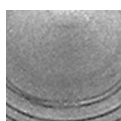


New deep-water brachiopod resilient assemblage from the South-Iberian Palaeomargin (Western Tethys) and its significance for the brachiopod adaptive strategies around the Early Toarcian Mass Extinction Event

JOSÉ F. BAEZA-CARRATALÁ, MATÍAS REOLID & FERNANDO GARCÍA JORAL



The Pliensbachian-Toarcian transition was a period of changes in long-term environmental conditions leading up to the Early Toarcian Mass Extinction Event (ETMEE), which resulted in a noticeable extinction and turnover in the marine biota. The westernmost Tethyan basins, especially the peri-Iberian platforms, provide an exceptional brachiopod record to better understand the adaptive strategies and the severe ecological effects of these faunas within the marine ecosystems. This event marks a critical interval in the evolutionary history of the Phylum Brachiopoda as two orders, the Athyridida and Spiriferinida, became extinct. Evolutionary patterns displayed by several taxa from these groups and some rhynchonellids typifying deep-water habitats are analyzed across this biotic crisis spanning several Mediterranean and NW-European basins. New work performed in La Cerradura section, a deep pelagic trough from the South-Iberian palaeomargin, reveals two new taxa (*Koninckodonta sumuntanensis* and *Atychorhynchia falsiorigo*) herein described. This newly documented fauna supports pre-extinction dwarfing and resilience in deep refugia linked to the ETMEE, and an episode of speciation which is interpreted in terms of a pre-extinction radiation. In the ETMEE repopulation phase an opportunistic strategy occurs typified by *Soaresirhynchia bouchardi*, and a case of homoplasy involving post-extinction pioneers (Elvis taxon) is detected. Similar adaptive strategies occurred associated with other mass extinctions such as the Permian/Triassic and the Cretaceous/Paleocene events, supporting a possible standard pattern in the response of the brachiopod fauna to such biotic crises and shedding light on the ecological effects of the mass extinction events. • Key words: Jurassic, Brachiopods, Western Tethys, Early Toarcian Mass Extinction, adaptive strategies.

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The Early Toarcian Mass Extinction Event (ETMEE) was one of the most important environmental perturbations of the Mesozoic which had a dramatic impact on the marine benthic and nekto-planktic biota (e.g. Hallam 1986, 1987; Little & Benton 1995; Harries & Little 1999; McArthur *et al.* 2000; Bailey *et al.* 2003; Wignall *et al.* 2005; Dera *et al.* 2010). The mass extinction was experienced by many organisms living at various levels within the water column. This includes benthic groups, such as bivalves (Aberhan & Fürsich 1997), brachiopods (Vörös 2002, García Joral *et al.* 2011, Baeza-Carratalá *et al.* 2015), cnidarians (Lathui-

lière & Marchal 2009), foraminifera (Nikitenko & Mickey 2004, Zakharov *et al.* 2006) and ostracodes (Arias 2009); as well as nekto-benthic/nektonic ammonites (Macchioni & Cecca 2002, Cecca & Macchioni 2004, Dera *et al.* 2010) and planktic forms, such as dinoflagellates (Bucefalo Palliani *et al.* 2002).

Some previous authors suggested that the ETMEE was actually a multi-phased event (*cf.* Little 1996, Macchioni & Cecca 2002, Wignall & Bond 2008, Dera *et al.* 2010, Caruthers *et al.* 2013, Arias 2013, Rita *et al.* 2016) the onset of which is detected in the late Pliensbachian–earliest

Toarcian, with the main phase coinciding with the early Toarcian Oceanic Anoxic Event (T-OAE; established in the westernmost Tethys within the *serpentinum/levisoni* Zone for the Sub-Mediterranean/Mediterranean Domain respectively) as a result of a period of changes in long-term environmental conditions prior to this event (*cf.* Harries & Little 1999, Dera *et al.* 2010, Suan *et al.* 2010, Gómez & Goy 2011, García Joral *et al.* 2011). This relatively long phase represents the so-called “extinction interval” where diverse environmental changes or pulses occurred.

After the significant compositional turnover that the end-Triassic extinction event produced in the brachiopod communities (Hallam 1990, 1996; Tomašových & Siblík 2007) with severe effects on several clades as spiriferinids and athyridids (Jablonski 2002, Vörös *et al.* 2016), the ETMEE was an important interval in brachiopod evolutionary history as these two (*i.e.* the Athyridida and Spiriferinida) of the five orders known prior to the event became extinct (*e.g.* Vörös 2002). Amidst the Early Jurassic brachiopods, the profuse record and extinction of the koninckinid fauna can be used as a precursor signal of the main biotic crisis event within this multi-phased extinction interval (Baeza-Carratalá *et al.* 2015). The present work analyzes the evolutionary trends of several taxa belonging to these extinct and survivor groups in La Cerradura Section (CE section hereinafter), located in the South-Iberian palaeomargin, close to the Gondwana palaeomargin, with ocean dynamics influenced by the convergence of the Spanish Corridor connecting the Western Tethys and the Proto-Atlantic seaway. In this locality, koninckinid fauna is recorded together with spiriferinids and new taxa typifying deep-water habitats in the final phases of the extinction interval, providing new data on the adaptive response of brachiopods that can be a crucial key to better understanding the ecologic adaptive strategies in relation to this biotic crisis.

Globally, the ETMEE is typified by a crisis of carbonate production in shallow-marine settings, an increase in organic matter content and a negative carbon isotope excursion (Jenkyns & Clayton 1997; Mattioli *et al.* 2004, 2009; Hesselbo *et al.* 2007; Suan *et al.* 2008; Hermoso *et al.* 2009; Al-Suwaidi *et al.* 2010, 2016; Littler *et al.* 2010; Caruthers *et al.* 2011). This event, so-called T-OAE (Toarcian Oceanic Anoxic Event) was originally considered as global on the basis of the prevailing record of organic-rich facies and anoxic conditions (Jenkyns 1988). However, the conditions recorded in deeper-water settings suggest considerable geographical variability (*e.g.* Gómez

et al. 2008; Hermoso *et al.* 2009; Rodríguez-Tovar & Reolid 2013; Reolid *et al.* 2014a, b). Recent analyses have documented the role of local and regional factors that overprint the typical pattern of the T-OAE (Braga *et al.* 1981; McArthur *et al.* 2008; Rodríguez-Tovar & Uchman 2010; Reolid *et al.* 2013a, b; Rodríguez-Tovar & Reolid 2013).

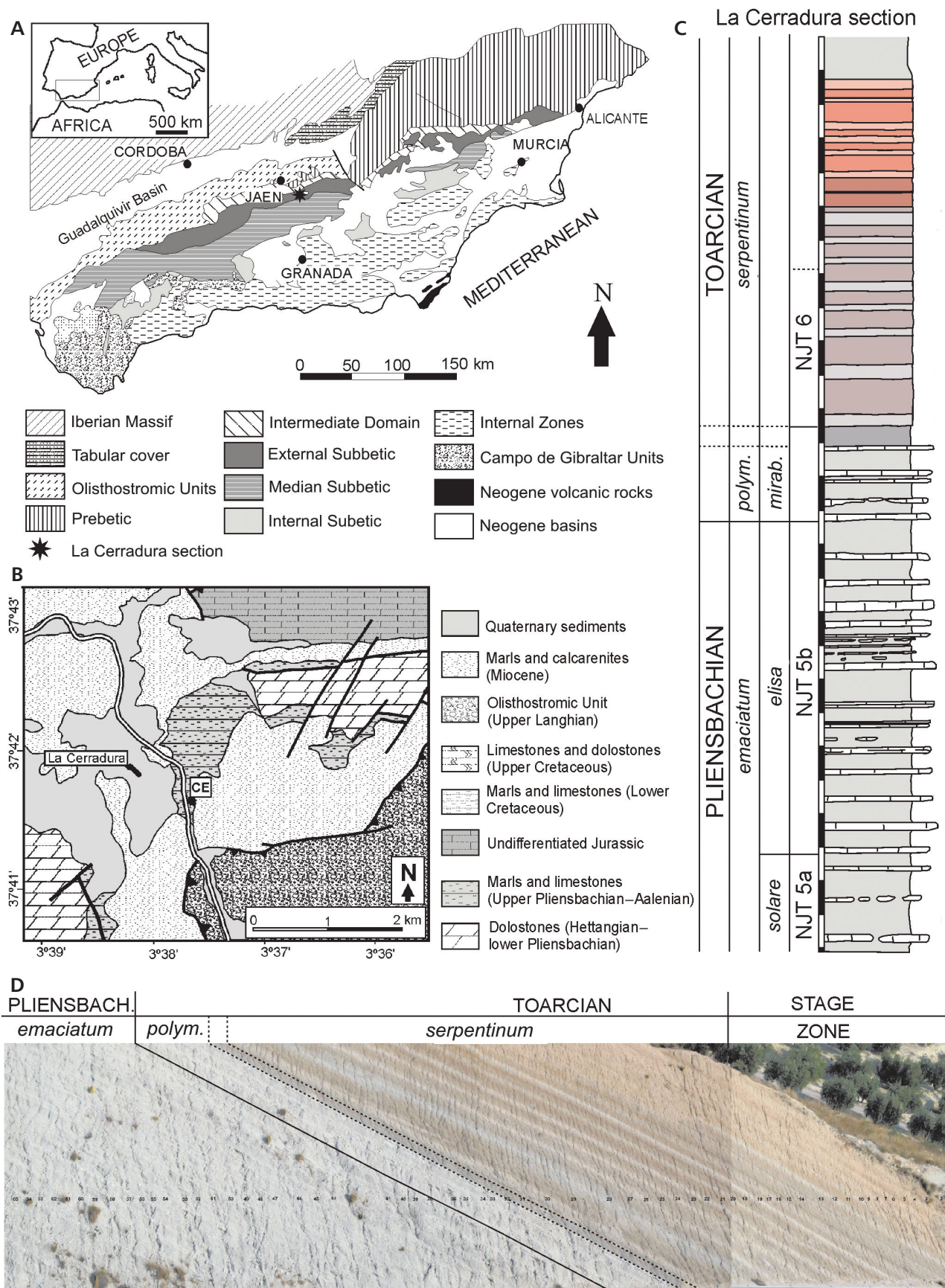
In the CE section, the main pulse of T-OAE was recorded in the lowermost *serpentinum* Zone, but with lower levels of total organic carbon (wt% TOC) than other Western Tethyan sequences (Reolid *et al.* 2014a). There is some uncertainty on the precise timing of the event in CE, but as brachiopods occur above the levels where the main pulse of T-OAE is detected, this area could have been a deep water “refugia”. Additionally, the record at CE contributes to enhanced analysis of an example of adaptive dwarfism in the extinction intervals in groups such as the koninckinids and spiriferinids, in contrast with the well-known Lilliput effect regarded as a post-extinction syndrome in the aftermath of the extinction boundaries.

Geological setting

The Early Jurassic brachiopods analyzed in this study were primarily derived from the External Subbetic (External Betic zones). The External Betic zones (Fig. 1) comprise the Prebetic and Subbetic, both made up of thick successions of Triassic to Miocene strata (Vera *et al.* 2004). The Prebetic rocks were deposited in shallow-marine shelfal, coastal plain and continental environments during the Jurassic and Cretaceous. During the Jurassic, the Subbetic was a relatively distal setting, characterized by pelagic swells with low rates of subsidence abutting subsiding central troughs (*e.g.* Braga *et al.* 1981, Reolid *et al.* 2015). Jurassic sedimentation in the External Subbetic is characterized by shallow shelf deposits in the lowermost Jurassic (Gavilán Formation), overlain by Pliensbachian–Aalenian hemipelagic facies of marls and marly limestones (Zegri Formation).

