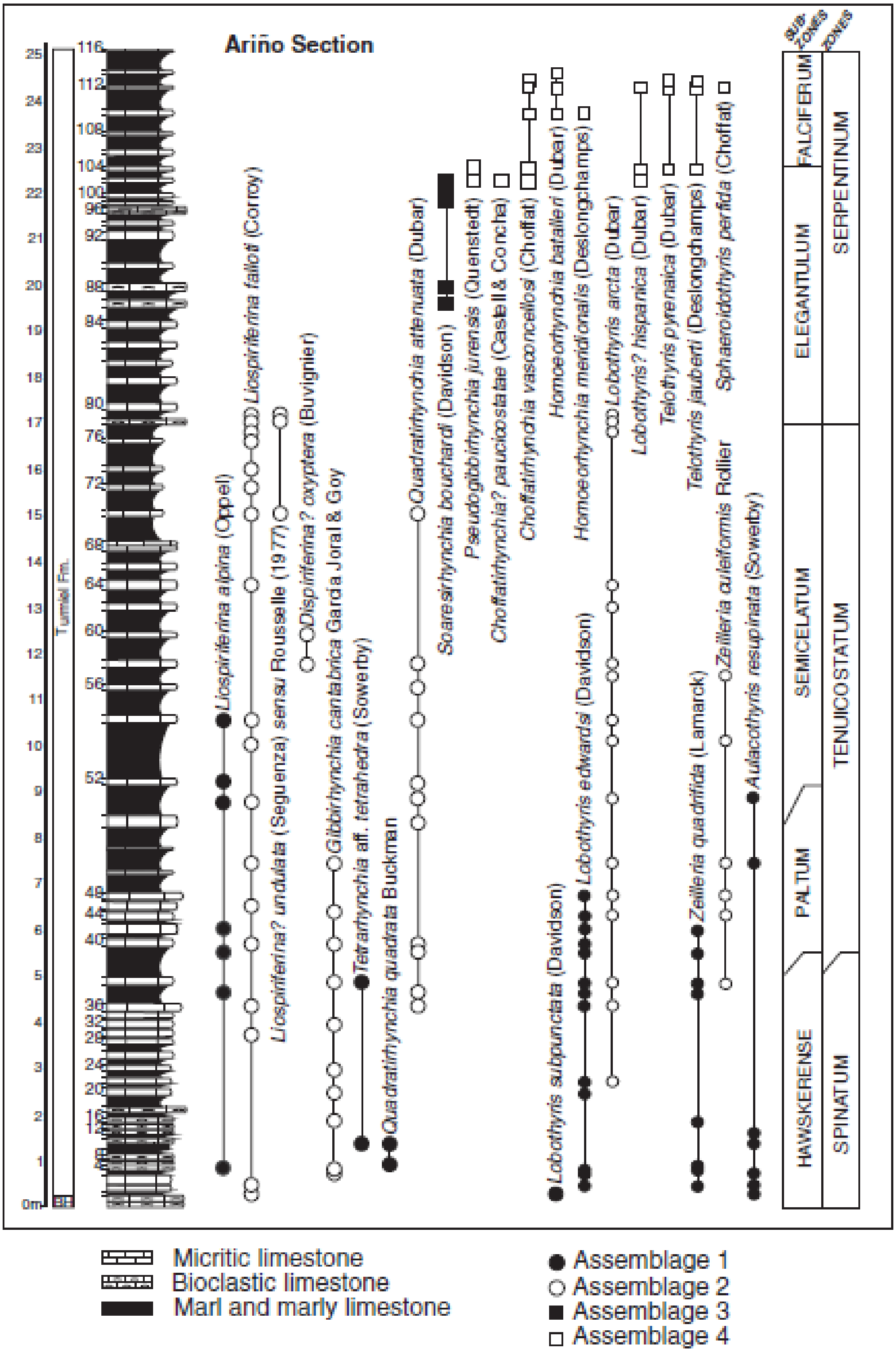


Fig. 3. Distribution of the species and assemblages of brachiopods in the Ariño section. Ammonites-based biochronostratigraphy in this section has been modified after Goy et al. (1997), Osete et al. (2007).

Ager, 1967, 1971; Hallam, 1971; Vörös, 1977, 1984, 1987; Manceñido, 2002). This assemblage can clearly be distinguished from others found in warmer Tethyan areas of the "Mediterranean" Province, though it includes genera of wide distribution (*Liospiriferina*, *Tetrarhynchia*, *Gibbirhynchia*, *Lobothyris*, and *Zeilleria*) that can be considered as nearly cosmopolitan. This provincialism has been primarily attributed to bathymetric/bottom controlled differences (Ager, 1965; Vörös, 2005). However, as shown in Fig. 6b, the species constituting assemblage 1 were mainly distributed at paleolatitudes between 30 and 45°N, suggesting a latitudinal/temperature control, and therefore inhabiting relatively cool waters.

Assemblage 2 is notably more restricted to paleolatitudes around 28°–35°N, and following the same reasoning, preferentially linked to warmer waters. It includes species of the same genera as assemblage 1 but of a more endemic distribution. The dominant species, *Gibbirhynchia cantabrica*, is characteristic of the northern Iberian platform system (Asturias, Basque–Cantabrian Basin and western Pyrenees), though this species can also been found in the central Iberian Range and to the south of the Armorican Massif (Alméras and Fauré, 2000; Alméras and Becaud, 2002).

Assemblage 3, composed of the single species *Soaresirhynchia bouchardi*, has a relatively wide geographical distribution, from southern England to Morocco and from Portugal to the Balkans, including some typically Mediterranean areas such as the High Atlas in Morocco (Rousselle, 1978), the eastern Betic Range in southern Spain (Baeza-Carratalá, 2008), Majorca Island (Álvaro et al., 1989) or the Central Apeninnes (Graziano et al., 2006). Except for a few occurrences, *S. bouchardi* is distributed in paleolatitudes lower than 35°N (Fig. 6), indicating a probable Mediterranean provenance, linked to warm environments. Anecdotically, this species was described in southern England (Davidson, 1852) where it is uncommon and represents the northernmost locality where this taxon has been reported.

