Diversity dynamics of Early Jurassic ostracods of the Cordillera Ibérica (Spain) and the re-evaluation of the Pliensbachian–Toarcian mass extinction

Carmen Arias

Abstract: The extinction and recovery of Ostracoda at the Pliensbachian–Toarcian (P–T) boundary are analyzed based on a database of taxonomically revised Pliensbachian to Toarcian transition ostracod assemblages. In contrast to earlier assertions, the results of this study indicate that ostracod extinction rates were significant in comparison with other marine invertebrates. An extinction rate of 54% has been calculated for upper Pliensbachian ostracod species occurring in more than one section. Diversification took place in the latest Pliensbachian (*Spinatum* Zone) and early Toarcian (*Tenuicostatum* Zone), whereas diversity decrease occurred in the middle early Toarcian (*Strangewaysi* Subzone, *Serpentinus* Zone). This notable diversity decline in the early Toarcian corresponds to a global mass extinction time, whose peak has been documented in the *Tenuicostatum* Zone. Meanwhile, the ostracod mass extinction occurred within the *Serpentinus* Zone and was followed by radiation and recovery in the succeeding *Bifrons* Zone. Similar diversity changes of ostracods are observed in other European areas, although in the Cordillera Ibérica, the demise began later. Many aspects of this event are still debated, and there is no common cause or single set of climatic or environmental changes common to this event. The supposed extinction-causing environmental changes resulting from anoxia episodes are unclear and are unlikely to have been of sufficient intensity or geographic extent to cause this global extinction. In this paper, the decrease in marine species diversity is explained by a new palaeoceanographic scenario, in which a rapid global cooling episode is regarded as the ultimate cause.

Résumé : L’extinction et le rétablissement des ostracodes à la limite Pliensbachien–Toarcien (P–T) sont analysés à la lumière d’une base de données sur des assemblages d’ostracodes caractéristiques de la transition du Pliensbachien au Taorcien ayant fait l’objet d’une révision taxonomique. À l’encontre d’assertions précédentes, les résultats de cette analyse indiquent que les taux d’extinction des ostracodes étaient importants comparativement à ceux d’autres invertébrés marins. Un taux d’extinction de 54 % a été calculé pour des espèces d’ostracodes du Pliensbachien tardif présents dans plus d’une section. Des diversifications se sont produites au Pliensbachien final (zone à *Spinatum*) et au Toarcien précoce (zone à *Tenuicostatum*), alors qu’une diminution de la diversité a eu lieu au milieu du Toarcien précoce (sous-zone à *Strangewaysi*, zone à *Serpentinus*). Cette diminution notable au Toarcien précoce correspond à une période d’extinction massive à l’échelle planétaire dont l’apogée a été documentée dans la zone à *Tenuicostatum*, alors que l’extinction massive des ostracodes est observée dans la zone à *Serpentinus* et est suivie par le rayonnement et la reprise dans la zone suivante, à *Bifrons*. Si des variations semblables de la diversité des ostracodes sont observées dans d’autres régions d’Europe, le déclin observé dans la Cordillera Ibérica a débuté plus tard. De nombreux aspects de cet évènement font toujours l’objet de débats, et il n’existe aucune cause commune ou ensemble unique de changements climatiques ou environnementaux pouvant l’expliquer. Les changements environnementaux présumés découlant d’épisodes d’anoxie ne sont pas bien documentés, et il est peu probable que leur intensité ou étendue géographique aient été assez importantes pour causer cette extinction d’envergure planétaire. Un nouveau scénario paléoocéanographique faisant appel à un épisode de refroidissement planétaire rapide est présenté pour expliquer la diminution de la diversité des espèces marines.

[Traduit par la Rédaction]

Introduction

The proposal that mass extinction events have occurred at regular intervals (with a regular spacing of 26.2 million years) was derived from statistical examinations of family- and genus-level compilations of global data on marine animals (Raup and Sepkoski 1984, 1986; Sepkoski and Raup 1986; Sepkoski 1989, 1996). As a result of the broad scope of most mass extinction research, most papers on the subject have concentrated on one of the “big five” mass extinctions

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(end-Ordovician, Late Devonian, Permian–Triassic, Triassic–Jurassic, or Cretaceous–Tertiary mass extinctions). Only a few papers deal with lesser known mass extinctions, such as the early Toarcian extinction event (Hallam 1961, 1987; Jenkyns 1988; Hori 1993; Little and Benton 1995; Aberhan and Fürsich 1997, 2000; Hallam and Wignall 1997, 1999; Harries and Little 1999; Guex et al. 2001; Wignall 2001; Jenkyns et al. 2002; Pálfy et al. 2002; Vörös 2002; Ruban 2004).

This second-order mass extinction took place during the Pliensbachian and Toarcian stages of the Early Jurassic. First recognized as a minor Pliensbachian peak in the global extinction rate, particularly among benthic marine invertebrates (Sepkoski 1982; Raup and Sepkoski 1984, 1986; Hallam 1986), it was alternatively interpreted as a regional response to an early Toarcian anoxic event. Hallam (1986) argued that this low-level event took place, not at the Pliensbachian–Toarcian (P–T) boundary, but in the early Toarcian. Subsequently, several detailed studies established it as a global long-term event spanning five successive ammonoid zones (Little and Benton 1995). Little and Benton (1995) analyzed the time distribution of global family extinctions and found that there was in fact an extended episode of extinction during the late Pliensbachian and early Toarcian, in which 33 of the 49 families disappeared between the *Margaritatus* and *Bifrons* zones. Little (1996) and Harries and Little (1999) showed a significant extinction event during the early Toarcian, documented in the *Tenuicostatum* Zone. Almost all research shows that a severe crisis affected different fossil groups at the P–T boundary and lasted during the time interval represented by the *Tenuicostatum* Zone. Global data on all marine biota suggest the beginning of their decimation occurred at the end of the *Tenuicostatum* Zone (Little and Benton 1995; Pálfy et al. 2002). Although the majority of the family extinctions occurred within the Boreal area, some extinctions also took place in the Tethyan and Austral realms (Little and Benton 1995; Arias 2006).

The late Pliensbachian – early Toarcian (Early Jurassic) ostracod mass extinction is one of the most significant events in geological history. Although it is often described as a "small" mass extinction in relation to such great biotic crises as the Permian–Triassic or Cretaceous–Tertiary extinctions, the disappearance of the suborder Healdioidea characterizes one of the major biotic crises in the Ostracoda record (Whatley and Stephens 1976; Lord 1982; Herrig 1988; Whatley 1988, 1990; Boomer 1990, 1992; Arias 2000).

