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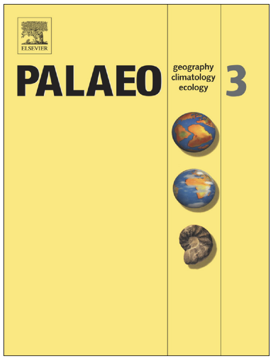

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PII: S0031-0182(20)30236-4

DOI: https://doi.org/10.1016/j.palaeo.2020.109791

Reference: PALAEO 109791

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 29 November 2019

Revised date: 30 April 2020

Accepted date: 3 May 2020

Please cite this article as: J.F. Baeza-Carratalá and F.G. Joral, Linking Western Tethyan Rhynchonellide morphogroups to the key post-Palaeozoic extinction and turnover events, *Palaeogeography, Palaeoclimatology, Palaeoecology* (2020), https://doi.org/10.1016/j.palaeo.2020.109791

Linking Western Tethyan Rhynchonellide morphogroups to the key post-Palaeozoic extinction and turnover events

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Abstract

Genetic control undoubtedly plays the most decisive role in the development of characters in rhynchonellides, especially in those structural features such as shell microstructure and brachidial architecture. However, considering the relationship between shell microstructure and type of crura in post-Palaeozoic rhynchonellides supported by recent growing research, the present study links this striking matching to the distribution of rhynchonellide morphogroups around the main post-Palaeozoic mass extinction and diversification events, innovatively introducing the ribbing pattern as a feature widely argued as indicator of deeper/shallower habitats and particular ecological conditions. The analyses performed on the Western Tethys rhynchonellide database and, directly on 28 species from the peri-Iberian margins around selected post-Palaeozoic extinction/diversification episodes, reveal a recurrent distribution pattern according to the habitat considered (epicontinental vs. epioceanic). The smooth, eurinoid, septifal/arcual body plan is the distinctive inhabitant of deeper epioceanic environments, also being the last to withdraw from the epicontinental platforms when the environmental conditions were adverse, and the pioneers or opportunistic taxa conducting repopulation of these epicontinental habitats when the conditions were re-established after crises.

The ribbed, eurinoid, falciform morphogroup seems to be the more resilient stock on epicontinental platforms in relation to ecological crises. Conversely, the ribbed, leptinoid, raducal group is typical inhabitant of epicontinental seas when normal conditions prevail and shows an uneven distribution unlinked to critical events, suggesting a more specialist pattern with a diversification related with a secondary differentiation. It is suggested that this distribution dynamic of morphogroups was controlled by the availability of requirements to generate each type of crura and microstructure in epicontinental/epioceanic habitats, such as metabolic or oxygen restrictions, or the filter-feeding efficiency of the lophophore. A research line starting-point is thus herein introduced which can lead to shed light into the adaptive strategies of rhynchonellides, relating particular morphotypes with potential triggering factors of mass extinction events.

Keywords: Brachiopoda; extinction events; adaptive strategies; environmental distribution; Western Tethys.

1. Introduction

Representatives of phylum Brachiopoda are frequently used in macroevolutionary studies (e.g. Ager 1956a; Johnson 1975; McNamara 1982; Ager 1983; Raup 1986; Valentine and Jablonski 2010; Carlson 2016; Stigall 2013) due to their wide-ranging record throughout the Phanerozoic, their considerable diversity and abundance, and relatively simple body plan, endowing this group with a reasonable morphological stability range (Kowalewski et al. 1997; Krause 2004; Harper et al. 2017; Topper et al. 2017; Vörös et al. 2019). Owing to their close connection with substrata and short mainly lecithotrophic larval stage (at least in post-Palaeozoic times), they are also exceptional proxies to shed light on the response of marine benthic ecosystems to environmental perturbations. In this sense, a number of marine biotic crises and mass extinctions recurrently affected this filter-feeding biota influencing the diversity dynamics and the evolutionary trajectories of the different brachiopod clades (Gould and Calloway 1980; Chen et al. 2005; Curry and Brunton 2007; García Joral et al. 2011; Harper et al. 2014; Carlson 2016; Vörös et al. 2016, 2019).

Notwithstanding the well-known homeomorphy experimented by several constituents of this phylum, among brachiopod clades, the post-Palaeozoic representatives of the Order Rhynchonellida Kuhn, are relatively standardised in both the external form (shape, beak features, rhizo- to pleni-pedunculate shells, *sensu* Ratcliffe 1991 and Harper and Moran 1997 respectively) and internal architecture (crural developments as skeletal supports of spirolophous lophophore), accordingly constituting effective ecological and evolutionary tools.

Concerning the external attributes, one of the most challenged features on the ecological interpretations in rhynchonellides is the ornamentation. It is stated that smooth brachiopods are more prolific in both deeper and warmer environments (Ager 1965; Rudwick 1970; cf. Fürsich and Hurst 1974; Vörös 2005). Smooth rhynchonellides stock is supposed to play a significant role in several crucial extinction and/or diversification events in the evolutionary history of brachiopods (Vörös 2005). In fact, several smooth evolutionary lineages mainly arranged into the families Basiliolidae and Norellidae were invoked by Vörös (2005) to be crucial in the Mesozoic marine diversification, hypothesizing that they survived the End-Triassic extinction and were resilient to the major post-Palaeozoic marine crises as inhabitants of bathyal deep-sea environments, thus facilitating the pioneering re-colonization of habitats in the aftermath of these crisis events.

On the other hand, after experimental substantiation, Manceñido and Motchurova-Dekova (2010) postulated a close correspondence between types of crura and the microstructure pattern of the secondary layer of the shell in most of the rhynchonellid groups. Using combination of both internal diagnostic criteria has been growing as innovative tool on the suprageneric taxonomy, also revealing major evolutionary lineages within rhynchonellides (Motchurova-Dekova and Simon 2007; Radulovic et al. 2007; Motchurova-Dekova et al. 2008, 2009; Manceñido and Motchurova-Dekova 2010; Schreiber et al 2014; Simon et al. 2018, among others).

In this paper, both aforementioned inter-related hypotheses are coupled and tested. Firstly, new data on the hypothesized positive crural architecture-shell microstructure relationship (Manceñido and Motchurova-Dekova 2010) are empirically evaluated in several smooth and ribbed rhynchonellides from the Mesozoic-Cainozoic peri-Iberian platforms-basins system, where brachiopod faunas are widely represented virtually in all periods and series, being specially studied in their Jurassic heydays and in crucial events (e.g. Choffat 1880; Jiménez de Cisneros 1923; Dubar 1925; 1931; Comas-Rengifo and Goy 1975; Calzada 1975, 1984, 1997; Calzada and Pocoví 1980; García Joral and Goy 1984, 2000, 2004, 2009; García Joral et al. 1990, 2011, 2018; Alméras et al. 1996; Alméras and Fauré 2000; Bitner and Martinell 2001; Reolid 2005; Andrade 2006; García-Ramos 2006; Baeza-Carratalá 2011, 2013; Comas-Rengifo et al. 2006, 2013, 2015; Baeza-Carratalá et al. 2015, 2016 a, b, 2018; Colás 2015; Berrocal-Casero et al. 2017, 2020; Giannetti et al. 2018). Subsequently, the external ribbing pattern is taken into account to perform an equivalence analysis coupling this external feature with the internal architecture/microstructure compiling an updated Western Tethys Meso-Cainozoic rhynchonellide database for that purpose.

Linking both internal and external primary systematic criteria with the occurrence of the different post-Palaeozoic rhynchonellide taxa, we can extend the hypothesis that substantial turnover events in the diversity dynamics of post-Palaeozoic rhynchonellides were undergone by smooth morphotypes (cf. Vörös 2005) also involving the role of other morphogoups in these events, in turn phylogenetically related to several evolutionary lineages (Vörös 2005; cf. Manceñido and Motchurova-Dekova 2010). Thus, comparing the rhynchonellide distribution curve derived from the global dataset of the Paleobiology Database (PaleoDB) with the possible matching predicted by two hypotheses, it is possible to deduce if particular rhynchonellide morphogroups could recurrently develop in the evolutionary history of brachiopods and if this may be explained in terms of ecological strategies or behaviours in response to ecological perturbations.

2. Materials and Methods

A number of 102 Western Tethyan post-Palaeozoic rhynchonellide genera dataset was built up in a matrix (supplementary material) with an initial geographical discrimination from the revised *Treatise* (Kaesler and Selden 1997-2007) combined with raw data of the Paleobiology Database (PaleoDB, http://paleobiodb.org/ accessed via the FossilWorks gateway, http://fossilworks.org/), and new recent generic attributions mainly from the peri-Iberian basins. Discrimination also took into account the availability of reliable documentation about internal features and microstructure in previous selected literature revealing crural and microstructure criteria (44 genera) either directly in descriptions or in the pictures. New data on 28 species (22 genera) from the peri-Iberian basins were analysed. The matrix dataset was supplemented by additional 36 genera on the basis of their suprageneric attribution, when crural architecture and shell microstructure were properly guaranteed from different confamiliar taxa.

The internal structure and microstructure of the shell was studied on 34 peri-Iberian rhynchonellide specimens using the conventional method of taking acetate peels after making transverse serial sections. The distance between serial sections was 0.1 mm. Using Scanning Electron Microscope (SEM) has been promoted as better exploratory method of the shell microstructure whenever possible, but SEM is not always available to all brachiopodologists (as pointed out by Motchurova-Dekova et al. 2008) and microstructural analysis performed in the present paper exposes that conventional light microscopy can be a suitable equipment to reveal the main microstructural patterns in proper serial sections. Thus, high resolution microphotographs of acetate peels were taken using a Nikon CFI60 600POL microscope. The fibres of the secondary layer were quantified as close as possible to the maximum shell width, as recommended by previous authors (Radulovic et al. 2007; cf. Manceñido and Motchurova-Dekova 2010). All specimens figured and acetate peels are deposited in the collections of the Earth and Environmental Sciences Department of the University of Alicante (DCTMA), the Department of Geodynamics, Stratigraphy and Palaeontology of the Complutense University of Madrid (DPUCM), and the Department of Palaeontology of the University of Granada (DPUGR).

With reference to the ribbing pattern criterion, Vörös (2010) defined four ornamentation categories in Mesozoic rhynchonellides: 1. smooth or capillate; 2. costate or antidichotomous; 3. strongly costate; and 4. spinose. Partly based on this categorization, we adopted the following groupings: 1. smooth or capillate with paucicostate shells, mainly restricted to the anterior margin; 2. strong multicostate or fully ribbed shells, 3. spinose shells.

Regarding the crural types, nomenclature herein followed is that proposed by Manceñido et al. (2007), later followed by Manceñido and Motchurova-Dekova (2010) considering four crural groups: ensimergal, raducal, septifal, and arcual. Concerning the shell microstructure on the secondary layer, the duality eurinoid/leptinoid (coarse/finer fibres respectively) established, among others, by Radulovic et al. (2007), Manceñido et al. (2007, in *Treatise*, v. 6), and Manceñido and Motchurova-Dekova (2010), is considered.

Several critical bioevents were plotted against the rhynchonellide diversity curve obtained using the global dataset of the PaleoDB. This diversity dynamics curve was processed to genus-level by means of a stage-level resolution. Biostratigraphical data of each taxon were taken into account to evaluate the range and distribution of each morphogroup. Environmental epioceanic/epicontinental duality was also considered, when available, in the interpretation of the graphics to better constrain the environmental objective of the research (see environmental occurrence data in the supplementary matrix for habitat preferences of each taxon; columns Q and R).

The binary (presence/absence) matrix, built up exclusively considering morpho-structural criteria, i.e. the crural type, microstructure, and ribbing criteria, was evaluated through hierarchical cluster analysis with the UPGMA algorithm using the Jaccard similarity coefficient. Independently, binary values were also considered to plotting the environmental preferences of each rhynchonellide morphogroup (columns Q and R in the supplementary matrix) against their biostratigraphic range. All statistical analyses were carried out by means of the PAST software package (Hammer et al. 2001).

3. Crural architecture plus shell microstructure.

Significance of type of crura as the main endoskeletal structure with most important taxonomic value has a long-way trajectory. Traditional systematics of rhynchonellides is based upon this character earlier in the morphological interpretations of Rothpletz (1886), Wisniewska (1932), and Muir-Wood (1934), subsequently followed by the comprehensive works of Ager (1956b-1967), Cooper (1959), Makridin (1964), Dagys (1968), Ager et al. (1972), Manceñido (2000), Manceñido and Owen (2001), Savage et al. (2002), Manceñido and Motchurova-Dekova (2010), Schreiber et al. (2014), among many others (for a recent revision on this issue, see e.g. two latter quoted works).

Over the last years, a more accurate taxonomical hierarchy has been achieved by means the exploration of the fibrous microstructure pattern on the secondary layer of the shell, simultaneously applied in correspondence with types of crura. In this sense, an extensive background (e.g. Motchurova-Dekova and Simon 2007; cf. Manceñido et al. 2007; Radulovic et al. 2007; Motchurova-Dekova et al. 2008, 2009; Manceñido and Motchurova-Dekova 2010; Simon et al. 2018) has improved the suprageneric taxonomy, also revealing major evolutionary lineages within rhynchonellides. Thus, an eurinoid coarse fibres pattern has been revealed corresponding with the arcual and septifal crural groups, contrasting with a finer leptinoid pattern which matches with the ensimergal and raducal crural groups (Manceñido and Motchurova-Dekova 2010).

As results of this previous extensive background, a starting point dataset has been built up herein. A total number of 102 genera has been considered, compiling information from 44 genera recorded in the Western Tethys Ocean, arranged into the Superfamilies Rhynchonelloidea, Hemithiridoidea, Rhynchotetradoidea, Dimerelloidea, Pugnacoidea, Wellerelloidea, and Norelloidea, taking previous comprehensive research of Manceñido and Motchurova-Dekova (2010) as a keystone, as well as data from some other authors revealing microstructure criteria either directly in descriptions or by observing the illustrations (e.g. Tomašových 2006; Dulai et al. 2008, Motchurova-Dekova et al. 2009, Simon et al. 2018, Berrocal-Casero et al. 2020). In all these genera, a positive correspondence between microstructure pattern and expected crural types was revealed (see supplementary material).

Additionally, new data testing this matching have been analysed in 23 Mesozoic-Cainozoic genera (29 species) recorded in the peri-Iberian platforms-basins system (Table 1), accomplishing therefore a profitable post-Palaeozoic database for further deductions (see supplementary material). These taxa are encompassed into 8 families: Wellerellidae (*Cirpa briseis, Cirpa* sp. aff. *latifrons, Salgirella albertii*), Tetrarhynchiidae (*Gibbirhynchia curviceps, Quadratirhynchia atenuatta*), Rhynchonellidae (*Cuneirhynchia cartieri, C. dalmasi, C. rastuensis, Homoeorhynchia meridionalis, Choffatirhynchia vasconcellosi, Rhynchonelloidea goyi*), Prionorhynchiidae (*Prionorhynchia guembeli, P. quinqueplicata, P. polyptycha*); Cyclothyrididae (*Alebusirhynchia vorosi, A. jorali, Globirhynchia subobsoleta*), Basiliolidae (*Apringia atlaeformis, Soaresirhynchia bouchardi, Pseudogibbirhynchia jurensis, Mondegia atla, Fortunella decipiens, Aphelesia bipartita*), Erymnariidae (*Septocrurella microcephala*), and Norellidae (*Nannirhynchia pillula, Atychorhynchia falsiorigo, Praemonticlarella distercica, Monticlarella triloboides*). The remaining 35 genera in the matrix are tentatively arranged in basis of their suprageneric taxonomic attribution widely substantiated from different confamiliar taxa from their respective lineages.

