

# Extinction pattern of marine Ostracoda across the Pliensbachian-Toarcian boundary in the Cordillera Ibérica, NE Spain: Causes and consequences<sup>☆</sup>

## Causes et conséquences de l'extinction de l'ostracofaune marine à la limite Pliensbachien-Toarcien dans la Cordillère ibérique, Espagne

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### Abstract

This paper discusses the extinction pattern of the Pliensbachian-Toarcian boundary (PTB) ostracod assemblages at the Almonacid de la Cuba section (Cordillera Ibérica, NE Spain), which has been recently proposed as auxiliary boundary stratotype for the PTB. The ostracod record shows that the main Early Jurassic ostracod extinction event occurred not at the end of the Pliensbachian, but near the top of the Mirabile ammonite Subzone, Tenuicostatum ammonite Zone (Early Toarcian). On the basis of the evaluation of PTB ostracod record, a new causal explanation for the Early Toarcian ostracod turnover is proposed. This paper suggests that a reorganization of surface and deep-water circulations caused by the opening of the Hispanic Corridor could have generated a mild cooling episode, finally affecting the survival of healdioid ostracods.

### Résumé

Les modalités d'extinction de l'ostracofaune à la limite Pliensbachien-Toarcien sont discutées pour la coupe d'Almonacid de la Cuba (Cordillère ibérique, NE Espagne), récemment proposée comme stratotype de limite complémentaire pour la limite Pliensbachien-Toarcien. L'extinction la plus intense affectant l'ostracofaune ne se situe pas au sommet du Pliensbachien, mais près du sommet de la sous-zone à Mirabilis (zone à Tenuicostatum). Les changements constatés au sein des associations d'ostracodes pourraient trouver leur origine dans la réorganisation de la circulation océanique superficielle et thermohaline, résultant de l'ouverture du Corridor Hispanique. Cela aurait pour conséquence la mise en place d'un épisode relativement froid, affectant finalement la survie des ostracodes healdioidés.

**Keywords:** Ostracoda; Pliensbachian-Toarcian boundary; Mass extinction; Palaeoceanography; Climate change; Cordillera Ibérica; Spain

**Mots clés :** Ostracodes ; Limite Pliensbachien-Toarcien ; Extinction massive ; Paléocéanographie ; Changement climatique ; Cordillère ibérique ; Espagne

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### 1. Introduction

In some of their initial investigations into periodic faunal extinctions, Raup and Sepkoski identified an important faunal turnover at, or about, the Pliensbachian-Toarcian boundary (PTB) (Raup and Sepkoski, 1986; Sepkoski and Raup, 1986; Sepkoski, 1996). Subsequent works on Lower Jurassic

successions in Europe, South America and Asia have shown that the most important faunal turnover took place in the early Toarcian (Pálffy and Smith, 2000; Wignall, 2001; Pálffy et al., 2002; Vörös, 2002). The mass extinction event across the PTB has raised many questions about the magnitude, duration, selectivity, geographic patterns and the subsequent recovery episode (Hallam, 1986; Little and Benton, 1995; Hallam and Wignall, 1999). Although it was initially documented in bivalves and brachiopods, the PTB event was subsequently described in other groups such as ostracods, ammonites, belemnites, and foraminifers (Lord, 1982, 1988; Little, 1994;

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Aberhan and Fürsich, 1997, 2000; Harries and Little, 1999; Guex et al., 2001; Arias, 2007).

The PTB extinction event in the Cordillera Ibérica is characterized by a distinct drop in species diversity and abundance at the top of the Tenuicostatum ammonite Zone (Early Toarcian), which mainly affected marine benthic invertebrates (benthic ostracods, deposit and suspension-feeding infaunal bivalves and brachiopods), while nektonic and pseudoplanktonic groups were largely unaffected, showing only some ecological response but almost no extinction (Goy et al., 2006).

This paper documents the ostracod extinction pattern across the PTB at the Almonacid de la Cuba section, Cordillera Ibérica (NE Spain), which has been recently proposed as a potential auxiliary Global Stratotype Section and Point (GSSP) for the PTB (Goy et al., 2006). In addition, this paper re-examines the ostracod record from several PTB sections exposed on the Cordillera Ibérica to assess the timing and severity of the ostracod extinction across the PTB. In its last part, this paper critically examines a new triggering mechanism that is suggested as responsible for the Early Toarcian extinction, analyzing the viability of their explanations in connection with the PTB ostracod extinction event.

## 2. Geological setting

In the last decade, a remarkable scientific research has been made to understand the main cause of the Early Toarcian mass extinction in the Cordillera Ibérica, NE Spain. However, many questions remain open, e.g., the succession and timing of the series of events, the nature and relative importance of controlling factors, and ultimate causes of this ecological disaster. There are only a few areas in the world where the PTB is exposed in an undisturbed, continuous marine succession, providing an opportunity to learn more about this global major event. The Cordillera Ibérica (NE Spain) is one such area with very detailed stratigraphic sections that allow us to describe complete ostracod successions across the PTB.

Proposed as a potential auxiliary GSSP for the PTB (Goy et al., 2006), the Almonacid de la Cuba section (Fig. 1)

encompasses major lithofacies changes and no important stratigraphic gap. The PTB has been defined at the base of level CU35 coinciding with the first record of *Dactylioceras* (*Eodactylites*) *simplex* (Fucini, 1935) (Comas-Rengifo et al., 1999). The boundary is also characterized by the occurrence of four successive ammonite assemblages: *Pleuroceras* (BH14–CU14), *Canavaria* (CU16–CU32), *Dactylioceras* (E.) (CU35–CU44) and *Dactylioceras* (*Orthodactylites*) (CU44–CU87).

The Upper Pliensbachian-Lower Toarcian Turmiel Formation comprises 8 to 9 m of an alternation of marls and mudstone carbonates, which are organized into sets of deepening and shallowing-upward sequences (Comas-Rengifo et al., 1999; Gómez and Goy, 2000; Goy et al., 2006). This unit overlies bioclastic limestones of the Upper Pliensbachian Barahona Formation, which consists mainly of lime wackestone to packstone, occasionally mudstone and grainstone, skeletal limestones and minor interbedded marls. This unit is organized into aggradational shallowing-upward sequences that were deposited on a shallow platform frequently influenced by storms (Gómez, 1991; Gómez and Goy, 2005).

The Almonacid de la Cuba section is characterized by the occurrence of biostratigraphically significant fossils of ammonoids, brachiopods, foraminifers and ostracods, allowing to understand the boundary position. A complete and precise local biozonation based on ammonite faunas of the Almonacid de la Cuba section has been previously published (Comas-Rengifo et al., 1999; Gómez and Goy, 2000; Goy et al., 2006). In Fig. 2, a simplified ammonite-based biostratigraphic zonation is correlated with the standard ammonite scales (Elmi et al., 1994, 1997; Page, 2003).

Latest studies of this section have shed light on biotic changes across the PTB that cannot simply be explained by well-known triggering mechanisms, e.g. anoxia episodes or sea level changes. In relation to the anoxic conditions, repeatedly described across Central Europe in the Early Toarcian (Jenkyne and Clayton, 1986, 1997; Harries and Little, 1999), the PTB event is only characterized by an impoverishment of the benthic biota during the Semicelatum Subzone (Tenuicostatum Zone), and no deposition of organic-rich shales in the Cordillera Ibérica (Goy et al., 2006).



Fig. 1. Geographical and geological setting of the studied sections.

	Iberian Range (this work)		Standard Subboreal Province (Page, 2003)		Standard NW Europe (Elmi et al., 1994, 1997)		Standard Mediterranean (Elmi et al., 1994, 1997)	
TOARCIAN	ZONES	SUBZONES	ZONES	SUBZONES	ZONES	SUBZONES	ZONES	SUBZONES
	Serpentinum	Falcifer	Serpentinum	Falciferum	Serpentinum	Falciferum	Levisoni	Falciferum
		Strangewaysi		Exaratum		Elegantulum		Levisoni
	Tenuicostatum	Semicelatum	Tenuicostatum	Semicelatum	Tenuicostatum	Semicelatum	Polymorphum	Semicelatum
		Mirabile		Tenuicostatum		Paltum		Mirabile
				Clevelandicum				
PLIENSBACHIAN	Spinatum	Hawskerense	Spinatum	Hawskerense	Spinatum	Hawskerense	Emaciatum	Elisa

Fig. 2. Correlation chart showing the standard and local ammonite zones and subzones of different areas of Europe (after Elmi et al., 1994, 1997; Page, 2003; Goy et al., 2006).