Although the P–T boundary is less well known in terms of ostracods than other fossil groups (Arias 2000), the data available on the late Pliensbachian and early Toarcian ostracods are sufficient to allow a short assessment of the general trends of ostracod assemblages. This is particularly true for the late Pliensbachian, for which there is an extensive literature, but earliest Toarcian ostracods are relatively little known. The reason primarily is because *Tenuicostatum* Zone deposition is not represented in many geological sections, and also as a consequence of very poorly preserved ostracod assemblages recovered at the boundary. The majority of published accounts of Lower Jurassic ostracods are from northwest Europe and include contributions from Britain, France, Germany, Switzerland, and Denmark. Relatively little is known about ostracod assemblages from southern Europe (Portugal, Spain, and Italy), and there are so few data available from the Americas and North Africa that the published information has failed to provide a complete record of the P–T boundary ostracod succession (Riegraf 1984, 1985; Bodergat and Donze 1988; Boomer 1990, 1992; Bodergat et al. 1991; Boomer and Whatley 1992; Harloff 1993; Harloff and Jäger 1994; Boomer et al. 1998; Arias 2000).

This often-called "minor" mass extinction has been very well recognized for many other fossil groups, including bivalves, foraminifers, brachiopods, ammonites, and dinoflagellates (Hallam 1986, 1987; Boomer 1990, 1992; Hori 1993; Vörös 1993, 1995, 2002; Bassoullet and Baudin 1994; Little and Benton 1995; Aberhan and Fürsich 1997, 2000; Hallam and Wignall 1997, 1999; Bucefalo-Palliani and Riding 1999, 2000, 2003; Harries and Little 1999; Arias 2000; Guex et al. 2001; Macchioni 2001; Wignall 2001; Bucefalo-Palliani et al. 2002; Jenkyns et al. 2002; Macchioni and Cecca 2002; Morard et al. 2003; Ruban 2004; Ruban and Tyszka 2005; van de Schootbrugge et al. 2005).

This study documents regional geographic patterns of extinction and recovery in ostracods in the Pliensbachian and Toarcian of the Cordillera Ibérica. Ostracoda are especially useful microfossils in such studies due to their relatively high diversity, widespread occurrence, and a high preservation potential. Particularly, this study emphasizes the intensity of the early Toarcian ostracod extinction and the pace of recovery, the ecological selectivity of ostracod extinctions, and the geographic patterns of ostracod extinction and recovery. In addition, it has made a comparison of the results of this research on ostracod assemblages with other benthic invertebrate groups.

Geological setting

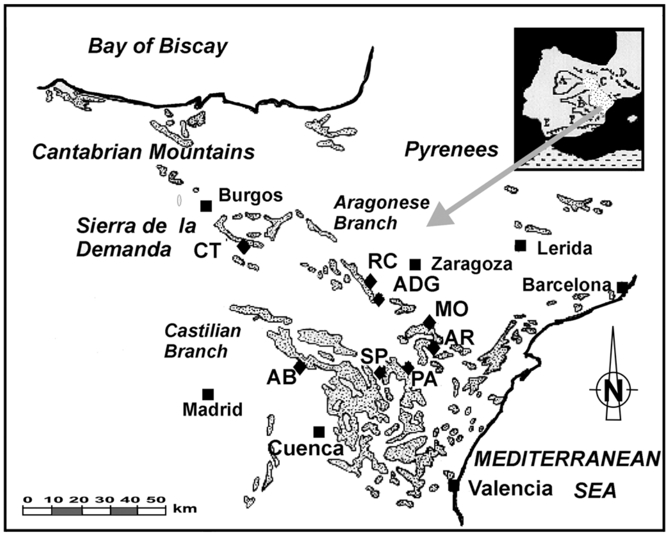
The Cordillera Ibérica was a northwesterly trending fold–thrust belt sited on the western margin of the Tethys Ocean. During the Early Jurassic, this area was characterized by the development of a system of shallow platforms on the progressively submerging Iberian block. Intracratonic extensional faulting controlled the paleogeographic evolution of these platforms (Fig. 1).

The Lias (Lower Jurassic) stratigraphy and lithology of the Cordillera Ibérica have been described by Goy (1974); Goy et al. (1976); Gómez and Goy (1979, 1981, 1998, 1999); Comas-Rengifo (1985); and Gómez et al. (2003). In the present study, the part investigated concerns the upper Pliensbachian Barahona Formation and the lower Toarcian Turmiel Formation (Fig. 2).

The bioclastic limestone of the Barahona Formation consists of wackestone to packstone, in some places mudstone and grainstone, with intercalations of marl. This unit is organized into aggradational shallowing-upward sequences that were deposited on a shallow platform, frequently influenced by storms (Gómez 1991). This unit covers a considerable part of the upper Pliensbachian *Margaritatus* and *Spinatum* zones (Comas-Rengifo 1985) and represents a minor regressive episode of a major transgressive phase developed during the early Pliensbachian – middle Toarcian (Gómez and Goy 2005).

During the time represented by the *Tenuicostatum* Zone (Fig. 2), a new generalized transgressive sub-cycle took place (LJ3–2), with a maximum water-deepening event at the base

Fig. 1. Studied sections of the Pliensbachian–Toarcian transition in the Cordillera Ibérica, NE Spain: AB, Ablanquejo; ADG, La Almunia de Doña Godina; AR, Ariño; CT, Barranco de las Alicantas; MO, Moneva; PA, Perales de Alfambra; SP, Sierra Palomera; RC, Ricla.