All the peri-Iberian Basiliolidae herein analysed reveal a eurinoid microstructure pattern (Fig. 1). Their coarse fibres show a rhomboidal cross-section outline and range from 45 to 75 µm width and 30 to 50 µm thickness. Crural developments in the studied Basiliolidae are represented by the hamiform type (figs. 1 A, B; 2C) in the Lower Jurassic representatives (*Apringia atlaeformis, Pseudogibbirhynchia jurensis*, and *Soaresirhynchia bouchardi*) and by the falciform type in the Middle Jurassic (*Mondegia atla*), Cretaceous (*Fortunella decipiens*), and Cainozoic (*Aphelesia bipartita*) counterparts (Fig. 1, C-E). Other taxon having an eurinoid pattern has been observed in Erymnariidae (*Septocrurella microcephala*), presenting coarse fibres with a mean of 70 µm wide and 45 µm thick, and septiform crura, thus satisfying the predicted pattern of the septifal crural group (Fig. 1F).

The remaining species revealing a eurinoid microstructure pattern are arranged into Wellerellidae (*Cirpa briseis, Cirpa*. sp. aff. *latifrons*, and *Salgirella albertii*). They present rhomboidal to subquadrate fibres in cross section, ranging from 60-70 µm wide and 35-40 µm thick, also corresponding with hamiform crural developments (Fig. 2). Taxa with arcual crural developments (*Nannirhynchia pillula, Monticlarella triloboides,* and *Atycorhynchia falsiorigo*) evidence slightly stacked and finer fibres (50-60 µm wide and around 20 µm thick) but also fitting the eurinoid pattern, with pseudo-rhombic fibres and rather homogeneous structure (Fig. 3). This eurinoid pattern is much more evident in *Praemonticlarella distercica*, also with arcual crural architecture (Fig. 3B).

By analysing the dataset matrix, the correspondence eurinoid/septifal can be extended to all the Basiliolidae, Erymnariidae, and Wellerellidae representatives as well as the eurinoid/arcual relationship can be broadened to Norellidae, as foreseen to some extent by Manceñido and Motchurova-Dekova (2010) and references therein.

On the other hand, a striking positive correspondence is detected between the leptinoid microstructure pattern and the raducal crural group (Fig. 4). It is substantiated in all the Jurassic families and genera studied with raduliform development, i.e. Tetrarhynchiidae (*Gibbirhynchia curviceps*), Rhynchonellidae (*Cuneirhynchia cartieri, C. dalmasi, C. rastuensis, Homoeorhynchia meridionalis,* and *Choffatirhynchia vasconcellosi*), Prionorhynchiidae (*Prionorhynchia quinqueplicata, P. guembeli* and *P. polyptycha*) and Cyclothyrididae (*Alebusirhynchia jorali, A. vorosi, Globirhynchia subobsoleta*). These taxa present finer halberd-like fibres in *Cuneirhynchia, Homoeorhynchia*, and *Prionorhynchia* (Fig. 4 A-F, L); subrectangular and finest in *Gibbirhynchia* (Fig. 4 G); being more irregular and heterogeneous in *Alebusirhynchia* and *Choffatirhynchia* (Fig. 4 I-K). The fibres size varies from 8-45 µm wide (exceptionally 55 µm in a few *Cuneirhynchia* cross sections) and 3-10 µm thick (except for some *Cuneirhynchia* fibres as well, with 15 µm thick).

The correlation leptinoid/raducal is also corroborated in all the Tetrarhynchidae, Rhynchonellidae, Prionorhynchiidae, and Cyclothyrididae representatives present in the dataset matrix, as also foreseen by Manceñido and Motchurova-Dekova (2010) and references therein.

4. Ribbing pattern reflected in the diverse crural-microstructure lineages of rhynchonellides

In his seminal work about smooth Mediterranean brachiopods, Vörös (2005) portrayed the evolutionary lineages of several smooth Norelloidea and Basiliolidae rhynchonellides, in part taking into account their internal architecture. The analysis now performed estimates the ornamentation pattern considering the Western Tethys post-Palaeozoic rhynchonellide database (see supplementary material), bearing in mind the crural/microstructure equivalence previously deduced in each evolutionary lineage. Considering the different ribbing pattern categories aforementioned in the materials and methods section, the dominant pattern in the diverse groups based on the internal structure is evaluated, resulting the following combinations (figs. 1-4):

1. Multicostate or fully strong-ribbed taxa are the abundant "ordinary-looking" post-Palaeozoic rhynchonellides. This ornamentation category is mainly distributed in the Western Tethys in two major groups according to their internal body plan:

1a. The raducal (unusually ensimergal)/leptinoid is the most numerous ribbed group (Fig. 4). Their representatives are arranged in several supra-generic positions: the better represented is Tetrarhynchiidae, with 23 genera (herein depicted with *Gibbirhynchia*). Superfamily Hemithiridoidea is also frequent in this class, emphasising 8 ribbed genera into the Family Cyclothyrididae (herein *Alebusirhynchia*). The Family Rhynchonellidae is typified by 6 ribbed genera (*Choffatirhynchia* and *Cuneirhynchia* herein). Further multicostate families such as Prionorhynchiidae (*Prionorhynchia* herein) or Peregrinellidae are less diverse.

1b. The septifal (exceptionally arcual)/eurinoid group is less abundant. Ribbed taxa are mainly arranged into the subfamilies Cirpinae (Family Welleriidae), Lacunosellinae (Superfamily Pugnacoidea), and, to a lesser extent, into the Subfamily Pamirorhynchiinae (Family Basiliolidae;

such as *Pseudogibbirhynchia* herein) and the Family Erymnariidae. The specimens illustrated in this work belonging to this group are mainly arranged in *Cirpa*, *Salgirella*, and *Pseudogibbirhynchia* (Fig. 2). Interestingly, some genera included in this group show a typical "bifurcate" ribbing pattern, more infrequent in the previous group. The ribbed representatives with arcual developments are arranged into Praemonticlarellinae, herein represented by *Praemonticlarella* (Fig. 3).

2. Spinose forms are completely embodied into the Family Acanthothirididae, all with raducal/leptinoid internal pattern.

3. Among the smooth, paucicostate, and capillate pattern there are different internal body plans, but major groups are included in Norelloidea and Basiliolidae.

3a. Smooth or paucicostate ribbing pattern with septifal/eurinoid structure is conspicuous in the Family Basiliolidae, showing falciform, subfalciform, and hamiform crura, and mainly arranged into the Subfamily Basiliolinae (13 genera). This subfamily is typified by *Apringia*, *Soaresirhynchia*, *Mondegia*, and *Fortunella* in this work (Fig. 1), also analysing Aphelesiinae (*Aphelesia*) and Pamirorhynchiinae representatives. Completing the septifal/eurinoid group there are three poorly ribbed genera belonging to Erymnariidae with septiform crura (*Septocrurella* herein).

3b. The paucicostate and smooth ornamentation is also recurrent in the rhynchonellides with arcual/eurinoid internal architecture. They are all arranged in Norelloidea (*Nannirhynchia*, *Monticlarella*, and *Atycorhynchia* herein, Fig. 3), mainly in the Subfamily Norellinae, as reflected in the matrix dataset.

3c. Leptinoid microstructure pattern is minority among the smooth (paucicostate) morphotypes. Five genera belonging to the Family Rhynchonellidae show this type of ornamentation with raducal/leptinoid structure (*Homoeorhynchia* herein, Fig. 4L) and three genera into Dimerelloidea fulfil the smooth leptinoid pattern with ensimergal crural development.

In summary, ribbing pattern is variable in almost all the groups defined by their crura-microstructure features, reinforcing its secondary role for phylogenetic relationships. Therefore, it seems to be an important feature in adaptive strategies, as will be discussed in the next paragraphs.

5. Discussion. Testing twofold hypothesis

5.1. Main post-Palaeozoic rhynchonellide morphogroups in the Western Tethys

Cluster multivariate analysis performed in the matrix dataset of Western Tethys rhynchonellides expose a clear grouping on the basis of microstructure pattern (eurinoid/leptinoid) as primary criterion (Fig. 5). The subsequent subordinate division takes the ribbing pattern as more relevant factor, being the crural group the last criterion of arranging.

These criteria are marked in the nodes of the cluster (Fig. 5) and apparently accomplish a discernible taxonomical component as primary factor for splitting morphogroups, i.e., leptinoid vs. eurinoid microstructure in turn related with the crural type, acquiring the ribbing pattern a decisive role in the clustering. However, all features globally considered acquire an environmental significance as discussed below, without diminishing its phylogenetic meaning.

In the eurinoid group, the phylogenetic and systematic relationship is evident, grouping on the basis of the similarity degree, the arcuiform Norellidae interrelated with the septifal crural architecture of the Erymnaridae (septiform) and Basiliolidae (hami/falciform). However, as previously mentioned, cluster distance gives more significance to the ribbing pattern than the crural group. Thus, several taxa diverge from the phylogenetic structure and we can observe ribbed eurinoid hamiform Basiliolidae, such as *Pseudogibbirhynchia*, *Stolmorhynchia,* and *Orbirhynchia* clustered together with ribbed eurinoid hamiform Welleridae such as *Cirpa, Salgirella,* or *Calcirhynchia*. Hence, this clustering releases an interesting systematic discussion. For instance, the so far assumed systematic arrangement of *Pseudogibbirhynchia* into Basiliolidae was obviously based on the type species *Pseudogibbirhynchia moorei* (Davidson), which is the only paucicostate species assigned to this genus. This species is very scarce and presumably endemic from the South-

England basins, since the occurrences attributed to this taxon outside its type area (Thévenin 1908; Comas-Rengifo and Goy 1975; Alméras 1996; Alméras and Becaud 2002; Baeza-Carratalá 2013) are tentative and/or ambiguous. On the other hand, the occurrences assigned to *Pseudogibbirhynchia* in the Upper Toarcian-Aalenian from Spain, Portugal, and the Alps (García Joral 1993; García Joral and Goy 2009; Andrade 2006; Andrade et al. 2016) are fully costate (frequently dichotomous) forms that can be considered closer to representatives of Welleridae, such as *Cirpa*, as resulted in our clustering analysis. It is therefore plausible postulating a phyletic relationship between *Pseudogibbirhynchia* and *Cirpa*, as envisaged by Ager (1962), and consequently, a systematic revision of *Pseudogibbirhynchia* and other ribbed Basiliolidae such as *Orbirhynchia*, both currently in the Subfamily Pamirorhynchiinae would be desirable.

5.2. Morphogroups linked to the key post-Palaeozoic turnover and extinction events

By analyzing the global diversity curve of rhynchonellides obtained using the global dataset of the PaleoDB, several events of extinction and diversification in the overall history of the group can be individualized (Fig. 6). We can distinguish four major post-Palaeozoic crises, entailing a considerable diversity decrease followed by subsequent noticeable recovery episodes: The Rhaetian, linked to the end-Triassic extinction (ETE) events; the Early Toarcian; the Oxfordian; and the Maastrichtian/Danian boundary. Several subordinate episodes involving loss of diversity, less conspicuous in the rhynchonellide groups, are also detected (e.g. Cenomanian-Turonian boundary or Messinian events in the Fig. 6). These secondary episodes took place just when brachiopods diversity was very low, even in the background conditions, and no relevant inferences can be obtained from their analysis. On the other hand, previous authors (e.g. Miller and Foote 2009) have confirmed that environmental perturbations during mass extinctions and their macroevolutionary signatures were manifested differently in epicontinental and epioceanic habitats (*sensu* Hallam 1971; Olóriz 2000). Connecting this aspect with the morphogroups resulting from the figure 5, allowing to organize the 9 groups previously determined by the cluster, arranging them into 4 stocks with palaeoenvironmental significance. For the sake of the accuracy of the analysis, only those morphogroups with relative abundance related to the extinction/diversification events have been considered, being the remaining groups too scarce to allow reliable interpretations. These groups are: 1. eurinoid arcuiform smooth; 2. eurinoid septifal smooth; 3. eurinoid septifal ribbed; and 4. leptinoid raducal ribbed. The chronostratigraphic distribution of the studied genera representing these four morphogroups is exposed in the Fig. 7, distinguishing epioceanic and epicontinental occurrences, and the main extinction and diversification events since the Early Triassic.

The eurinoid pattern of microstructure occurs in three of these morphogroups, all consistent with habitats related with pre- or post-stressed environmental conditions. The smooth eurinoid arcuiform morphogroup has been interpreted as constituted by deeper epioceanic taxa (cf. Vörös 2005). However, if we interrelate this morphogroup with the stratigraphical distribution and the epicontinental/epioceanic occurrences of the taxa analysed from the Western Tethys post-Palaeozoic database (Fig. 7), it can be deduced also for this group a resilient pattern in epicontinental platforms around extinction episodes as well as a pioneer post-extinction occurrence after three events, the early Toarcian, the Callovian/Oxfordian and the Cenomanian/Turonian extinctions. Likewise, it can be observed that the smooth eurinoid septifal morphogroup is mainly constituted by deeper epioceanic inhabitants, which conducted opportunistic post-crisis epicontinental colonization; while the distribution of the eurinoid falciform ribbed morphogroup is consistent with epicontinental resilient taxa.

Finally, the leptinoid, raducal, and ribbed forms, seems to be linked to epicontinental specialist taxa with secondary adaptations, depending on ecological factors such as the substrate type, trophic source, hydro-dynamics, or reproductive adaptations. This specialistic component is noticed also for the leptinoid ensimergal representatives (not represented in the figure 7). Thus, several dimerelloids such as *Peregrinella*, *Sulcirostra*, and *Rhynchonellina* have been related with cold seeps or chemosynthesis-based ecosystems (Campbell and Bottjer 1995; Sandy 1995, 2010; Dulai 2002; Peckmann et al. 2007, 2013; Kiel et al. 2014; Sandy and Peckmann 2016; Palfy et al. 2017, among others); in the same way, the raducal spinose Acanthothyrids, have been often related with pararecifal environments (e.g. Childs 1969) and *Cryptopora* could be adapted to deeper (up to abyssal) environments (Surlyk and Johansen 1984). The role of the leptinoid raducal smooth or paucicostate morphogroup is more difficult to analyse because of their scarcity, but it is noticeable its record just prior to the first occurrence of the leptinoid raducal ribbed forms in epicontinental areas, both in the Triassic and in the Paleogene.

With this analysis, a matching seems to appear between major post-Palaeozoic rhynchonellide turnover events after ecological crises and a specific body plan, consisting in smooth/eurinoid, arcual (Norellidae) or falciform and derived (mainly Basiliolidae) genera, otherwise typical inhabitants of epioceanic areas. Conversely, those ribbed leptinoid, raducal (some ensimergal) types do not reveal such a patent distribution pattern around critical events, but they are the main components of the assemblages in the diversification events in epicontinental environments. On the other hand, ribbed falciform (and derived) eurinoid types, recurrently recorded both in epicontinental and epioceanic environments, seem to be more resilient to these events (Fig. 8).

One of these a priori deeper epioceanic lineages (Norelloidea) was previously presumed as responsible of the rhynchonellide diversity recovery after the End-Permian and End-Triassic (ETE) crises (Manceñido and Owen 2001; Vörös 2005). These authors hypothesized that minute Norelloidea could lead the post-Palaeozoic radiation from paedomorphic survivors of this family, performing the recovery of brachiopod lineages after the Permian-Triassic biotic catastrophe. According to the rhynchonellide global diversity curve (Fig. 6), from the minimal richness values reached in the End-Permian extinction, when other 5 rhynchonelliform orders were extinct (Curry and Brunton 2007), the first rhynchonellide re-diversification pulse in the Western Tethys was recorded in the Anisian, probably conducted by smooth, arcuiform, eurinoid, *Norella* and *Holcorhynchella* (Vörös 2005; Gradinaru and Gaetani 2019) arranged into the Norelloidea lineage (Fig. 7). *Holcorhynchella* did not evolve beyond the Middle Triassic, but the epioceanic *Norella* lasted up to the End-Triassic crisis, in the Rhaetian. Thus, Norellidae (and most of the resulting morphogroups herein) apparently are consistent with a pattern of declining diversity in the ETE (at least in the westernmost Tethyan areas) whose onset was detected also in other fossil groups at or around the Norian/Rhaetian boundary by several previous authors (e.g. Rigo et al. 2020).