Assemblage 4, which is centered at a paleolatitude of about 35°N (Fig. 6), is characteristic of the so-called "Spanish Fauna" (Choffat, 1880; Dubar, 1931; Delance, 1972) or of the Spanish Bioprovince (García Joral and Goy, 1984, 2004). Besides the Iberian Range, this assemblage extends throughout the Middle Atlas in Morocco and Western Algeria (Elmi et al., 1985, 1991), Portugal (Alméras et al., 1996), Southern Spain (Eastern Subbetic) (Bizon et al., 1966; Baeza- Carratalá, 2008), Eastern Spain (Catalonian Coastal Ranges) (Dubar, 1931; Fernández-López et al., 1998), Eastern Pyrenees (Alméras and Fauré, 2000) and Southeastern France (Alméras and Moulan, 1982; Alméras, 1996; Alméras et al., 1997). Some components of this as- semblage (often congeneric, even sometimes conspecific), have been found in South America at a similar paleolatitude (Manceñido, 1990, 2002; Manceñido and Dagys, 1992), not only supporting the exis- tence of a connection between Europe and South America through the already open Hispanic Corridor (cf. Manceñido, 2002) (Fig. 6a) but also the control of temperature in the didemic distribution of this assemblage.

6. Oxygen isotope and paleotemperatures

Correlation of the $\delta^{18}O_{bel}$ curves obtained in Asturias, in the Basque–Cantabrian Basin and in the Iberian Range shows strong similarities among the three areas (Fig. 7). Late Pliensbachian, $\delta^{18}O_{bel}$ average values are relatively high (about 0‰ in Asturias). However, throughout the lowermost Toarcian Tenuicostatum Zone, $\delta^{18}O_{bel}$ values progressively decreased, reaching minimal values at the Sepentinum Zone. This was the beginning of an important negative excursion that developed from the Elegantulum Subzone (Serpenti- num Zone) up to the upper Bifrons Subzone (Middle Toarcian Bifrons Zone), in which the $\delta^{18}O_{bel}$ values severely became more negative, reaching peak values of up to −3.8‰ at La Almunia section.

The curve illustrating the seawater temperature variations during the Early to Middle Toarcian (Fig. 8) shows that the paleotem- peratures recorded at the latest Pliensbachian Spinatum Zone in the West Rodiles section were relatively low, averaging 11.6 °C. Similar temperatures were obtained by Rosales et al. (2004) in the Basque–Cantabrian Basin, in northern Spain, in Germany (Bailey et al., 2003), and in several localities of Central Europe (Dera et al., 2009), indicating the presence of a notable cooling interval in the latest Pliensbachian.

The beginning of the Toarcian was coincident with the transition from this cooling interval to a progressively warmer climate. During this transition, which extends up to the upper part of the Tenuicostatum Zone, the measured average paleotemperature was 15.5 °C in the West Rodiles section, 14.8 °C in the San Andres section and 16.3 °C in the La Almunia section. This represents a first interval of increasing seawater temperature at the Iberian platform system in the order of 4–5 °C. The progressive warming represents an important change in the environmental conditions under which brachiopods were living. It coincides with the extinction interval, marked by the progressive replacement of brachiopods of assemblage 1, more adapted to cooler conditions, by the species of assemblage 2, better adapted to warmer environments.

Close to the Tenuicostatum–Serpentinum zonal boundary, a notable increase in seawater temperature began. The onset of this rapid warming coincides with the extinction boundary, in which all the brachiopods of assemblages 1 and 2 disappeared. Average paleotemperatures of 20 °C in the West Rodiles section, and 23 °C in the La Almunia section were attained during this rapid warming, which extended up to the upper part of the Bifrons Zone (Bifrons Subzone) (Fig. 8). This implied an increment of temperature in the order of 4.5 °C in the West Rodiles section, and about 6.7 °C in the southerly La Almunia section.

The range of seawater temperatures reached during the Toarcian is compatible with the temperature values measured in current oceans (NOAA). Considering that the paleolatitude of Madrid, calculated for Toarcian times, was approximately 30–35°N (Osete et al., 2000), the inferred paleotemperatures indicate for this warming interval values 3–6 °C above the temperatures measured in to-days oceans.