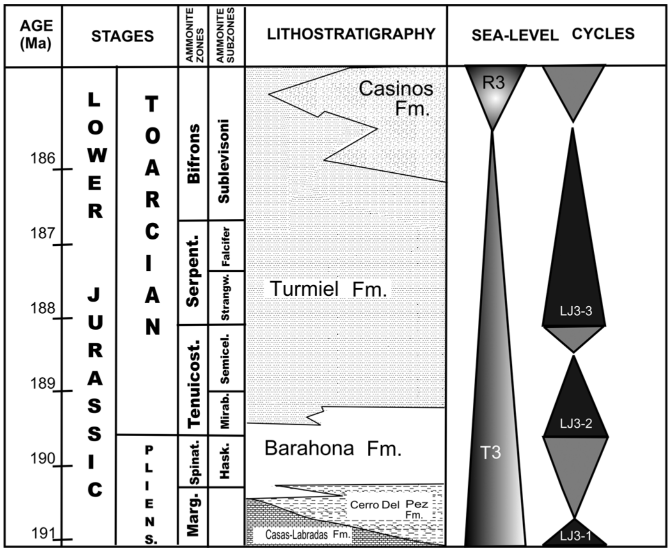
of the *Semicelatum* Subzone. This transgressive interval is represented by the alternation of marls and mudstone carbonates of the Turmiel Formation. The succession exhibits a cyclic organization with sets of deepening- and shallowing-upward sequences (Goy et al. 1997; Comas-Rengifo et al. 1996, 1999; Gómez and Goy 2000). No deposition of "black shale" took place in this area, i.e., no bottom anoxia (Goy et al. 1997). This transgressive episode ended with a regressive period near the boundary between the *Tenuicostatum* and the *Serpentinus* zones (Gómez and Goy 2005). A second transgressive sub-cycle developed from the lower part of the *Serpentinus* Zone up to the *Bifrons* Zone and represented the maximum transgression phase (Gómez and Goy 2000). This transgressive unit consists of deepening-upward sequences composed of rhythms of marl and carbonate within the Turmiel Formation (Gómez and Goy 2005).

Ostracods were sampled from eight sections and 113 levels situated in the Cordillera Ibérica (Fig. 1), four situated in the Aragonese Branch (La Almunia de Doña Godina, Ariño, Moneva, and Ricla), three in the Castilian Branch (Ablanquejo, Perales de Alfambra, and Sierra Palomera), and one at the Sierra de la Demand (Barranco de las Alicantas). These samples embrace the stratigraphic range of both formations, from the *Spinatum* ammonite zone in the upper Pliensbachian, to the *Sublevisoni* ammonite subzone in the *Bifrons* ammonite zone of the lower Toarcian. Samples used in this study are almost exclusively from mudstones and marls (Fig. 2).

Materials and methodology[2]

Lower Jurassic ostracods of the Cordillera Ibérica are moderately well studied. The first complete revision was made by Arias (1995), followed by works of Arias (1997) and Arias and Comas-Rengifo (1992). The most complete and taxonomically revised data on stratigraphic distribution of Spanish ostracods have been presented by Arias (1995) and Arias and Lord (1999*a*, 1999*b*). These sources have been used to compile the diversity data, with some revisions and stratigraphical corrections. These data were revised, checked, and amended for possible synonymy and for stratigraphic occurrences.

Fig. 2. Stratigraphy and biostratigraphy of the Lower Jurassic deposits of northeast Spain and sea-level cycles (T, transgression; R, regression) (after Gómez and Goy 2005). Fm., Formation. Pliens., Pliensbachian; Marg., *Margaritatus*; Spinat., *Spinatum*; Hask., *Hawskerense*; Tenuicost., *Tenuicostatum*; Mirab., *Mirabile*; Semicel, *Semicelatum*; Serpent., *Serpentinus*; Strangew., *Strangewaysi*.



Wherever possible, the elements, valves and carapaces (v = 1 and c = 2), were counted ($n = 14113$; n = number of valves + 2× number of carapaces), and sorted into species; 59 species belonging to 39 genera were distinguished. An additional 123 highly abraded ostracods were summarized into six taxa at the genus level because their preservation prevented determination to the species level. These taxa from poorly preserved material were excluded from further analysis (Fig. 3).

Diversity, extinction, and turnover rates were plotted against the time scale of Gradstein et al. (1995) and de Graciansky et al. (1998), and ammonite biostratigraphy (Goy 1974; Comas-Rengifo 1985). The duration of the ammonite zones was uneven, thus making average values just not reasonable, but this arbitrary procedure allows a rough estimation of turnover changes.

Diversity was measured as species richness (Simpson and Shannon–Weaver indices) and evenness, which are based on the proportional abundance of species (Yule 1944; Magurran 1988). The Simpson index, which is affected by the 2–3 most abundant species, and the Shannon–Weaver index, which is more strongly affected by species in the middle of the rank sequence of species, are the most commonly employed measures of diversity (Shannon and Weaver 1949;

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[2] Most of the text in this section is taken from Margaleff (1981) and Magurran (1988). It has been translated from the original Spanish and then modified by CA.