The succeeding record of this lineage is detected during the main Early Jurassic diversification event after the End-Triassic crisis (Sinemurian) due to the occurrence of the small-sized arcual, eurinoid, and paucicostate *Pisirhynchia* in epioceanic habitats (Vörös 2005; Vörös and Dulai 2007), together with the minute Pliensbachian-Bathonian *Nannirhynchia* (arcual, eurinoid, and mostly paucicostate species). This last genus has been repeatedly associated to relatively deep and oxygen-depleted environments (Ager 1967; Alméras et al. 1989, 1995; Andrade 2006).

As can be deduced from the figures 6 and 7, rhynchonellides suffered a Late Jurassic-Lower Cretaceous debacle with development of unfavourable conditions for brachiopod settlement in the Western Tethys as a whole, specially noticed in the epioceanic Mediterranean habitats by the so-called "*age of radiolarites*" (Vörös 2005; Colás and García Joral 2012) from the Callovian onwards. The only Norellidae genus recorded at this time is *Monticlarella*, which seemingly was capable of surviving this crisis by colonizing the epicontinental platforms of the northern margin of Western Tethys, just like other epioceanic brachiopods such as nucleatids (Colás and García Joral 2012).

Later representatives of this smooth lineage are very scarce up to their extant counterparts, e.g. *Abyssorhynchia*, *Neorhynchia*. The lineage probably survived in deeper epioceanic habitats establishing steady communities in deep faunal reservoirs (Vörös 2005; Thuy et al. 2014). This can be corroborated by the occasional record of this lineage in deep epioceanic environments, as typified by *Atycorhynchia* in deep Subbetic grabens around the Early Toarcian Mass Extinction Event (ETMEE) crisis (Baeza-Carratalá et al. 2017), which has revealed a eurinoid arcuiform smooth morphotype (Fig. 3).

On the other hand, a virtually uninterrupted trajectory can be detected in the smooth falciform (and related subfalciform, hamiform) Basiliolidae (Vörös 2005), also with eurinoid microstructure. This evolutionary lineage, clearly represented early in the Jurassic by the hamiform *Apringia*-group

(*Apringia, Serrataprinigia, Megapringia*) probably started with the Triassic representatives of *Austriellula*. It should be mentioned that *Austriellula* was arranged with uncertainty in Norellinae in the revised Treatise (Manceñido et al. 2002), but subsequent authors (Vörös 2005; Dulai et al. 2008; Baeza-Carratalá et al. 2017) preferred considering this taxon as the baseline of the evolutionary lineage *Austriellula* (Triassic)-*Fortunella* (Early Cretaceous). First records of *Austriellula* (Carnian-Norian) are reported in the maximum of the Triassic rhynchonellide diversification and persisted until the End-Triassic extinction event (except for the tentative attribution to it of Renz's Toarcian material from Western Greece by Manceñido (1993), with inaccessible internal features).

The following record in this lineage is typified by the epioceanic *Apringia* group in the main speciation recovery event that took place in the Sinemurian (Dulai 2003; Vörös and Dulai 2007; Baeza-Carratalá 2013), leading to the subsequent heyday of the brachiopod Mediterranean smooth fauna in the Pliensbachian (Vörös 2005, 2009; Vörös and Dulai 2007) and not exceeding the Early Toarcian Mass Extinction Event (ETMEE).

After the ETMEE, monospecific beds bearing the prolific *Soaresirhynchia bouchardi* are recorded throughout the Western Tethys Ocean (e.g. Alméras 1994; García Joral and Goy 2000; Graziano et al. 2006; García Joral et al. 2011; Baeza-Carratalá 2013; Baeza-Carratalá et al. 2017). This Basiliolidae species is characterized by a smooth to paucicostate shell, moderately small, hamiform crura, and eurinoid microstructure (Fig. 1). The post-ETMEE pattern of recovery led by *S. bouchardi* in the Serpentinum Chronozone (Elegantulum Subchronozone) of the Early Toarcian, occupying vacant ecospaces, is distinctive of an opportunistic strategy in the repopulation interval of the aforementioned biotic crisis (e.g. García Joral and Goy 2000; Gahr 2005; García Joral et al. 2011; Baeza-Carratalá et al. 2017). This turnover episode has been considered as the most important post-Palaeozoic renewal interval in the brachiopod fauna in the Western Tethys (García Joral et al. 2011; Andrade et al. 2016) subsequently allowing, in the stabilization of the background conditions, the settlement of the leptinoid radical morphotypes (i.e. *Homoeorhynchia, Choffatirhynchia*).

The subsequent taxon recorded in this evolutionary lineage is *Mondegia*, also showing smooth, eurinoid, and falciform morphotypes (Andrade 2006; Baeza-Carratalá et al. 2011; Fig. 1 herein). In the mainly epioceanic Mediterranean bioprovince, the onset of the first post-ETMEE diversification episode was conducted by smooth brachiopods (Vörös 2005), with this maximum in diversity dated in the Early Bajocian with the pervasive occurrence of *Mondegia atla* in most of the epioceanic basins (e.g. Oppel 1863; Ferrari 1962; Vörös 1997; Vörös and Dulai 2007; Baeza-Carratalá et al. 2011, 2014) preceding the rhynchonellide bloom in the Bajocian-Callovian interval (Fig. 7). *Mondegia* was also recorded in the Sauzei Chronozone (Lower Bajocian) in relatively deep areas of the epicontinental NW-European bioprovince (Lusitanian basin), subsequently to the dominance of the Basiliolidae (*Soaresirhynchia*) and Norellidae (*Nannirhynchia*), thus conducting these smooth eurinoid morphotypes the diversification episode in the Aalenian-lowermost Bajocian of this area (Andrade 2006). The Bajocian-Callovian interval represents the maximum diversity peak in the post-Palaeozoic history of rhynchonellides, highly contributing the deep-epioceanic smooth taxa to reaching this bloom (cf. Vörös 2005), after which *Mondegia* became extinct.

After the Late Jurassic crisis, the smooth eurinoid/falciform lineage continued in the Jurassic-Cretaceous transition with the genus *Fortunella*. This taxon appeared and diversified after recovery of environmental stress conditions, marked (similarly to the ETMEE) by a negative isotopic oxygen excursion (Curry and Brunton 2007). This genus, just like some other aforementioned Basiliolidae taxa, also reveals an opportunistic strategy, showing high morphologic plasticity, being widely diversified from the Oxfordian to the Aptian, and attaining a nearly cosmopolitan distribution, from East-Spain to the Alps and from Algeria to the Russian Platform (Sulser and Calzada 1991). In this sense, *Fortunella* could play a decisive role in the colonization of vacant ecospaces in this Upper Jurassic-Cretaceous rhynchonellide decline interval, since it was considered by Vörös et al. (2018) as pioneer taxon in the repopulation phases after crucial perturbation events, such as the Early Cretaceous Weissert anoxic event (Upper Valanginian), when monospecific levels of *Fortunella* were recorded recolonizing intra-Tethyan basins (Vörös et al. 2018).

The record of this lineage is virtually disrupted up to the Turonian times (Vörös 2005) when, once again, after the Bonarelli extinction event, the phylogenetic line of the extant *Basiliola* seems to emerge (figs. 6, 7) leading to a diversification phase of this morphogroup which lasted up to the Maastrichtian. The renowned Cretaceous-Paleogene (K-Pg) event also affected brachiopod fauna (Curry and Brunton 2007, Dulai et al. 2008, Vörös et al. 2019) leading to a very low rhynchonellide diversity. Once again, Basilioloidea representatives occurred as opportunistic brachiopod fauna after K-Pg event. Thus, Dulai et al. (2008) recorded numerous individuals of *Basiliocostella* (an eurinoid falciform and weakly ribbed morphotype) forming monospecific assemblages in the Danian.

Similar situation occurred with the Neogene counterparts of this lineage. The smooth Mesozoic Basiliolidae lineage depicted by Vörös (2005) continued with the Neogene *Aphelesia*. This taxon is profusely recorded in the Upper Miocene-Lower Pliocene of the Mediterranean basins. In the westernmost peri-Iberian basins (Mediterranean-Atlantic seaway), *Aphelesia* is recorded in the Late Tortonian, and re-emerged again in the earliest Pliocene (Bittner and Martinell 2001, Bittner and Moissette 2003, García-Ramos 2004, Toscano-Grande et al. 2010; Giannetti et al. 2018) when the background conditions after the Messinian Mediterranean Salinity Crisis were re-established (Giannetti et al. 2018).

The extant representatives of this lineage (e.g. *Basiliola, Basiliolella*) are typical inhabitants of cryptic or deeper habitats (Zezina 1994, 2010; Vörös 2005). If we consider the present-day as a declining episode in the rhynchonellides diversity, we can postulate that the smooth eurinoid arcual (or falciform) body plans of the Norellidae and Basiliolidae respectively withstand singular environmental conditions (caves, crevices, bathyal habitats) expecting future better conditions or less competitive pressure on the platforms, constituting "reservoirs" for potential diversification, since they are the clear dominant rhynchonellide fauna: 14 of the total 19 extant genera are arranged into Norellidae and Basiliolidae, and a great number of them are smooth and micromorphic forms, especially in the extant arcual Norelloidea. The same occurs to species-level: 24 of 38 total extant rhynchonellide species are arranged in these body plans.

The eurinoid/septifal ribbed morphogroup is consistent with an epicontinental resilient pattern in the Early and Middle Jurassic. *Cirpa* seems to be the only big-sized rhynchonellide that survives until the last levels prior to the Early Toarcian crisis (García Joral et al. 2018), and *Pseudogibbirhynchia* is the typical representative of the impoverished brachiopod communities that are frequent in the Late Toarcian and the Early Aalenian in epicontinental areas (Garcia Joral and Goy 2009; Andrade et al. 2016). Some representatives of this group have even been considered as disaster-taxa flourishing during Cretaceous OAEs or platform drowning events (Graziano and Taddei-Ruggiero 2008). Thus, *Orbirhynchia* blooms coincided with the Early Aptian Selli OAE and *Costerymnaria* beds are recorded concurring with both the Early Cenomanian and Late Campanian drowning episodes. This lineage seems to become extinct at the Cretaceous-Paleogene boundary.

The leptinoid radical group is present in epicontinental environments when "normal" conditions prevail in the Jurassic and the Cretaceous, with maximum of diversity in the Pliensbachian, the Bajocian-Bathonian, the Aptian to Cenomanian and the Santonian to Maastrichtian stages, and is scarce or absent during crisis events.

5.3. Functional adaptive body plan

As can be deduced from the previous analysis, there is a correspondence between the rhynchonellide morphogroup consisting of smooth eurinoid, mainly with arcual or septifal crura and crucial episodes in the post-Palaeozoic evolutionary history of rhynchonellides. Thus, the smooth eurinoid arcual structure is the most recurrent pattern just in the pre-extinction boundary intervals, but also is regularly recorded in the post-extinction recoveries, thus contributing to the main diversification events in both the epioceanic and epicontinental areas (Fig. 8). In the same way, the smooth eurinoid septifal structure seems to be the most effective pattern to conduct the recolonization and diversification events from the deeper seas, when the environmental conditions have been re-established in shallow-water environments after ecological perturbations, as opportunistic or pioneer taxa indicative of the onset of repopulation episodes in both epicontinental and epioceanic platforms (figs. 7, 8). Finally, the leptinoid microstructure with ribbed radical morphotype, is characteristic of the diversification climax, mainly in epicontinental areas (Fig. 8), and does not seem to play an important role in these critical bioevents.

Although genetic was probably the most determinant factor on the shell microstructure, the eurinoid type seemingly requires more metabolic energy and oxygenated habitats to construct coarser fibres than the leptinoid pattern (cf. Simon et al. 2018), and cannot be excluded that its iterative occurrence after extinction may have been a consequence of heterochrony processes (heterochronic "Lazarus effect" *sensu* Flesa and Jablonsky 1983; Jablonsky 1986; Vörös 2018). In this sense, Manceñido and Motchurova-Dekova (2010) considered that eurinoid microstructure could represent an "apomorphic stage" of development. Among the eurinoid morphogroups, all Basiliolidae and Norellidae develop a simple spirolophous lophophore, but the falciform (and derived) crural architecture of Basiliolidae may represent a more developed type of crura than those raduliform or arcual types developed in other rhynchonellide clades. The septifal crural developments entail a better attachment and consequently a less effective ciliate retractable lophophore (cf. Vörös et al. 2016). The proliferation of taxa with this better-attached lophophore can be consistent just when the record of the eurinoid septifal group increase, i.e. in the background conditions in the epioceanic environments and the onset of the repopulation intervals, since in such environmental contexts with abundant resources, redirecting flow regime through retractile lophophore is not essential for filter-feeding.

However, while the epicontinental environments are constrained by adverse conditions or oxygen-depleted habitats, the smooth eurinoid falciform group is mostly restricted to the deeper habitats (Fig. 8) and the eurinoid pattern (with higher metabolic and oxygen requirements) is only represented in the epicontinental settings by small smooth eurinoid rhynchonellides which developed relatively smaller-type arcuiform cruras (e.g. *Norella*, *Nannirhynchia*). These arcual crura provide a lesser-attached lophophore, thus achieving major surface of retractable ciliate lophophore, more efficient for filtering in less advantageous conditions. Likewise, spinuliform representatives of this arcual crural group were invoked as capable to separate the two coils of the spirolophe lophophore anteriorly (cf. Schreiber et al. 2013, p. 561), enhancing the flow regime within some mantle cavities. These adaptive strategies could lead to Norelloidea and related groups to tolerate the short-term impoverished conditions of the pre-extinction intervals.

Additionally, it is inferred that the small, smooth or paucicostate Erymnariids, with septifal crura and eurinoid microstructure (e.g. *Septocrurella*) could only develop a schizolophous lophophore stage (Manceñido and Motchurova-Dekova 2010, p. 209). Speculatively, the simple physiology and the conservative external morphotype of Erymnariids led them to play the role of a resilient stock diversified in epioceanic deeper refugia.

Conversely, the leptinoid pattern associated to radical (or ensimergal) crura, and mainly ribbed shell, shows an uneven distribution unlinked to critical events, suggesting, as previously deduced, a more specialized pattern. This type of crura and microstructure require less metabolic and environmental restrictions. The more primitive crural architecture (mainly radical) supports a simple spirolophous lophophore whose versatility, together with the less-resources consuming microstructure, makes this morphogroup consistent with a strategy that promotes specialization based on trophic efficacy. As previously mentioned, the diversification of this leptinoid group seems to be related with niche partitioning and adaptations to different substrate types or even to chemosynthesis processes.

According to the raised hypothesis linking the morphogroups distribution (epicontinental/ epioceanic) around the extinction and posterior diversification events, and taking into account the fixation of lophophore and the metabolic requirements to generate the different microstructure, the eurinoid ribbed falciform morphogroup, whose distribution can be consistent with a resilient pattern both in epioceanic and epicontinental environments, does not fulfil the proposed model. As postulated above, the lower versatility in terms of filter-feeding efficiency conditioned by falciform crura does not accomplish the requirements to be resilient in epicontinental areas during adverse conditions. The development of the ornamentation on this morphogroup could then come into play in these shallower platforms. These rhynchonellides develop strong angular ribs in the shell to better restrict the coarse particles potentially transferred into the mantle cavity (e.g. Rudwick 1964; Fürsich and Hurst 1974). On the other hand, lophophore tends to occupy all the available space within the shell. Consequently, a strong ribbed shell, apart from playing the role as a defence against shell-crushing predators (cf. Vörös 2010), may be efficient for both functions, the restriction of coarse sediment from entering the mantle cavity and the amplifying of the lophophore surface, which, in turn, improves the filter-feeding efficiency, allowing inhalant currents with a minor gaping of the shell (cf. Fürsich and Hurst 1974). This could be an alternative to the development of a retractile lophophore, enabling the resilience in a disfavoured environmental situation.