Sea-level variations in this area show a clear transgressive pattern. The Toarcian started with a generalized transgressive episode at the beginning of the Early Jurassic Tenuicostatum Zone (maximum deepening is reached in the lower portion of the Semicelatum Subzone), which extended up to the Late Toarcian Variabilis Zone (Goy et al., 1997). This major cycle can be subdivided into three minor sub-cycles, a first transgressive one during the early part of the Tenuicostatum Zone, a second regressive one near the boundary between the Tenuicostatum and the Serpentinum zones, and a third one developed up to the lower part of the Serpentinum Zone (Goy et al., 1997).

### 3. Material and methods

Best-studied marine sections relevant to the PTB mass extinction event in Spain are mainly concentrated in the Cordillera Ibérica. Among the most completed PTB sections, the Lower Jurassic section at Almonacid de la Cuba includes one of the best PTB ostracod record in this area. The section is located about 1.8 km northwest of Almonacid de la Cuba (GPS: N 41°18'38"; E 20°52'35") province of Zaragoza, Northeast Spain (Fig. 1).

Previous studies of the Early Jurassic ostracod content of this area were given by Arias (1995) and Arias and Lord (1999a, 1999b). A total of 25 samples were collected from the Upper Pliensbachian and Lower Toarcian mudstones and marls materials. From these samples, 741 ostracod specimens were recovered, which were referred to 23 species belonging to 13 genera, 12 families, five superfamilies and two orders. In addition, belemnites from the Lower Toarcian sediments of this section have been collected and analyzed for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  (Gómez et al., 2008; Fig. 3).

### 4. The Late Pliensbachian-Early Toarcian ostracod record in the Almonacid de la Cuba section (NE Spain)

Late Pliensbachian (Spinatum Zone) ostracod assemblages of the Almonacid de la Cuba section (Fig. 4) are marked by a high abundance of cytheroids: *Ektypocythere* aff. *E. vitiosa* (Apostolescu, 1959) (Fig. 5[11]), *Kinkelina tenuicostata* Martin (1960) (Fig. 5[12]) and *Grammannella apostolescui*

(Gramann, 1962) (Fig. 5[15]); healdioids such as *Ogmoconchella adenticulata* (Pietrzenuk, 1961), *Ogmoconchella* aff. *O. aspinata* (Drexler, 1958) (Fig. 5[7, 8]) and *Ogmoconchella propinqua* Malz (1971) (Fig. 5[4–6]); and the cypridoid species *Liasina lanceolata* (Apostolescu, 1959) (Fig. 5[10]). The lower levels of the Upper Pliensbachian Barahona Formation are dominated by two healdioid species: *O. adenticulata* (Pietrzenuk, 1961) and *O. aff. O. aspinata* (Drexler, 1958). Of the Late Pliensbachian horizons considered herein, the upper levels within the Upper Pliensbachian Turmiel Formation (CU19) exhibit the first evidence of a biotic change: a sharply defined decline in some smooth healdioids (e.g., *O. adenticulata* [Pietrzenuk, 1961] and *O. aff. O. aspinata* [Drexler, 1958]) and their replacement by large cytheroid species (*E. aff. E. vitiosa* [Apostolescu, 1959] and *G. apostolescui* [Gramann, 1962]) accompanied by *L. lanceolata* (Apostolescu, 1959) (Fig. 4). At the PTB, within the Turmiel Formation (CU35), ostracod assemblages are initially dominated by *E. aff. E. vitiosa* (Apostolescu, 1959) associated with *L. lanceolata* (Apostolescu, 1959) and *Ogmoconchella aequalis* (Herrig, 1969) (Fig. 5[9]). This change occurred synchronously with an initial negative carbon-isotope excursion (CIE) and with a new reversed magnetozone (R2) (Fig. 3). Consequently, healdioid ostracods dominate the Upper Pliensbachian Barahona Formation (basal part of the Spinatum Zone) assemblages, and cytheroids together with healdioids are the leading components of the Upper Pliensbachian Turmiel Formation ostracod assemblages (Figs. 4 and 6).

Above the PTB (CU35) continues the dominance of *E. aff. E. vitiosa* associated with *L. lanceolata* (Apostolescu, 1959) and appears a new healdioid ostracod, *Ogmoconchella aequalis* (Herrig, 1969), which typifies the Mirabile Subzone ostracod assemblage (Tenuicostatum Zone). The most abrupt and dramatic turnover in benthic and pelagic ostracods is coeval with the Mirabile-Semicelatum subzones transition (CU43/47) (Fig. 4). This faunal change is characterized by a sharply defined disappearance of all healdioid species together with the nearly total disappearance of two of the well-represented Late Pliensbachian species of large and ornamented cytheroids, *E. aff. E. vitiosa* (Apostolescu, 1959) and *G. apostolescui* (Gramann, 1962). This episode is also characterized by the appreciable decrease in abundance of *L. lanceolata*