The main fragmentation stage of the large carbonate platform occurred during the earliest Jurassic (García-Hernández *et al.* 1987, 1989; Vera 2001; Vera *et al.* 2004), when rocks of the Gavilán Formation were deposited. Blocks were tilted along a number of listric faults (Vera 2001), and those which experienced less subsidence became pelagic swells with condensed *ammonitico rosso* facies (*e.g.* Braga *et al.* 1981, Reolid *et al.* 2015). The differential block subsidence resulted in remarkable thickness variation (Vera *et al.* 2004).

Figure 1. Geological setting and stratigraphical succession studied. • A – situation of La Cerradura section in the context of the Betic Cordillera, Spain (modified after Vera *et al.* 2004). • B – geological map around the La Cerradura locality (modified after Roldán *et al.* 1991). • C – synthetic Lower Jurassic lithostratigraphical column from La Cerradura. • D – outcrop view of La Cerradura section showing the distribution of the ammonites chronozones.



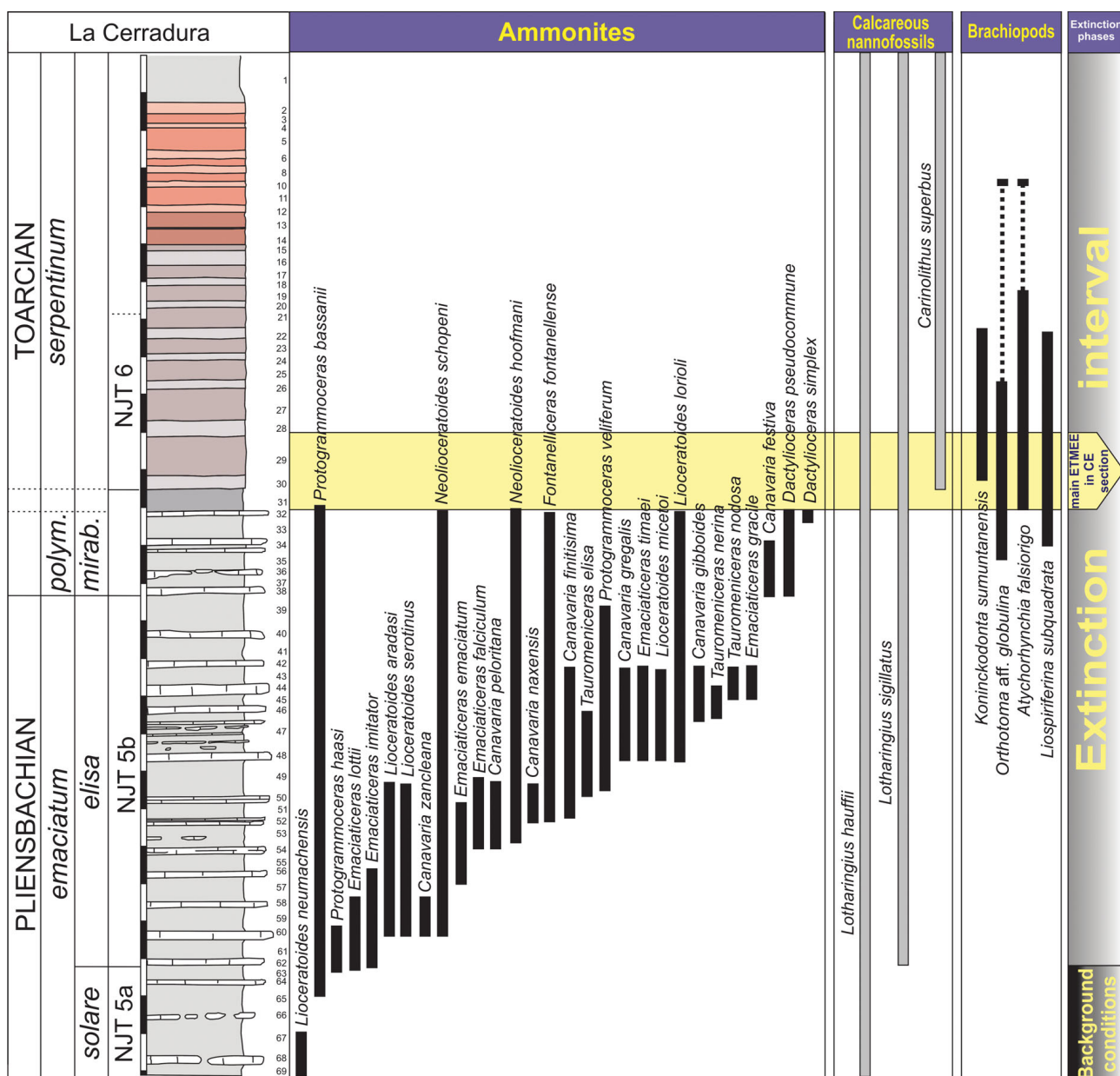


Figure 2. Brachiopod occurrences in La Cerradura section together with the ammonite and calcareous nannofossil distributions. The main early Toarcian Mass Extinction Event in La Cerradura is marked after Reolid *et al.* (2014a) on the basis of geochemical and palaeontological proxies within NJT-16 Zone. Extinction phases of the brachiopod fauna have been pointed out (sources for their establishment are cited in the text). Ammonite distribution is based on Braga (1983), Jiménez (1986) and Reolid *et al.* (2014a) and calcareous nannofossils in Reolid *et al.* (2014a).

New sampling in the External Subbetic has been carried out at the La Cerradura section (37° 41' 47.8" N; 3° 37' 57.6" W). The section (Fig. 1) is 15 km south of the Jaen City (Spain). Early studies of this area were carried out by Mouterde *et al.* (1971) and the ammonite fauna was primarily studied by Braga (1983) and Jiménez (1986). Recently, Sandoval *et al.* (2012) dealt with this section in a comprehensive study on the Toarcian Subbetic facies, mainly focused on ammonite and calcareous nannofossil bioevents.

The rocks comprising the CE section represent a pelagic marine setting with deep habitats below storm wave base in the South-Iberian palaeomargin, close to the Hispanic Corridor and the passage between the Western Tethys and the Proto-Atlantic seaway (Aberhan 2001, Bailey *et al.* 2003), at a palaeolatitude of ~ 20° N (Jiménez *et al.* 1996, Rodríguez-Tovar & Reolid 2013). The Zegrí Formation exposed at CE section was deposited in a subsiding area with an expanded sedimentation and a greater cumulative thickness (Reolid *et al.* 2014a).

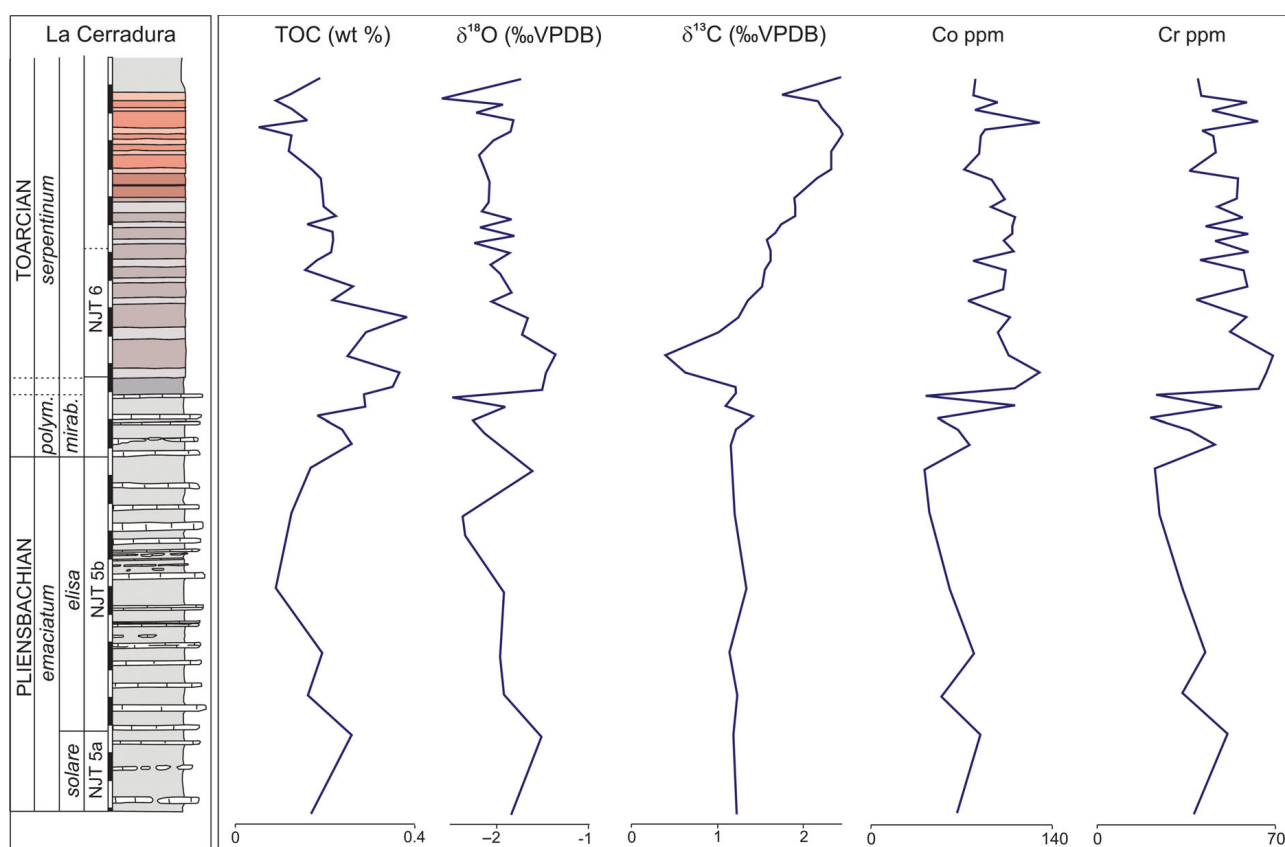


Figure 3. Geochemical proxies. Stratigraphic distribution in the La Cerradura section of the total organic carbon (TOC), $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ from bulk sample, and content of redox sensitive elements (ppm).

The CE section is composed of 27.5 m of marl-marly limestone rhythmite and 12 m of dark marls (Fig. 1, 2). The marly limestone succession consists of mudstone and occasional wackestone beds with sporadic mollusc bioclasts. The marly layers are rich in illite, smectite and chlorite (Caniço *et al.* 2015). Recently, Reolid *et al.* (2014a) identified the early Toarcian Oceanic Anoxic Event in the CE stratigraphic column by the increase in redox sensitive elements, total organic carbon (TOC) and total sulfur (TS), the record of a negative carbon isotopic excursion (CIE), changes in calcareous nannofossils, and absence of benthic remains and trace fossils. This interval corresponds to the first 60 cm above the top of the marl-limestone rhythmite (Figs 2, 3). Brachiopod-bearing levels are found in both marl-marly limestone rhythmite and dark marls beds (levels 35 to 10 in Fig. 2), extending above the main T-OAE pulse recorded by Reolid *et al.* (2014a).

Material and methods

New bed-by-bed sampling in the CE section has been exhaustively carried out to achieve a high-resolution record, resulting 112 newly collected brachiopods. Mean biomet-

ric parameters (length, width, thickness) were measured for complete specimens. Generic assignments follow published determinations mainly in the Treatise (Kaesler & Selden, 1997–2007). The internal structure of brachiopods was studied using the conventional method of taking acetate peels after making transverse serial sections. The distance between serial sections was 0.1 mm. All the sectioned and figured specimens are deposited in the Departamento de Ciencias de la Tierra y del Medio Ambiente (University of Alicante, Spain).