A particular case after the well-known K-Pg event recovery can lead to masking the true pattern of post-extinction recolonization carried out by the eurinoid morphogroups. After a barren interval just after the extinction boundary, the record of rhynchonellides in some epicontinental settings immediately starts in the Danian with raducal leptinoids, consisting of micromorphic species belonging to the smooth *Cryptopora* and the ribbed *Cretirhynchia* (e.g. Johansen 1989, Hakansson and Thomsen, 1999). However, *Cretirhynchia* is a raducal leptinoid genus which is also widely recorded in the Campanian-Maastrichtian background conditions prior the extinction interval (Johansen 1989). This genus commonly occurred in the assemblages from the Cenomanian-Turonian event onwards. Thus, it cannot be considered as opportunistic taxon, but an epicontinental resilient suffering miniaturization as a solution to the environmental deterioration and the shortage of resources. Otherwise, *Cryptopora* is a peculiar raducal leptinoid genus seemingly adapted to deeper environments (Surlyk and Johansen 1984). Seemingly, the epioceanic eurinoid and falciform *Basiliocostella* could have found an effective substitute in this depth-adapted micromorphic leptinoid forms to recolonize some platforms.

Accordingly, we suggest that the diversity dynamics of the smooth rhynchonellides stock can be globally affected by post-Palaeozoic biotic crises, since diversity turnovers after crisis events are documented to a genus (or species) level, but the body plan (smooth, eurinoid, septifal/arcual) persisted: they were the typical inhabitants of the deeper epioceanic environments (Vörös 2005) who are the last to withdraw the epicontinental platforms (Norellidae, Erymnaridae?) when the environmental conditions were not propitious, and the pioneers and opportunistic taxa when the conditions are re-established in the aftermath of the biotic crises (Norellidae, Basiliolidae).

6. Conclusions

An updated Western Tethys post-Palaeozoic rhynchonellide database has been compiled to appraise conclusive inter-relationship coupling the crural architecture, microstructure of the secondary layer of the shell, and the ribbing pattern of 101 genera, testing both previous available data and new observations empirically evaluated in several taxa from the peri-Iberian basins. This analysis allows to differentiate four main rhynchonellide morphogroups: smooth eurinoid arcuiform, smooth eurinoid septifal, ribbed eurinoid septifal, and ribbed leptinoid raducal).

The changing relative occurrence of these morphogroups in response to the key extinction and diversification events recorded in the overall post-Palaeozoic history of rhynchonellides reveals a recurrent pattern with an adaptive significance beyond the phylogenetic meaning of the grouping:

The smooth, eurinoid, arcual morphogroup is a distinctive inhabitant of deeper epioceanic environments as well as the last to withdraw from the epicontinental platforms when the environmental conditions are adverse and, together with the smooth (epioceanic), eurinoid, septifal morphogroup played the role of pioneers and opportunistic taxa conducting repopulation of epicontinental habitats when the conditions were re-established after biotic crises. The ribbed, eurinoid, falciform morphogroup seems to be the more resilient stock in relation to ecological crises. Finally, the ribbed, leptinoid, raducal group mainly represents the faunal core of epicontinental communities when normal conditions predominate, evidencing an uneven distribution unlinked to critical events, thus suggesting a more specialist pattern with a diversification related to a secondary differentiation.

The relationship between morpho-structural features defining morphogroups and their predominance or scarcity in substantial ecological crises or replacement events is probably controlled by the availability and utilization of resources. In the progressively deteriorating conditions of extinction events, the more effective and versatile forms, represented by smooth eurinoid arcual morphologies, otherwise resilient in deep environments, are dominant in both epioceanic and epicontinental habitats. Severe ecological perturbations in epicontinental seas could be only short-term withstood by the ribbed eurinoid falciform morphogroup, as the increasing of the filter-feeding efficiency of the lophophore is postulated for this group. When resources become abundant after crises, the repopulation is conducted mainly by smooth eurinoid septifal morphologies with opportunistic strategies, together with the aforesaid versatile smooth arcual group. When diversity increases towards normal background levels, the leptinoid radical ribbed morphotypes are benefited due to their trophic efficiency, with economic structures and more specialized strategies.

Acknowledgements

This research is a contribution to the IGCP-655 Toarcian Oceanic Anoxic Event: Impact on marine carbon cycle and ecosystems, and was supported by project CGL2015-66604-R (MINECO, Government of Spain), and the Research Group VIGROB-167 (University of Alicante). Authors thank Dr. M. Company for access to the Cretaceous brachiopod collection (where *Fortunella* specimens prepared by Dr. Calzada were selected) deposited in the University of Granada. We are also grateful to Dr. J. Colás (University of Zaragoza) for kindly providing the material of *Monticlarella triloboides*. We appreciate the insightful comments and suggestions from the Journal Editor and Reviewers (M.O. Manceñido and A. Vörös). This is Paleobiology Database publication # 365.

References

Ager, D.V., 1956a. Geographical factors in the definition of fossil species. In: Sylvester-Bradley, P.C. (ed.). The species concept in Palaeontology. Systematics Association Publication 2, 105–109.

Ager, D.V., 1956b. A Monograph of the British Liassic Rhynchonellidae Part. I. Palaeontographical Society London 110, 1–50.

Ager, D.V., 1962. A Monograph of the British Liassic Rhynchonellidae, Part III. Palaeontographical Society London 116, 85–136, pl. 8–11.

Ager, D.V., 1965. The adaptation of Mesozoic brachiopods to different environments. Palaeogeography, Palaeoclimatology, Palaeoecology 1, 143–172.

Ager, D.V., 1967. A Monograph of the British Liassic Rhynchonellidae. Part. IV. Palaeontographical Society London 121, 137–172.

Ager, D.V., 1983. Allopatric speciation, an example from the Mesozoic Brachiopoda. Palaeontology 6 (3), 555–565.

Ager, D.V., Childs, A., Pearson, D.A.B., 1972. The evolution of the Mesozoic rhynchonellida. Geobios 5 (3), 205–235.

Alméras, Y., 1994. Le genre *Soaresirhynchia* nov. (Brachiopoda, Rhynchonellacea, Welleleridae) dans le Toarcien du sous-bassin nord-lusitanien (Portugal). Doc. Lab. Géol. Lyon 130, 1–136.

Alméras, Y., 1996. The genus *Pseudogibbirhynchia* (Brachiopoda, Rhynchonellacea) from the Toarcian of Portugal. In: Copper P., Jin, J. (Eds.), Brachiopods. Proceedings of the 4th International Brachiopod Congress, in: Balkema, A.A. (Ed.), Rotterdam, pp. 7–12.

Alméras, Y., Elmi, S., Mouterde, R., Ruget, C., Rocha, R., 1989. Evolution Paléogéographique du Toarcien et influence sur les peuplements, in: Rocha, R.B., Soares, A.F. (Eds.), International Symposium on Jurassic Stratigraphy, Lisboa. 1988. pp. 687–698.

Alméras, Y., Mouterde, R., Elmi, S., Rocha, R., 1995. Le genre *Nannirhynchia* (Brachiopoda, Rhynchonellacea, Norellidae) dans le Toarcien Portugais. Sonder-Abdruk aus Palaeontographica 237, 1–38.

Alméras, Y., Mouterde, R., Benest, M., Elmi, S., Bassoullet, J.-P., 1996. Les brachiopodes toarciens de la rampe carbonatée de Tomar (Portugal). Doc. Lab. Géol. Lyon 138 (21), 125–191.

Alméras, Y., Fauré, P., 2000. Les Brachiopodes liasiques des Pyrénées. Paléontologie, Biostratigraphie, Paléobiogéographie et Paléoenvironnements. Strata 36, 1–395.

Alméras, Y., Becaud, M., 2002. Les zones charnières entre provinces paléobiogéographiques. Géologie de la France 3, 17–29.

Andrade, B., 2006. Los braquiópodos del tránsito Jurásico Inferior–Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56, 5–194.

Andrade, B., Duarte, L.V., García Joral, F., Goy, A., Henriques, M.H., 2016. Palaeobiogeographic patterns of the brachiopod assemblages of the Iberian Subplate during the Late Toarcian-Early Aalenian (Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 442, 12–22.

Baeza-Carratalá, J.F., 2011. New Early Jurassic brachiopods from the Western Tethys (Eastern Subbetic, Spain) and their systematic and paleobiogeographic affinities. Geobios 44, 345–360, sup. 1–9.

Baeza-Carratalá, J.F., 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). Palaeogeography, Palaeoclimatology, Palaeoecology 381-382, 76–91.

Baeza-Carratalá, J.F., Vörös, A., Dulai, A., Tent-Manclús, J.E., 2011. Brachiopod assemblages from the Early-Middle Jurassic transition in the Eastern Subbetic (SE Spain): Systematic and palaeobiogeographic implications and palaeoenvironmental significance. Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen 262 (2), 171–197.

Baeza-Carratalá, J.F., García Joral, F., Sandoval, J., 2014. Bajocian-Early Bathonian (Jurassic) brachiopods from the Subbetic domain (Betic Cordillera, SE Spain): Taxonomy and palaeobiogeographic implications. Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen 274 (1), 1–24.

Baeza-Carratalá, J.F., García Joral, F., Giannetti, A., Tent-Manclús, J.E., 2015. Evolution of the last koninckinids (Athyridida, Koninckinidae), a precursor signal of the Early Toarcian mass extinction event in the Western Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology 429, 41–56.

Baeza-Carratalá, J.F., Pérez-Valera, F., Pérez-Valera, J.A., 2016a. The oldest post-Paleozoic (Ladinian, Triassic) brachiopods from the Betic Range, SE Spain. Acta Palaeontologica Polonica 63 (3), 71–85.

Baeza-Carratalá, J.F., Manceñido, M.O., García Joral, F., 2016b. *Cisnerospira* (Brachiopoda, Spiriferinida), an atypical Early Jurassic spire bearer from the Subbetic Zone (SE Spain) and its significance. Journal of Paleontology 90 (6), 1081–1099.

Baeza-Carratalá, J.F., Reolid, M., García Joral, F., 2017. 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. Bulletin of Geosciences 92 (2), 233–256.

Baeza-Carratalá, J.F., García Joral, F., Goy, A., Tent-Manclús, J.E., 2018. Arab-Madagascan brachiopod dispersal along the North-Gondwana palaeomargin towards the Western Tethys Ocean during the Early Toarcian (Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 490, 252–268.

Berrocal-Casero, M., Barroso-Barcenilla, F., García Joral, F., Segura, M., 2017. Functional meaning of asymmetrical commissures in Coniacian (Upper Cretaceous) rhynchonellide brachiopods from Northern Spain. Cretaceous Research 79, 77–90.

Berrocal-Casero, M., Barroso-Barcenilla, F., García Joral, F., 2020. Coniacian (Upper Cretaceous) rhynchonellides from Northern Spain: Taxonomy and palaeobiogeography. Cretaceous Research 106, art. 104216.

Bitner, M.A., Martinell, J., 2001. Pliocene brachiopods from the Estepona area (Málaga, South Spain). Rev. Española de Paleontología 16 (2), 9–17.

Bitner, M.A., Moissette, P., 2003. Pliocene brachiopods from north-western Africa. Geodiversitas 25 (3), 463–479.

Calzada, S., 1975. Braquiópodos infracretácicos del Levante español. Trab. Museo Geol. Seminario Barcelona 14: 86 pp.

Calzada, S., 1984. Sobre algunos braquiópodos liásicos. Boletín Geológico y Minero 95 (6), 540–552.

Calzada, S., 1997. Miscelánea sobre braquiópodos. Batalleria 7, 31–34.

Calzada, S., Pocovi, A., 1980. Braquiópodos senonienses de la sierra del Montroig (Prepirineo de Lérida). Bol. R. Soc. Española Historia Natural 78, 5–19.

Campbell, K.A., Bottjer, D.J., 1995. Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. Geology 23 (4), 321–324.

Carlson, S.J., 2016. The Evolution of Brachiopoda. Annual Review Earth and Planetary Sciences 44, 409–438.

Chen, Z.-Q., Kaiho, K., George, A.D., 2005. Survival strategies of brachiopod faunas from the End-Permian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 224, 232–269.

Childs, A., 1969. Upper Jurassic rhynchonellid Brachiopods from North-western Europe. Bulletin of the British Museum (Natural History) Geology, Supp. 6, 1–119.

Choffat, P., 1880. Etude stratigraphique et paléontologique des terrains jurassiques du Portugal: Le Lias et le Dogger au Nord du Tage. Mémoires du Service des Ttravaux Géologiques de Portugal, 1–72.

Colás, J., 2015. Los Rinconélidos (Brachiopoda, Rhynchonellida) del intervalo Calloviense-Oxfordiense en el Sector Central de la Cordillera Ibérica. Unpublished PhD Thesis, Univ. Zaragoza, Spain, 249 pp., 7 pl.

Colás J., García Joral F., 2012. Morphology and environment in the Jurassic Nucleatidae (Brachiopoda) from Western Tethys. Lethaia 45 (2), 178–190.

Comas-Rengifo, M.J., Goy, A., 1975. Estratigrafía y paleontología del Jurásico de Ribarredonda (Guadalajara). Estudios Geológicos 31, 297–339.

Comas-Rengifo, M.J., García Joral, F., Goy, A., 2006. Spiriferinida (Brachiopoda) del Jurásico Inferior del NE y N de España: distribución y extinción durante el evento anóxico oceánico del Toarciense inferior. Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.) 101 (1–4), 147–157.

Comas-Rengifo, M.J., Duarte, L.V., García Joral, F., Goy, A., 2013. Los braquiópodos del Toarciense Inferior (Jurásico) en el área de Rabaçal-Condeixa (Portugal): distribución estratigráfica y paleobiogeografía. Comunicações Geológicas 100 (1), 37–42.

Comas-Rengifo, M.J., Duarte, L.V., Félix, F.F., García Joral, F., Goy, A., Rocha, R.B., 2015. Latest Pliensbachian–Early Toarcian brachiopod assemblages from the Peniche section (Portugal) and their correlation. Episodes 38, 2–8.

Cooper, G.A., 1959. Genera of tertiary and recent rhynchonelloid brachiopods. Smithsonian Miscellaneous Collections 139 (5), 1–90.

Curry, G.B., Brunton, C.H.C., 2007. Stratigraphic distribution of brachiopods, in: Kaesler, R.L., Selden, P.A. (Eds.), 1997–2007, Vol. 6 (Sup.), pp. 2901–3081. Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Rev.). Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Dagys, A.S., 1968. Jurassic and Early Cretaceous brachiopods from north Siberia. Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR 41, 1–167.

Dubar, G., 1925. Étude sur le Lias des Pyrénées Françaises. Mémoires de la Société Géologique du Nord 9 (1), 1–332.

Dubar, G., 1931. Brachiopodes liassiques de Catalogne et des régions voisines. Butlletí Inst. Catalana Historia Natural 31, 103–180.

Dulai, A., 2002. A Dunántúli-középhegység hettangi és kora-szinemuri (kora-jura) brachiopoda faunája I. Diverzitás, rétegtani elterjedés, paleoökológia, paleobiogeográfia, faunafejlődés: A Bakony Természettudomány Kutatásának Eredményei 26, 112 p.

Dulai, A., 2003. A Dunántúli-középhegység hettangi és kora-szinemuri (kora-jura) brachiopoda faunája II. A Bakony Természettudomány Kutatásának Eredményei 27, 144 p.

Dulai, A., Bitner, M.A., Müller, P.Á.L., 2008. A monospecific assemblage of a new rhynchonellide brachiopod from the Paleocene of Austria. Fossils and Strata 54, 193–201.

Ferrari, A., 1962. Brachiopodi giurassici dei dintorni di Rovereto (Trentino). Giorn. Geologia 29 (2), 91–153.

Flessa, K.W., Jablonski, D., 1983. Extinction is here to stay. Paleobiology 9 (4), 315–321.