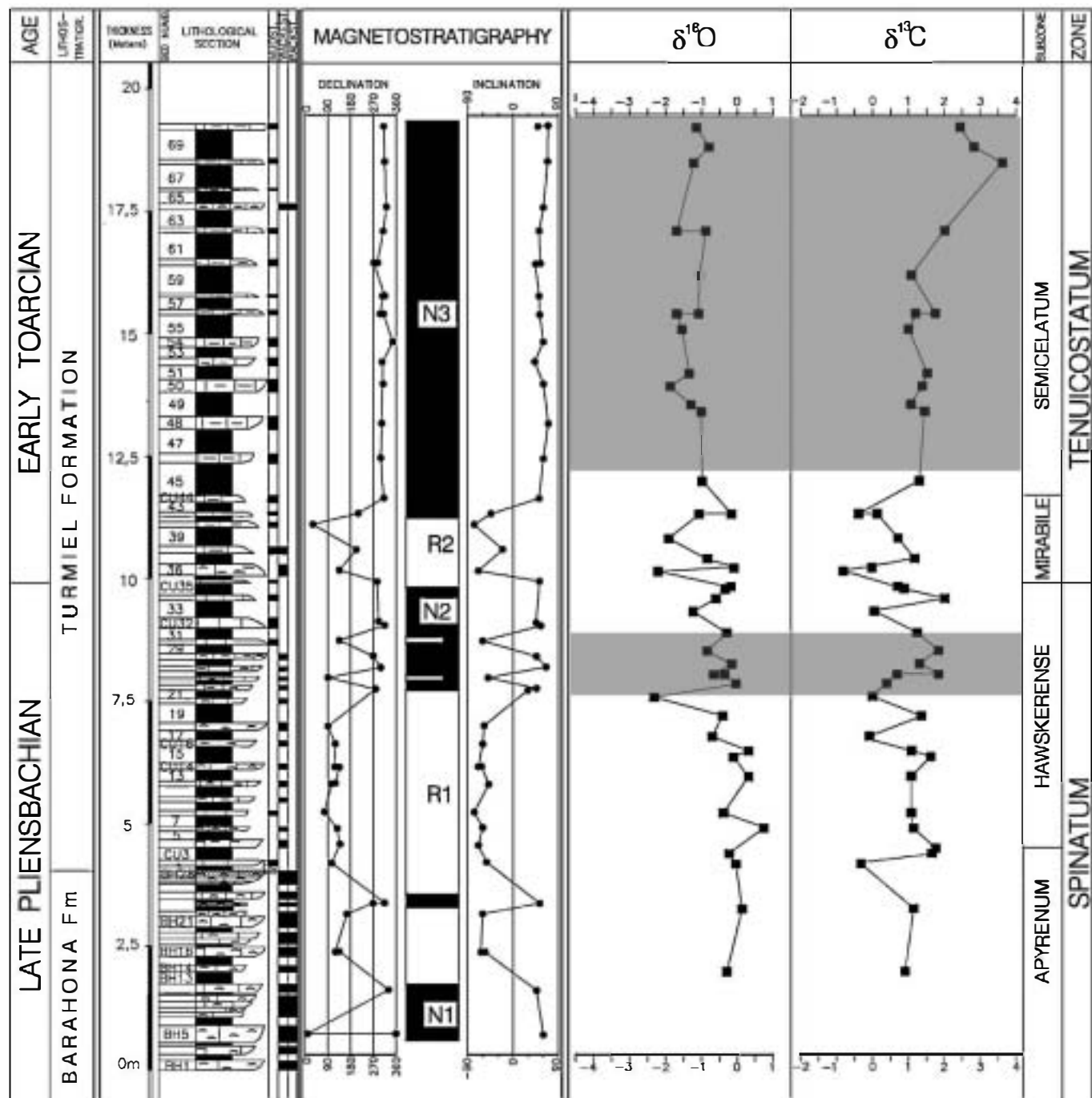


Fig. 3. Magnetostratigraphy and  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  records from the Alnonaci de la Cuba section. Chronology and ammonite biostratigraphy after Goy et al. (2006).

(Apostolescu, 1959). The last appearance of the healdioid taxa occurred almost synchronously with an initial positive CIE, within an extended normal magnetozone (N3) at the top of the Mirabile Subzone, Tenuicostatum Zone (Figs. 3 and 4). Then, healdioids survived into the Early Toarcian Tenuicostatum Zone and they did not disappear from the fossil record at the PTB.

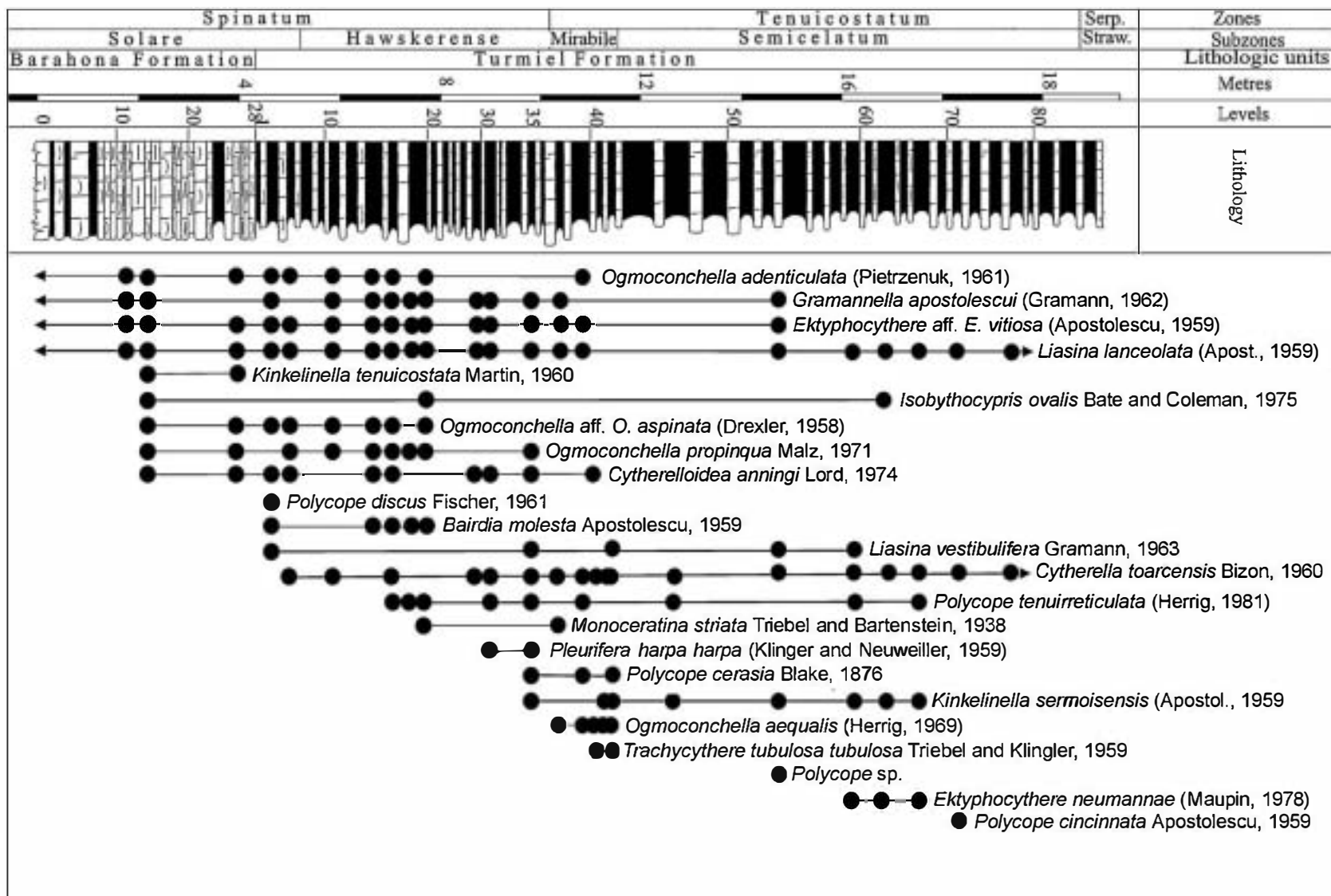
Above this level (CU47), Semicelatum Zone assemblages are dominated by cytheroids (*Kinkelina sermoensis* [Apostolescu, 1959]) and cytherellids (*Cytherella toarcensis* Bizou, 1960; Fig. 5[2]); meanwhile *L. lanceolata* (Apostolescu,

1959) that has survived the Mirabile-Semicelatum crisis becomes one of the dominant species in the Early Toarcian Semicelatum Subzone.

##### 5. Selectivity pattern of the Early Toarcian (Jurassic) marine ostracod extinction in the Cordillera Ibérica (Spain)

As previously mentioned, the most recent revision of ostracod extinction chronology across the Spanish PTB showed that a major PTB catastrophic ostracod extinction in this area

Fig. 4. Location of samples in the Ammoniac de la Cuba section, showing the Upper Pleistocene Barahona Formation and the overlying Lower Tertiary Mirabile Formation.