The ammonite zonal/subzonal scheme follows the commonly used zonation for the Betic Range, based on the standard proposed by Cariou & Hantzpergue (1997) for the Mediterranean Domain, supplemented by biochronological data from Braga (1983) and Jiménez & Rivas (1979). Their equivalent in the Sub-Mediterranean European Domain has been pointed out when necessary for correlations (Fig. 4B). The Pliensbachian and Toarcian ammonites in the CE section were studied by Braga (1983) and Jiménez (1986), respectively. Coccolith distributions (Reolid *et al.* 2014a) allow calibration according to the scheme of Mattioli & Erba (1999) for the South-Tethyan region. Other recent biochronological data (Mattioli *et al.* 2004, 2013) are also applied.

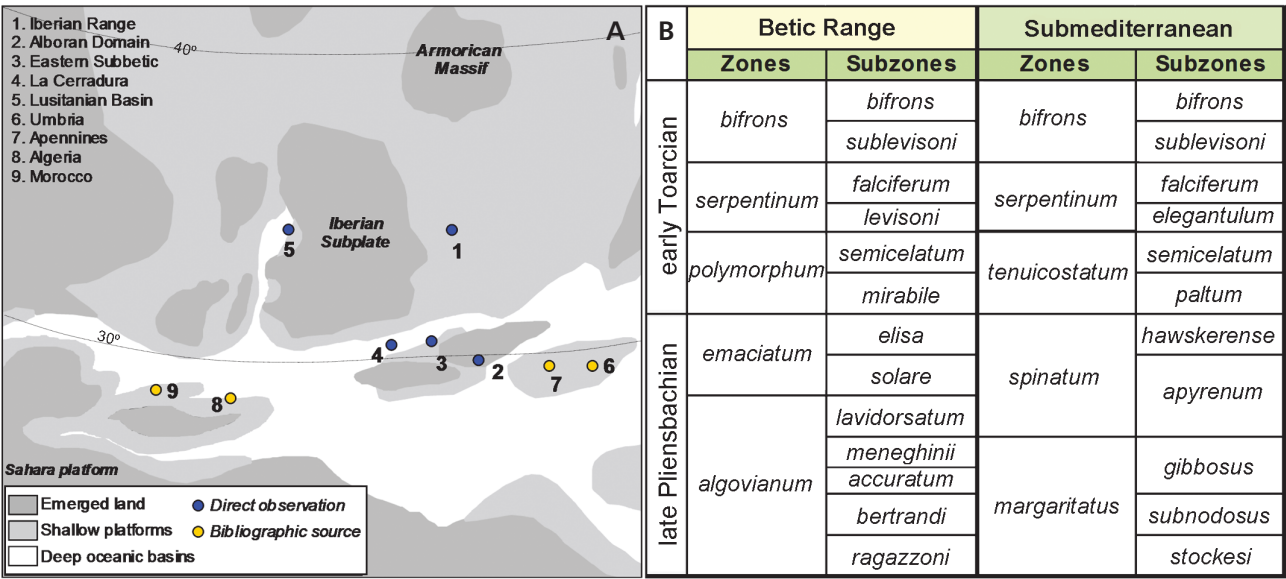


Figure 4. Palaeogeographical and chronostratigraphical context of the analysis. • A – situation of the brachiopod fauna datasets (bibliographic/directly examined sources) referred to in this study, plotted on an Early Jurassic palaeomap, slightly modified after Bassoullet *et al.* (1993). • B – sketch showing the biochronozones commonly used for the Betic Range, and their equivalent in the Sub-Mediterranean Domain to perform correlations.

Stable isotopic records from Reolid *et al.* (2014a) are used for determining the position of the negative CIE in the section. In addition, the analysis of redox sensitive trace elements such as Co, Cr, Cu, Th and U, which are less soluble under reducing conditions and enriched in the sediment under suboxic and anoxic conditions, constituted a tool for confirming oxygen reducing biofacies during the negative CIE (Reolid *et al.* 2014a). Total organic carbon content (TOC) was calculated as percentage of the sample weight.

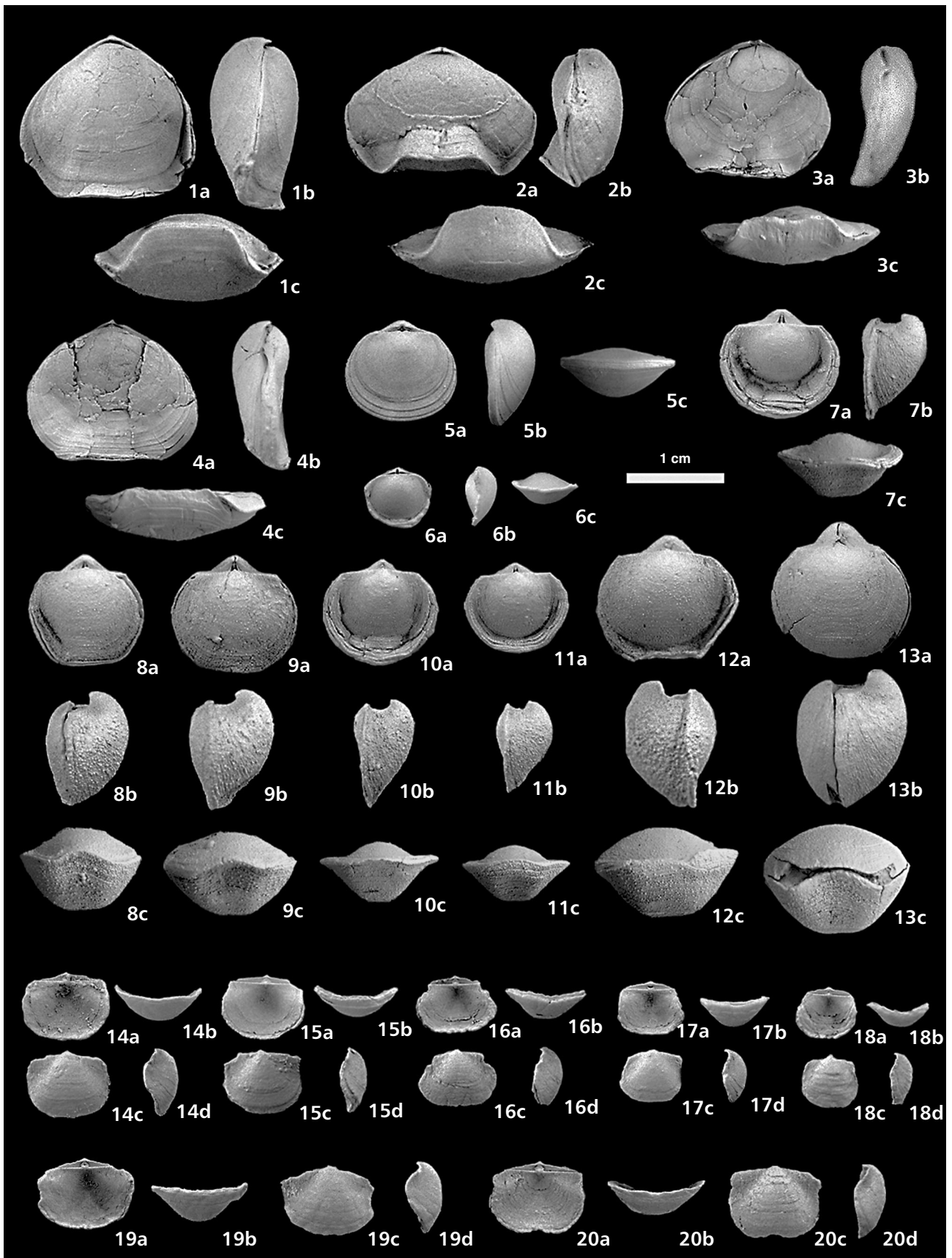
A comparative analysis was performed after review of the dataset from several Mediterranean and NW-European basins; mainly by means of the newly collected brachiopods in the CE section, 503 athyridid and spiriferinid specimens from the easternmost Subbetic area (Baeza-Carratalá 2008, 2013), located 300 km eastward from CE, and several bibliographical sources of Mediterranean (Pozza & Bagaglia 2001, Vörös 2003), and Portuguese (Comas-Rengifo *et al.* 2013, 2015) koninckinid faunas. This latter material was directly examined by one of the authors (FGJ). Previous data from the Internal Betic Zone (Baeza-Carratalá *et al.* 2011) and the Iberian Range (García Joral *et al.* 2011) have also been taken into account

(Fig. 4A). These brachiopod faunas were analysed through cluster analysis computed using the Jaccard similarity coefficient from the PAST software package (Hammer *et al.* 2001). Paleobiogeographic categorization of biochores follows the nomenclature proposed by Westermann (2000), subsequently adapted for the brachiopod fauna by several authors (*e.g.* Manceñido 2002, Vörös 2016).

Compositional analysis of the brachiopod-bearing deposits in the CE section

Taxonomic analysis performed in the brachiopod fauna from the CE section reveals the occurrence of an assemblage recorded around the ETMEE consisting of *Liospiriferina subquadrata* (Seguenza, 1885), *Orthotoma* aff. *globulina* (Davidson, 1851), *Koninckodonta sumuntanensis* nov. sp. and *Atychorhynchia falsiorigo* gen. et sp. nov. (Fig. 5). The two new taxa constituting the faunal core of this assemblage must be emphasized since they are herein recorded and formally described for the first time:

Figure 5. Some representative taxa of the brachiopod assemblage from La Cerradura. All specimens were coated with magnesium oxide. Images from 1 to 13 are arranged thus in (a) dorsal, (b) lateral, and (c) anterior views. Images from 13 to 20 are ordered in (a) dorsal, (b) anterior, (c) ventral, and (d) lateral views. • 1–4 – *Atychorhynchia falsiorigo* gen. et sp. nov.; 1 – specimen CE28.Rh1 (holotype); 2 – specimen CE28.Rh2; 3 – specimen CE19.Rh1; 4 – specimen CE19.Rh2 (2–4 with severe diagenetic distortion). • 5–6 – *Orthotoma* aff. *globulina* (Davidson): 5 – specimen CE32.O1; 6 – specimen CE26.O1. • 7–13 – *Liospiriferina subquadrata* (Seguenza); 7 – specimen CE27b.LS1; 8 – specimen CE24.LS2; 9 – specimen CE27.LS1; 10 – specimen CE27.LS2; 11 – specimen CE27.LS3; 12 – specimen CE26.LS1; 13 – specimen CE24.LS1. • 14–20 – *Koninckodonta sumuntanensis* sp. nov.; 14 – specimen CE28.K1 (holotype); 15 – specimen CE22.K1; 16 – specimen CE28.K2; 17 – specimen CE28.K3; 18 – specimen CE29B.K1; 19 – specimen CE29B.K2; 20 – specimen CE26.K1.



Order Rhynchonellida Kuhn, 1949
Superfamily Norelloidea Ager, 1959
Family Norellidae Ager, 1959
Subfamily Norellinae Ager, 1959

Genus *Atychorhynchia* gen. nov.

Type Species. – *Atychorhynchia falsiorigo* nov. sp.

Derivation of name. – From [*atycha*]: Greek = unfortunate.

Diagnosis. – Smooth subpentagonal Norellidae with rather flat valves and short and pointed beak containing a minute foramen. Anterior commissure clearly uniplicate. Very short dental plates fused to the ventral valve; dorsal median septum and septalium absent. Short arcuiform crura.