Fürsich, F.T., Hurst, J.M., 1974, Environmental factors determining the distribution of brachiopods. Palaeontology 17 (4), 879–900.

Gahr, M.E., 2005. Response of Lower Toarcian (Lower Jurassic) macrobenthos of the Iberian Peninsula to sea level changes and mass extinction. Journal of Iberian Geology 31 (2), 197–215.

García Joral, F., 1993. The Aalenian Rhynchonellids from the Northern Calcareous Alps in the Rothpletz Collection, in: Pálfy, J., Vörös, A. (Eds.), Mesozoic Brachiopods of Alpine Europe, pp. 39–40. Budapest.

García Joral, F., Goy, A., 1984. Características de la fauna de braquiópodos del Toarciense Superior en el Sector Central de la Cordillera Ibérica (Noreste de España). Estudios Geológicos 40, 55–60.

García Joral F., Goy, A., 2000. Stratigraphic distribution of Toarcian brachiopods from the Iberian Range and its relation to depositional sequences. Georesearch Forum 6, 381–386.

García Joral, F., Goy, A., 2004. Caracterización de *Choffatirhynchia* nov. gen. (Brachiopoda, Rhynchonellida) en el Toarciense (Jurásico) de la Cordillera Ibérica (España). Bol. R. Soc. Esp. Historia Natural 99, 237–250.

García Joral, F., Goy, A., 2009. Toarcian (Lower Jurassic) brachiopods in Asturias (Northern Spain): stratigraphic distribution, critical events and palaeobiogeography. Geobios 42, 255–264.

García Joral, F., Goy, A., Ureta, S., 1990. Las sucesiones de braquiópodos en el tránsito Lías-Dogger en la Cordillera Ibérica. Cuadernos de Geología Ibérica 14, 55–65.

García Joral, F., Gómez, J.J., Goy, A., 2011. Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in northern and central Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 302, 367–380.

García Joral, F., Baeza-Carratalá, J.F., Goy, A., 2018. Changes in brachiopod body size prior to the Early Toarcian (Jurassic) Mass Extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 506, 242–249.

García-Ramos, D., 2004. Braquiópodos pliocenos de Águilas. Bol. Asoc. Cult. Paleont. Murciana 3, 18–39.

García-Ramos, D., 2006. Nota sobre Terebratulinae del Terciario de Europa y su relación con los representantes neógenos del sureste español. Bol. Asoc. Cult. Paleont. Murciana 5, 23–83.

Giannetti, A., Baeza-Carratalá, J.F., Soria, J.M., Dulai, A., Tent-Manclús, J.E., Peral-Lozano, J., 2018. New paleobiogeographical and paleoenvironmental insight through the Tortonian brachiopod and ichnofauna assemblages from the Mediterranean-Atlantic seaway (Guadix Basin, SE Spain). Facies 64 (3):24, 1–20.

Gould, S.J., Calloway, C.B., 1980. Clams and brachiopods -ships that pass in the night. Paleobiology 6, 383–396.

Grădinaru, E., Gaetani, M., 2019. Upper Spathian to Bithynian (Lower to Middle Triassic) brachiopods from North Dobrogea (Romania). Riv. It. Paleontol. Strat. 125 (1), 91–123.

Graziano, R., Taddei-Ruggiero, E., 2008. Cretaceous brachiopod-rich facies of the carbonate platform-to basin transitions in southern Italy: stratigraphic and paleoenvironmental significance. Boll. Società Geologica Italiana 127 (2), 407–422.

Graziano, R., Buono, G., Taddei Ruggiero, E., 2006. Lower Toarcian (Jurassic) brachiopod-rich carbonate facies of the Gran Sasso range (central Apennines, Italy). Boll. Società Paleontologica Italiana 45(1), 61–74.

Håkansson, E., Thomsen, E., 1999. Benthic extinction and recovery patterns at the K/T boundary in shallow water carbonates, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 154 (1-2), 67–85.

Hallam, A., 1971. Provinciality in Jurassic faunas in relation to facies and palaeogeography, in: Middlemiss, F.A., Rawson, P.F., Newall, G. (Eds.), Faunal Provinces in Space and Time. Geological Journal Spec. Iss. 4, 129–152.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9.

Harper, D.A.T., Moran, R., 1997. Brachiopod life styles. Geology Today 13(6), 235–238.

Harper, D.A.T., Hammarlund, E.U., Rasmussen, C.M.Ø., 2014. End Ordovician extinctions: A coincidence of causes. Gondwana Research 25 (4), 1294–1307.

Harper, D.A.T., Popov, L.E., Holmer, L.E., 2017. Brachiopods: origin and early history. Palaeontology 60, 609–631.

Jablonski, D., 1986. Causes and consequences of mass extinction: a comparative approach. In: Elliott, D.K. (ed.). Dynamics of Extinction. J. Wiley & Sons, pp. 184–229.

Jiménez de Cisneros, D., 1923. La Fauna de los estratos de "Pygope Aspasia" Menegh. del Liásico Medio del Rincón de Egea en el W de la provincia de Murcia: Junta para Ampliación de Estudios e Investigaciones Científicas. Trabajos del Museo Nacional de Ciencias Naturales. Serie Geológica 30, 1–55.

Johansen, M.B., 1989. Adaptive radiation, survival and extinction of brachiopods in the northwest European Upper Cretaceous-Lower Paleocene chalk. Palaeogeography, Palaeoclimatology, Palaeoecology 74 (3-4), 147–204.

Johnson, J.G., 1975. Allopatric Speciation in Fossil Brachiopods. Journal of Paleontology 49 (4), 646–661.

Kaesler, R.L., Selden, P.A. (Eds.), 1997–2007. Treatise on Invertebrate Paleontology. Part H, Brachiopoda, (Rev.), vols. 1–6. Geological Society of America and Paleontological Institute, Boulder, Colorado and Lawrence, Kansas.

Kiel, S., Glodny, J., Birgel, D., Bulot, L.G., Campbell, K.A., Gaillard. C., Graziano, R., Kaim, A., Lazər, I., Sandy, M.R., Peckmann, J., 2014. The paleoecology, habitats, and stratigraphic range of the enigmatic Cretaceous brachiopod *Peregrinella*. PLoS ONE 9 (10): e109260.

Kowalewski, M., Dyreson, E., Marcot, J.D., Vargas, J.A., Flessa, K.W., Hallman, D.P., 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology 23, 444–469.

Krause, R.A., 2004. An assessment of morphological fidelity in the sub- fossil record of a terebratulide brachiopod. Palaios 19, 460–476.

Makridin, V.P., 1964. Brakhiopody Iurskikh otlozhenii Russkoi Plataformy i nekotorykh prilezhasnchikh k nei oblastei. Moscú, pp. 1–395.

Manceñido, M.O., 1993. Early Jurassic Brachiopods from Greece: a review, in: Pálfy, J., Vörös, A. (Eds.), Mesozoic Brachiopods of Alpine Europe, pp. 79–100. Hungarian Geological Society, Budapest.

Manceñido, M.O., 2000. A systematic summary of the stratigraphic distribution of Jurassic rhynchonellide genera (brachiopoda). Advances in Jurassic Research, in: Hall, R.L., Smith, P.L. (Eds.), Proceedings of the Fifth International Symposium on the Jurassic System, GeoResearch Forum 6, pp. 387–396.

Manceñido, M.O., Motchurova-Dekova, N., 2010. A review of crural types, their relationships to shell microstructure, and significance among post-Paleozoic Rhynchonellida, in: Álvarez, F., Curry, G. (Eds.), Evolution and development of the brachiopod shell. Special Papers in Palaeontology 84, 203–204.

Manceñido, M.O., Owen E.F., 2001. Post-Paleozoic Rhynchonellida (Brachiopoda): classification and evolutionary background, in: Cocks, L.R.M., Brunton, C.H.C., Long, S.L. (Eds.), Brachiopods past and present. Proceedings of the Millennium Brachiopod Congress. Systematics Association spec. vol. 63, pp. 189–200. London.

Manceñido, M.O., Owen, E.F., Dagys, A.S., Dong-Li, S., 2002. Norelloidea, in: Kaesler, R.L. (Ed.): Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Rev.), Vol. 4, Rhynchonelliformea (part). Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, pp. 1308–1325.

Manceñido, M.O., Owen, E.F., Sun, D.L., 2007. Post-Paleozoic Rhynchonellida. In: Selden, P.A. (ed.). Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Rev.), Vol. 6 (Supp.). Geological Society of America & University of Kansas, pp. 2727–2741.

McNamara, K., 1982. Heterochrony and Phylogenetic Trends. Paleobiology 8 (2), 130–142.

Miller, A.I., Foote, M., 2009. Epicontinental seas versus open-ocean settings: the kinetics of mass extinction and origination. Science 326, 1106.

Motchurova-Dekova, N., Simon, E., 2007. *Homaletarhynchia* Simon and Owen, 2001, a genus transferred to the Basiliolidae (Pugnacoidea, Rhynchonellida, Brachiopoda). Bull. Inst. Royal Sc. Nat. Belgique, Sciences de la Terre 77, 117–129.

Motchurova-Dekova, N., Long, S., Saito, M., 2008. Unravelling taxonomy of some Post-Palaeozoic rhynchonellides by using multiple techniques to investigate their internal morphology. Fossils and Strata 54, 231–239.

Motchurova-Dekova, N., Radulovic, V., Metodiev, L., 2009. Shell microstructure used to unveil homoeomorphy in rhynchonellide brachiopods. *Pseudocapillirhynchia platoni*, New Early-Middle Jurassic genus and species from Bulgaria. Comptes rendus de l'Académie bulgare des Sciences 62 (10), 1299–1310.

Muir-Wood, H.M., 1934. On the internal structure of some Mesozoic brachiopoda. Phil. Trans. R. Soc. Lond. B 223, 511–567.

Olóriz, F., 2000. Time averaging and long term palaeoecology in macroinvertebrate fossil assemblages with ammonites (Upper Jurassic). Revue de Paléobiologie, Genève vol. spéc. 8, 123–140.

Oppel, A., 1863. Ueber das Vorkommen von jurassischen Posidonomyen-Gesteinen in den Alpen. Zeitschrift der Deutschen geologischen Gesellschaft 15, 188–277.

Pálfy, J., Kovács, Z., Price, G.D., Vörös, A., Johannson, G.G., 2017. A new occurrence of the Early Jurassic brachiopod *Anarhynchia* from the Canadian Cordillera confirms its membership in chemosynthesis-based ecosystems. Canadian Journal of Earth Sciences 54 (12), 1179–1193.

Peckmann, J., Campbell, K.A., Walliser, O.H., Reitner, J., 2007. Late Devonian hydrocarbon-seep deposit dominated by Dimerelloid brachiopods, Morocco. Palaios 22, 114–122.

Peckmann, J., Sandy, M.R., Taylor, D.G., Gier, S., Bach, W., 2013. An Early Jurassic brachiopod-dominated seep deposit enclosed by serpentinite, eastern Oregon, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 390, 4–16.

Radulović, B., Motchurova-Dekova, N., Radulović, V., 2007. New Barremian rhynchonellide brachiopod from Serbia and the shell microstructure of Tetrarhynchiidae. Acta Palaeontologica Polonica 52 (4), 761–782.

Ratcliffe, K.T., 1991. Palaeoecology, taphonomy and distribution of brachiopod assemblages from the Much Wenlock Limestone Formation of England and Wales. Palaeogeography, Palaeoclimatology, Palaeoecology 83 (4), 265–293.

Raup, D.M., 1986. Biological Extinction in Earth History. Science 231 (4745), 1528–1533.

Reolid, M., 2005. Asociaciones de braquiópodos del Oxfordiense medio-Kimmeridgiense inferior en la Zona Prebética (Sureste de España): Relación con las litofacies y el gradiente proximal-distal de la plataforma. Rev. Española de Paleontología 20 (1), 21–36.

Rigo, M., Onoue, T., Tanner, L.W., Lucas, S.G., Godfrey, L., Katz, M.E., Zaffani, M., Grice, K., Cesar, J., Yamashita, D., Maron, M., Tackett, L.S., Campbell H., Tateo, F., Concheri, G., Agnini, C., Chiari, M., Bertinelli, A., 2020. The Late Triassic Extinction at the Norian/Rhaetian boundary: Biotic evidence and geochemical signature. Earth-Science Reviews 204, 103180.

Rothpletz, A., 1886. Geologische-palaeontologische Monographie der Vilser-Alpen, mit besonderer Berücksichtigung der Brachiopoden-Systematik. Palaeontographica 33, 1–180.

Rudwick, M.J.S., 1964. The function of zig-zag deflections in the commissures of fossil brachiopods. Palaeontology 7, 135–171.

Rudwick, M.J.S., 1970. Living and Fossil Brachiopods, London: Hutchinson University Library, Biological Sciences, 1–199.

Sandy, M.R., 1995. A review of some Palaeozoic and Mesozoic brachiopods as members of cold seep chemosynthetic communities: ‘‘unusual’’ palaeoecology and anomalous palaeobiogeographic patterns explained. Földtani Közlöny 125, 241–258.

Sandy, M.R., 2010. Brachiopods from ancient hydrocarbon seeps and hydrothermal vents, in: Kiel, S. (Ed.), The vent and seep biota. Topics in Geobiology 33, pp. 279–314. Berlin.

Sandy, M.R., Peckmann, J., 2016. The Early Cretaceous brachiopod Peregrinella from Tibet: a confirmed hydrocarbon-seep occurrence for a seep-restricted genus. Palaontologische Zeitschrift 90 (4), 691–699.

Savage, N.M., Manceñido, M.O., Owen, E.F., Carlson, S.J., Grant, R.E., Dagys, A.S., Dong-Li, S., 2002. Rhynchonellida, in: Kaesler, R.L. (Ed.): Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Rev.), Vol. 4, Rhynchonelliformea (part). Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, pp. 1027–1040.

Schreiber, H.A., Bitner, M.A., Carlson, S.J., 2013. Morphological analysis of phylogenetic relationships among extant rhynchonellide brachiopods. Journal of Paleontology 87 (4), 550–569.

Schreiber, H.A., Roopnarine, P.D., Carlson, S.J., 2014. Three-dimensional morphological variability of Recent rhynchonellide brachiopod crura. Paleobiology 40 (4), 640–658.

Simon, E., Motchurova-Dekova, N., Mottequin, B., 2018. A reappraisal of the genus *Tethyrhynchia* Logan, 1994 (Rhynchonellida, Brachiopoda): a conflict between phylogenies obtained from morphological characters and molecular data. Zootaxa 4471(3), 535–555.

Stigall, A.L., 2018. How is biodiversity produced? Examining speciation processes during the GOBE. Lethaia 51 (2), 165–172.

Sulser, H., Calzada, S., 1991. The genus *Fortunella* (Brachiopoda, Rhynchonellida) and its related species in the Upper Jurassic and Lower Cretaceous. Eclogae Geologicae Helvetiae 84 (3), 851–871.

Surlyk, F., Johansen, M.B., 1984. End-Cretaceous brachiopod extinctions in the chalk of Denmark. Science 223 (4641), 1174–1177.

Thévenin, A., 1908. Paléontologie de Madagascar, 5: fossiles liasiques. Annales de Paléontologie 3 (3), 1–39.

Thuy, B., Kiel, S., Dulai, A., Gale, A.S., Kroh, A., Lord, A.R., Numberger-Thuy, L.D., Stöhr, S., Wisshak, M., 2014. First glimpse into Lower Jurassic deep-sea biodiversity: in situ diversification and resilience against extinction. Proc. R. Soc. B 281, 20132624.

Tomašových, A., 2006. A new Early Jurassic rhynchonellid brachiopod from the Western Tethys and implications for systematics of rhynchonellids from the Triassic-Jurassic boundary. Journal of Paleontology 80 (2), 212–228.

Topper, T.P., Strotz, L.C., Skovsted, C.B., Holmer, L.E., 2017. Do brachiopods show substrate- related phenotypic variation: a case study from the Burgess Shale. Palaeontology 60, 269–279.