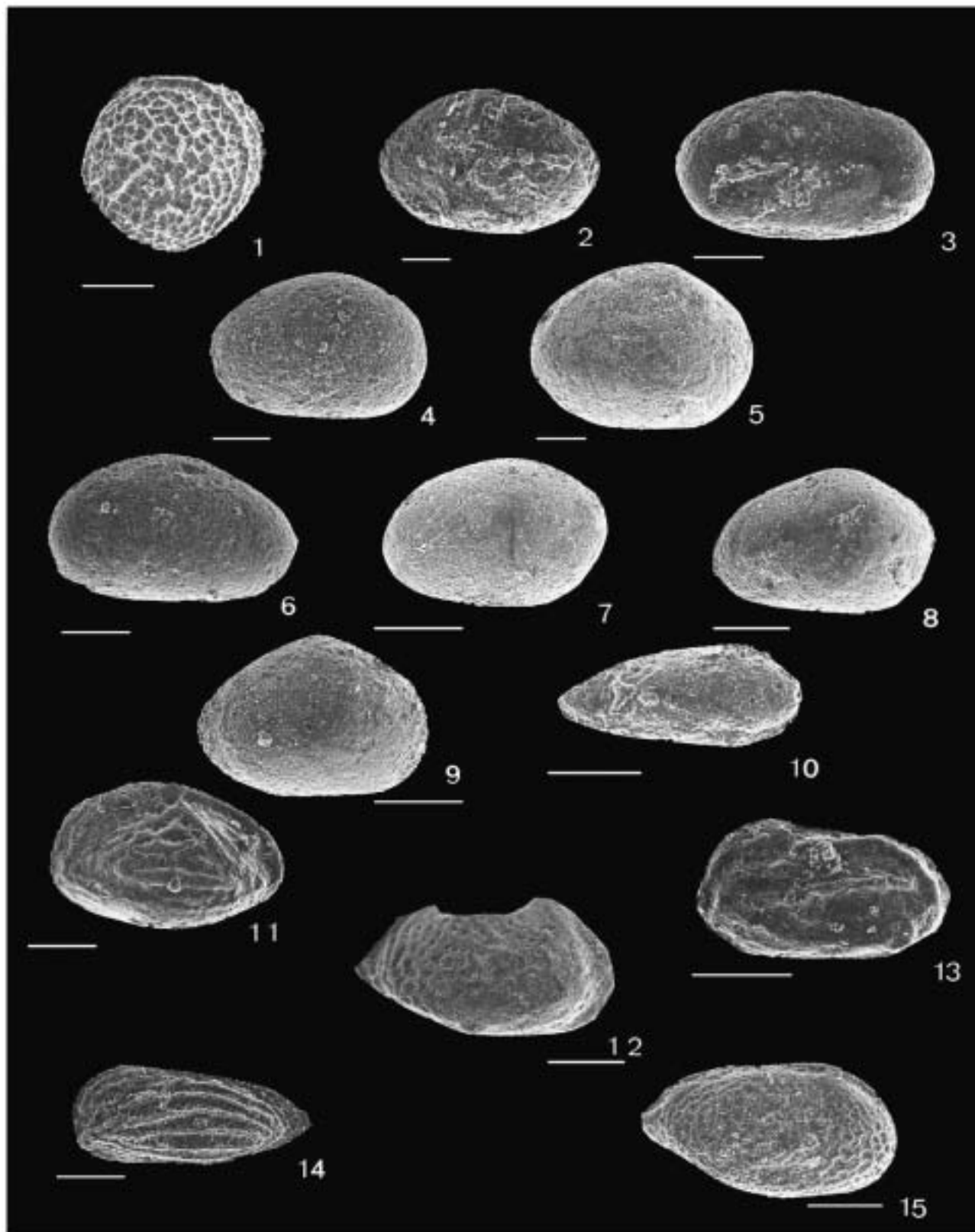


Fig. 5. 1. *Polycopse cerasia* Blake, 1876: carapace, left lateral view, Mirabile Subzone, Tenuicostatum Zone. 2. *Cytherella toarcensis* Bizon, 1960: left valve, Hawskerense Subzone, Spinatum Zone. 3. *Isobythocypris ovalis* Bate and Coleman, 1975: carapace, right lateral view, Semicelatum Subzone, Tenuicostatum Zone. 4–6. *Ogmoconchella propinqua* Malz, 1971: left valve, Solare Subzone, Spinatum Zone (4); left valve, Solare Subzone, Spinatum Zone (5); right valve, Solare Subzone, Spinatum Zone (6). 7, 8. *Ogmoconchella* aff. *O. aspinata* (Drexler, 1958): left valve, Solare Subzone, Spinatum Zone (7); left valve, Hawskerense Subzone, Spinatum Zone (8). 9. *Ogmoconchella aequalis* (Herrig, 1969): left valve, Mirabile Subzone, Tenuicostatum Zone. 10. *Liasina lanceolata* (Apostolescu, 1959): carapace, right lateral view, Mirabile Subzone, Tenuicostatum Zone. 11. *Ekythocythere* aff. *E. villosa* (Apostolescu, 1959): left valve, Mirabile Subzone, Tenuicostatum Zone. 12. *Kinkelina tenuicostata* Martin (1960): right valve, Solare Subzone, Spinatum Zone. 13. *Pleurifera harpaharpa* (Klingler and Neuweiler,

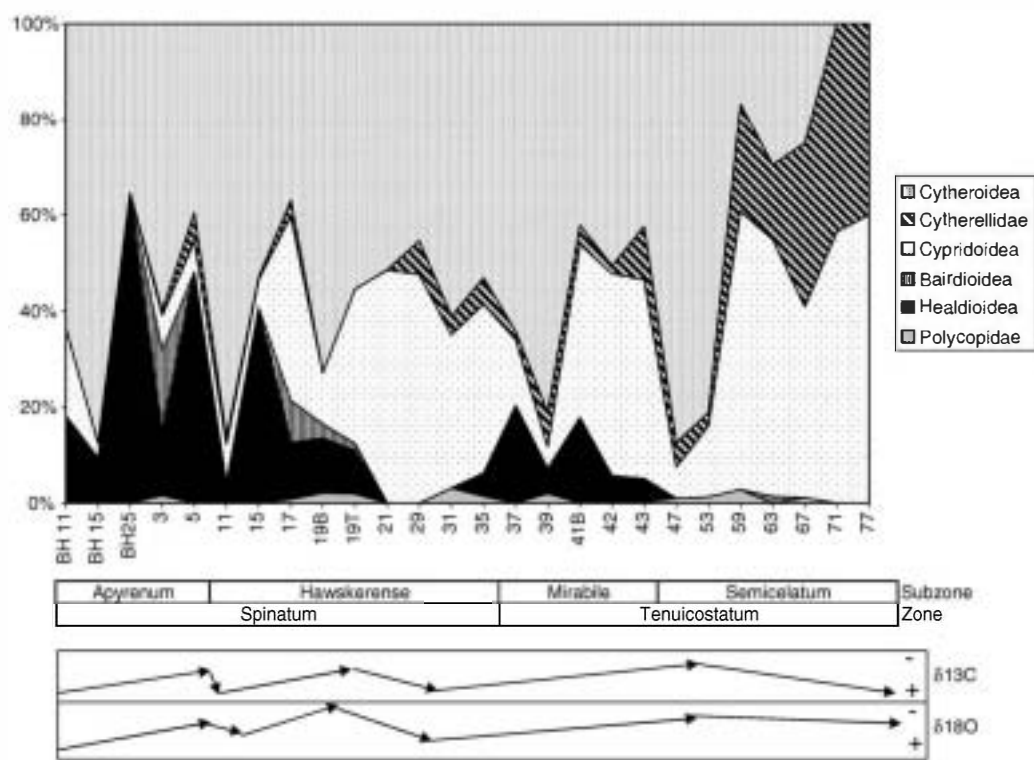


Fig. 6. Relative abundance of main ostracod groups at the Almonacid de la Cuba section. The horizontal scale corresponds to numbers of the samples in the Almonacid de la Cuba section. The lower part of figure denotes the interval of Early Toarcian  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  excursions with respect to the ammonite biostratigraphy.

was less likely than a drawn-out, stepped ostracod extinction (Arias, 2000). The best examined Spanish PTB ostracod succession comes from the Cordillera Ibérica, northeastern Spain (Arias, 1995, 1997, 2000). High-resolution sampling and detailed studies of the ostracod fauna through several sequences in the Cordillera Ibérica illustrate that ostracod assemblages were affected by an Early Toarcian Tenuicostatum event with significant effects on the composition of ostracod assemblages: the smooth healdioids (*Ogmoconchella* and *Ledahia*), which dominated the Late Pliensbachian ostracod assemblages, are largely replaced by ornamented cytheroids (*Kinkelinella* and *Ektyphocythere*) in the Early Toarcian (Arias and Lord, 1999a, 1999b).

Late Pliensbachian ostracod assemblages are characterised by the occurrence of seven healdioid species: *O. aequalis* (Herrig, 1969), *O. aff. O. aspinata* (Drexler, 1958), *O. adenticulata* (Pietrzenuk, 1961), *Ogmoconchella gruendeli* Malz, 1971, *O. propinqua* Malz, 1971, *Ogmoconchella convexa* Boomer, 1991 and *Ledahia septenaria* (Gründel, 1964); three cytheroid species: *E. aff. E. vitiosa* (Apostolescu, 1959), *G. apostolescui* (Gramann, 1962) and *Pleurifera harpa harpa* (Klingler and Neuweiler, 1959; Fig. 5[13]); one cypridoid species, *L. lanceolata* (Apostolescu, 1959); and some accessories ostracod species: *C. toarcensis* Bizon, 1960, *Liasina vestibulifera* Gramann, 1963, *K. tenuicostata* Martin,

1960, and *Gramannicythere aubachensis* Riegraf, 1984 (Fig. 7).