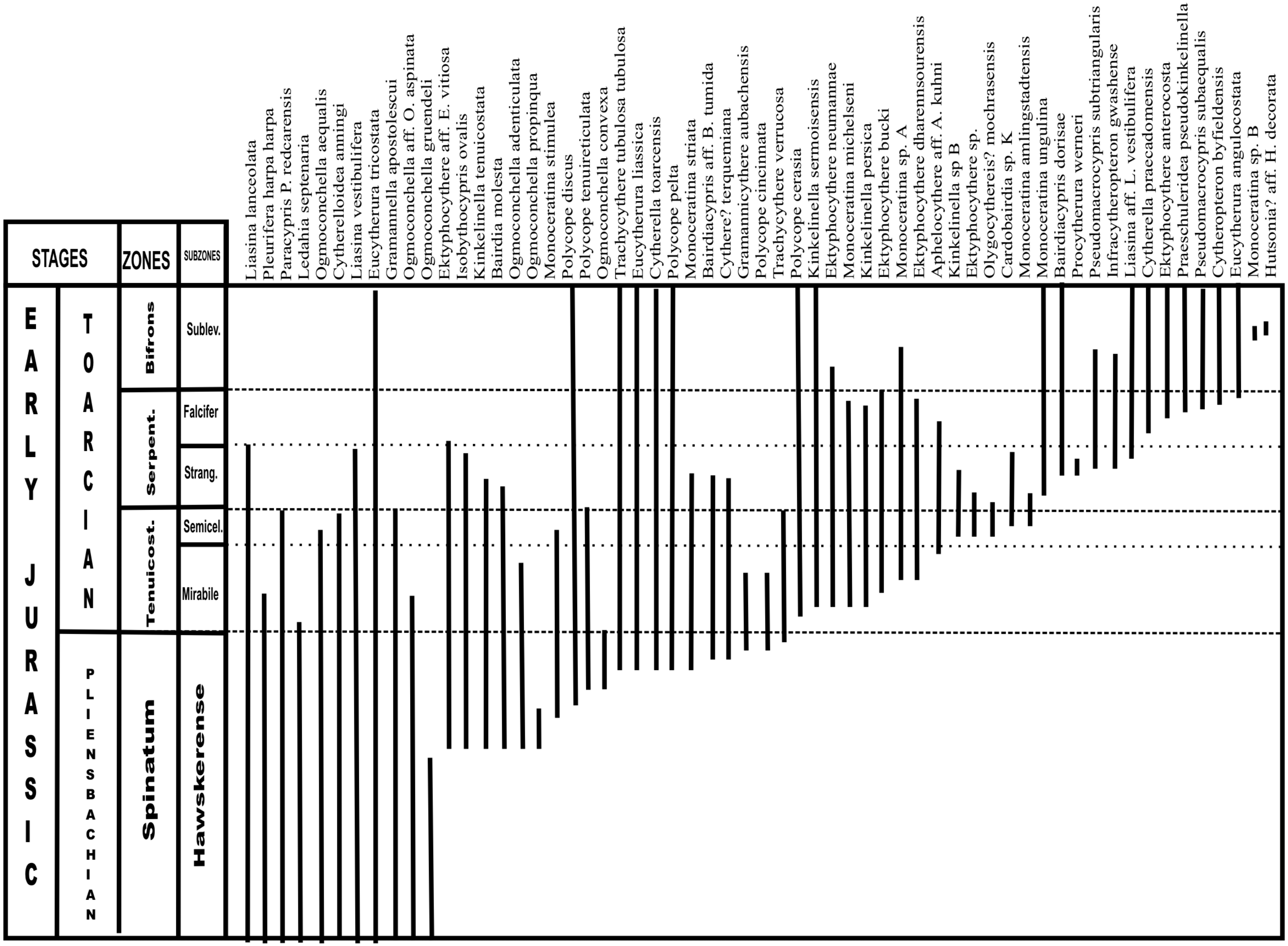


Fig. 3. Stratigraphical ranges of ostracods across the late Pliensbachian – early Toarcian boundary in the Cordillera Ibérica (Spain). Tenuicost., *Tenuicostatum*; Semicel, *Semicelatum*; Serpent., *Serpentinus*; Strang., *Strangewaysi*; Sublev., *Sublevisoni*.

Michelsen 1975; Pielou 1975; Pokorný 1978; Blondel 1986; Odum 1989).

Simpson's Index measures the probability that two individuals randomly selected from a sample will belong to the same species. In this paper, the inverse of Simpson's index (1/D) is used. The inverse of the Simpson index (D′) was calculated as follows:

$$\mathrm{D}' = N(N-1) / \sum n(n-1)$$

where N is the total number of individuals of all species and n is the total number of individuals of a particular species. The value of D′ ranges between 0 and 1 and it starts with 1 as the lowest possible figure. This value would represent a community containing only one species. "The higher the value, the greater is the diversity" (Margalef 1981, p. 367; Magurran, 1988, pp. 107, 108, 239).

Dominance is measured with entropy and is the probability that two individuals drawn randomly from a sample are the same species. The Shannon Index (H) is used in this study to measure dominance (Shannon and Weaver 1949). "The Shannon diversity index (H) is commonly used to characterize species diversity in a community. Like the Simpson index, the Shannon index accounts for both abundance and evenness of the species present" (Magurran 1988, p. 107). The proportion of species i relative to the total number of species (p_i) is calculated and then multiplied by the natural logarithm of this proportion (ln p_i). The resulting product is summed across species, and multiplied by (–1):

$$H = -\sum p_i \ln p_i$$

If there is only one species in the community, the Shannon Index will equal zero. Therefore, the closer the measured value is to zero, the more dominant a particular species is (Daget 1979; Schneider 1988; Odum 1989).

"Another index used was Shannon's equitability (E_H), which can be calculated by dividing H by $H_{\max}$; and S is the total number of species in the community. Equitability assumes a value between 0 and 1 with 1 being complete evenness" (Magurran 1988, p. 108; Margaleff 1981, p. 369):

$$E_H = H / H_{\max} = \ln S$$

Another approach for investigating the effect of the Pliensbachian–Toarcian boundary event on ostracod fauna was by means of the quantitative indices proposed and described by Lasker (1978) and Sepkoski (1978):

$$\text{Rate of origination } r_o = (1/D) \times (S/t)$$

$$\text{Rate of extinction } r_e = (1/D) \times (E/t)$$

Where D indicates the number of species present in a specific interval, S is the number of species originations, E is the number of species extinctions, and t is the time interval (in Ma).

Other indices, which have been used in the present paper, were from Lasker (1978):

$$\text{Rate of diversification } r_d = r_o - r_e$$

$$\text{Rate of recovery } r_d = r_o + r_e$$

Diversification occurs after the survival phase is complete. But the rate of recovery, in this paper, is defined as the point at which the rate of new originations per taxon peak and begin to drop off. Both indices show when the main extinction episode took place. They are calculated, respectively, to establish the diversity of ostracods in the latest Pliensbachian and in the early Toarcian. Regrettably, adequate data on the precise temporal and spatial distribution of first appearance datum (FAD) and last appearance datum (LAD) of species, as well as additional age occurrences, were not always available. As a result, all FADs are considered here to be Pliensbachian. FADs, LADs, and species unaffected through the Pliensbachian–Toarcian were also determined in percentages.

Results

In this paper the extinction, survival, and origination rates at species level across the P–T boundary have been measured (Fig. 3). There are 59 species known in the early Toarcian, of which three species have the LADs in the late Pliensbachian. From the early Toarcian, 56 species are documented, with one species representing a Lazarus taxon (*Monoceratina michelseni*). Twenty-eight species (48%) cross the P–T boundary event, including all major ecological groups, from 31 species (53%) that have been described in the late Pliensbachian. Consequently, a decrease in species diversity is not evident across the P–T boundary. The actual decrease took place during the *Tenuicostatum–Serpentinus* transition, when 16 species became extinct (27%), while six species are encountered in the *Strangewaysi* Subzone of the *Serpentinus* Zone for the first time (10%). A new increase at the end of the *Falcifer* Subzone of the *Serpentinus* Zone took place, where 21 species (35%) passed through the *Serpentinus–Bifrons* boundary, eight species (14%) disappeared, and two species (3%) appeared for the first time.

The analysis displays a decrease for Healdioidea from the late Pliensbachian to the early Toarcian, until its total disappearance at the end of the *Tenuicostatum* Zone. The last species of Healdioidea (*Ogmoconchella aequalis*) disappears at the end of the *Semicelatum* Subzone. Subsequent to the disappearance of metacopids, Cytheroidea becomes dominant in the ostracod assemblages. Cytheroidea are characterized by only 19 species in the *Tenuicostatum* Zone (32%) and 25 species (42%) in the *Serpentinus* Zone.