Toscano-Grande, A., García-Ramos, D., Ruiz-Muñoz, F., González-Regalado, M.L., Abad, M., Civis, J., González-Delgado, J.A., Rico-García, A., Martínez-Chacón, M.L., García, E.X., Pendón-Martín, J.G., 2010. Braquiópodos neógenos del suroeste de la depresión del Guadalquivir (sur de España). Rev. Mexicana Ciencias Geológicas 27 (2), 254–263.

Valentine, J.W., Jablonski, D., 2010. Origins of marine patterns of biodiversity: Some correlates and applications. Palaeontology 53 (6), 1203–1210.

Vörös, A., 1997. Magyarország jura brachiopodái. Studia Naturalia 11, 1–110.

Vörös, A., 2005. The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders? Palaeogeography, Palaeoclimatology, Palaeoecology 223, 222–242.

Vörös, A., 2009. The Pliensbachian brachiopods of the Bakony Mountains (Hungary). Geologica Hungarica, series Paleontologica 58, 1–300.

Vörös, A., 2010. Escalation reflected in ornamentation and diversity history of brachiopod clades during the Mesozoic marine revolution. Palaeogeography, Palaeoclimatology, Palaeoecology 291, 474–480.

Vörös, A., 2018. Mass extinctions and fatal extinctions in the history of brachiopods: review and post-Paleozoic cases. Permophyle, Newsletter of the Subcommission on Permian Stratigraphy 66 (Sup. 1), 118–119.

Vörös, A., Dulai, A., 2007. Jurassic Brachiopods of the Transdanubian Range (Hungary); stratigraphical distribution and diversity changes: Fragmenta Palaeontologica Hungarica 24–25, 51–68.

Vörös, A., Dulai, A., Főzy, I., 2018. Brachiopods and the Early Cretaceous Weissert event (Bakony Mountains, Hungary). Permophyle, Newsletter of the Subcommission on Permian Stratigraphy 66 (Sup. 1), 120.

Vörös, A., Kocsis, Á.T., Pálfy, J., 2016. Demise of the last two spire-bearing brachiopod orders (Spiriferinida and Athyridida) at the Toarcian (Early Jurassic) extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology 457, 233–241.

Vörös, A., Kocsis, Á.T., Pálfy, J., 2019. Mass extinctions and clade extinctions in the history of brachiopods: brief review and a post-Paleozoic case study. Riv. Italiana di Paleontologia e Stratigrafia 125 (3), 711–724.

Wisniewska, M., 1932. Rhynchonellidae Górnej Jury w Polsce. Palaeontologia Polonica 2 (1), 1–71.

Zezina, O.N., 1994. Deep-sea brachiopods. Their peculiarities in morphology and evolution. Sarsia 79, 59–64.

Zezina, O.N., 2010. Checklist of Holocene brachiopods annotated with geographical ranges of species. Paleontological Journal 44 (9), 1176–1199.

Table and Figure captions

Table 1. Peri-Iberian post-Palaeozoic rhynchonellides integrated in the analysis with internal and external features description. See repository acronyms in the material and methods section.

Fig. 1. Representative post-Palaeozoic rhynchonellid species from the peri-Iberian basins, combining eurinoid microstructure with septifal crural architecture and smooth ribbing pattern. **A.** *Apringia atlaeformis*, specimen O4.2. TS3, Pliensbachian, westernmost Subbetic area. A1, A2. Serial sections at 2.60 and 3.20 mm respectively from the apex showing hamiform crural development. A3, A4. Microphotographs of the secondary layer of the shell at the same sections respectively (2.60 and 3.20 mm) showing eurinoid microstructure. A5. Anterior view of the same specimen. **B.** *Soaresirhynchia bouchardi*, Early Toarcian of the Iberian Range. B1. Serial section performed at 5.00 mm from the apex on the specimen VO0.2 showing hamiform crura. B2, B3.

Microstructure of the secondary layer of the shell in a section performed at 1.70 mm from the apex (B2) in the Esc.Bo1 specimen, and at 1.30 mm from the apex in the PT.ES.1 specimen (B3). B4. Dorsal view of the SC2a.bo.1 specimen. **C**. *Mondegia atla*, Early Bajocian, Western Subbetic. C1. Serial section performed at 3.80 mm from the apex in the specimen LSR-Map-sec.1, showing incipient falciform crura. C2, C3. Microphotographs on the same specimen showing eurinoid microstructure at 1.80 and 4.60 mm from the apex respectively. C4. Dorsal and anterior views of specimen LSR.A-Aap6. **D**. *Fortunella decipiens*, specimen XA28.276, Barremian, Prebetic domain. D1. Serial section performed at 3.00 mm from the apex, showing falciform crura. D2. Detailed view of the shell in the same section showing eurinoid microstructure. D3. Dorsal and anterior view of the same specimen. **E**. *Aphelesia bipartita*, Late Tortonian, Guadix post-orogenic Betic basin. E1. Serial section performed at 2.20 mm from the apex in the specimen AL6.AB9, showing an incipient stage of the falciform crura. E2. Dorsal and anterior view of the AL1.AB1 specimen (note that shell microstructure is not exposed because of the poor preservation of the material). **F**. *Septocrurella microcephala*, Early Bajocian, Subbetic area. F1. Serial section performed on the specimen O.7.3.Ts.1 at 2.10 mm from the apex showing septiform crura. F2. Microphotograph of the same specimen in a section at 1.80 mm from the apex showing eurinoid microstructure. F3. Anterior view of the specimen O.7.3.Ts.5.

Fig. 2. Representative post-Palaeozoic rhynchonellid species from the peri-Iberian basins, combining eurinoid microstructure with septifal crural architecture and multicostate ribbing pattern. A, B, and D derive from the Pliensbachian from the westernmost Subbetic area, and C from the Early Toarcian from the Iberian Range **A.** *Cirpa briseis*. A1. Serial section performed on the specimen CCC.3 at 2.60 mm from the apex showing fused hinge plates which evolve onwards to hamiform crura. A2. Dorsal view of the CCA.8.Cb.1 specimen**.** **B**. *Cirpa* sp. aff. *latifrons*. B1. Microphotograph of the I.12.T26(26).1 specimen in a section at 2.60 mm from the apex showing eurinoid microstructure. B2. Dorsal view of the same specimen. **C**. *Pseudogibbirhynchia jurensis*,

1.AR.103.1 specimen. C1. Serial section at 2.50 mm from the apex showing hamiform crura. C2. Dorsal and anterior views of the same specimen. C3. Eurinoid microstructure pattern revealed in the previous section (2.50 mm). **D**. *Salgirella albertii*. D1. Serial section at 3.30 mm from the apex performed in the I12.T26(26).2 specimen, showing hamiform crura. D2. Dorsal view of O8.20.T5.1 specimen. D3. Microphotograph of the I.12.T26(26).2 specimen in a section at 2.30 mm from the apex showing eurinoid microstructure.

Fig. 3. Representative post-Palaeozoic rhynchonellid species from the peri-Iberian basins, combining eurinoid microstructure with arcual crural architecture. **A**. *Atycorhynchia falsiorigo*, Early Toarcian, Subbetic area. A1. Serial section performed on the specimen CE.28b.Rh1 (paratype) at 3.20 mm from the apex showing arcuiform crura. A2. Microphotograph of the same specimen in a section at 3.50 mm from the apex showing eurinoid microstructure. A3. Dorsal view of the specimen CE.28.Rh1 (holotype). **B.** *Praemonticlarella distercica*, Aalenian, Iberian Range. B1. Serial section performed at 2.10 mm from the apex on the specimen FZ.68.17 (paratype) showing arcual development. B2. Microphotograph of the same specimen in a section at 1.10 mm from the apex showing wide and coarse eurinoid microstructure. B3. Dorsal and anterior views of specimen FZ.74.3 (paratype). **C**. *Nannirhynchia pillula*, Late Pliensbachian, Subbetic area. C1. Serial section performed on the specimen O4.1.T1.7 at 0.80 mm from the apex showing arcuiform crura. C2. Microphotograph of the same specimen in a section at 1.40 mm from the apex showing eurinoid microstructure. C3. Anterior view of O8.23.6 specimen. **D.** *Monticlarella triloboides*, specimen TO3 R51-9.1, Middle Oxfordian, Iberian Range. D1. Partial view of serial section at 3.20 mm from the apex showing arcuiform crura. D2. Detailed microphotograph of the same specimen in a section at 1.40 mm from the apex showing eurinoid microstructure. D3. Dorsal and anterior views of the same specimen.

Fig. 4. Representative post-Palaeozoic rhynchonellid species from the peri-Iberian basins, combining leptinoid microstructure with a raducal crural architecture and multicostate ribbing pattern. A-H derive from the Pliensbachian from the westernmost Subbetic area and J-K from the Sinemurian of the same Subbetic Domain. I, L derive from the Toarcian from the Iberian Range. **A**. *Cuneirhynchia cartieri*, specimen Cu.Ca1. A1. Section at 1.60 mm from the apex showing initial stage of raduliform crura. A2. Dorsal view of the same specimen. **B**. *Cuneirhynchia rastuensis*, specimen LL.A.Cu.1, B1. Section at 3.90 mm from the apex showing leptinoid microstructure of the shell. B2. Dorsal view of the same specimen. **C**. *Cuneirhynchia dalmasi*, specimen Cu.Da1. C1. Section at 3.40 mm from the apex showing leptinoid microstructure. C2. Dorsal view of the same specimen. **D**. *Prionorhynchia polyptycha*, specimen O.5.B4c. D1. Section at 3.20 mm from the apex showing raduliform crura. D2. Anterior view of the same specimen. **E**. *Prionorhynchia quinqueplicata*, specimen O.9.2.1. E1. Section at 4.70 mm from the apex showing leptinoid microstructure. E2. Dorsal view of the same specimen. **F**. *Prionorhynchia guembeli*, specimen I.12.26c. F1. section at 5.10 mm from the apex showing leptinoid microstructure. F2. Anterior view of the same specimen. **G-H**. *Gibbirhynchia curviceps*, specimen O.8.20.3. G1. Section at 3.10 mm from the apex showing raduliform crura. G2. Dorsal view of the same specimen. H1. Section at 5.00 mm from the apex showing leptinoid microstructure of the shell. **I.** *Choffatirhynchia vasconcellosi*, specimen AR.11.501, paratype. I1. Section at 3.60 mm from the apex showing raduliform crura. I2. Dorsal and anterior views of the same specimen. I3. section at 2.50 mm from the apex showing leptinoid microstructure. **J.** *Alebusirhynchia jorali*, specimen O.12.10.2, paratype. J1. Section at 5.30 mm from the apex showing raduliform crura. I2. Dorsal view of the same specimen. **K**. *Alebusirhynchia vorosi*, specimen SG1.ANP7. K1. section at 3.20 mm from the apex showing leptinoid microstructure. K2. Dorsal and anterior views of the holotype of this species (specimen SG1.ANP1). **L.** *Homoeorhynchia meridionalis*, specimen VO.345. L1. Section at 3.50 mm from the apex showing raduliform crura. L2. Dorsal and anterior views of the same specimen. L3. Section at 2.10 mm from the apex showing leptinoid microstructure.

Fig. 5. Phenogram of the rhynchonellide dataset studied based on a cluster analysis performed with the Jaccard similarity index. The nodes in this multivariate approach are understood as the most significant internal and external diagnostic features herein used to link/discriminate among genera (shell microstructure, ornamentation, type of crura).

Fig. 6. Global diversity curve of post-Palaeozoic Western Tethys rhynchonellides (from PaleoDB, http://paleobiodb.org/, slightly modified after addition of several new recent genera) remarking the main critical ecological crises and extinction events and the major post-Palaeozoic diversification episodes.

Fig. 7. Stratigraphic range distribution and diversity of the four rhynchonellide morphogroups analysed in relation to the main extinction and diversification events of the post-Palaeozoic rhynchonellide record. Ranges are differentiated after the occurrences of the genera in epicontinental (left) or epioceanic (right) environments. When genera occur in both environments, they are represented on both sides of the logs.

Fig. 8. Schematic model explaining the spatial distribution pattern (epicontinental vs. epioceanic environments) of post-Palaeozoic rhynchonellide morphogroups (1 to 4) in relation to ecological crises or critical bioevents taking into account the different phases around mass extinction events.

Taxa	Author/year	Repository/specimen	Family	Age	Locality	Crural type
Cirpa briseis	(Gemmellaro, 1874)	DCTMA/CCC.3	Wellerellidae	Pliensbachian	Subbetic	hamifor
Cirpa sp. aff. *latifrons*	-	DCTMA/I.12.T26(26).1	Wellerellidae	Pliensbachian	Subbetic	hamifor
Salgirella albertii	(Oppel, 1861)	DCTMA/I12.T26(26).2	Wellerellidae	Pliensbachian	Subbetic	hamifor
Gibbirhynchia curviceps	(Quenstedt, 1852)	DCTMA/O.8.20.3	Tetrarhynchidae	Pliensbachian	Subbetic	raduca
Quadratirhynchia attenuata	(Dubar, 1931)	DPUCM/AR.7.102	Tetrarhynchidae	E. Toarcian	Iberian Range	raduca
Cuneirhynchia cartieri	(Oppel, 1861)	DCTMA/Cu.Ca1	Rhynchonellidae	Pliensbachian	Subbetic	raduca
Cuneirhynchia dalmasi	(Dumortier, 1869)	DCTMA/Cu.Da1	Rhynchonellidae	Pliensbachian	Subbetic	raduca
Cuneirhynchia. rastuensis	(Benigni, 1978)	DCTMA/LL.A.Cu.1	Rhynchonellidae	Pliensbachian	Subbetic	raduca
Homoeorhynchia meridionalis	(Deslongchamps, 1863)	DPUCM/VO.3.45	Rhynchonellidae	E. Toarcian	Iberian Range	raduca
Choffatirhynchia vasconcellosi	(Choffat in Dubar, 1931)	DPUCM/AR.11.501	Rhynchonellidae	E. Toarcian	Iberian Range	raduca
Rhynchonelloidea goyi	García Joral, 1982	DPUCM/RE.6	Rhynchonellidae	L. Toarcian	Iberian Range	raduca
Prionorhynchia guembeli	(Oppel, 1861)	DCTMA/I.12.26c	Prionorhynchiidae	Pliensbachian	Subbetic	raduca
Prionorhynchia quinqueplicata	(Zieten, 1832)	DCTMA/O.9.2.1	Prionorhynchiidae	Pliensbachian	Subbetic	raduca
Prionorhynchia polyptycha	(Oppel, 1861)	DCTMA/O.5.34c	Prionorhynchiidae	Pliensbachian	Subbetic	raduca
Globirhynchia subobsoleta	(Davidson, 1852)	DPUCM/RE.M.36	Cyclothyrididae	Aalenian	Iberian Range	raduca
Alebusirhynchia jorali	Baeza-Carratalá, 2011	DCTMA/O.12.10.2	Cyclothyrididae	L. Sinemurian	Subbetic	raduca
Alebusirhynchia vorosi	Baeza-Carratalá, Dulai & Sandoval, 2018	DCTMA/SG1.ANP7	Cyclothyrididae	L. Sinemurian	Subbetic	raduca
Apringia atlaeformis	(Böse, 1897)	DCTMA/O4.2.TS3	Basiliolidae	Pliensbachian	Subbetic	hamifor
Soaresirhynchia bouchardi	(Davidson, 1852)	DPUCM/VO.0.2 DCTMA/Esc.Bo1 DCTMA/PT.ES.1	Basiliolidae	E. Toarcian	Iberian Range	hamifor
Mondegia atla	(Oppel, 1863)	DCTMA/LSR-Map-sec.1	Basiliolidae	E. Bajocian	Subbetic	falcifor
Pseudogibbirhynchia jurensis	(Quenstedt, 1858)	DPUCM/1.AR.103.1	Basiliolidae	E. Toarcian	Iberian Range	hamifor
Aphelesia bipartita	(Brocchi, 1814)	DCTMA/AL6.AB9	Basiliolidae	L. Tortonian	post-orogenic Betic basins	falcifor
Fortunella decipiens	(D'Orbigny, 1847)	DPUGR/XA28.276	Basiliolidae	Barremian	Prebetic	falcifor
Septocrurella microcephala	(Parona, 1896)	DCTMA/O.7.3.Ts.1	Erymnariidae	E. Bajocian	Subbetic	septifor
Praemonticlarella distercica	García Joral, 1993	DPUCM/FZ.68.17	Norellidae	Aalenian	Iberian Range	arcual
Atychorhynchia falsiorigo	Baeza-Carratalá, Reolid & García Joral, 2017	DCTMA/CE.28b.Rh1	Norellidae	E. Toarcian	Subbetic	arcual
Monticlarella triloboides	(Quenstedt, 1858)	DPUCM/TO3 R51-9.1	Norellidae	M. Oxfordian	Iberian Range	arcual
Nannirhynchia pillula	(Schlosser in Böse & Schlosser, 1900)	DCTMA/O4.1.T1.7	Norellidae	L. Pliensbachian	Subbetic	arcual