7. Discussion

7.1. Correlation between the distribution of the brachiopods and temperature changes

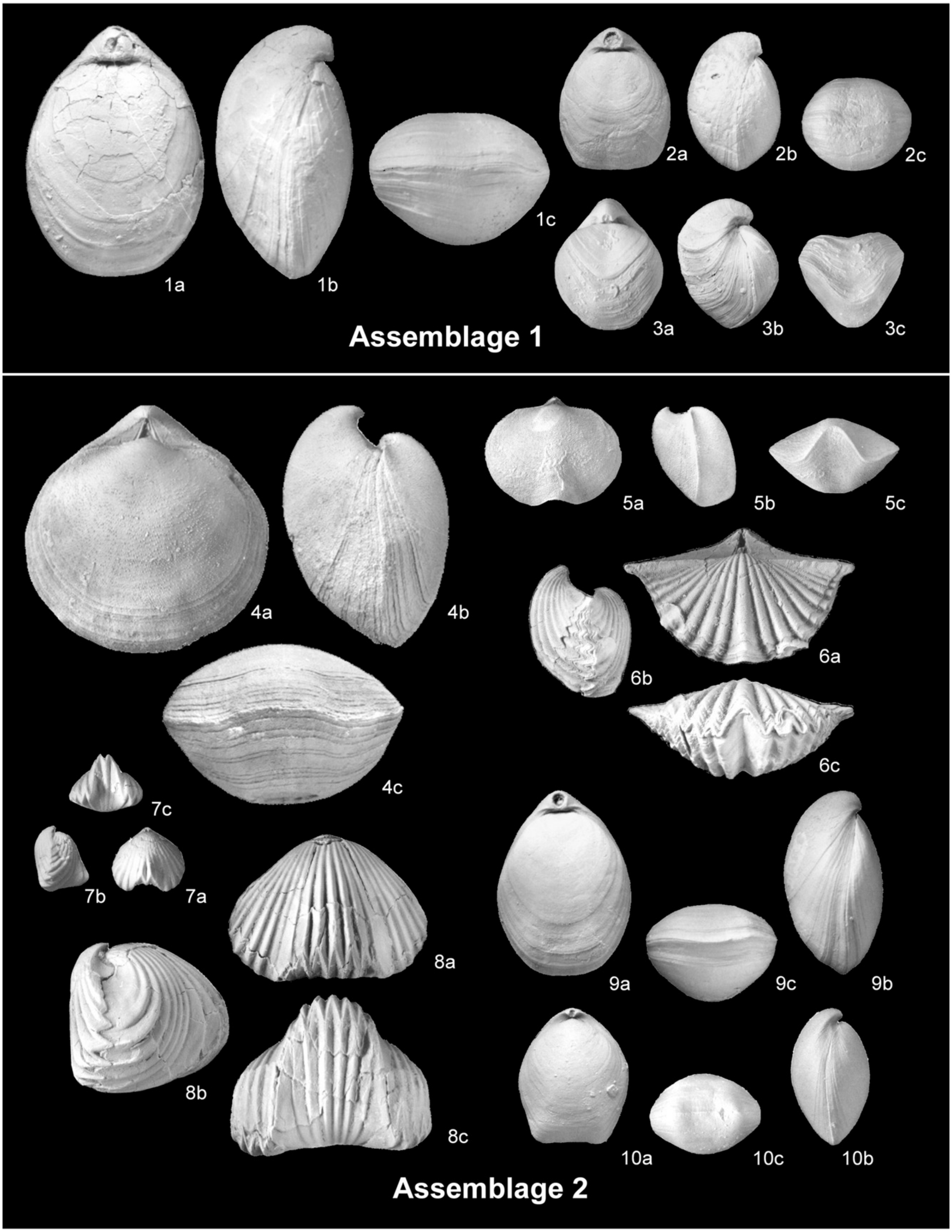
Inferred seawater temperatures, stratigraphical distribution of the brachiopod assemblages, and the number of species in the stud- ied sections show a close correlation (Fig. 8). The progressive warm- ing during the Tenuicostatum Zone time correlates with a progressive loss of brachiopod species and the replacement of assemblage 1 by assemblage 2. The rapid warming at the Tenuicostatum–Serpentinum zonal boundary correlates with the disappearance of all brachiopods in the studied sections. The stable high temperatures recorded in the Serpentinum and Bifrons zones correlate with the occurrence of assemblages 3 and 4, in which a progressive increase of species is observed.

Not enough information on the influence of temperature on the brachiopods is available. However, provinciality among many Mesozoic brachiopods approximately follows latitudinal belts, indi- cating that temperature has been an important controlling factor (Middlemiss, 1984; Price, 1999). Vörös (2002) described how some species of Koninckinidae of the Upper Pliensbachian and Lower

Fig. 4. Photographs of some representative species of assemblages 1 and 2 described in this paper. 1: *Lobothyris subpunctata* (Davidson, 1851). Specimen labeled Ar.7.157, from the Spinatum Zone (Hawskerense Subzone) of the Ariño Section. 2: *Lobothyris edwardsi* (Davidson, 1851). Specimen labeled Ar.7.152, from the Spinatum Zone (Hawskerense Subzone) of the Ariño Section. 3: *Aulacothyris resupinata* (Sowerby, 1818). Specimen labeled Ar.7.302, from the Spinatum Zone (Hawskerense Subzone) of the Ariño Section. 4: *Liospiriferina falloti* (Corroy, 1927). Specimen labeled 1Ar.79, from the Tenuicostatum Zone (Semicelatum Subzone) of the Ariño Section. This specimen has been figured in Comas-Rengifo et al., 2006, Fig. 4:5. 5: *Liospiriferina? undulata* (Seguenza, 1885 *sensu* Rousselle, 1977). Specimen labeled Ar.8.201, from the Tenuicostatum Zone (Semicelatum Subzone) of the Ariño Section. 6: *Dispiriferina? oxyptera* (Buvignier, 1843). Specimen labeled Ar.7.101, from the Tenuicostatum Zone (Semicelatum Subzone) of the Ariño Section. 7: *Gibbirhynchia cantabrica* García Joral and Goy, 2009. Specimen labeled 1Ar.45.2, from the Tenuicostatum Zone (Paltum Subzone) of the Ariño Section. 8: *Quadratirhynchia attenuata* (Dubar, 1931). Specimen labeled Ar.7.102, from the Tenuicostatum Zone (Semicelatum Subzone) of the Ariño Section. 9: *Lobothyris arcta* (Dubar, 1931). Specimen labeled Ar.8.101, from the Tenuicostatum Zone (Semicelatum Subzone) of the Ariño Section. 10: *Zeilleria culeiformis* Rollier, 1919. Specimen labeled Ar.7.301, from the Tenuicostatum Zone (Paltum Subzone) of the Ariño Section. (a = dorsal view, b = lateral view, and c = frontal view). The figured specimens are deposited in the collections of the Department of Palaeontology UCM. All photographs (X1).