Remarks. – Internal and external features suggest the arrangement of these rhynchonellids within the Family Norellidae Ager, 1959 and almost certainly into the Subfamily Norellinae Ager, 1959, but they cannot be assigned to any genus currently belonging to this Subfamily. Their similarity is obvious, except for the distinctive sulcation present in most of the representatives. In fact, based on external morphology *Atychorhynchia* would be better related with the smooth and uniplicate representatives of this Subfamily such as the Triassic-Early Jurassic *Austriellula*, which was placed with uncertainty into the Norellinae in the revised *Treatise* (Savage *et al.* 2002).

Occurrence. – Late Pliensbachian–early Toarcian (*polymorphum*–*serpentinum* chronozones).

***Atychorhynchia falsiorigo* sp. nov.**

Figures 5.1–5.4, 6, 7

Holotype. – CE28.Rh1. Dimensions (in mm): L: 17.01; W: 17.79; T: 8.63. Deposited in the Departamento de Ciencias de la Tierra y del Medio Ambiente (University of Alicante, Spain).

Type locality. – La Cerradura, Jaén Province, Betic Cordillera, Spain.

Derivation of name. – [*falsum*, -i]; [*origo*]: Latin = false, failed; origin. It is referred to its condition of “failed crisis progenitor” leading the repopulation phase in the aftermath of the Early Toarcian Mass Extinction Event.

Diagnosis. – As for genus.

Description. – Medium-sized shells (Fig. 7), biconvex with rather flat valves and triangular to subpentagonal outline.

Specimens are wider than long, the maximum width lying in the mid-length and the maximum convexity shifted toward the posterior third. The beak is very short and pointed and shows a minute and mesothyrid foramen with well-developed beak ridges. The lateral commissure is straight and the anterior commissure is uniplicate with a trapezoidal dorsal median fold. The shells are usually smooth but there are rare forms with anteromarginal rounded plicae. They often display spaced growth lines. The specimens frequently show diagenetic distortions (compressed and flattened lateral profiles).

Internal structure (Fig. 6): small pedicle cavity with pedicle collar present, very short dental plates fused to the ventral valve and hinge teeth slightly crenulated and inserted in broad sockets parallel to the commissural plane. Hinge plates dorsally oriented. Dorsal median septum and septalium are absent. Crura are short. First stages of the crural architecture have a dorsal development acquiring distally a clear ventral arcuiform progression.

Remarks. – Most of the external features of *A. falsiorigo* such as the biconvex profile, smooth uniplicate form, with subpentagonal outline, are similar to those shown by the smooth (or slightly plicate) varieties of *Soaresirhynchia bouchardi*. Essential differences can be found in the beak features, very short and pointed in *A. falsiorigo* and the major convexity of the valves in *S. bouchardi*. Crural development is also different, arcuiform in *A. falsiorigo* as opposed to hamiform-subfalciform in *S. bouchardi*. The same is applicable for the classical smooth and uniplicate Pliensbachian representatives of the genus *Apringia*, recently revised and split into several genera by Vörös (2009), all showing characteristic hamiform-subfalciform crura.

Occurrence. – Zegrí Fm., late Pliensbachian–early Toarcian (*polymorphum*–*serpentinum* chronozones).

Order Athyridida Boucot, Johnson & Staton, 1964
Suborder Koninckinidina Harper, 1993
Superfamily Koninckinoidea Davidson, 1853
Family Koninckinidae Davidson, 1853

Genus *Koninckodonta* Bittner, 1893

***Koninckodonta sumuntanensis* sp. nov.**

Figures 5.14–5.20, 7

Holotype. – CE28.K1. Dimensions (in mm): L: 6.45; W: 8.20; T: 3.20. Deposited in the Departamento de Ciencias de la Tierra y del Medio Ambiente (University of Alicante, Spain).

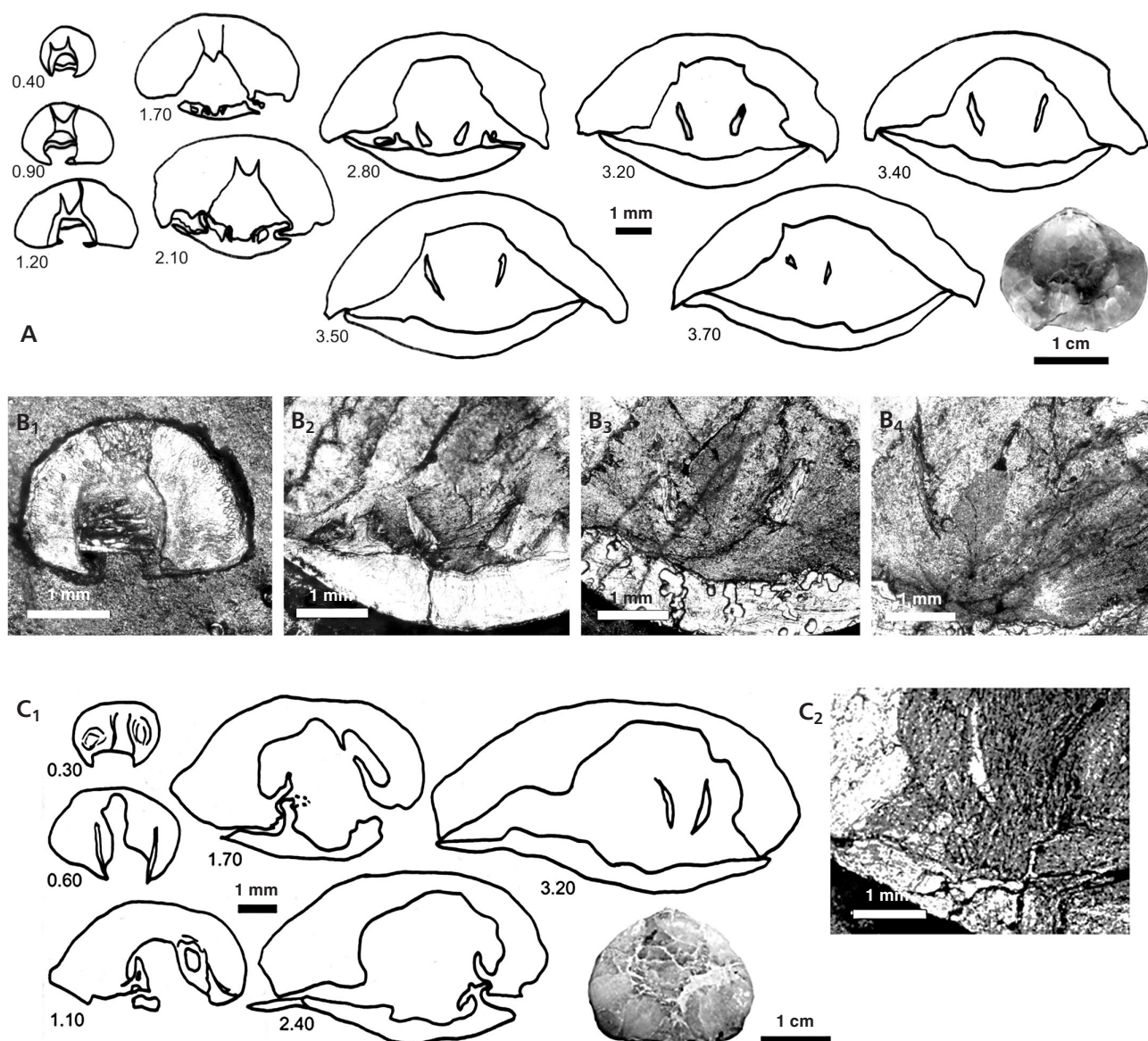


Figure 6. Internal structure of *Atychorhynchia falsiorigo* gen. et sp. nov. • A – transverse serial sections through specimen CE28b.Rh1 (distance from the apex in mm). • B1–B4 – photomicrographs of acetate peels from specimen CE28b.Rh1; B1 – section at 0.40 mm from the apex, showing the delthyrial cavity with vestiges of the pedicle collar; B2, B3 – sections at 2.80 and 3.20 mm from the apex, respectively showing the initial stages of crural development, close to the brachial valve; B4 – section at 3.50 mm from the apex, showing arcuiform crural development. • C1 – transverse serial sections through specimen CE10.Rh1 (distance from the apex in mm). • C2 – photomicrograph of acetate peel at 3.20 mm from the apex in specimen CE28b.Rh1 showing a detailed view of the arcuiform crura.

Type locality. – La Cerradura, Jaén Province, Betic Cordillera, Spain.

Derivation of name. – from *Sumuntan*, the ancient toponym of Sierra Mágina, the region where this species is recorded for the first time.

Diagnosis. – Smooth small-sized shells with subrectangular outline, wider than long. Wing-shaped and curved posterior margins and large cardinal areas. The beak is pointed and sharp. Anterior commissure with a wide to vague sinus.

Description. – Small-sized *Koninckodonta* (Fig. 7) with subquadrate to rectangular outline, wider than long and with maximum convexity near the mid-length or slightly shifted toward the anterior third of the shell. Hinge margins and cardinal areas large and widening-expanded. It shows distinctive posterolateral expansions, giving a wing-shaped outline to the posterior margin. These winged extensions are well-delimited due to their ventral curving. The beak is nearly pointed and sharp and the shell often shows densely packed growth lines, mainly in the anterior third. The anterior commissure shows a wide sinus, which in some specimens is nearly indiscernible.

Remarks. – The subquadrate-rectangular outline of this taxon and their wing-shaped posterior extensions assign this species to the broad group of specimens attributed to *K. davidsoni* in the Western Tethys as a whole. Its shape is comparable to that in species such as *K. davidsoni*, *K. geyeri* and *K. auriculata*. However, *K. sumuntanensis* has the cardinal line and posterior margins less straight than *K. geyeri* and *K. davidsoni*, also showing a more convex ventral valve. The closest affinity is found to representatives of *K. auriculata* (Vörös 2003), due to their similar wing-shaped profile, tilted towards the ventral valve, but the beak is rather massive and incurved in *K. auriculata* while it is sharper and pointed in *K. sumuntanensis*, the latter also showing a wide anterior sinus, not present in *K. auriculata*. Also remarkable is the difference in size, the length of *K. auriculata* being more than twice that of *K. sumuntanensis*.

Occurrence. – Zegrí Fm., late Pliensbachian–early Toarcian (*polymorphum*–*serpentinum* chronozones).

Record of the ETMEE in the CE section

Recent works explain the ETMEE as a pronounced biotic crisis consisting in a multi-phased interval with episodes of changing environmental conditions, which started in the late *spinatum* Chronozone up to the extinction boundary within the early *serpentinum* Chronozone. In the expanded hemipelagic facies of the CE section, Reolid *et al.* (2014a) reported the main T-OAE pulse by the increase in redox sensitive elements, TOC and TS, the record of a negative CIE, calcareous nannofossil changes and a barren interval of benthic remains.

The geochemical proxies typifying the event in this section indicate an abrupt change at the beginning of the dark marly interval (Fig. 3) with decreasing values of carbonate content and increasing TOC values (0.4% wt, but low if it is compared with the Central and North-European outcrops, lying in the lower range of those recorded in the Tethyan Toarcian sections (see discussion in Rodríguez-Tovar & Reolid 2013). Additionally, the onset of a negative $\delta^{13}\text{C}$ excursion is located 2 m above the top of the rhythmite interval and a negative $\delta^{18}\text{O}$ isotopic excursion at the rhythmite/marly interval contact and the subsequent positive isotopic excursion in the first dark marly bed are also detected. Likewise, the highest values of redox-sensitive elements (Co, Cr) occur in the first 2 m of the dark marly interval (Fig. 3).