Linking Western Tethyan Rhynchonellide morphogroups to the key post-Palaeozoic extinction and turnover events

José Francisco Baeza-Carratalá[a*] and Fernando García Joral[b]

Highlights:

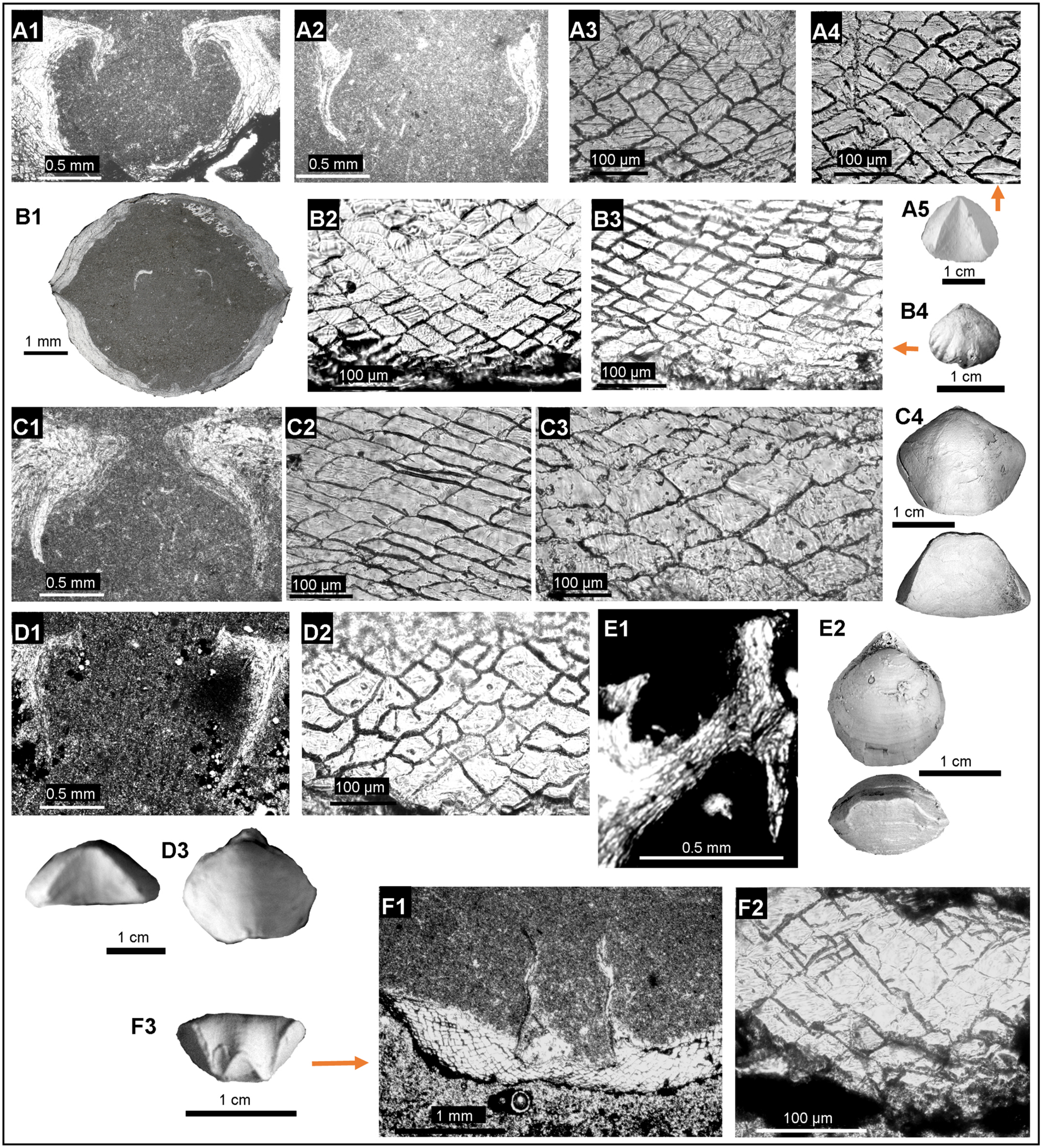
Rhynchonellides are arranged coupling shell-microstructure, crural type and costation

Singular morphogroups are linked to key post-Palaeozoic crisis/diversification events

A recurrent pattern with adaptive meaning beyond a phylogenetic meaning is revealed

Adaptive response to extinction events differ in epicontinental/epioceanic seas

Resources availability or filter-feeding efficiency regulated distribution of groups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C1
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C3
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C4
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D1
0.5 mm
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F1
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F2
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F3
1 cm

Figure 1

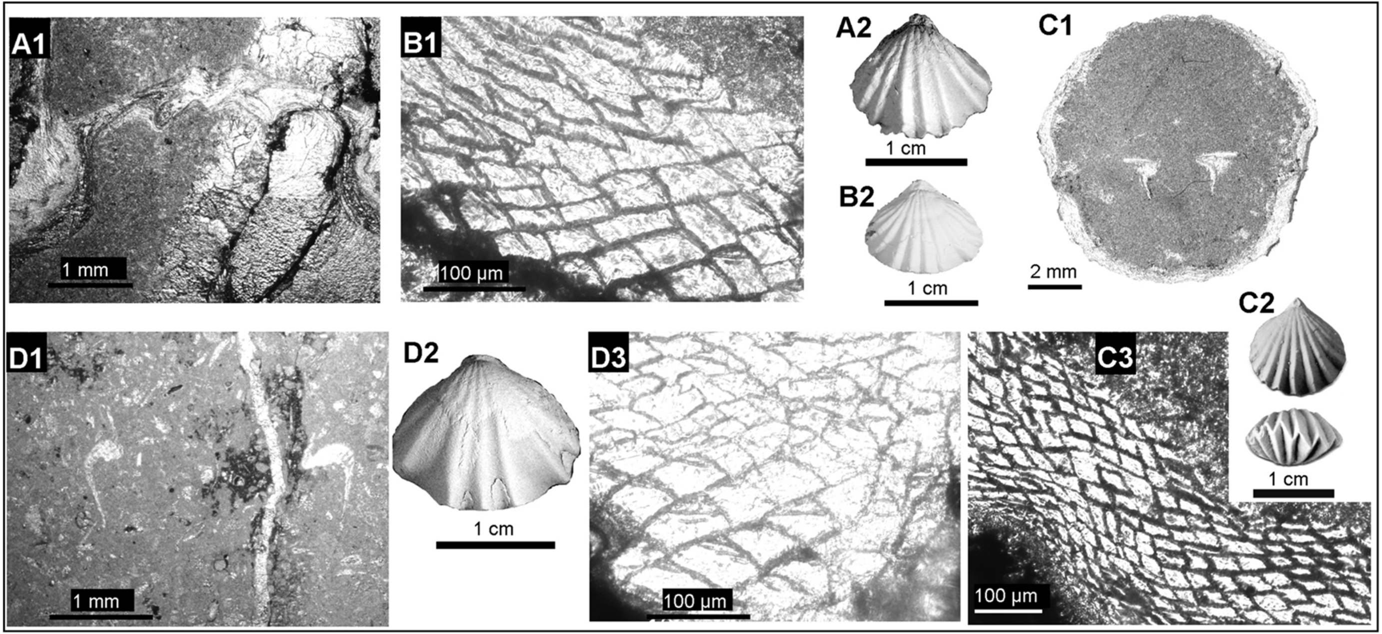
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Figure 2

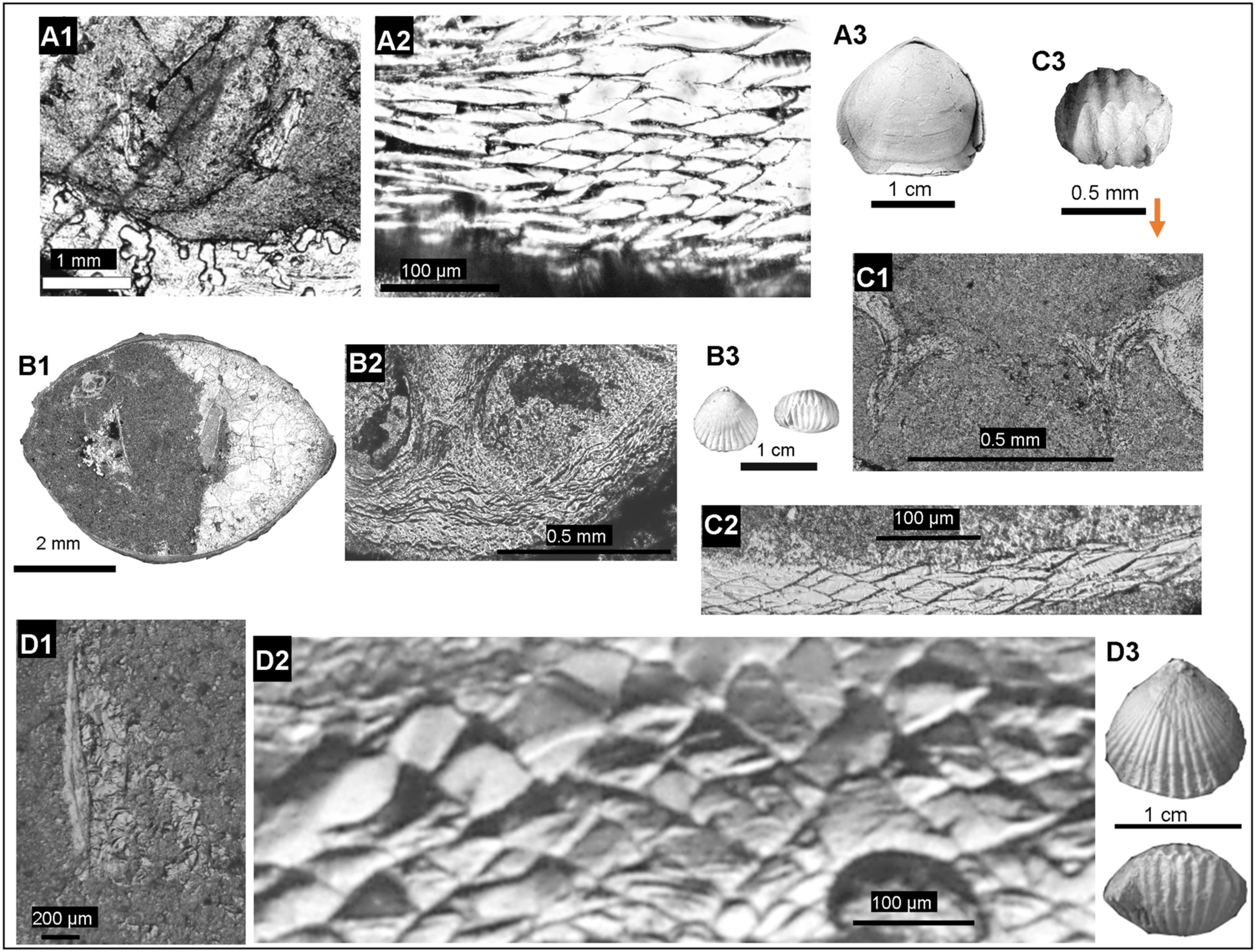
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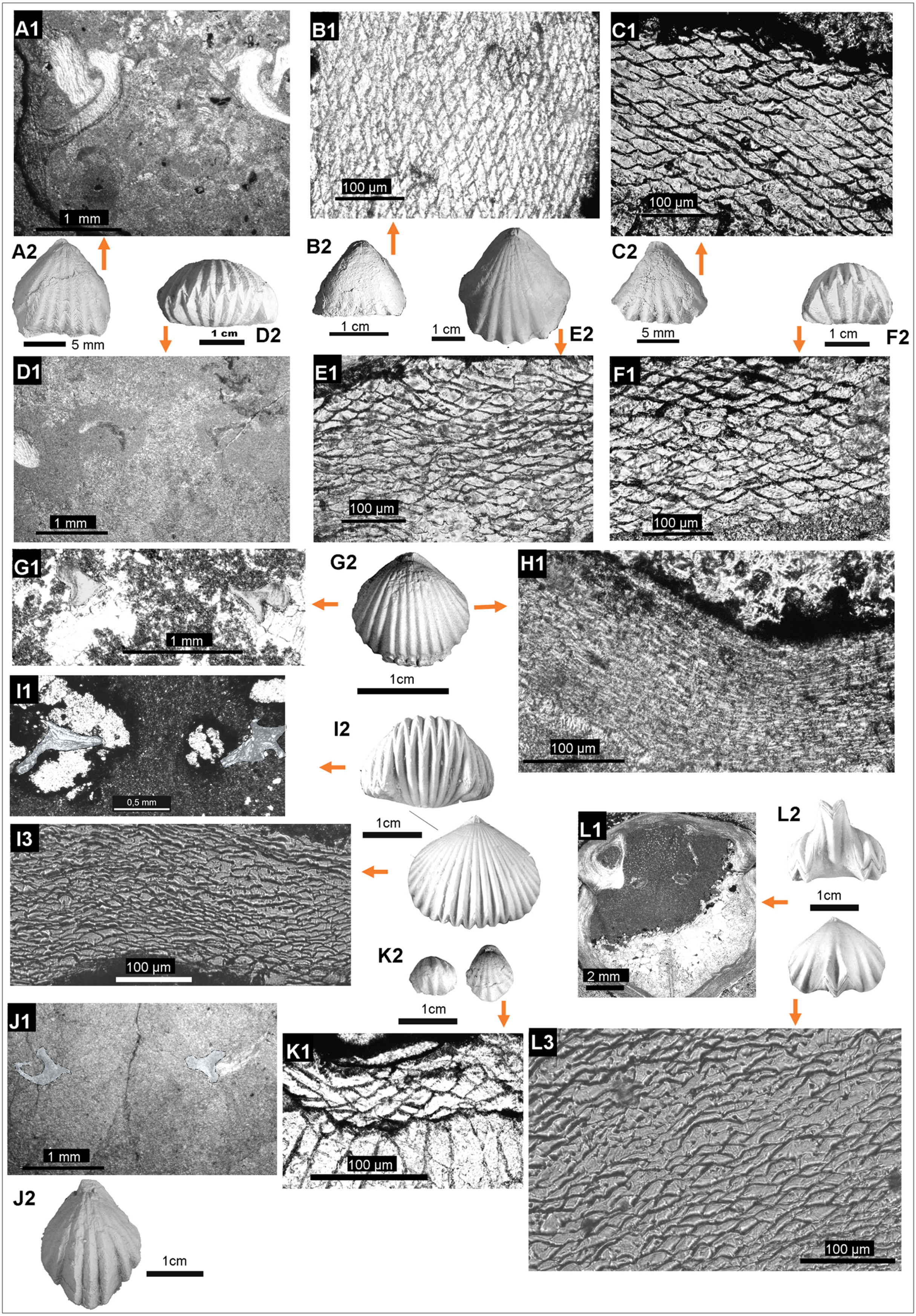
Figure 3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E1
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G1
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G2
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I1
0,5 mm
I2
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I3
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K2
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J1
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K1
100 µm
L3
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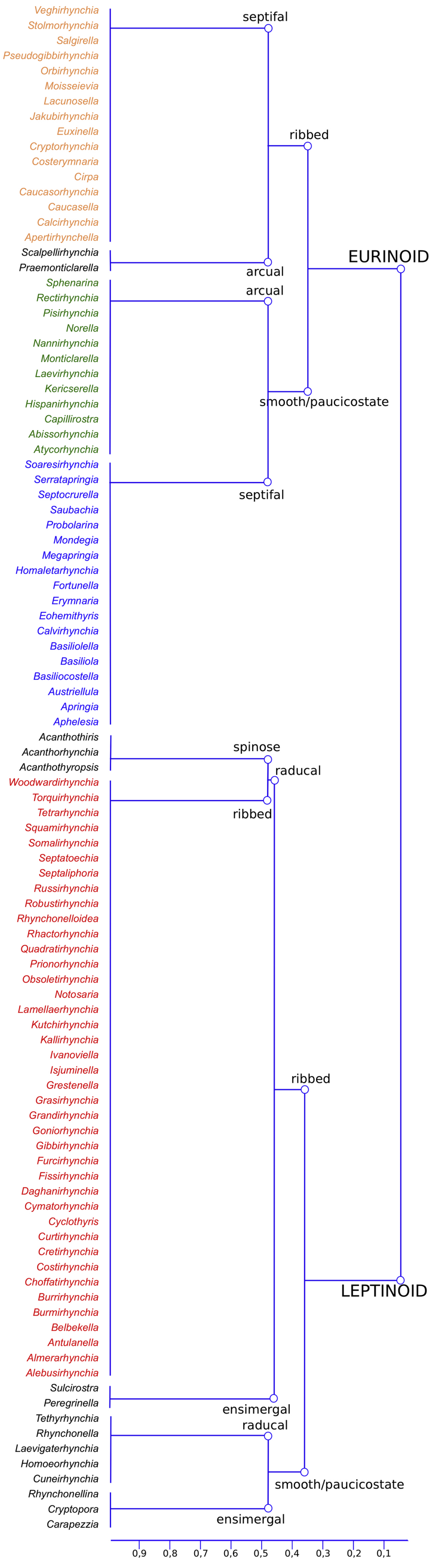
J2
1cm