Consequently, species diversity of ostracods did not change dramatically in the Cordillera Ibérica during the P–T transition (Figs. 4*a*, 4*b*). After the great diversification in the late Pliensbachian – earliest Toarcian (*Semicelatum* Subzone, *Tenuicostatum* Zone), a severe diversity decline occurred in the next ammonite zone, the *Serpentinus* Zone (*Falcifer* Subzone), subsequent to the disappearance of the healdioids at the end of the *Semicelatum* Subzone. In the *Bifrons* Zone a new gradual diversification took place, although it did not compensate for the previous decline. Consequently, there is a steady decrease in taxonomic diversity from the end of the *Semicelatum* Subzone to the end of the *Strangewaysi* Subzone, and a steady even increase to the *Sublevisoni* Subzone (Figs. 4*a*, 4*b*). Data from the Mochras Borehole, Wales, by Boomer (1990) points to a significant gradual turnover at the P–T transition. However, in northeast Spain, the duration of this event covers a long quiet interval,

Figs. 4. Plot of species diversity measured by Shannon–Weaver and Simpson indices, and equitability index per studied sample. The horizontal scales are the sampled levels and the ammonite zonation. Sections of Ablanquejo (AB), La Almunia de Doña Godina (ADG), Ariño (AR), and Barranco de las Alicantas (CT).

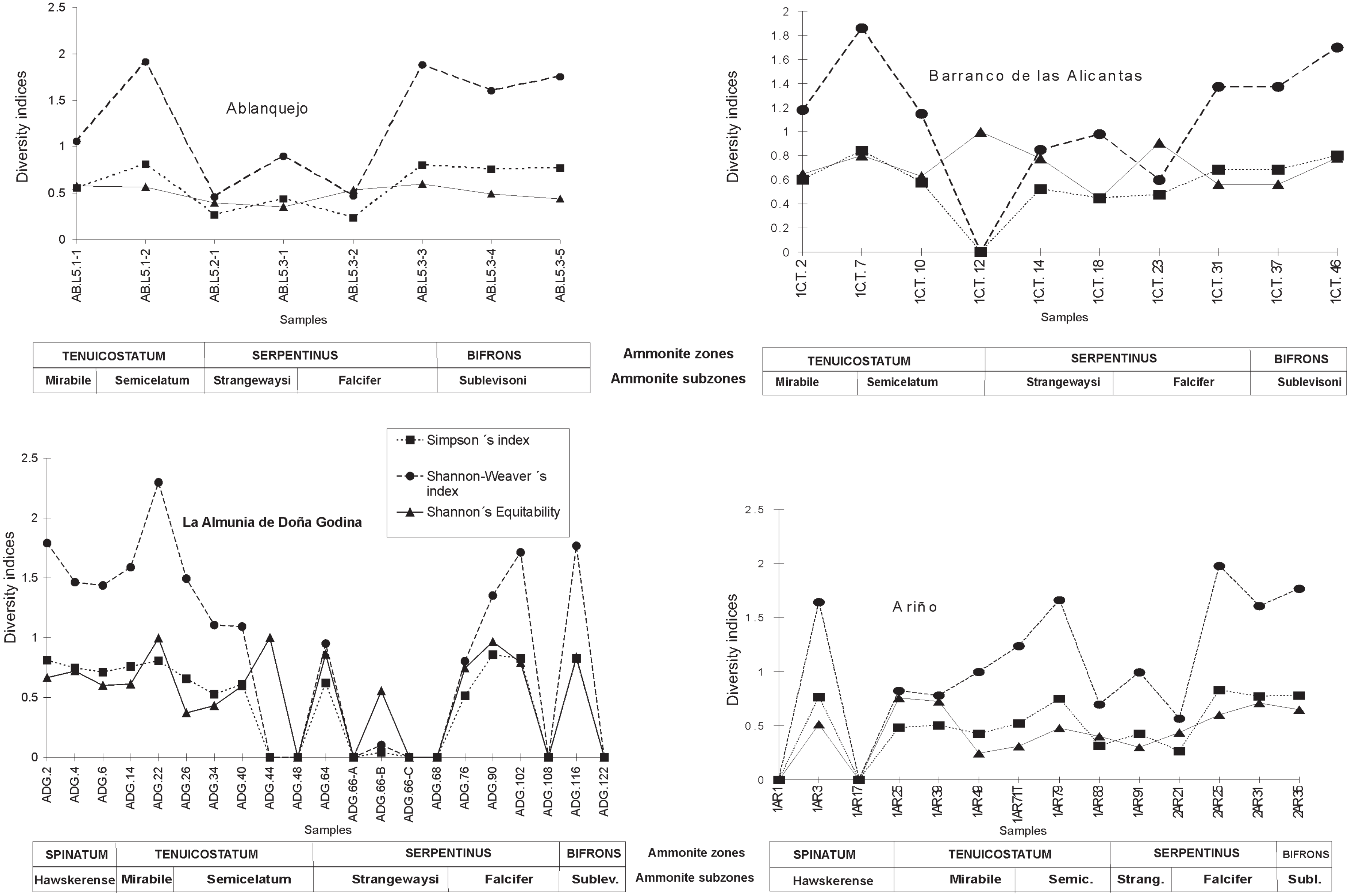


Fig. 4 (*concluded*). Sections of Moneva (MO), Perales de Alfambra (PA), Sierra Palomera (SP), and Ricla (RC).