The main T-OAE pulse was placed at the first 60 cm of dark marls above the top of the marl-limestone rhythmite (Figs 2, 3). From a biostratigraphic standpoint, the occurrence of ammonites is restricted to the marl-limestone rhythmites. The record of *Dactyloceras pseudo-commune*, *D. polymorphum* and *D. simplex* at the top of

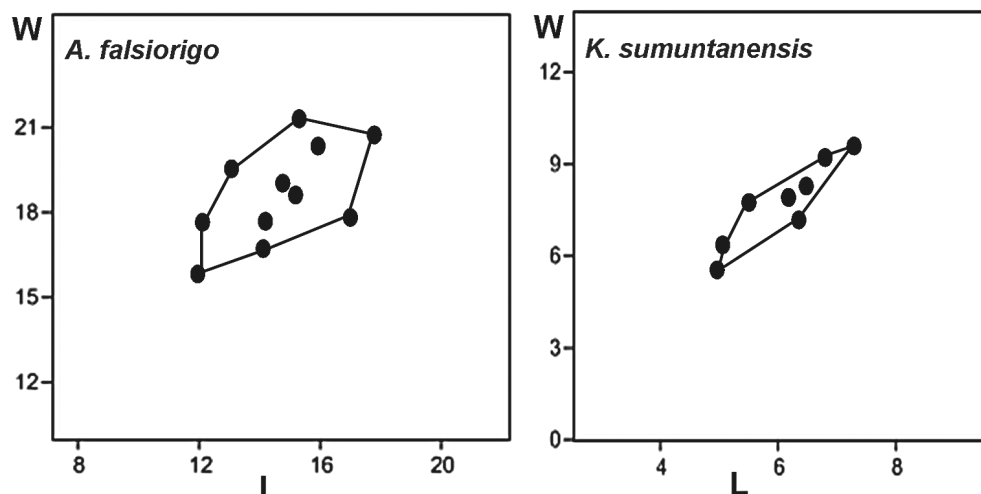
that sequence is correlative with the *polymorphum* Zone according to Braga (1983) and Jiménez (1986) (see Reolid *et al.* 2014a for more details).

The ammonites are absent in the beginning of the dark marly interval, which include the levels containing the negative CIE. Calcareous nannoplankton has been studied in these marls. Sandoval *et al.* (2012) assigned this interval to the NJT5b Zone (CNZ), not evidencing the negative CIE. Subsequently, Reolid *et al.* (2014a) recorded the negative CIE as well as the first occurrence (FOD) of the marker *Carinolithus superbus* (Fig. 2) from bed 30 upwards, assigning this interval to the NJT6 Zone (CNZ). This zone usually contains the T-OAE record (Mattioli *et al.* 2004, 2008, 2009; Casellato & Erba 2015), and, in other Tethyan basins, it spans the uppermost *polymorphum*–lower *serpentinum* ammonite zones.

In terms of the brachiopods, the biochronologic data from the CE section place the last occurrence datum (LOD) of *Liospiriferina subquadrata* within sample 22 (Fig. 2). This is the youngest record of this species worldwide, as occurrences of *L. subquadrata* have never been recorded from above the *polymorphum*–*serpentinum* boundary. Records of this species in nearby basins are constrained to the *mirabile* Subzone in Algeria (Elmi *et al.* 2006, Alméras *et al.* 2007); the *mirabile*–*semicelatum* subzones in Portugal (Comas-Rengifo *et al.* 2013, 2015), and the *semicelatum* Subzone in Pyrenees (Alméras *et al.* 2007). In fact, apart from this new record in the CE section, the presence of the representatives of the Order Spiriferinida above the *polymorphum*–*serpentinum* boundary are restricted to the La Almunia section (Iberian Range; García Joral *et al.* 2011) and Portugal (Comas-Rengifo *et al.* 2013). These authors recorded *L. falloti* and *L.?* aff. *undulata*, respectively, in the bed immediately overlying this boundary, together with *Eleganticeras elegantulum*, but never positioned above the record of the T-OAE.

On the other hand, *Orthotoma* aff. *globulina* shows a continuous record in the CE section up to sample 26, and its occasional occurrence in the 10 marks its LOD (Fig. 2). The LOD of *O. globulina* occurs in the *polymorphum* Zone in the Western Tethys as a whole. It is mainly recorded in Portugal and the North-African basins forming part of the koninckinid fauna (Choffat 1947, Alméras *et al.* 1988, Alméras & Elmi 1993, Alméras *et al.* 2007) as well as in England (Ager 1990). Further records are also assigned to *Orthotoma* in deposits assigned even to the Pliensbachian–Toarcian transition such as *Orthotoma* sp. from the latest *emaciatum*–lowermost *polymorphum* zones (*elisa*–*mirabile* subzones) in the easternmost Subbetic area (Baeza-Carratalá 2013, Baeza-Carratalá *et al.* 2015) and *Orthotoma quenstedti* regarded as becoming extinct within the extinction interval of the Pliensbachian–Toarcian boundary (Harries & Little 1999).

Figure 7. Scatter plots of the width/length ratios (in mm) on a type series of the new species *Atychorhynchia falsiorigo* and *Koninckodonta sumuntanensis*.



The remaining brachiopod fauna recorded does not allow biostratigraphic correlations as they are new taxa, probably endemic to this area. However, the record of koninckinids (beds 30–22 in CE, Fig. 2) never extends above the main extinction boundary in the Western Tethys as a whole (Vörös 2002, Baeza-Carratalá et al. 2015). The species of the classic British *Leptaena* beds (e.g. Davidson 1876–1878, Ager 1990) and their equivalent French *Koninckella* fauna (e.g. Deslongchamps 1853, Almérás et al. 1988, Almérás & Elmi 1993, Elmi et al. 1997) become extinct at approximately the *tenuicostatum-falciferum* boundary, with some British records even showing that the taxon extends into the lower part of the *serpentinum* Zone (Vörös 2002). Their North African and Mediterranean counterparts are even recorded earlier, in the uppermost Pliensbachian-lowermost Toarcian (see Vörös 2002 and Baeza-Carratalá et al. 2015 for a revision).

Summing up, the biochronologic brachiopod data hitherto reported in the Western Tethys indicate that the CE brachiopod-bearing levels correlate with the uppermost *tenuicostatum*–lowermost *serpentinum* chronozones (*semicelatum*–lowermost *elegantulum* subchronozone). Nevertheless, the remaining fauna and geochemical proxies (Reolid et al. 2014a) suggest a younger date for this assemblage within the *elegantulum* Subzone and the NJT6 Zone (CNZ), but without reaching the upper part of this subchronozone, as indicated by the FOD of *Soaresirhynchia bouchardi*, regarded as an initial coloniser in the extinction aftermath in most of the Western Tethyan basins (e.g. García Joral & Goy 2000, García Joral et al. 2011, Baeza Carratalá et al. 2011, Andrade et al. 2016). This is consistent with the record of an early T-OAE pulse in the CE section plausibly in the basal layers of the *serpentinum* Zone (Reolid et al. 2014a), bearing in mind that the expanded section in the CE area supports a significant thickness for the basal *serpentinum* Zone deposits.

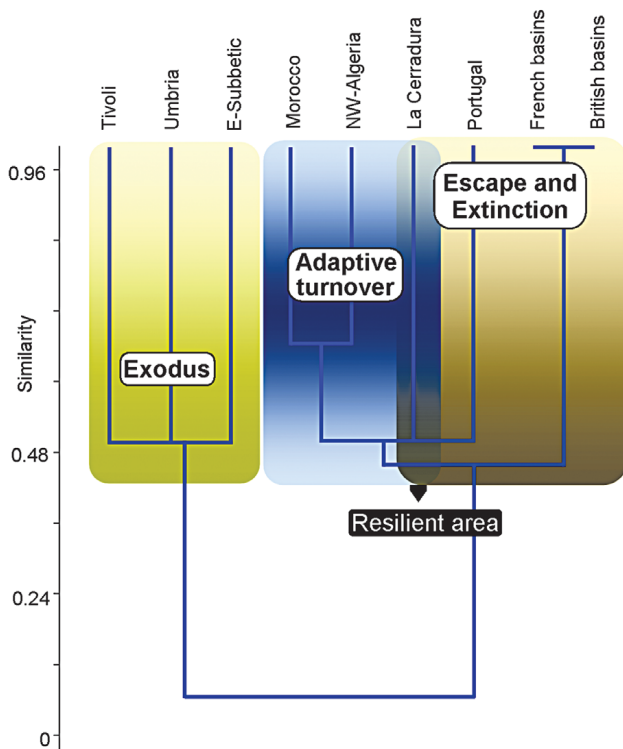
Palaeobiogeographical affinity of the CE brachiopod assemblage

Except for *Atychorhynchia falsiorigo*, which can be regarded as a standard-sized form, the minute morphotypes and species comprising this assemblage suggest a relationship with those recorded in the more western North-African and Lusitanian basins. Thus, similar morphologies to *Liospiriferina subquadrata* and *Orthotoma* aff. *globulina* were recorded together within the *Koninckella* fauna in Algeria (Almérás et al. 1988, 2007; Elmi et al. 2006). These authors initially assigned the minute spiriferinid specimens recorded in Algeria and Portugal to *L. villosa*. Subsequently, the Algerian material was reassessed as *L. subquadrata* (Elmi et al. 2006, Almérás et al. 2007) including the nearly rectimarginate forms and the uniplicate ones (Almérás et al. 2007). Likewise, Comas-Rengifo et al. (2013, 2015) considered the minute Portuguese *Liospiriferina* as *L. subquadrata*.

Therefore it can be deduced from the cluster analysis (occurrences) constructed using the Jaccard coefficient of faunal similarity (Fig. 8, Tab. 1) and from the size comparison (Fig. 9), that the presence of minute *L. subquadrata*, *Orthotoma* aff. *globulina* and *Koninckodonta* species suggest that the assemblage from the CE section has closer links with the westernmost Tethyan areas (North-African, Portugal) than with the larger koninckinid faunas from the intra-Mediterranean bioprovince (Easternmost Subbetic, Tivoli and Umbria; Baeza-Carratalá et al. 2015). However, the brachiopod fauna from the CE section can be regarded as a separate assemblage from the Algerian and Lusitanian basins (Fig. 8, Tab. 1) due to the distinctive occurrence of new taxa such as *K. sumuntanensis* and *Atychorhynchia falsiorigo* as representative elements in the assemblage. The absence of *Nannirhynchia* and *Pseudokingena* in the CE section, genera typically recorded in Algeria and Portugal (e.g. Almérás et al. 2007; Comas-Rengifo et al. 2013, 2015), is also noteworthy.

Table 1. Compositional table with data of the representative faunal elements in the assemblages considered in cluster analysis of the koninckinid fauna (see Fig. 8).