Toarcian migrated to the Western European platforms escaping from the high seawater temperatures developed in the areas where they were living, and finally disappeared at the extinction boundary. A marked latitudinal didemic distribution (mainly bipolar) of other benthic organisms, such as bivalves, has been pointed out by many authors (e.g., Damborenea, 1993, 1998, 2002). This didemic distribution is, for some authors, mostly due to temperature (Liu et al., 1998; Westermann, 2000).

Other factors may be important controlling the geographic distribution of these organisms. Many authors agree in the importance



of oceanic currents for most benthic organisms, and more specifically for the brachiopods, since currents strongly determine larval dispersion (Richardson, 1997). In the case of the Iberian platform system, the southward currents through the Laurasian Seaway hampered northward migration of the benthic organisms toward northern cooler waters, making temperature changes insurmountable events for brachiopods.

The extinction and recovery observed in the brachiopods of this study fit well with the models proposed by Walliser (1986) and other authors (see Twitchett, 2006 for a revision), with an extinction interval, an extinction boundary and a repopulation interval (García Joral et al., 2000; Gahr, 2002, 2005).

7.2. The extinction interval

This interval is characterized by an evident relationship between the progressive seawater warming and the progressive brachiopod turnover from assemblage 1 to assemblage 2. Besides, a marked latitudinal gradient in the diversity and in the size of the brachiopods is observed. In the Lower Toarcian Tenuicostatum Zone, brachiopods are less diverse and show an important decrease in size towards the northwestern sections. Taxa number is maximum at the southernmost section of Ariño (Figs. 1 and 3), in La Almunia section, located approximately 90 km to the northwest (Fig. 1), the number of taxa of assemblages 1 and 2 is still high, but several species such as *Liospiriferina falloti*, *Quadratirhynchia attenuata* and *Lobothyris arcta* present smaller sizes. At the Castrovido section, in the northern Iberian Range, few beds contain brachiopods at the Tenuicostaum Zone. In the Basque–Cantabrian Basin, at the San Andres section, the brachiopod diversity is notably lower (Figs. 2 and 8); only assemblage 2 is present and it consists of only two species (*Gibbirhynchia cantabrica* and *Zeilleria culeiformis*), the two smaller species of assemblage 2. In the northernmost section (West Rodiles) some species of assemblage 1 are recorded, all of them represented by individuals of a smaller size than in the Iberian Range; assemblage 2 is represented by just one species (*G. cantabrica*). It is important to emphasize that the smaller sizes observed towards the north is not only due to miniaturization processes, but rather to the northward predominance of the smaller sized taxa. These gradients mark a notable north–south polarity in the environmental conditions which parallels a progressive deepening of the platform to the north.

Beside this spatial gradient, most species of assemblage 2 in some sections of the Iberian Range, as in Ariño, are present in the uppermost bed before the extinction without a noticeable size decrease or changes in morphology. In fact, some species like *Liospiriferina falloti* increase their size, the largest specimens often appearing at the uppermost Tenuicostatum Zone, immediately before the final extinction of the order Spiriferinida. A similar pattern is exhibited by *Gibbirhynchia cantabrica* (cf. García Joral and Goy, 2009, Fig. 5).

Miniaturization within a lineage is a very common phenomenon in brachiopods, and has been related with developmental heterochronies linked to environmental stress (cf. Laurin and García Joral, 1990; García Joral and Goy, 1994). In the case described in this paper, the changes observed in the size of the brachiopods show both a spatial gradient, attaining smaller sizes towards the northwest, and a temporal gradient, the larger sizes within several species found in the uppermost Tenuicostatum Zone. Thus, though miniaturization seems to be related in this case to certain environmental constraints, these do not seem to be the same constraints that led to the extinction since spatial and temporal patterns are in disagreement. A similar situation has been described by He et al. (2007) from the Upper Permian at Dongpan, Southern China, where miniaturized forms appear in deep environments before the Permian–Triassic Extinction Event.

In particular, no correlation between the progressive brachiopod turnover and mass extinction and the presence of anoxic environments were observed. Only in the West Rodiles section the extinction boundary coincides with a thinly laminated deposit, indicative of the absence of bioturbation and hence, of the lack of benthic organisms. The deposits of all the remaining sections are strongly bioturbated, revealing the presence of normal oxygen levels. In addition, the low to inexistent values obtained for organic content in most of the sections studied in this paper do not support the presence of euxinic conditions at the time of the extinction interval and at the extinction boundary.

Only in the West Rodiles section the laminated organic facies where the zonal/extinction boundary is included, contain up to 3.2 wt.% TOC (Gómez et al., 2008). As a consequence, anoxia cannot be argued as the main cause for the brachiopod mass extinction that took place in the Early Toarcian.

7.3. The extinction boundary

The extinction boundary in all the studied sections is located close to the Tenuicostatum–Serpentinum zonal boundary. At this boundary a massive extinction of brachiopods took place (García Joral and Goy, 2000; Gahr, 2002).