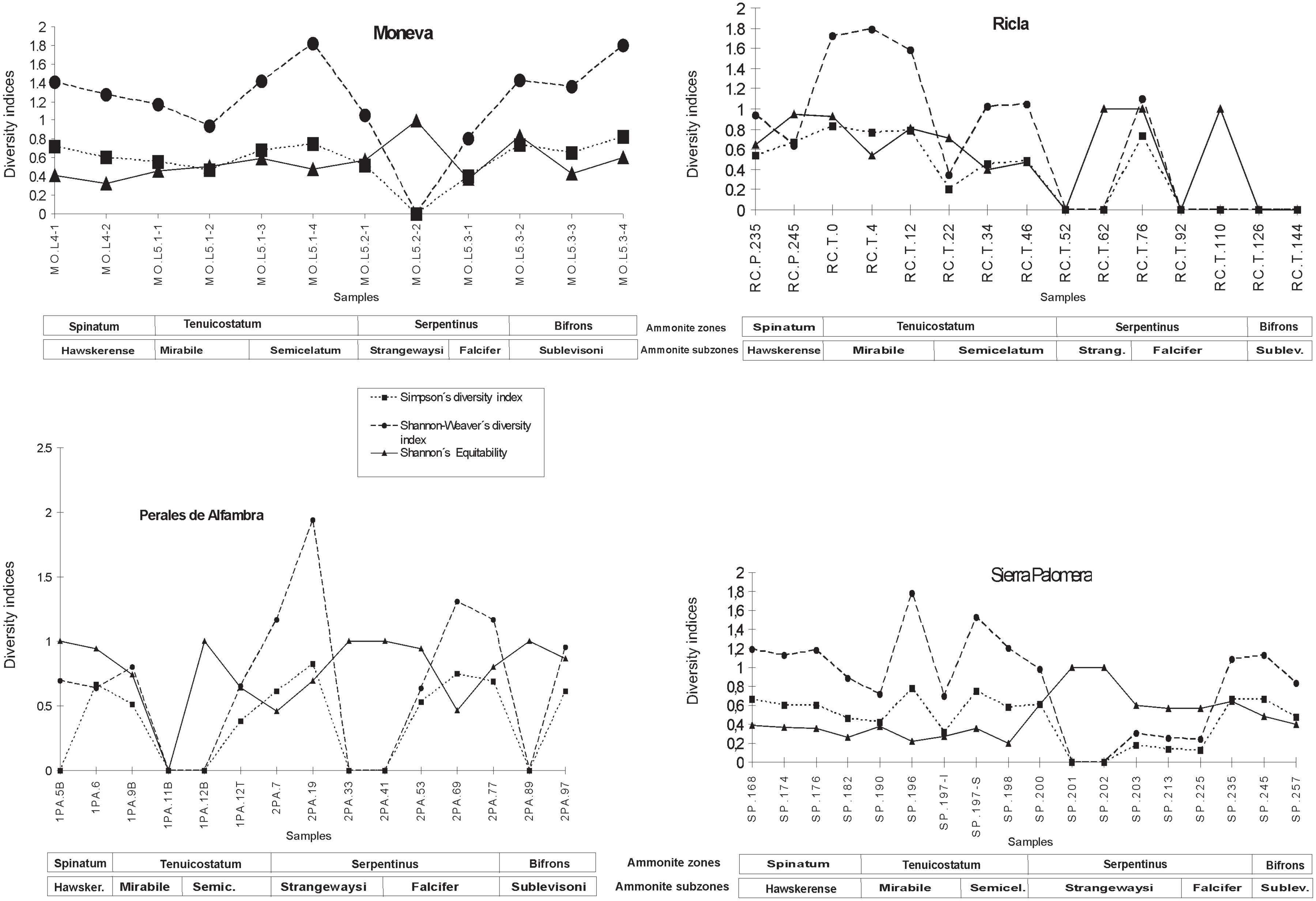
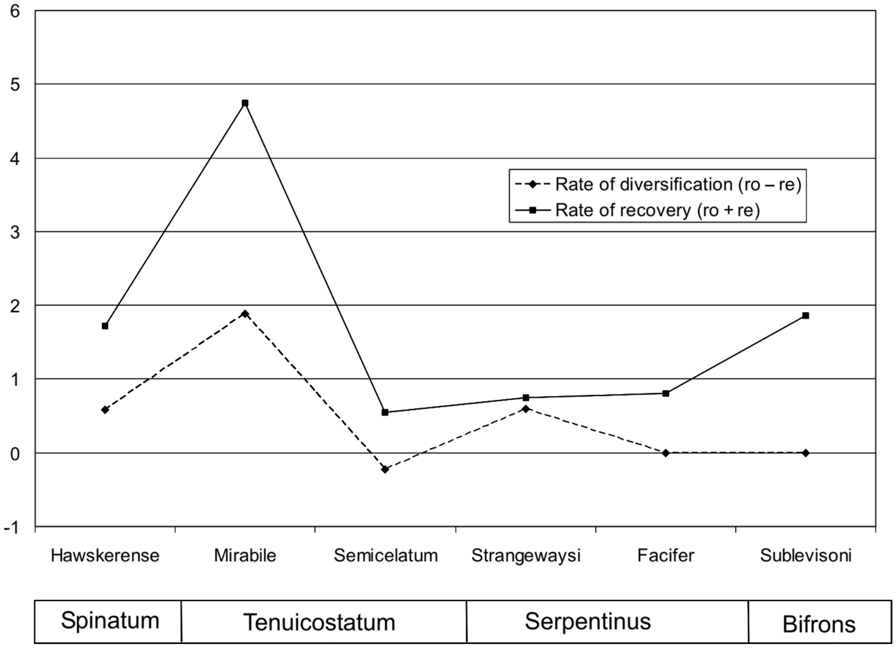


Fig. 5. Patterns of diversification of ostracods at specific levels in the late Pliensbachian and early Toarcian in terms of rate of diversification and rate of recovery recorded for each Early Jurassic ammonite subzone and zone.



represented by the *T–S* zone transition (*Semicelatum–Strangewaysi* subzones) in the early Toarcian.

As a result, the most outstanding feature of the regional ostracod history is the early Toarcian demise. The origination and extinction rates can help us to understand the causes of such turnovers (Fig. 5). Late Pliensbachian diversification is followed by decrease both of origination and extinction during the time of the *Tenuicostatum* Zone. Both values (origination and extinction rates) start to increase from this zone, but the rate of recovery continues to rise, while the diversification does not. Therefore, the early Toarcian demise of ostracods corresponded to collapse of both diversification and recovery rates.

An analysis of events connected with disappearance of fossils should always take into account the so-called Lazarus taxa effect (Flessa and Jablonski 1983; Jablonski 1986; Wignall and Benton 1999; Twitchett et al. 2000; Fara 2001). The Lazarus effect represents a significant gap in any taxon's range. Among Early Jurassic ostracods of the studied region only one Lazarus taxon has been found, *Monoceratina michelseni*. The interval of its absence covers the *Semicelatum* Zone, early Toarcian in the Cordillera Ibérica. It is evident that such a negligible Lazarus effect could not significantly influence the above-mentioned results.