The ostracod assemblages recovered from the lowest part of the Tenuicostatum Zone did not show any important initial compositional change. The assemblages described above occur before and after the PTB and no significant change is observed in the ostracod assemblage across the PTB. The most prominent feature in relation to the Spanish PTB ostracod assemblages took place in the Mirabile Subzone (Fig. 7), where the healdioids progressively disappear, being initially replaced by one cypridoid species, *L. lanceolata* (Apostolescu, 1959), as the main component of the assemblage, and then, by one cytherellid species, *C. toarcensis* Bizon, 1960.

As a result of the mentioned crisis, some new cytheroids species, *Kinkelinella* sp. B, *Ektyphocythere dharennsourensis* Boutakiout et al., 1982, *Ektyphocythere neumannae* (Maupin, 1978) (Fig. 5[14]) and *K. sermoensis* (Apostolescu, 1959), together with *C. toarcensis* Bizon, 1960 and *L. lanceolata* (Apostolescu, 1959), became prevailing in the Semicelatum Zone, although with important fluctuations in their respective abundances (Fig. 7). After the gentle recovery of ostracod assemblages in the Semicelatum Zone, a second faunal turnover took place at the beginning of the Serpentinum Zone; diversity abruptly fell and reached a minimum at the base of the Strangewaysi Subzone, Serpentinum Zone. This second event



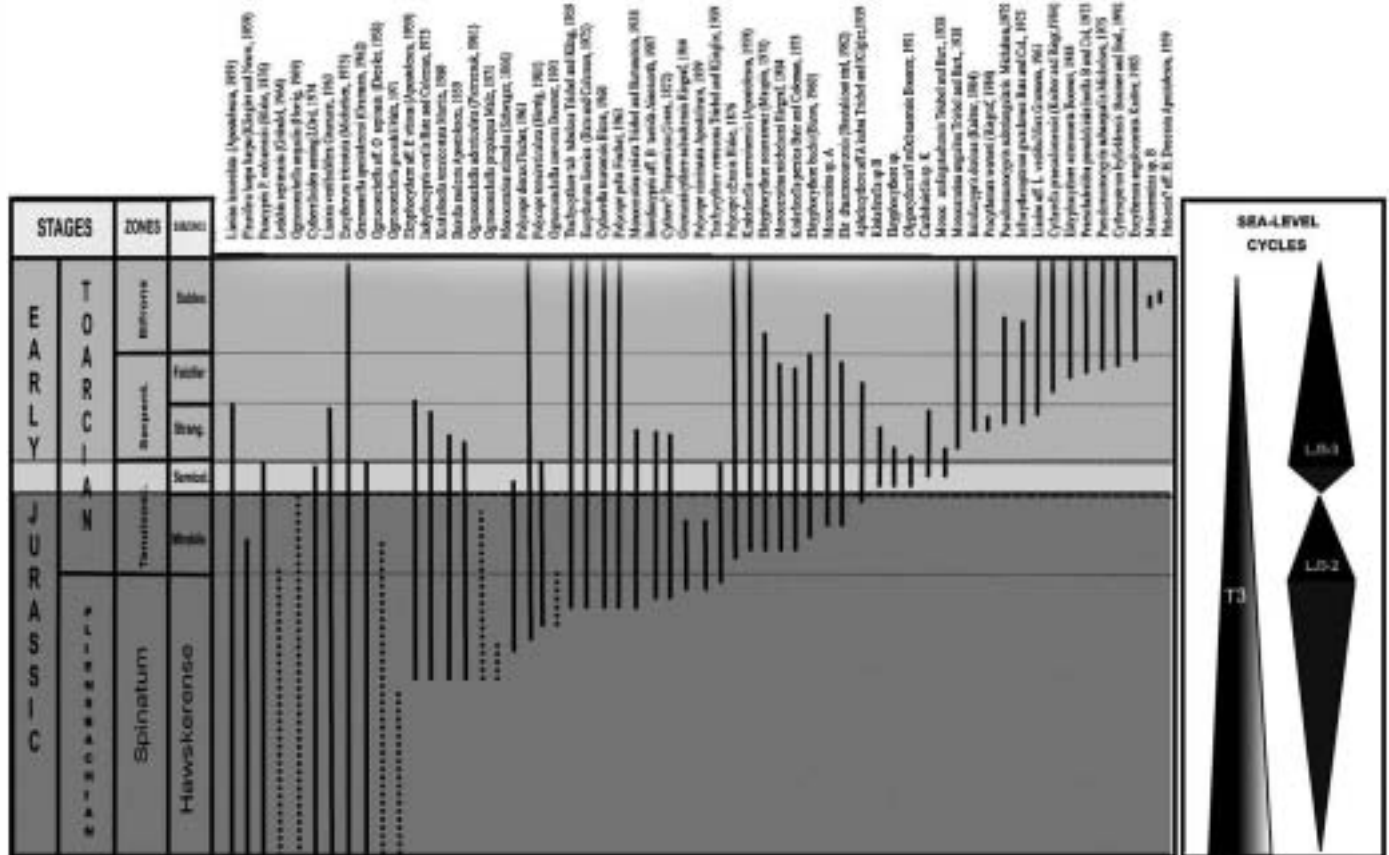


Fig. 7. Range chart of ostracod species across the Pliensbachian-Toarcian boundary and relative sea-level changes in the Cordillera Ibérica, Spain (after Gómez and Goy, 2005).

altered the whole character of Early Toarcian ostracod assemblages and the superfamily Cytheroidea, which survived the Early Toarcian extinction event, became the most successful Toarcian marine ostracod. In summary, the detailed review of the Spanish ostracod record and its biostratigraphic significance emphasizes that ostracods suffered a first episode of extinction at the end of the Mirabile Subzone, Tenuicostatum Zone, then followed by a second biological crisis at the beginning of the Serpentinum Zone (Fig. 7).

## 6. PTB ostracod assemblages

With a few exceptions, ostracod faunas from Western Europe have contributed little to the PTB discussion because, for the whole time interval studied (PTB), accurate data on the biostratigraphical ostracod distribution are infrequent at the biohorizon scale (Arias, 1995, 1997, 2000; Bodergat, 1997; Arias and Whatley, 2004, 2005).

A couple of well-detailed biostratigraphical studies of the Paris Basin and Quercy area, respectively, dealt with the presence of complete stratigraphical PTB sequences (Bodergat et al., 1985; Bodergat and Donze, 1988; Andreu et al., 1995). In this area, the whole disappearance of healdioids is recorded in the Tenuicostatum Zone with the last records of *Ogmoconchella hagenowi* Drexler, 1958 (*O. convexa* Boomer, 1991) and *Ogmoconchella* sp. (*O. aff. O. aspinata* [Drexler, 1958]) and

*Ogmoconcha* sp. A (*Hermiella ambo* Lord and Moorley, 1974). The healdioid disappearance appeared coincident with the development of large cytheroids, such as *K. tenuicostata* Martin (1960), *K. sermoisensis* (Apostolescu, 1959), and *Ektocythere* sp. A (*P. harpa harpa* [Klingler and Neuweiler, 1959]), and a pair of *Trachycythere* species (Bodergat et al., 1985; Bodergat and Donze, 1988; Andreu et al., 1995).

One of the best documented PTB ostracod successions has been described from southwestern Germany (Riegraf, 1984, 1985; Richter, 1987). Riegraf (1985) described the occurrence of the last healdioid species, *Ogmoconcha rotunda* Dreyer, 1967, in the earliest *Semicelatum* Subzone (Tenuicostatum Zone), together with last records of *Isocythere tatei* (Coryell, 1963), *K. tenuicostata* Martin, 1960 and *L. lanceolata* (Apostolescu, 1959). Because across the Tenuicostatum-Serpentinum interval there is no data, it is difficult to establish the complete sequence of the extinction event. Richter (1987) described the disappearance of a succession of healdioid species: *O. amalthei rotunda* Dreyer, 1967, *Ogmoconchella conversa* Malz, 1971, *Hermiella circumvallata* Dreyer, 1967 and *Hermiella intercedens* Dreyer, 1967 at the base of the succeeding *Elongatum* Subzone (Falciferum Zone). This episode of extinction affected the Tenuicostatum rich fauna of cytheroids, bairdioids and cypridioids as well, with no ostracod data at the top of the Exaratum Subzone (Richter, 1987).