Localities	Main components of “ <i>Koninckella</i> fauna” considered	Age	References
British basins	<i>Koninckodonta davidsoni</i> <i>Orthotoma globulina</i>	<i>tenuicostatum</i> –lowermost <i>serpentinum</i> zones (<i>exaratum</i> Subzone)	Davidson (1876), Ager (1990), among others
French basins	<i>Koninckella bouchardii</i> , <i>Koninckodonta davidsoni</i> <i>Orthotoma globulina</i>	<i>tenuicostatum</i> – <i>falciferum</i> zonal boundary	Deslongchamps, (1853), Alm��ras <i>et al.</i> (1991)
La Cerradura	<i>Liospiriferina subquadrata</i> , <i>Orthotoma</i> aff. <i>globulina</i> , <i>Koninckodonta sumuntanensis</i> , <i>Atychorhynchia falsiorigo</i>	uppermost <i>polymorphum</i> –lowermost <i>serpentinum</i> zones (<i>semicelatum</i> –lower <i>elegantulum</i> subzones).	herein
Portugal	<i>Koninckella liasiana</i> , <i>L. subquadrata</i>	<i>polymorphum</i> Zone–earliest <i>levisoni</i> Zone (beds with <i>Eleganticeras elegantulum</i>)	Alm��ras & Elmi (1993), Comas-Rengifo <i>et al.</i> (2013, 2015)
Morocco Beni Snassen	<i>Koninckella liasiana</i> , <i>Orthotoma globulina</i> , <i>Liospiriferina subquadrata</i>	<i>tenuicostatum</i> Zone (<i>semicelatum</i> Subzone)	Alm��ras <i>et al.</i> (1988), Alm��ras & Elmi (1993)
NW-Algeria	<i>Koninckella liasiana</i> , <i>Liospiriferina subquadrata</i>	uppermost Pliensbachian (<i>emaciatum</i> Zone, <i>elisa</i> – <i>solare</i> subzones) to the lowermost Toarcian (<i>polymorphum</i> Zone, <i>mirabile</i> Subzone)	Elmi <i>et al.</i> (2006), Alm��ras <i>et al.</i> (2007)
Easternmost Subbetic	<i>Koninckella bolivari</i> , <i>K. gibbosula</i> , <i>Koninckodonta fornicata</i> , <i>K. cf. fornicata</i> , <i>K. davidsoni</i> , <i>K. waehneri</i> , <i>Orthotoma</i> sp.	<i>spinatum</i> – <i>polymorphum</i> zones (<i>elisa</i> – <i>mirabile</i> subzones?)	Baeza-Carratal�� (2013), Baeza-Carratal�� <i>et al.</i> (2015)
Apennines: Tivoli	<i>Koninckella tiburtina</i> (= <i>K. bolivari</i>), <i>K. gibbosula</i> , <i>K. ? choffati</i> , <i>Koninckodonta ? auriculata</i> , <i>K. fornicata</i> , <i>K. cf. waehneri</i> , <i>K. davidsoni</i> , <i>K. sicula</i> , <i>K. styriaca</i> ?, <i>K. cf. geyeri</i>	earliest Toarcian	V��r��s (2003)
Umbria: Monte Serrone	<i>Koninckella gibbosula</i> , <i>K. liasiana</i> , <i>Orthotoma apenninica</i> ; <i>Liospiriferina villosa</i> = <i>L. subquadrata</i>	<i>polymorphum</i> Zone: Pozza & Bagaglia (2001), attributed subsequently to the lowermost <i>semicelatum</i> Subzone = mid- <i>polymorphum</i> Zone (Bilotta <i>et al.</i> 2010)	Pozza & Bagaglia (2001)

**Figure 8.** Cluster analysis of the koninckinid fauna in several basins using the Jaccard similarity index, including the CE section as a resilient area. This multivariate approach is interpreted in terms of the phases in koninckinid evolution, prior to their global extinction in westernmost Tethys (*sensu* Baeza-Carratal   *et al.* 2015).

Palaeobiogeographic correlations with regions from the northern margin of the Neo-Tethys Ocean were not performed because in most of the documented areas, such as the Northern Caucasus, regional factors triggered a decline of brachiopods long before the ETMEE and therefore evidence of this event is ambiguous (Ruban 2004, 2009; Ruban *et al.* 2015).

Extinction phases of the brachiopod fauna around the ETMEE

Several previous authors have established an extinction pattern around the ETMEE for the macrobenthic fauna which, from a broad perspective, holds for the extinction models proposed by Kauffman & Erwin (1995) and Kauffman & Harries (1996), although with some modifications (see Twitchett 2006 for a revision of these models).

From the wide-ranging analysis undertaken by Harries & Little (1999) covering nektonic, planktic and benthic fauna, as regards the brachiopod fauna we can identify patterns of the (a) background conditions, (b) extinction and (c) repopulation phases. Harries & Little (1999) detected a mass extinction with a relatively long extinction interval and an extensive survival phase into the repopulation interval (Fig. 10). Subsequent analyses specifically focused on brachiopod faunas from the westernmost Tethys Ocean (Gahr 2005, Garc  a Joral *et al.* 2011) resulted in new data

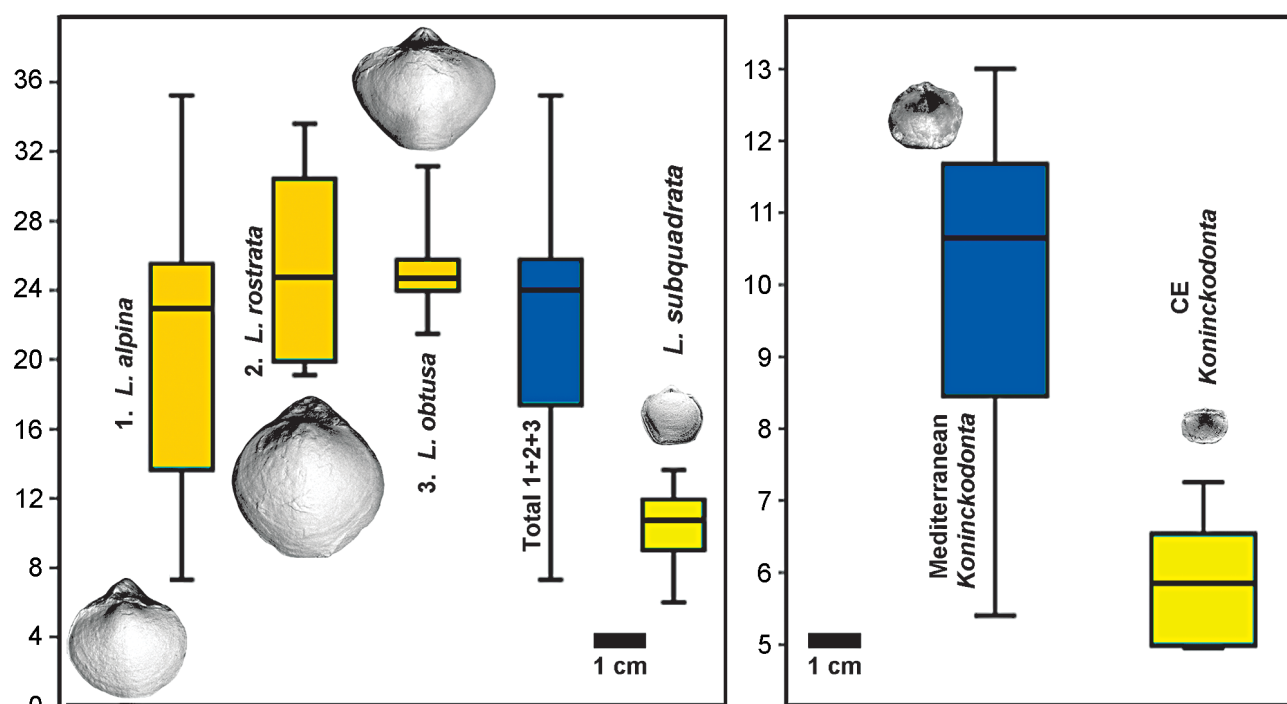


Figure 9. Boxplots showing difference in size (Length in mm) between the CE populations and (A) the easternmost Subbetic spiriferinids, and (B) the global occurrences of Mediterranean koninckinids. Easternmost Subbetic dataset from Baeza-Carratalá (2008). Global Mediterranean koninckinid data from Pozza & Bagaglia (2001), Vörös (2003), and Baeza-Carratalá (2008, 2013).

to better constrain these phases. The newly described CE brachiopod fauna documented herein offers important insight into these biotic crisis phases, as further discussed below.

In terms of the extinction interval, there are some discrepancies related to the timing of its onset and in giving support to a twofold phase in the repopulation interval after the main extinction boundary, consisting of an initial survival phase and finally a true recovery interval (Fig. 10). The present work regards these phases taking into account recent data on the evolutionary history of brachiopods around the ETMEE (e.g. Vörös 2002, 2005; García Joral *et al.* 2011; Baeza-Carratalá *et al.* 2015; Comas-Rengifo *et al.* 2015; Gómez *et al.* 2016) by adding biochronological data acquired from the westernmost Tethys areas (Braga 1983; Jiménez 1986; Sandoval *et al.* 2012; Comas-Rengifo *et al.* 2013, 2015; Reolid *et al.* 2014a, Baeza-Carratalá *et al.* 2015), and also analyzing the correlation with the isotopic curve fluctuations and palaeotemperature data in several peri-Iberian basins (Gómez & Goy 2011, García Joral *et al.* 2011, Sandoval *et al.* 2012).

The extinction phases herein proposed (Fig. 10) closely resemble the initial pattern suggested by Harries & Little (1999), but the extinction interval has been expanded according to the new data, with the extinction boundary placed in the basal part of the *elegantulum* Subzone. The definition of the extinction interval is consistent with the

latter occurrences and evolution of koninckinid fauna (Baeza-Carratalá *et al.* 2015), which can be used as a precursor signal of a multi-phased interval with episodes of changing environmental conditions in accordance with the main isotopic excursion pulses and temperature changes. This interval is detected from the *elisa–mirabile* subzones, when the first evolutionary changes related to the extinction occurred, lasting up to the extinction boundary in the basal *elegantulum* Subzone (Baeza-Carratalá *et al.* 2015).

In this extinction interval, the pathway through, which koninckinid fauna passed from an initial migration to more favourable environments, to an adaptive turnover and finally to their extinction, can be followed across the Western Tethys by a species turnover, involving a general decrease in size and diversity loss. In the basins where koninckinid fauna is not recorded, this interval is characterized by the occurrence of species seemingly better adapted to warmer environments, as they are restricted to paleolatitudes around 28°–35° N and this interval represents an increasing in the seawater temperature at the Iberian platform system in the order of 4–5 °C (García Joral *et al.* 2011).

Thus, brachiopod data might endorse the research trend which suggests that the onset of ETMEE occurred in the late Pliensbachian–earliest Toarcian, and the extinction boundary coinciding with a thermal maximum resulting of long-term changes in environmental conditions prior to

this event (e.g. Gómez *et al.* 2008, Dera *et al.* 2010, Suan *et al.* 2010, García Joral *et al.* 2011, Baeza-Carratalá *et al.* 2015).

The extinction boundary established into the lower *serpentinum* Zone is marked by the conspicuous impact suffered by the brachiopod fauna at a global scale. Two orders, Spiriferinida and Athyridida, which survived with low diversity since the End-Triassic Extinction (Vörös *et al.* 2016) became extinct (Vörös 2002, 2005; Comas-Rengifo *et al.* 2006; García Joral *et al.* 2011; Baeza-Carratalá *et al.* 2015) whereas the ~70% of the genera within the Order Rhynchonellida disappeared (cf. Manceñido 2000, García Joral *et al.* 2011), and the Order Terebratulida underwent an important renewal (García Joral *et al.* 2011).

The onset of the repopulation interval into the *elegantulum* Zone is marked by the FOD of *Soaresirhynchia bouchardi* at many localities of the westernmost Tethyan basins (cf. García Joral *et al.* 2011, Comas-Rengifo *et al.* 2015). *S. bouchardi* fulfills the standard pattern of a bloom of opportunistic species in the sense of Levinton (1970) or Harries *et al.* (1996, p. 45) occupying an environment where competitors were lacking (García Joral & Goy 2000; Gahr 2002, 2005). It is only recorded in the aftermath of the extinction, being probably the precursor of the Middle Jurassic–Cretaceous Basiliolidae. Its record marks the beginning of the repopulation interval, whose lower boundary is marked by the onset of the post-extinction radiation (cf. Kauffman & Harries 1996).