Figs. 4*a* and 4*b* show Pielou's evenness and the Shannon–Weaver and Simpson diversity indices for each section. There is a trend of decreasing evenness with increasing species richness in the diversity study, caused by a large influx of the dominant species. There are no significant differences in evenness between late Pliensbachian and early Toarcian samples (the curve of evenness stays low for most of the studied period, except for a marked drop in the *Strangewaysi* Subzone and slightly elevated values in the *Falcifer* Subzone). Shannon–Weaver and Simpson diversity indices differed significantly between the P–T and the *T–S* transitions (high diversity in the first and low diversity in the last). The Shannon–Weaver diversity index shows minimum values during the *Falcifer* Subzone, following a slight increase during the *Strangewaysi* Subzone and then the diversity is on the rise again. The curve of Simpson's Index closely mirrors that of the Shannon–Weaver's Index (Figs. 4*a*, 4*b*).

To increase additional insight into the biotic changes across the P–T boundary, it is essential to see whether diversity changes are accompanied by changes in the composition of ostracod assemblages, i.e., relative proportions of the six major compositional ostracod groups: Polycopidae, Cytherellidae, Healdioidea, Bairdioidea, Cypridoidea, and Cytheroidea (Figs. 6*a*, 6*b*).

Most of the ostracod species recovered from the latest Pliensbachian belong to the superfamilies Cytheroidea and Healdioidea, with smaller numbers of taxa of the Cypridoidea and Bairdioidea. Generally, ostracod faunas in late Pliensbachian strata are of high diversity, but yield abundant large instars of species of the Healdioidea. Figs. 4*a*, 4*b* show a diversity drop from the *Semicelatum* Subzone to the *Sublevisoni* Subzone, coinciding with a substantial variation in the relative dominance of the three major components of the ostracod fauna, the Healdioidea, Cypridacea, and Cytheroidea.

Figures 6*a* and 6*b* show an interesting relationship, almost of mutual exclusion, between the last two superfamilies and the first one. Healdioids are dominant in the late Pliensbachian assemblages, followed by the cytheroids, which continuously increase in diversity up to the P–T boundary. From there to the end of the *Mirabile* Subzone, *Tenuicostatum* Zone, Cytheroidea accounted for 70% to 80% of the total ostracod taxa, coinciding with the disappearance of Healdioidea. Cytherellidae are poorly represented in the uppermost Pliensbachian, but at the beginning of the *Tenuicostatum* Zone increase in importance up to the *T–S* boundary, where they reach values comparable to those of Cytheroidea, around 50%, and then, during the *Strangewaysi*

Fig. 6. Relative abundance of the main ostracod groups: Polycopidae, Cytherellidae, Healdioidea, Bairdioidea, Cypridoidea, and Cytheroidea. The horizontal scales are the sampled levels and the ammonite zonation. Sections of Ablanquejo (AB), La Almunia de Doña Godina (ADG), Ariño (AR), and Barranco de las Alicantas (CT).