Our knowledge of the PTB ostracod biostratigraphy in the British Isles is sparse because of the lack of basal Toarcian faunas (Lord, 1974, 1978, 1982; Bate and Coleman, 1975). Boomer (1991) documented the most complete section at the Mochras borehole (Wales). In this work, Boomer described for the first time the extinction of the healdioids during the uppermost Tenuicostatum zone, coinciding with the last appearance of *Ogmoconcha convexa* Boomer, 1991. He also indicated the extinction of the healdioids was followed by a new ostracod assemblage completely composed of the cypridoid ostracod *L. lanceolata* (Apostolescu, 1959), which was subsequently replaced by a cyclical dominance relationship between cytheroids (*Ektyphocythere debilis* Bate and Coleman, 1975 and *Ektyphocythere intrepida* Bate and Coleman, 1975) and cytherellids throughout the Middle Toarcian (Boomer, 1991). Exploration drilling in the Fasnet Basin, offshore southwestern Ireland, in spite of the poor stratigraphic resolution, showed the progressive disappearance of the healdioids across the PTB (*O. adenticulata* [Pietrzenuk, 1961], *O. gruendeli* Malz, 1971, *O. aequalis* [Herrig, 1969] *Pseudohealdia etaulensis* [Apostolescu, 1959]), indicating as the last healdioid record the occurrence of *O. aff. O. rotunda* (Ainsworth, 1990).

Pliensbachian-Toarcian ostracod assemblages from southern Europe are not very well preserved, despite the fact that they revealed a surprising diversity (Exton, 1979; Arias, 1995; Exton and Gradstein, 1984; Boomer et al., 1998). A remarkable exception is the Zambujal section in the Lusitanian Basin, Portugal (Exton, 1979; Exton and Gradstein, 1984; Boomer et al., 1998). Relatively numerous healdioid species (*O. aequalis* (Herrig, 1969), *Ledahia bispinosa* (Gründel, 1964), *L. septenaria* (Gründel, 1964) and *Pseudohealdia gruendeli* Malz, 1971) disappeared in the Late Pliensbachian and only *O. convexa*, *Hermiella inflata* and *Ogmoconchella* spp. have their last records at the beginning of the Tenuicostatum Zone. Above the PTB, the ostracod assemblage shows a different composition, with bairdioids (*Bairdiacypris rectangularis* Ainsworth, 1986 and *Bairdiacypris triangularis* Ainsworth, 1986), polycopids and cytheroids dominating the Early Toarcian assemblages (Boomer et al., 1998).

Consequently, the limited PTB ostracod record shows that the healdioid extinction event was not instantaneous but it spanned three ammonite zones (Spinatum, Tenuicostatum and Serpentinum zones) from the Late Pliensbachian to the Early Toarcian, and that this extinction event was distributed unequally in northwestern Europe deposits of these ages. Another aspect to consider regarding the PTB extinction is to know why the Superfamily Cytheroidea survived the PTB extinction and evolved rapidly in the Middle Toarcian, becoming the leading group of Early Jurassic ostracods.

## 7. The PTB ostracod extinction: a long-term climate change and the reorganization of the ocean circulation

Only a handful of papers have systematically explored the fate of healdioid ostracods around the PTB. Lord (1982, 1988), summarizing earlier works, showed that the complete extinction

of the most characteristic Pliensbachian ostracods, the healdioids, was coeval with a basal Jurassic diversification of the cytheroid genera *Kinkelinella* and *Ektyphocythere*. Most noteworthy are the papers of Herrig (1988) and Boomer (1991), which analyzed the extinction and recovery of ostracods based on multiple sources and discussed the ecological selectivity and geographic patterns. Arias (2000) reported that total ostracod specific extinctions in the Cordillera Ibérica (Spain) were around 60%. She showed that healdioids were more strongly affected by the Tenuicostatum Zone extinction than cytheroids, and that the earliest Toarcian progress of cytherellids, bairdioids and cypridoids may have been a consequence of the previous healdioid extinction.

The ostracod record from the PTB sediments of the Almonacid de la Cuba section shows a patent extinction episode in the Tenuicostatum Zone, which affected the most distinctive Pliensbachian ostracods, the healdioids. However, this episode did not affect the entire ostracod fauna; actually, this event was coincident with a basal Toarcian diversification of the cytheroid genera *Kinkelinella* and *Ektyphocythere*. The question is if the cytheroids could endure, why not the healdioids?

Despite the relative severity of the PTB mass extinction episode, associated environmental changes have been poorly documented in comparison to other extinction events. One thing that should be obvious is that a single overarching cause of mass extinctions as advocated in the past (e.g. marine regressions or transgression, climatic cooling or warming, volcanism, etc.) appears extremely unlikely. Indeed, all these mechanisms should be implicated to some degree. It is not the purpose of this paper to evaluate all of the many hypotheses proposed to account for the PTB mass extinction, but rather to examine one of the most recently suggested ones and to see what consequences involving the Spanish Toarcian ostracod extinction would result.

### 7.1. Long-term climate change: a cool episode?

According to the sedimentological record, the Early Jurassic climate may have been warmer than the present-day one (Crowley et al., 1989; Kutzbach and Gallimore, 1989; Parrish, 1993). However, there is some doubt that the climate in high latitudes had become warmer (Epshteyn, 1978; Brandt, 1986; Frakes et al., 1992; Arias and Whatley, 2004). Cooling episodes during generally warm Early Jurassic conditions have been explained by the influx of cool water onto the northwest European Epicontinental Sea (EES) via the Viking Strait (Bjerrum et al., 2001) or by the presence of more saline and cool water masses during the Late Pliensbachian (Riding and Hubbard, 1999; McArthur et al., 2000; Bailey et al., 2003; Rosales et al., 2004; Van de Schootbrugge et al., 2005; Arias, 2007). The Late Pliensbachian influxes of cool water into the high-latitude EES could also explain the migration of Boreal faunas southward as far as North Africa (Van de Schootbrugge et al., 2005; Arias, 2007).

At the Almonacid de la Cuba section, positive excursions in  $\delta^{18}O$  are seen through the basal and mid Hawskerense Subzone (Spinatum Zone) and negative excursions through the Mirabile

Subzone, Tenuicostatum Zone (Fig. 3). Assuming that this episode represents a regional signal, positive Hawskerense Subzone excursions may be interpreted as a period where cool and relative saline waters existed on the northeast Spain. This conclusion would be consistent with previously published data measured in belemnites from Yorkshire coast sections (Bailey et al., 2003) and from northern Spain (Rosales et al., 2004), suggesting a probable cooling period coming with a shift toward more saline water from the Late Pliensbachian to the Toarcian.

### 7.2. Large Igneous Provinces, carbon cycle perturbations and sea floor methane hydrates: a subsequent global warming episode?

As it was previously mentioned, the Early Toarcian sedimentary record is characterized by a global episode of enhanced organic carbon deposition (Jenkyns and Clayton, 1997), which is reflected by a negative CIE of ~5‰ in both marine organic and inorganic carbon reservoirs. This negative CIE has been widely, but not universally, interpreted as a major variation in the Early Jurassic carbon cycle (Hesselbo et al., 2000; Van de Schootbrugge et al., 2005; Arias, 2007).

Our belemnite  $\delta^{13}\text{C}$  isotope record (Fig. 3) is one of the most complete long-term records available for the PTB interval, calibrated with ammonites in this area. Bulk  $\delta^{13}\text{C}$  isotope values fluctuate around 0‰ Pee Dee Belemnite (PDB) (from -1 to +2‰ PDB) from the Spinatum Zone up to the middle Tenuicostatum Zone. These moderately steady values are interrupted by few more significant short-term negative excursions (reaching -1‰ PDB) during the Mirabile Subzone. From the upper Mirabile to the Semicelatum subzones,  $\delta^{13}\text{C}$  isotope record shows a relatively rapid increase from -1 to ~4‰. Interestingly, our trends in the  $\delta^{13}\text{C}$  isotope record are consistent with the minimum  $\delta^{13}\text{C}$  isotope data in the Tenuicostatum Zone from the Mochras core, Wales (Röhl et al., 2001; Bailey et al., 2003; Van de Schootbrugge et al., 2005), although the most cited negative CIE described across Europe is recorded in the Falciferum Zone (Jenkyns and Clayton, 1997; Hesselbo et al., 2000; Schouten et al., 2000; Van de Schootbrugge et al., 2005).