Significance of the CE assemblage for the brachiopod adaptive strategies linked to the ETMEE

Considering the brachiopod records in the CE section and analyzing the evolutionary trend in the westernmost Tethyan basins of the groups making up the studied assemblage, different strategies developed in the extinction phases can be deduced (Fig. 11):

Pre-extinction dwarfing

Fluctuations in the body size of several macroinvertebrates through the Pliensbachian–Toarcian extinction interval and in the aftermath of the ETMEE were studied by Morten & Twitchett (2009) with variable results depending on the analyzed group. As a rule, size-decrease patterns linked to mass extinction events have been widely documented mainly in the aftermath of extinction boundaries through the well-known “Lilliput effect” as a post-extinction syndrome in the survival taxa (e.g. Urbanek 1993; Twitchett

2001, 2006, 2007; Harries & Knorr 2009). However, among the significant bioevents that occurred during the brachiopod’s extensive macroevolutionary history, reduction in size within an extinction interval preceding extinction boundary is, generally considerably understudied except for some noticeable data (see e.g. He *et al.* 2007, Zhang *et al.* 2016).

Previous authors (e.g. Marshall & Corruccini 1978, Harries & Knorr 2009) used the term “dwarfing” to designate a size pattern consisting of progressive smaller sizes within a lineage prior to, during, and in the repopulation phases of a mass extinction event. This term was then used by Wade & Olsson (2009) for descendant populations smaller than ancestral ones preceding an extinction interval in Cenozoic planktic foraminifera, suggesting the presence of smaller size in the same lineage as an adaptive response to environmental perturbations of the water column. In terms of brachiopods, dwarfing in chonetids prior to the end-Permian mass extinction event was detected by Zhang *et al.* (2016).

Pre-extinction dwarfing related to ETMEE is also detected in several brachiopod stocks such as the koninckinid fauna through a spatial gradient in the westernmost Tethys (Baeza-Carratalá *et al.* 2015), which is related to the taxonomic composition of the assemblages. These authors identified several stages in the koninckinid fauna evolution within the extinction interval prior to the its extinction, triggering a migration from the Mediterranean mainly epi-oceanic areas (where the stock of large *Nannirhynchia* and koninckinids proliferated, e.g. *N. reynesi*, *N. gemmellaro*, *N. pilulla*, *K. fornicata*, *K. gibbosula*) to the Atlantic/NW-European basins, where mostly miniaturized and paucispecific koninckinid faunas (e.g. *N. pygmaea*, *K. liasiana*) were widespread. The occurrences of this dwarf fauna recorded to date supported the hypothesis that this adaptive response started in the North-African basins (Baeza-Carratalá *et al.* 2015).

The taxonomic and morphologic composition of the brachiopod assemblage from the CE section certainly suggests affinities with the earlier North-African assemblages, which probably contained the adaptation (Figs 8, 9). Otherwise, the studied assemblage is also comparable with the younger assemblages recorded in localities from the Lusitanian Basin (Fig. 8, Tab. 1), which typify the first stages of the “escape and extinction” phase in the higher latitude Atlantic basins. In this sense, from a palaeogeographical point of view, the CE section would be located in a hemipelagic trough connected with the Hispanic Corridor (Sandoval *et al.* 2012, Rodríguez-Tovar & Reolid 2013, Reolid *et al.* 2014a), allowing both migration through the Atlantic seaway and surviving of long-lasting species up to their total extinction within the *serpentinum* Zone.

Referring to the spiriferinids, the size-distribution pattern prior to their extinction is slightly more complex.

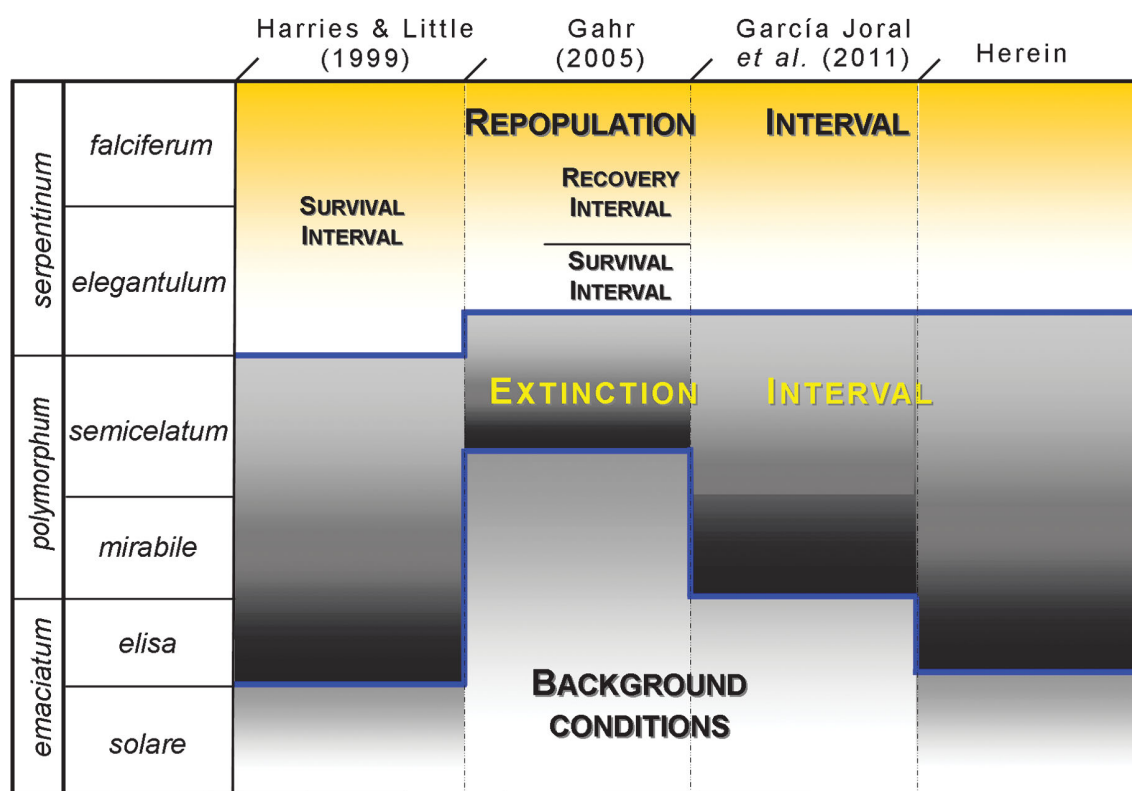


Figure 10. Pattern of the extinction phases linked to the early Toarcian Mass Extinction Event for the brachiopod fauna. The new intervals herein proposed are mainly based on data of García Joral *et al.* (2011) and Baeza-Carratalá *et al.* (2015), and also supported by several groups of macrobenthic fauna (sources in the text).

A spatial-size-decrease gradient from the Mediterranean or well-oxygenated areas to the epicontinental NW-European seas is observed also affecting the taxonomic composition of the assemblages (Fig. 9).

Minute spiriferinids such as *Liospiriferina subquadrata* and *L. villosa* are recurrently recorded in the extinction interval together with the T-OAE-precursor koninckinid fauna in NW-Algeria, Portugal, and now in the South-Iberian palaeomargin (CE section), but they are also eventually recorded with standard-size or even larger spiriferinids like *L. falloti* or *L. rostrata* in the North Gondwana Palaeomargin (Algeria), even reaching the Pyrenean Basin (Alméras & Fauré, 2000), but never being recorded in either the background interval or in the repopulation phases.

To explain a similar uneven pattern in size change in chonetids associated with the end-Permian extinction, Zhang *et al.* (2016) alluded to an interspecific competition for trophic resources supply and interactions between closely related species. Dwarfing within a brachiopod lineage can be related to developmental heterochronies linked to environmental stress (*cf.* Laurin & García Joral 1990). As probably occurs in other taxonomic groups (Guex 2016), the progressive increase of temperature and consequently low oxygen availability in most intra-Tethyan

zones triggered such adaptive responses in the brachiopod fauna (García Joral *et al.* 2011, Baeza-Carratalá *et al.* 2015).

In this context, within the extinction interval, spatial dwarfing would have been an effective short-term adaptive response to the adverse changing environmental conditions such as extreme temperatures, oxygen-depleted habitats, restricted nutrients availability, and/or turbidity. Zhang *et al.* (2016) inferred the reduction of food supply as a cause of the pre-extinction dwarfism in the end-Permian chonetids. In La Cerradura case, however, trophic resources were surely not the restrictive parameter as high nutrients concentration has been reported for this time interval (*e.g.* Jenkyns *et al.* 2001, Dera & Donnadieu 2012, Rodríguez-Tovar & Reolid 2013, Reolid *et al.* 2014a, Casellato & Erba 2015), probably introduced by higher run-off and warming (weathering-induced nitrification). A quantitative study on brachiopod body size in the extinction interval will be approached by the authors in a further work to better understand this adaptive response.

On the other hand and to some extent related to this pre-extinction dwarfing, a global perspective of the koninckinid fauna in the Western Tethys as a whole can fit with a failed crisis progenitor model (*cf.* Kauffman & Harries 1996, Harries & Little 1999) (Fig. 11). In the

Pliensbachian-Toarcian transition, koninckinids mainly proliferated in the extinction interval. They successfully survived a diverse set of severe ecological perturbations, which characterize the multi-phase extinction interval, as can be deduced from several pulses and excursions displayed by biotic and isotopic signals (Vörös 2002, Baeza-Carratalá *et al.* 2015). They originated a premature pre-extinction radiation (Figs 8, 11), but they are not recorded in the repopulation interval marked by the *S. bouchardi*-beds in the Western Tethys, not providing the successful stock for the post-extinction radiation.

Resilience

It is well-known that smooth brachiopods are representative inhabitants of deep-sea environments, especially in the Mediterranean province of the Western Tethys (*cf.* Ager 1967; Vörös 1993, 2005). Vörös (2005) ascertained that, in the post-Palaeozoic history of brachiopods, deeper-water marine habitats might have operated as long-term reservoirs where the evolutionary lineages of smooth morphotypes survived marine crises and, under appropriate conditions, expanded to re-occupy shallow habitats. After the end-Triassic and early Toarcian extinctions, the recovery of brachiopod fauna in shallow-water marine environments was conducted by surviving smooth stocks from the deep-sea reservoir (Vörös 2005).

Several authors (*e.g.* Thuy *et al.* 2014, Andrade *et al.* 2016) suggested that the deep-sea fauna is not only more resilient to an extinction event than those inhabiting shallow-water, but that *in situ* diversification in these deeper-water habitats was probably higher than generally supposed. Hence, these areas should not be considered only refugia but as resilient environments that can produce and export high taxonomic diversity (Vörös 2005, Lindner *et al.* 2008, Thuy *et al.* 2014).

The CE section is located in a deep-water, subsiding area with expanded sedimentation and represents a pelagic marine trough situated close to the Hispanic Corridor and the passage between the Western Tethys and the Proto-Atlantic seaway (Bailey *et al.* 2003, Rodríguez-Tovar & Reolid 2013, Reolid *et al.* 2014a). Thus, fragmentation of the South-Iberian palaeomargin in horst and graben/semi-graben basins could produce such deeper sub-basins giving a potential interpretation as resilient area for the CE fauna.

All the brachiopods recorded in the CE section (*Liospiriferina*, *Koninckodonta*, *Orthotoma*, *Atychorhynchia*) are consistent with a very stable external morphotype consisting of a smooth ornament or very faint ribbing pattern (Fig. 5), indicative of deep-water habitats (Vörös 2005). The high evolutionary stability of this kind of deep and resilient environment enabled smooth latest Pliensbachian–early Toarcian morphotypes to withstand

several perturbation peaks within the extinction interval. The assemblage of the CE section is never recorded throughout the Subbetic area. They not only survived the main ETMEE probably recorded in the lowermost *serpentinum* Zone in the expanded CE section, but also underwent a radiation during the extinction interval (Fig. 11) as CE brachiopods diversified their lineages developing new taxa such as *Koninckodonta sumuntanensis* and *Atychorhynchia falsiorigo*. This speciation event is consistent with the hypothesis previously mentioned of deep areas which can serve as evolutionary factories.