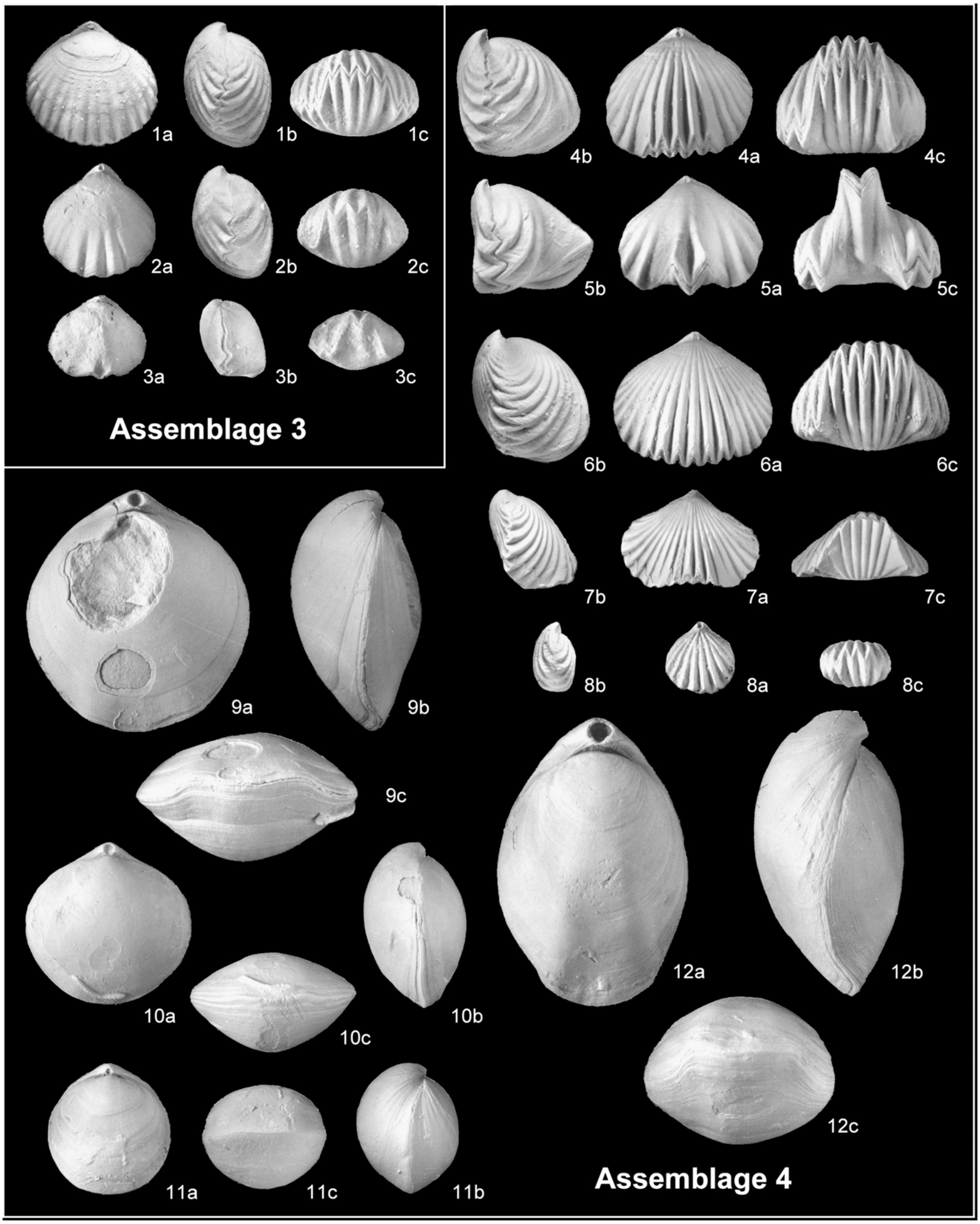
From a taxonomical point of view, the effects of this extinction event among the brachiopods are extraordinarily important at a global scale. As a consequence of this event, two major orders, Spiriferinida (Comas-Rengifo et al., 2006) and Athyridida (Vörös, 2002) disappeared. The order Rhynchonellida suffered a notable renewal and according to Manceñido (2000) about 2/3 of the genera belonging to this order disappeared. The order Terebratulida seems to be less affected, particularly the Superfamily Zeillerioidea.

The extinction undergone by the brachiopods in the Early Toarcian can be considered as the most important turnover in post-Paleozoic times. According to the most updated data of the "*Treatise on Invertebrate Paleontology*" (Kaesler and Selden, 1997–2007), two of the seven orders, and five of the twelve superfamilies present before the extinction, disappeared. Comparison with other extinction events reveals that only the major latest Permian extinction, in which four orders of brachiopods became extinct, was more severe. No new disappearances of brachiopods at the order level has been recorded since the Early Toarcian, and after this extinction only three superfamilies disappeared, one at the Middle Jurassic, other at the Early Cretaceous and the third one at the latest Cretaceous.

Fig. 5. Photographs of some representative species of assemblages 3 and 4 described in this paper. 1–3: *Soaresirhynchia bouchardi* (Davidson, 1852) from the Serpentinum Zone (Elegantulum Subzone) of Villar del Cobo Section (Albarracín, Teruel). 1: specimen labeled Vo.0.1; 2: specimen labeled Vo.0.2; 3: specimen labeled Vo.1.15. 4: *Homoeorhynchia batalleri* (Dubar, 1931). Specimen labeled Vo.4.1, from the Serpentinum Zone (Falciferum Subzone) of Villar del Cobo Section (Albarracín, Teruel). 5: *Homoeorhynchia meridionalis* (Deslongchamps, 1863). Specimen labeled Vo.3.45, from the Serpentinum Zone (Falciferum Subzone) of Villar del Cobo Section (Albarracín, Teruel), the type locality of the species. 6: *Choffatirhynchia vasconcellosi* (Choffat *in* Dubar, 1931). Specimen labeled Ar.11.401, from the Serpentinum Zone (Falciferum Subzone) of the Ariño Section (specimen figured in García Joral and Goy, 2004, L.1, Fig. 3). 7: *Choffatirhynchia? paucicostatae* (Castell and Concha, 1956). Specimen labeled 1Ar.101.7, from the Serpentinum Zone (Elegantulum Subzone) of the Ariño Section. 8: *Pseudogibbirhynchia jurensis* (Quenstedt, 1858). Specimen labeled 1Ar.103.1, from the Serpentinum Zone (Elegantulum Subzone) of the Ariño Section. 9: *Telothyris jauberti* (Deslongchamps, 1863). Specimen labeled Tu,5/3.51 from the Serpentinum Zone (Elegantulum Subzone) of Turmiel Section (Guadalajara) that is in the type area of the species. 10: *Telothyris pyrenaica* (Dubar, 1931). Specimen labeled Ar.11.405, from the Serpentinum Zone (Falciferum Subzone) of the Ariño Section. 11: *Telothyris? perfida* (Choffat, 1947). Specimen labeled 2Ar.31.1, from the Serpentinum Zone (Falciferum Subzone) of the Ariño Section. 12: *Lobothyris? hispanica* (Dubar, 1931). Specimen labeled Ar.11.301, from the Serpentinum Zone (Falciferum Subzone) of the Ariño Section. (a = dorsal view, b = lateral view, and c = frontal view). The figured specimens are deposited in the collections of the Department of Paleontology UCM. All photographs (X1).