Figure 4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Pseudogibbirhynchia
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Jakubirhynchia
Euxinella
Cryptorhynchia
Costerymnaria
Cirpa
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Calcirhynchia
Apertirhynchella
Scalpellirhynchia
Praemonticlarella
Sphenarina
Rectirhynchia
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Norella
Nannirhynchia
Monticlarella
Laevirhynchia
Kericserella
Hispanirhynchia
Capillirostra
Abissorhynchia
Atycorhynchia
Soaresirhynchia
Serratapringia
Septocrurella
Saubachia
Probolarina
Mondegia
Megapringia
Homaletarhynchia
Fortunella
Erymnaria
Eohemithyris
Calvirhynchia
Basiliolella
Basiliola
Basiliocostella
Austriellula
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Acanthothiris
Acanthorhynchia
Acanthothyropsis
Woodwardirhynchia
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Tetrarhynchia
Squamirhynchia
Somalirhynchia
Septatoechia
Septaliphoria
Russirhynchia
Robustirhynchia
Rhynchonelloidea
Rhactorhynchia
Quadratirhynchia
Prionorhynchia
Obsoletirhynchia
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Kutchirhynchia
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Ivanoviella
Isjuminella
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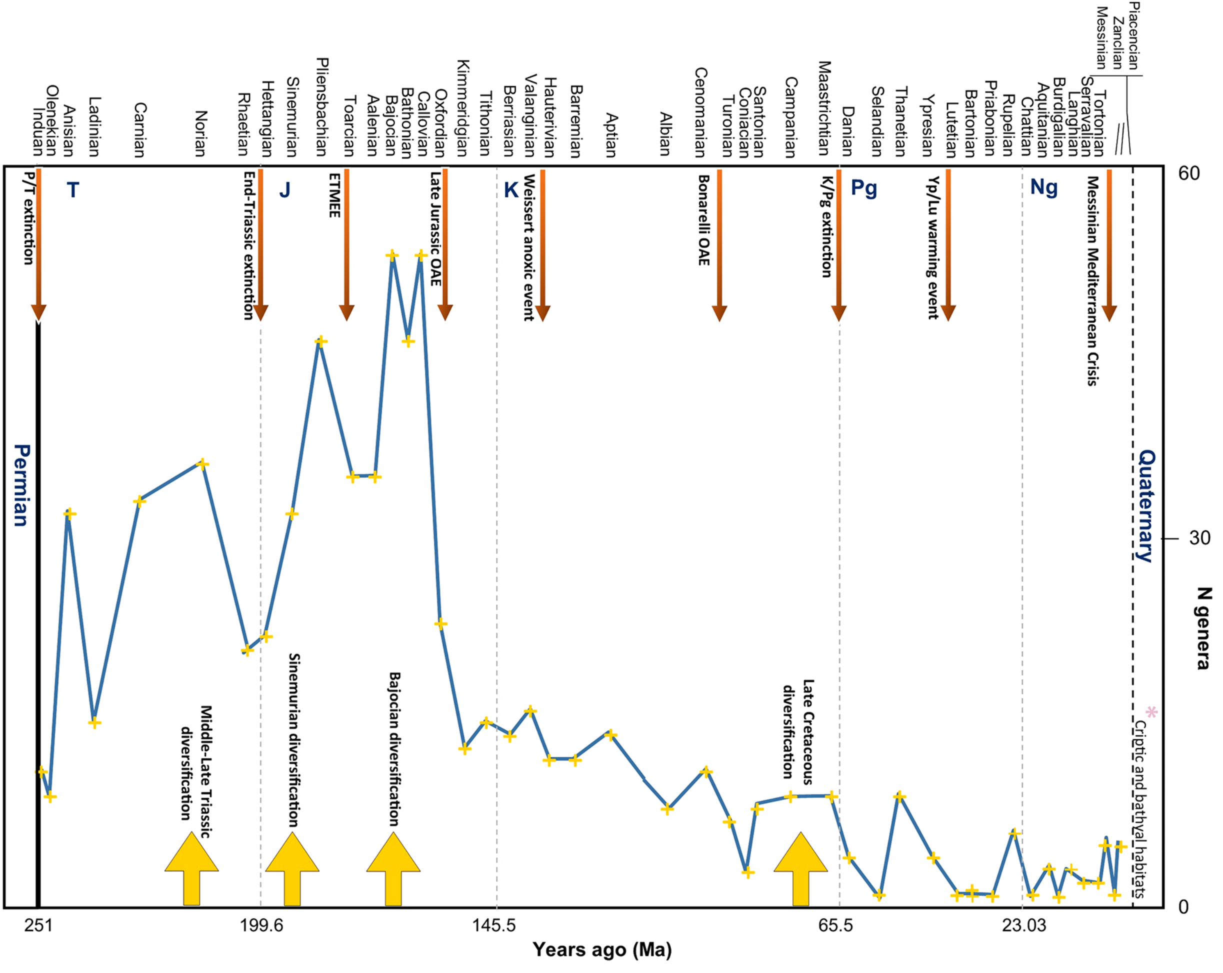
Figure 5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Chattian
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ETMEE
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Bonarelli OAE
K/Pg extinction
Yp/Lu warming event
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Middle-Late Triassic diversification
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Bajocian diversification
Late Cretaceous diversification
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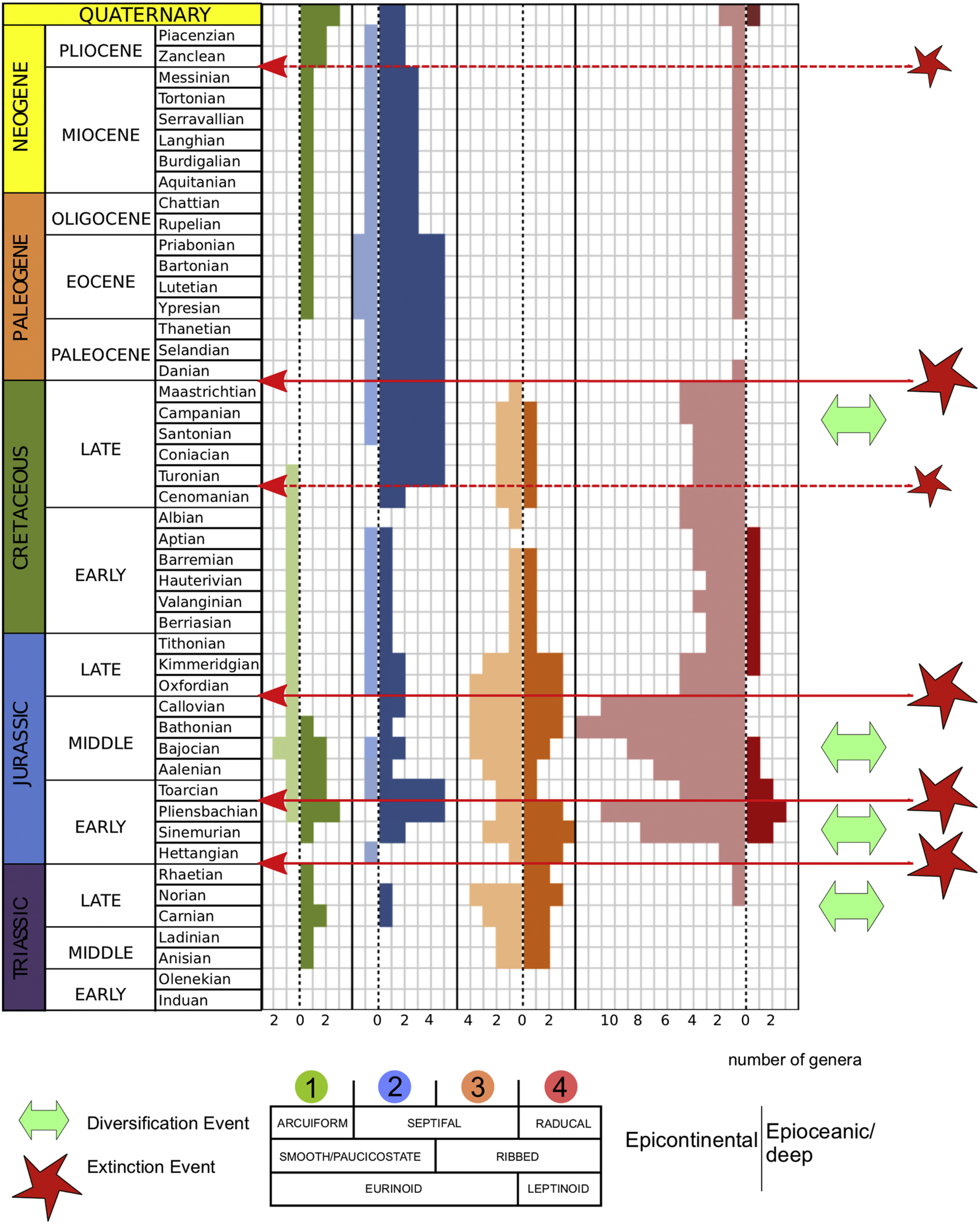
Figure 6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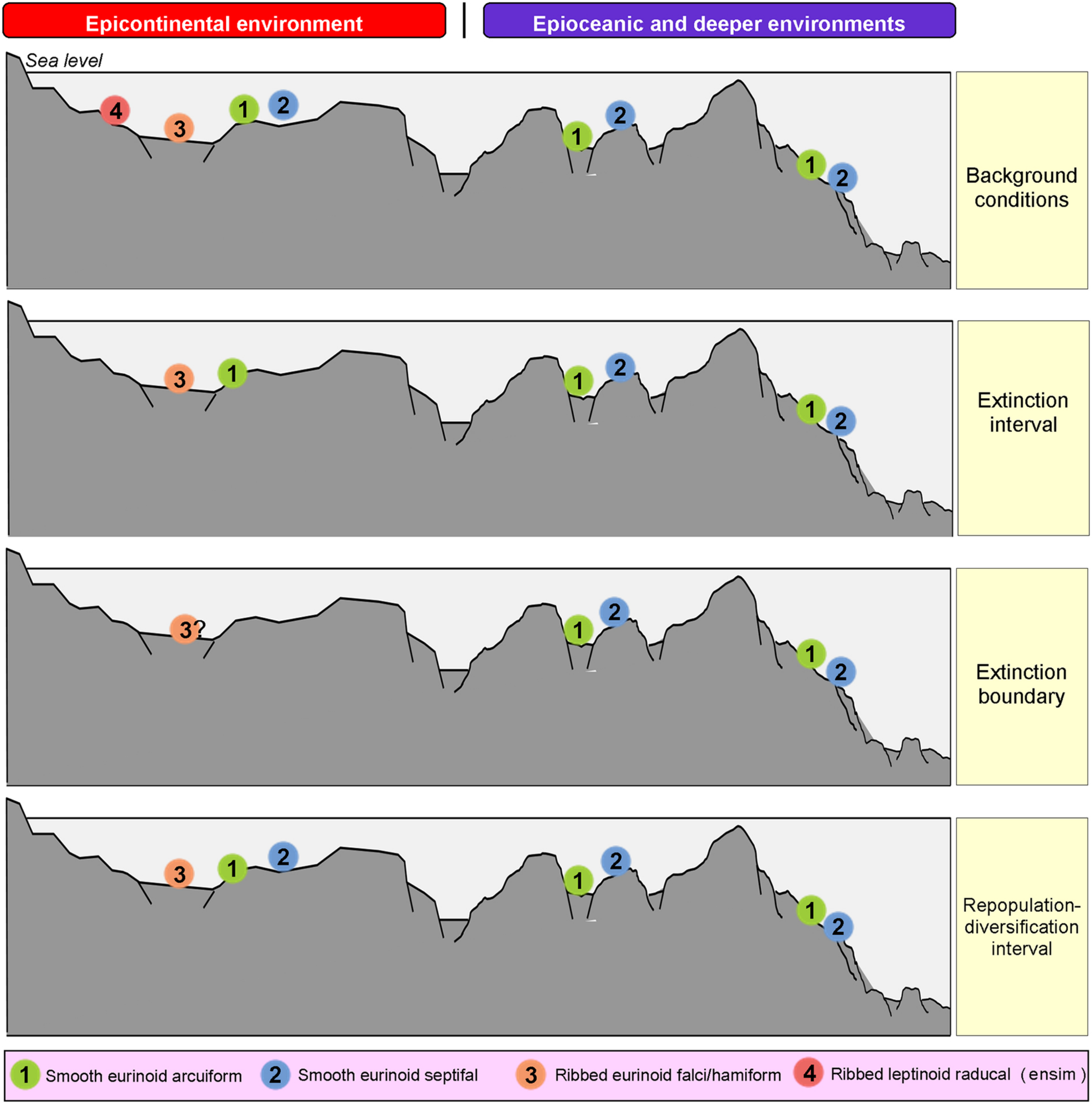
ARCUIFORM
SEPTIFAL
RADUCAL
SMOOTH/PAUCICOSTATE
RIBBED
EURINOID
LEPTINOID
Epicontinental
Epioceanic/ deep
Diversification Event
Extinction Event

Figure 7


Epicontinental environment
Epioceanic and deeper environments
Sea level
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Background conditions
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Extinction interval
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Extinction boundary
3
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2
2
1
1
2
Repopulation-diversification interval
1 Smooth eurinoid arcuiform
2 Smooth eurinoid septifal
3 Ribbed eurinoid falci/hamiform
4 Ribbed leptinoid radical (ensim)

Figure 8