Several hypotheses have been proposed to explain the CIE episode, e.g. the release of massive amounts of volcanic  $\text{CO}_2$  related to the onset of the Karoo-Ferrar flood volcanism (Tanner et al., 2004; Beerling and Brentnall, 2007); episodes of thermal metamorphism caused by magmatic intrusions on organic rich sedimentary successions (McElwain et al., 2005; Svensen et al., 2007); or the local recycling of remineralized carbon and its subsequent incorporation into phytoplankton biomass (Van de Schootbrugge et al., 2005).

Another of the most successful theories to explain the negative  $\delta^{13}\text{C}$  excursion invokes the input of large quantities of isotopically light  $\text{CH}_4$  from the dissociation of gas hydrates buried in marine sediments (Hesselbo et al., 2000; Cohen et al., 2004; Kemp et al., 2005, 2006). Dickens et al. (1995) were the first to propose that this massive release of ocean-floor methane could have generated a significant ocean warming episode,

dropping off the thermocline, which may result in a continued dissociation and a “runaway greenhouse” effect.

Beerling et al. (2002), Hesselbo et al. (2000, 2007) and Pálffy et al. (2002) indicated that the onset of the Karoo-Ferrar eruption and the rapid expulsion into the atmosphere of significant quantities of light carbon was not sufficient, as it is unlikely to produce such a large amount of methane in such a very short time. Nevertheless, they indicated that methane hydrates could become unstable under conditions of reduced hydrostatic pressures associated with sea-level rise and warming of bottom waters as a consequence of the intensified rift-related tectonic activity of the Karoo-Ferrar volcanism (Pálffy et al., 2002; McElwain et al., 2005). They suggested a new possibility for the Toarcian event: an alteration in the global thermohaline circulation. This change could have caused an increase in the Tethyan bottom-water temperature by up to 5 °C, triggering the methane hydrates dissociation. All these authors seem to indicate that during the Toarcian a warmer, greenhouse climate may have produced periodic release of gas hydrates into the atmosphere. This proposition raises a new provocative question related to the Toarcian CIE: was the Toarcian CIE the result of a sudden methane release as the consequence of a climate change (greenhouse episode), or was the existence of global warming conditions in the Toarcian the consequence of this methane release?

Nevertheless, both proposals (a first cooling episode followed by a warming episode) could coincide in a possible explanation of the observed changes. First, a cool episode could have favoured the formation of greater gas hydrate deposits (Van de Schootbrugge et al., 2005) during the Pliensbachian. Subsequently, a different triggering mechanism (Cohen et al., 2007) may have destabilized these gas hydrates buried in the sediments, releasing large amounts of isotopically light methane into the water column, and eventually into the atmosphere, turning out the global shift of marine carbon-isotope signatures to more negative values as it was recorded in marine organic and inorganic carbon reservoirs (Jenkyns et al., 2002; Hesselbo et al., 2000, 2007; Röhl et al., 2001).

Although the arguments for correlations between the Pliensbachian-Toarcian extinction episode and some flood basalt events are convincing (as a possible triggering mechanism for the warming episode), it should be noted that the greatest problem is the temporal asynchrony between this catastrophic kill mechanism and the haldoid extinction in the Cordillera Ibérica. Therefore, in spite of a clear evidence of some episode of release of hydrated methane, it is not at all certain that this episode could have much, if any, effect on the ostracod fauna from the Cordillera Ibérica. This new scenario could have been the last act in the PTB ostracod extinction episode, explaining the Lack of recovery of Toarcian haldoid faunas and the decline in diversity described at the end of the Tenuicostatum Zone in the Cordillera Ibérica.

### 7.3. Palaeoceanographic changes

Apart from changes in the biosphere and those of atmospheric composition, the essential role of the ocean circulation



in long-term climate changes should be recognized. By transporting huge amounts of heat, ocean circulation constitutes a major component of the climate system. Any change of the palaeoceanographic configuration, therefore, would modify the latitudinal thermal gradient. Studies based on climate models indicated that during the Early Jurassic, Sea Surface Temperatures (SST) at low latitudes were estimated to be just above 20 °C, whereas high-latitude SSTs were probably about 10 °C (Chandler et al., 1992). This would indicate that the meridional SST gradient during the Early Jurassic was less than half its present value. Interestingly, our  $\Delta\delta^{13}\text{C}$  record denote only a couple of minimum values in the Mirabile Subzone on a long-term Late Pliensbachian-Early Jurassic increase, reaching the maximum value in the Semicelatum Zone, thus indicating a cool episode at the end of the Tenuicostatum Zone.

A decrease in the SST gradient magnitude could have occurred during the Early Jurassic due to the opening of the Hispanic Corridor Passage, an embryonic seaway between the eastern Pacific and western Tethyan oceans (Boomer and Ballent, 1996; Damborenea, 2000; Aberhan, 2001; Arias, 2006). The opening of this Central America seaway (since the Late Pliensbachian) would have produced a total reorganization of the superficial ocean circulation in the western corner of the

EES because of the termination of a “pre-Gulf Stream” Current and the beginning of a westward flow of warm and saline Tethyan water, driven by equatorial easterly winds (Arias, 2007). This palaeogeographic change stopped the warm water transportation to northeastern EES and would have also decreased the salinity of the Western Tethys Sea, diminishing deepwater formation in the EES and producing drastic variations of water temperatures in many areas around the EES (Arias, 2007).

A global cooling episode would be also responsible for the general migration pattern of boreal faunas towards the Tethys. One example of this phenomenon would be the sudden change of the migration pattern of the ostracod fauna at the end of the Pliensbachian (Arias, 2007). Early Jurassic ostracod migrations, which followed a clockwise circulation in the eastern side of the EES during the Pliensbachian (with a leading northeast–southwest movement and the frequent arrival of Tethyan faunas into the central and western parts of the EES), changed in the Early Toarcian with a leading east–west movement and the end of the Tethyan ostracod flux into the EES (Arias, 2006, 2007). The opening of the Hispanic Corridor could have also distorted the ostracod round migration described in the EES, because of its role in the dramatic