7.4. The repopulation interval

After the extinction event, brachiopods apparently did not recover in Asturias and in the Basque–Cantabrian Basin until the Middle Toarcian Variablilis Zone (2 Ma after the extinction boundary, following the scale of Ogg, 2004) (García Joral and Goy, 2009). A similar repopulation pattern is recorded throughout most of Western Europe, whereas in the Iberian Range a colonization and diversification phase, representing the repopulation interval, started after a brief episode, of a shorter duration than the equivalent to a subzone, in the order of 0.5 Ma. This situation reproduces a similar pattern as observed in the Permian–Triassic Extinction Event, where recovery is



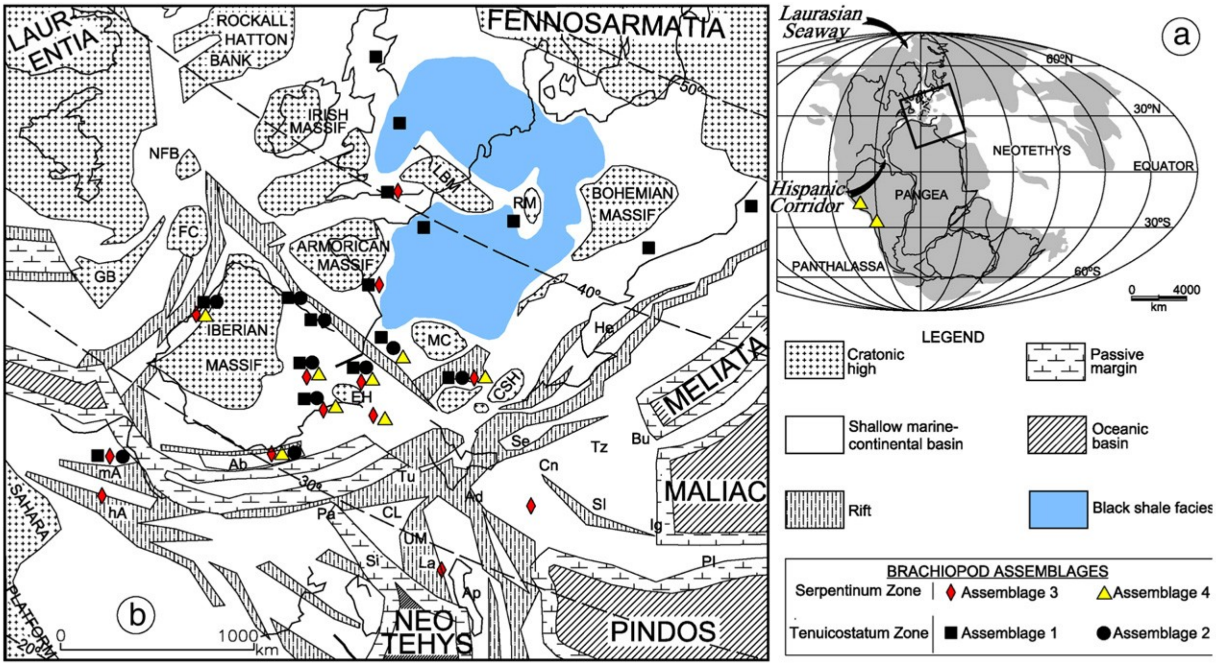


Fig. 6. a) Paleogeographical map of the Toarcian, modified after Golonka (2006), showing the position of the Viking Straits (Poulton and Callomon, 1977; Callomon, 1979) or Laurasian Seaway (Bjerrum et al., 2001) and the Hispanic Corridor (Smith, 1983; Damborenea, 2000; Aberhan, 2001). b) Paleogeographical and paleobiogeographical map of Eastern Europe and Northern Africa at the Toarcian (modified after Ziegler, 1990; Vera, 2001; Stampfli and Borel, 2004; Osete et al., 2010). Western Europe was partly occupied by an euxinic sub-basin where black-shale facies were deposited. The paleobiogeographical distribution of brachiopod assemblages shows that the species composing assemblage 1 were preferentially distributed at paleolatitudes between 30 and 45°N, indicating that they were preferentially inhabiting relatively cool waters. Assemblage 2 is notably more restricted to paleolatitudes around 30–35°N, indicating that they were preferentially linked to warmer waters. Brachiopods of assemblage 2 substituted to the components of assemblage 1 when warming started in the Early Toarcian Tenuicostatum Zone. Except for a few occurrences north of 35° of paleolatitude, assemblage 3 constituted by *S. bouchardi*, is mainly distributed in paleolatitudes lower than 35°N, indicating that this is a Mediterranean species, well adapted to warm waters. This species colonized the Southern European and Northern African platforms after the extinction boundary, marking the onset of the repopulation interval. A similar distribution pattern is shown by assemblage 4, which is specially concentrated at a paleolatitude of about 35°N, not only in the northern hemisphere, but also in South America (a). This fact supports the communication between the Neotethys and Panthalassa through the Hispanic Corridor, as well as the didemic distribution of the species constituting this assemblage. Abbreviations: Ab — Alboran. Ad — Adria s. str. Ap — Apulia s. str. Bu — Bucovinian. Bv — Budva. CL — Campania Lucania. Cn — Carnic–julian. CSH — Corsica–Sardinia High. EH — Ebro High. FC — Flemish Cap. GB — Grand Bank. hA — High Atlas. He — Helvetic rim basin. Ig — Igal trough. La — Lagonegro. LBM — London–Braband Massif. mA — Middle Atlas. MC — Massif Central High. NFB — East Newfoundland Basin. Pa — Panormides. Pl — Pelagonian. RM — Rhenish Massif. Se — Sesia (western Austroalpine). Si — Sicanian. Sl — Slavonia. Tu — Tuscan. Tz — Tisia. UM — Umbria–Marche.