The FODs of these taxa are recorded within the extinction interval and did not reach the repopulation interval as defined by the FOD of *S. bouchardi*. Thus, they can be regarded as failed crisis progenitors (*cf.* Kauffman & Harries 1996; Harries & Little 1999), as they could have played the role of pioneers that *S. bouchardi* achieved.

In fact, *A. falsiorigo* exemplifies the possible pattern followed by *S. bouchardi*, which can be regarded as an analogous morphotype. *S. bouchardi* likely originated in another similar resilient deep-water environment and, in favourable environmental conditions, colonised peri-Iberian basins (Andrade *et al.* 2016). Furthermore, the development of very simple and conservative morphotypes in these resilient habitats allows reaching a high diversification and provides them the potential to export taxonomic diversity, once again confirming the great dispersal potential of the deep-sea benthic biota (Vörös 2005, Thuy *et al.* 2014).

This scenario connects with the *evolutionary factories* model proposed by Andrade *et al.* (2016) as supplier for the late Toarcian-early Aalenian peri-Iberian brachiopod biohermas. This evolutionary model can predispose the biogeographical distribution of Recent brachiopods already established for the Early Jurassic faunas (Vörös 2005, Zezina 2008, Thuy *et al.* 2014, Andrade *et al.* 2016).

Opportunism and homoplasy

Analyzing brachiopod trends round the ETMEE, Harries & Little (1999) detected a clear pattern consisting of the extinction of most of the pre-boundary taxa followed by an early initial evolutionary burst in the repopulation interval. Taking into account the aforementioned pre-extinction dwarfing and resilience models, some new insights of this repopulation can be further developed by analyzing several specific groups.

New findings in the Subbetic CE section of *Atychorhynchia falsiorigo* and its homeomorphic external similarity with *Soaresirhynchia bouchardi*, regarded as the coloniser in the aftermath of the extinction marking the repopulation interval, suggests a possible crisis progenitor/survival descendant relationship. Both species are biconvex, smooth to slightly antero-marginal ribbed forms,

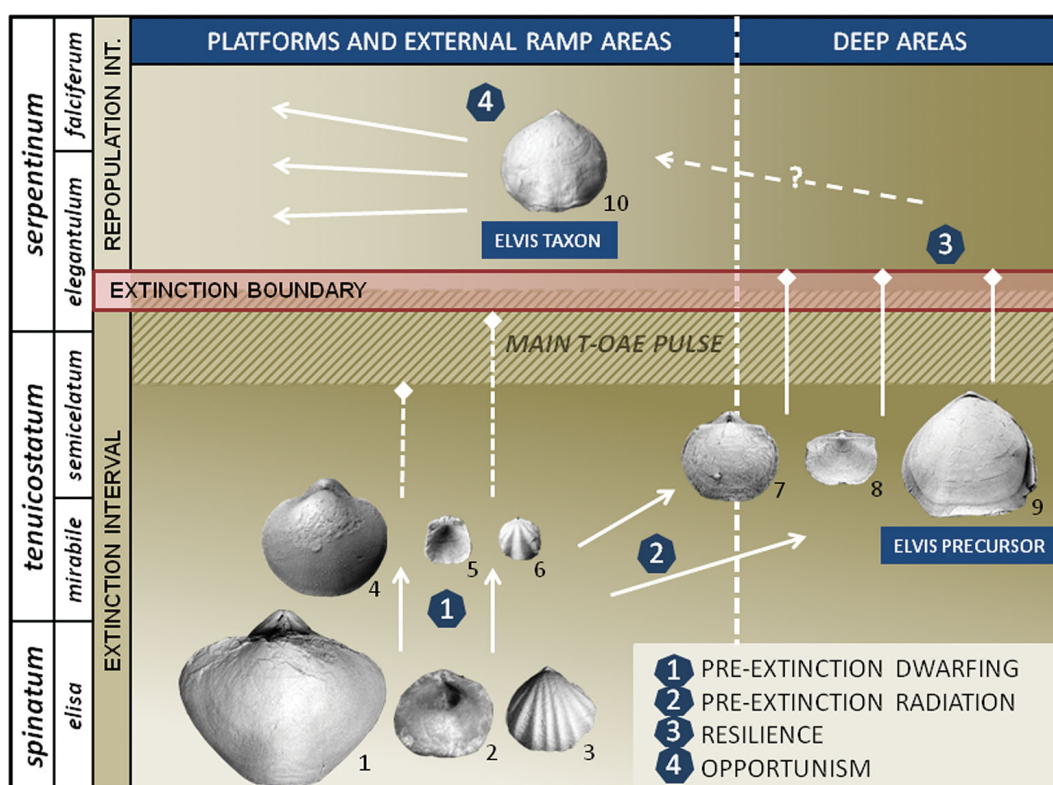


Figure 11. Summary-sketch of the evolutionary trends and adaptive strategies linked to the Early Toarcian Mass Extinction Event inferred for the brachiopod fauna in the westernmost Tethys Ocean. 1. *Liospiriferina obtusa* (Oppel); 2. *Koninckodonta fornicata* (Canavari); 3. *Nannirhynchia pilulla* (Schlosser in Böse and Schlosser); 4. *Liospiriferina cf. falloti* (Corroy); 5. *Nannirhynchia pygmaea* (Morris); 6. *Koninckella liasiana* (Bouchard in Davidson); 7. *Liospiriferina subquadrata* (Seguenza); 8. *Koninckodonta sumuntanensis* sp. nov.; 9. *Atychorhynchia falsiorigo* gen. et sp. nov.; 10. *Soaresirhynchia bouchardi* (Davidson).

uniplicate, with rounded to subpentagonal outlines, occurring above and below the mass extinction boundary.

In this situation, it would be feasible to infer a phyletic relationship between these two taxa within the evolutionary lineage *Apringia* (Pliensbachian)–*Soaresirhynchia* (early Toarcian) suggested by García Joral *et al.* (2011), belonging to the virtually continuous smooth uniplicate evolutionary lineage *Austriellula* (Triassic)–*Fortunella* (Early Cretaceous) pointed out by Vörös (2005), who stated that the record of this lineage suffered short gaps during the end-Triassic and early Toarcian crises and its re-appearance typifies a Lazarus effect.

Nevertheless, the accurate analysis of the internal architecture of *A. falsiorigo* has revealed quite different features mainly related to crural development, which enables the new taxon to be split from this lineage. Serial sections performed on the new rhynchonellids from the CE section show internal features related more to representatives within the Norellidae than those of the *Apringia*–*Soaresirhynchia*–*Mondegia* lineage that belong to the Basiliolidae. Although some of the accessory criteria such as the absence of a dorsal median septum and septalium are coincident in both families, the crural architecture found in

the studied specimens shows a clear arcuiform development, indicative of the Early Jurassic Norellidae instead of the hamiform-subfalciform crura shown by the Basiliolidae. This situation can hence be interpreted in terms of a reasonable case of homoplasy between these taxa (Fig. 11).

Homoplasy, so-called Elvis taxa (Ervin & Droser 1993) is a documented trend in brachiopod lineages through mass extinction events (*e.g.* Dulai & Pálffy 2003) as a consequence of the relatively simple morphology of brachiopods and the adaptation of different taxa to analogous environmental conditions. In fact, external homeomorphism is a common feature among brachiopod taxa, and particularly in the smooth brachiopods, likely as a result of a convergent adaptation to deeper marine environments (Vörös 2005). Smooth forms are very simple and conservative morphotypes developed and diversified in resilient habitats such as the CE area. Thus, if *A. falsiorigo* from this locality represents a separate taxon from *S. bouchardi* and their Pliensbachian counterparts, *S. bouchardi* can be regarded as an Elvis taxon (Fig. 11) in correspondence with *A. falsiorigo*, the latter can be understood as an Elvis precursor (not in the phylogenetic sense of “progenitor” but by

the earlier occurrence of heterochronous homeomorphic forms).

The pattern of repopulation led by *S. bouchardi*, recorded in the *elegantulum* Subzone, occupying vacant ecospace after the extinction boundary in both epicontinental (e.g. García Joral *et al.* 2011) and epi-oceanic areas (e.g. Baeza-Carratalá 2013), is distinctive of an opportunistic strategy (*sensu* Levinton 1970, Harries *et al.* 1996) as it shows basic external features (nearly smooth shells, subrounded outlines), morphological plasticity and simple internal architecture (Fig. 11). *S. bouchardi*-beds are also characterized by monospecific assemblages with copious specimens.

This opportunistic strategy has been perceived in the repopulation interval of several biotic crises. Thus, smooth brachiopods could also lead the Early Triassic repopulation (*cf.* Vörös 2005) and Basiliolidae species, probably linked to the *Apringia-Fortunella* lineage (like *S. bouchardi*), are also recorded leading the repopulation interval after the end-Cretaceous mass extinction, since Dulai *et al.* (2008) reported a monospecific assemblage composed of *Basiliocostella*. This genus survived in deep-water areas during the end-Cretaceous extinction interval and invaded shallow-water habitats again in the Danian (Dulai *et al.* 2008). The recurrent morphological similarity showed by all these taxa is indicative of an evolutionary pattern that can be generalized.

Conclusions

Lower Toarcian deposits of the peri-Iberian platform system include one of the most significant brachiopod faunas from the Western Tethys Ocean, allowing an appraisal of the epibenthic fauna in the marine ecosystems around the ETMEE.

The present analysis reviews the early Toarcian extinction phases taking into account recent data on the evolutionary history of noteworthy brachiopod groups round the ETMEE. The extinction interval has been expanded, establishing its onset likely in the *elisa-mirabile* subzones and the extinction boundary into the basal part of the *elegantulum* Subzone. The definition of the extinction interval is consistent with the later occurrences and evolution of the koninckinid fauna and the extinction boundary is marked by the conspicuous impact suffered by the brachiopod fauna at a global scale. The onset of the repopulation interval into the *elegantulum* Zone is marked by the FOD of *Soaresirhynchia bouchardi*.

The newly documented fauna recorded from La Cerradura, External Subbetic (Spain), a deep pelagic trough in the South-Iberian palaeomargin, close to the Hispanic Corridor and the passage between the Western Tethys and the Proto-Atlantic seaway, enhances compre-

hensive understanding of some unique examples of adaptive strategies. Essential supplementary systematic work has to be done to identify undescribed species from the new CE site, resulting in two new taxa, *Koninckodonta sumuntanensis* new species and *Atychorhynchia falsiorigo* new genus and species.

These data support evidence of pre-extinction dwarfing and resilience in deep refugia linked to the ETMEE. An episode of speciation has been recognized in the late extinction interval which can be interpreted in terms of a pre-extinction radiation. In the same way, *Atychorhynchia falsiorigo* fits well with the failed crisis progenitor model, thus typifying a homoplasy case of an Elvis taxon with the pioneer opportunistic species that colonise the Western Tethys in the aftermath of the extinction, *Soaresirhynchia bouchardi*.

Similar strategies (pre-extinction dwarfing, resilience in deep refugia and opportunistic pioneers of similar morphology) occurred related to other mass extinction intervals such as the Permian-Triassic or the Cretaceous-Paleocene events, reinforcing the scheme of a possible standard pattern of the brachiopod fauna in response to such biotic crises and shedding light on the ecological effects of mass extinction events.

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