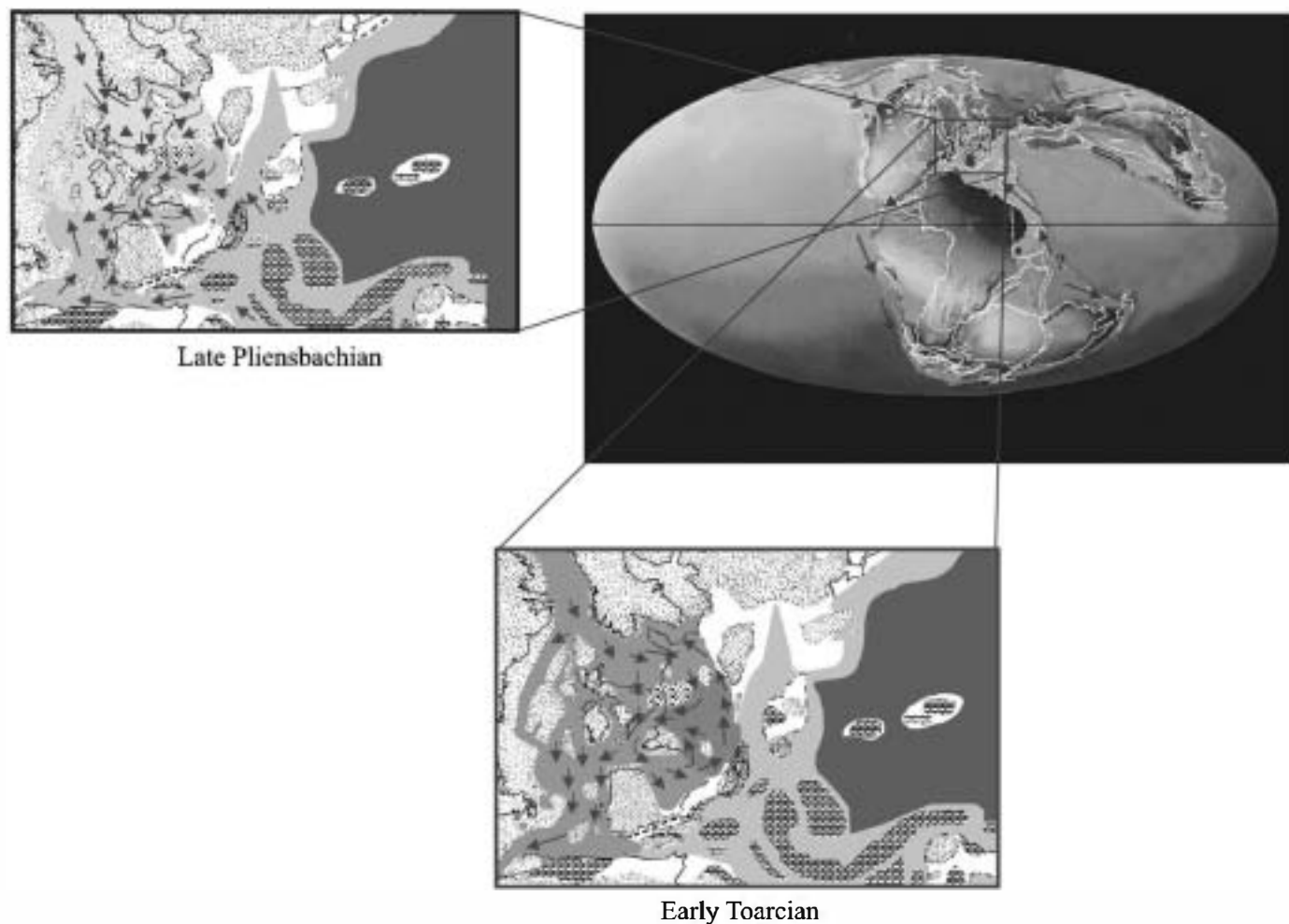


Fig. 8. Patterns of ostracod migration in the European Epicontinental Sea (palaeogeography after Scotese (1991)) and Panthalassa oceans during the Early Toarcian (modified from Arias, 2006, 2007). Black arrows illustrate ostracod migration patterns.



weakening of the north-south SST gradient and in the reorganization of surface ocean currents as well as the disruption of the deep-water circulation (Fig. 8).

#### 7.4. Faunal composition and environmental changes

Low temperatures are as lethal as excessively high temperatures: global cooling episodes usually lead to the loss of high latitude habitats and the general migration of boreal faunas toward the Equator. The low temperatures resulting from this event would have affected the ostracod fauna at the beginning of the Toarcian, because such a cold episode would have favoured those ostracod species that were well adapted to temperate or warm water conditions, being particularly severe for those ostracods that could not cope with this thermal change. The Early Toarcian ostracod mass extinction in the Cordillera Ibérica shows the characteristic succession of events in a mass extinction episode (Harries and Kauffman, 1990; Harries, 1993).

This event would be initiated by an extinction phase during which diversity falls rapidly (affecting the generalists), followed by a survival or lag phase of minimal diversity (with the dominance of disaster and opportunists) and then, a recovery phase of rapid diversity increase (with the dominance of ecological generalists). Ecological ostracod assemblages may consist of high diversity *K*-strategy species (e.g. large sizes, complex and specialized taxa, such as Healdioidea or Cytheroidea) and in minor proportion, low-diversity *r*-strategy species (small-sized ecologic generalists as Bairdioidea or Cypridoidea) (Fig. 6). Bodergat et al. (1991, 1998) initially recognized this type of adaptative strategies among Toarcian ostracods. They considered that one species of the genus *Ogmoconcha*, *O. amalthei*, could be an example of such opportunistic species.

A major environmental perturbation, as was a global cooling episode, may have modified the ecosystem and may have eliminated specialized niches of *K*-strategy ostracod species and some of the *r*-strategists, resulting in a patent extinction episode. This progression might product a regional segregation of all large and complex species of ecological generalists (healdioids). First ecological opportunists to recover would be groups of small size and low-oxygen-tolerant species as may be the bairdioids, cytherellids and cypridooids (Whatley et al., 1994), which would be constantly represented in pre-extinction environments at the PTB. They would occupy minor ecological roles (small populations in locally distributed areas), dominating during the beginning of stressed conditions. Cytherelloidea would be one of these groups of most stress-tolerant ostracod species, as well as the first opportunist to thrive after the environmental change. The extensive niche of these organisms would allow adaptation to variable environmental conditions and, hence, would permit the survival of these stress-tolerant species (Boomer and Whatley, 1992; Whatley et al., 1994; Arias and Whatley, 2004). Without competitors, these species rapidly increased their populations exponentially. *Cytherella* and *Cytherelloidea* would symbolize this type of ecological strategy.

The recuperation of stable environmental conditions, the increase of ecological competition and niche development and the restoration of well-stratified water masses, would permit the recovery of new specialized *K*-strategists, replacing the opportunist species and disaster specialists, which became rare during the ecosystem recovery. The restoration of highly diverse ostracod assemblages (mainly formed by large cytheroids *Kinkelina* or *Ektypocythere*) would represent the full recovery of the ecological sequence during the Tenuicostatum-Serpentinum zones transition after this major environmental perturbation (Fig. 6).

However, this proposal is only a very simplified scenario. Another aspect to consider is the phenoplasticity (the response of a genotype to environmental changes). Among ostracods, phenoplasticity depends on ontogenic variations and environmental factors (Bodergat et al., 1991, 1998). High levels of plasticity occur in aquatic habitats characterized by factors that vary over small spatial or short-term temporal scales. An environmental change (such as ocean temperature change) could be the main factor which induced a significant plastic variation in the population. Plasticity could give an explanation for the colonization of species in habitats with different degrees of disturbance. Some species can adopt different types of strategies (*K* or *r*) according to morphological traits adapted to the physical environment. Evolutionary theory dictates that all species would follow an *r*- and *K*-strategy simultaneously but environmental conditions force them into one alternative or another. For example, Bodergat et al. (1991) indicated that *K. sermoensis* (Apostolescu, 1959) could have adopted this strategy, shifting in a "*r* to *K* continuum" toward a *r*-strategy. As a result, the plasticity would give it advantages that explain its ability to colonize different types of habitats.

## 8. Conclusions

One of the most prominent faunal groups cited in identifying the PTB mass extinction, the Ostracoda, experienced a gradual extinction episode across the Late Pliensbachian-Early Toarcian time interval, being particularly intense during the earliest Toarcian in the Cordillera Ibérica. The complete disappearance of healdioids from the Almonacid de la Cuba section at the Mirabile-Semicelatum subzones transition is the commencement of the extinction event, which is followed by a decrease in diversity and abundance of all ostracod groups during the Semicelatum Subzone, finishing with a major faunal turnover which is characterized by the dominance of Cytheroidea during the Serpentinum Zone.

In addition, this research has brought some new facts to light about a new plausible causal mechanism to explain the ostracod extinction event related to a new reorganization of surface and deep-water circulations as a result of the opening of the Hispanic Corridor. These palaeoceanographic changes could have transformed surface and deep-water masses, which in turn cooled and destabilized the marine ecosystem. However, because a good hypothesis for the extinction of the ostracods should be general enough to explain the whole extinction

recorded at the beginning of the Toarcian, it seems unreasonable to believe that only one process could have driven the extinction of the belemnites and other species. Other proposed mechanisms, e.g. the sudden eruption of a large igneous province (Karoo-Ferrar) and the associated SO<sub>2</sub>, CO<sub>2</sub> and methane emissions could have been involved in the PTB ostracod extinction, particularly in the last part of the faunal crisis, during the recovery stage.

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