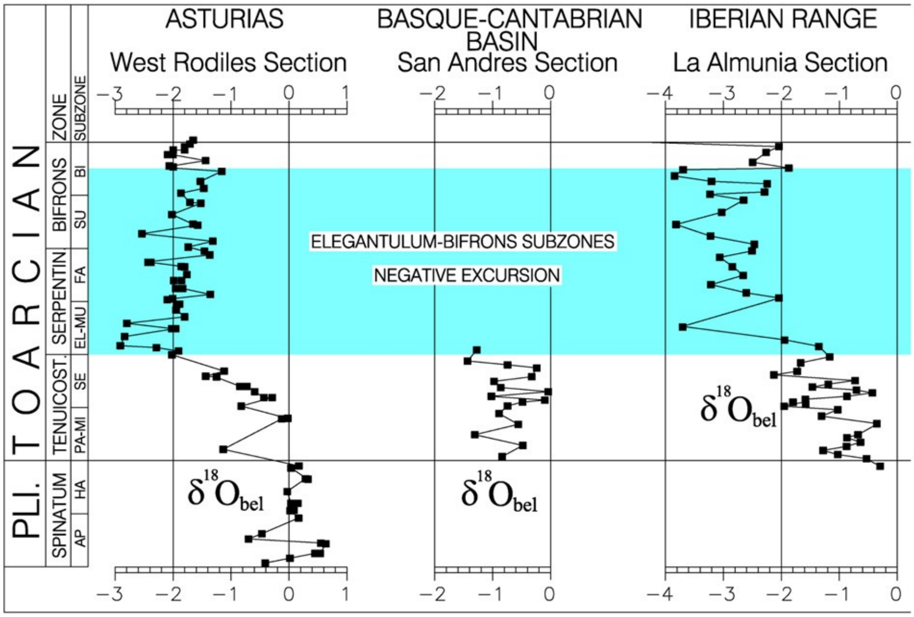


Fig. 7. Correlation of the $\delta^{18}O_{bel}$ curves obtained from belemnite rostra calcite in northern Spain (West Rodiles and San Andres sections) and in central Spain (La Almunia section), plotted against the standard ammonite zones and subzones. The $\delta^{18}O_{bel}$ values are progressively more negative through the uppermost Pliensbachian (Spinatum Zone) and lowermost Toarcian (Tenuicostatum Zone). They are followed by a prominent negative excursion which develops from the Tenuicostaum–Serpentinum zonal boundary to the Middle Toarcian Bifrons Zone. Subzones abbreviations: AP — Apyrenum. HA — Hawskerense. PA — Paltum. MI — Mirabile. SE — Semicelatum. EL — Elegantulum. MU — Murleyi. FA — Falciferum. SU — Sublevisoni. BI — Bifrons.

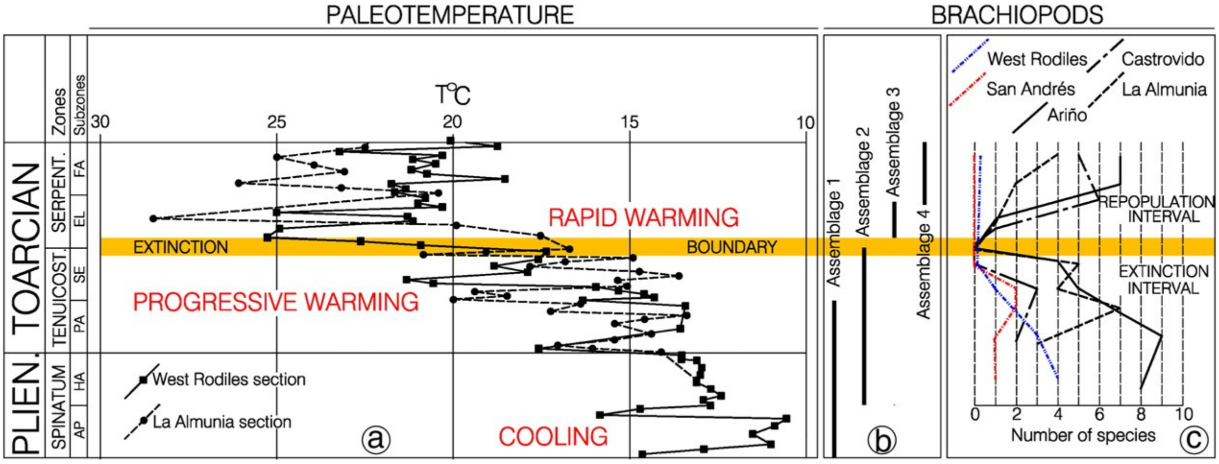


Fig. 8. Correlation between (a) variations of seawater temperature, (b) stratigraphical distribution of the four distinguished brachiopod assemblages and (c) number of species of brachiopods in each studied section, plotted against ammonite zones and subzones. Brachiopod assemblage 1, mainly composed of species that thrived in relatively cool waters, disappeared in all the sections as temperature increased through the lowermost Toarcian Tenuicostatum Zone. After disappearance of assemblage 1, assemblage 2 composed of species probably better adapted to relatively warm environments, became dominant, but the number of species progressively decreased through this first warming interval. Rapid and notable increase in seawater temperature around the Tenuicostaum–Serpentinum extinction and zonal boundary conditioned the total extinction of the brachiopods in all the studied sectors of the platform, as well as in many other areas of Western Europe and north Siberia and Arctic regions. After mass extinction, population of the platform started about 0.5 Ma later in the Iberian Range, but 2 Ma later (Variabilis Zone) in northern Spain as well as in many areas of NW Europe. Subzones abbreviations: AP — Apyrenum. HA — Hawskerense. PA — Paltum. MI — Mirabile. SE — Semicelatum. EL — Elegantulum. MU — Murleyi. FA — Falciferum. SU — Sublevisoni. BI — Bifrons.

rapid in well oxygenated areas, but delayed in areas affected by anoxia (Twitchett et al., 2004).

The onset of the repopulation interval in the Iberian Range is marked by the presence of numerous and polymorph individuals of *Soaresirhynchia bouchardi*, rarely associated with *Pseudogibbirhynchia jurensis*, constituting assemblage 3. *S. bouchardi* shows a wide geographical distribution (Fig. 6) and a simple morphology, with few derived characters. It forms dense populations within which a high morphological variability can be recognized. All these features correspond with those of an “opportunist” in the sense of Levinton (1970) or Harries et al. (1996, p. 45) occupying an environment where competitors were lacking (García Joral and Goy, 2000; Gahr, 2002, 2005). However, to link assemblage 3 with the “survival interval” of Kauffman–Erwin model as suggested by Gahr (2002, 2005) is not adequate, because *S. bouchardi* cannot be considered as a survivor to the extinction, but rather as a colonizer or pioneer marking the onset of the repopulation interval. Based on its external and internal morphology, *S. bouchardi* probably derived from some species of the genus *Apringia* of the Pliensbachian and Toarcian of the Mediterranean area, better adapted to warmer Tethyan environments.

Within the last beds containing *Soaresirhynchia bouchardi*, several taxa of the so-called Spanish Bioprovince, are progressively recorded, forming assemblage 4. This assemblage mainly includes species of the genera *Homoeorhynchia* and *Telothyris*. It reached an important development at the Serpentinum and Bifrons zones, showing more complex morphologies, giving rise to the presence of geographically separate varieties. This is the case of the genus *Homoeorhynchia*, which shows similar morphologies but with local peculiarities in different parts of the Spanish Bioprovince. Assemblage 4 clearly involves a significant increase in the diversity and in the degree of specialization, thus representing the culmination of the repopulation that started with the colonizers of assemblage 3.

8. Conclusions

Calculated seawater paleotemperatures from the δ^{18}O values obtained in belemnite rostra calcite, shows a notable seawater warming interval during the Early Jurassic that started around the Pliensbachian–Toarcian boundary, when relatively cool temperatures have been inferred. Temperatures progressively increased during the Early Toarcian Tenuicostatum Zone and suffered a notable and rapid increased during the Tenuicostatum–Serpentinum zonal boundary.

The dynamics of the brachiopod assemblages studied in central and northern Spain show an excellent correlation with the detected climate change. During the latest Pliensbachian cooling interval, a group of brachiopods here referred to as assemblage 1, thrived under favorable lower seawater temperature conditions. As temperatures rose, through the Tenuicostatum Zone, assemblage 1 was replaced by assemblage 2 which become dominant in all the studied area up to the extinction boundary.

Coinciding with the rapid and pronounced increase in temperature recorded around the Tenuicostatum–Serpentinum zonal boundary, brachiopods disappeared. This extinction event is synchronous not only in the studied area, but also in the whole of Western Europe, and probably in Northern Siberia and the Arctic region. The extinction event appears to be clearly independent from sea bottom oxygenation conditions, as extinction is recorded both in areas where the basin had euxinic conditions as well as in areas where waters were well oxygenated, suggesting a different cause for the extinction other than sea bottom anoxia.

The notable increase in seawater temperature recorded at the Tenuicostatum Zone and the rapid and notable warming interval that started around the Tenuicostatum–Serpentinum zonal boundary are the most plausible causes of the mass extinction. The predominant southward currents along the Laurasian Seaway (or Viking Straits) obstructed or precluded the dispersion of the brachiopods living in the Western Tethys epicontinental platforms toward the northern and cooler Arctic waters. These severe changes in the environmental conditions caused a massive extinction of most of the benthos.

The taxonomical impact of this extinction for the brachiopods at a global scale is very significant. It represents the disappearance of two orders, the Spiriferinida and Athyridida, together with the disappearance of around 70% of the genera of the order Rhynchonellida and an important renewal of the order Terebratulida. The extinction event occurred when many of these groups, at least locally, showed a relatively high diversity, including both generalists as well as specialized taxa.

The recovery pattern of the brachiopods after the extinction event is in agreement with the classic models of extinction–pause– radiation, and constitutes a good example of these evolutionary processes. The time of recovery is relatively short at the Iberian Range of central Spain (around 0.5 Ma). The approximately 2 Ma lag-time observed both in Northern Spain as in Western Europe in the recovery of the brachiopods (Early Toarcian Serpentinum Zone to Middle Toarcian Variabilis Zone), is probably linked to the persistence of unfavorable environmental conditions in these areas. In the case of the euxinic sub-basin located in Central Europe, anoxia could be one of the main causes for the delay in the recovery, as laminated black-shale facies persist until the Middle Toarcian.

Acknowledgements

This research work was financed by projects CGL 2008-03112 and CGL 2008-01273 of the Spanish Ministerio de Educación y Ciencia, and the projects GR58/08B/910431, GR58/08A/910429 and GR58/08A/ 91039 of the Universidad Complutense de Madrid. We gratefully acknowledge Editor F. Surlyk, and reviewers M. Manceñido and A. Vörös for their valuable comments and constructive reviews.

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