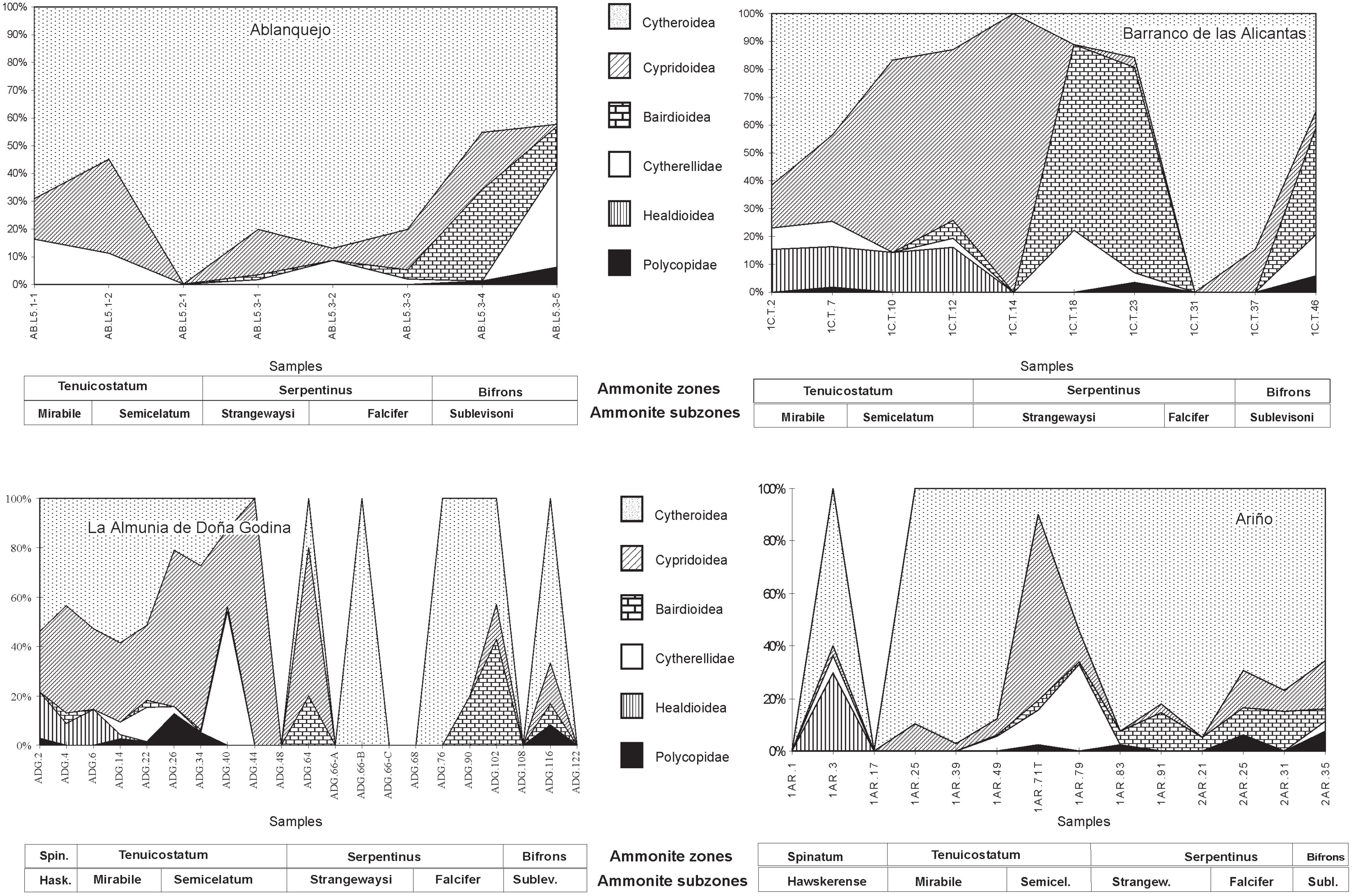
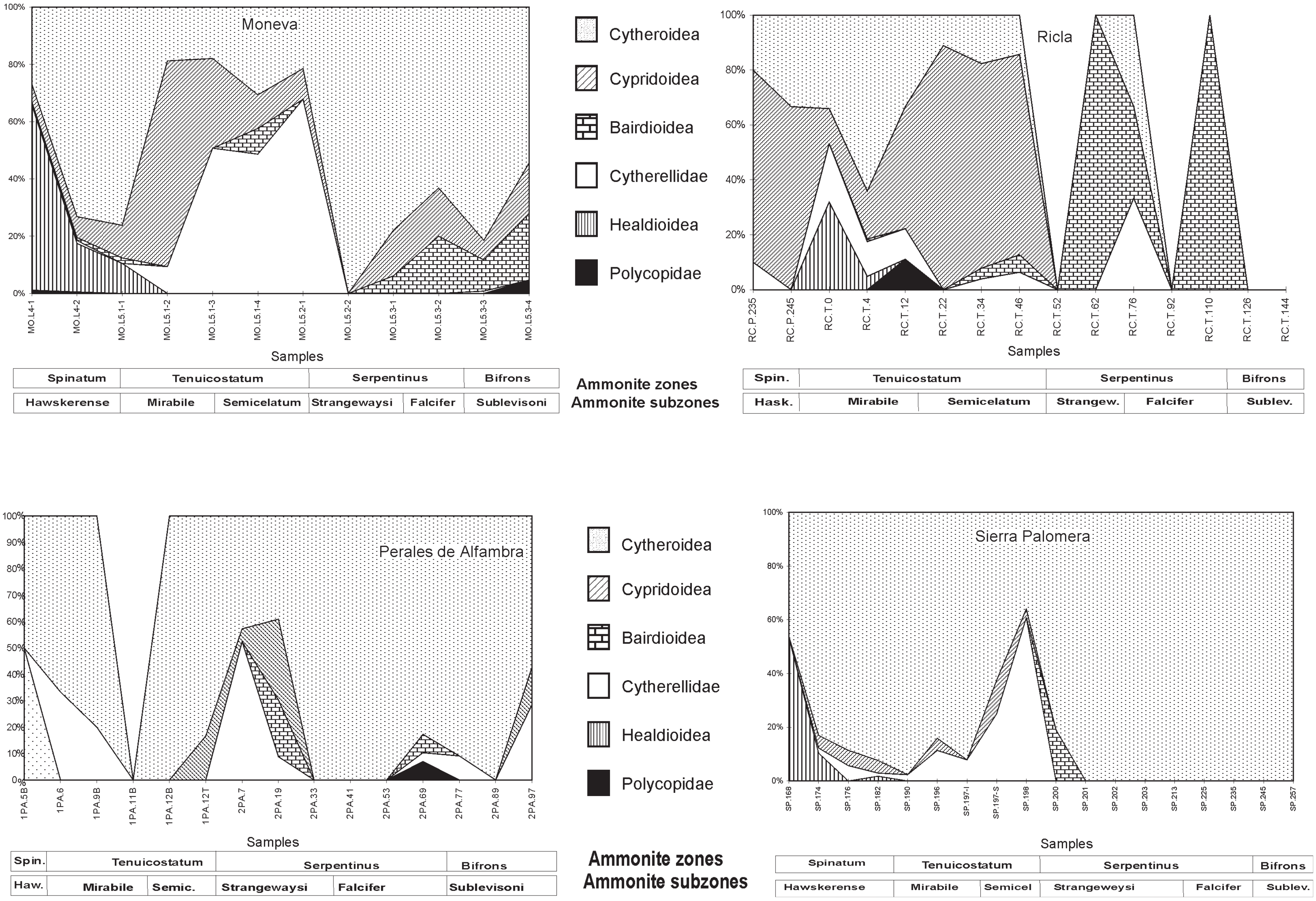


Fig. 6 (*concluded*). Sections of Moneva (MO), Perales de Alfambra (PA), Sierra Palomera (SP), and Ricla (RC).



Subzone, diminished. Cypridoidea is only well represented at the beginning of the *Tenuicostatum* Zone and at the base of *Serpentinus* Zone, and Bairdioidea is only common during the *Serpentinus* Zone, just like the Polycopidae. Consequently, the Healdioidea and Cytheroidea are the most significant elements at the P–T boundary, and after the disappearance of the Healdioidea, Cytheroidea dominate ostracod assemblages.

Interpretation and discussion

The results clearly demonstrate that a distinctive change in composition and diversity took place within the Cordillera Ibérica area from the late Pliensbachian to the early Toarcian. All species of the superfamily Healdioidea disappeared by the end of the *Tenuicostatum* Zone (Lord 1982, Arias 2000).

This important turnover would be related to some environmental change. For this reason, the taxa of the *Tenuicostatum* Zone were analyzed to examine the decline in diversity and were assigned to three categories: (1) ecological generalists, (2) disaster opportunists, and (3) ecological opportunists (Harries and Kauffmann 1990; Harries 1993). A simple model may express the biotic response to this major environmental stress. An optimum ecological assemblage consists 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 (e.g., small sized ecologic generalists, such as Bairdioidea, Cypridoidea). A major environmental perturbation severely modified the ecosystem and eradicated the specialized niches of K-strategy species and most of the r-strategists, resulting in mass mortality. This may result in a regional segregation of all large complex species and many ecological generalists, which may explain the different behaviour of the healdioids.

The first ecological opportunists to recover would be groups of small size and low-oxygen-tolerant species, the bairdioids and cypridoids (Whatley et al. 1994). These groups of ecological opportunists are constantly common members in pre-extinction environments (P–T boundary). They would occupy minor ecological roles, as small populations in locally distributed areas. They would have been high-diversity communities and dominant during the beginning of stressed conditions because they could have had special adaptations for environmental conditions, which produce high levels of biological stress. These special ecological adaptations would allow them to occupy primary habitats through biological competition.

Biostratigraphical distribution of Cytherellidae indicates that this group is the most stress-tolerant, as well as the first opportunist to thrive after an environmental change. They are disaster opportunists. The extensive niche of these organisms enables adaptation to variable environmental conditions and hence permits the niche drift that assures survival of these stress-tolerant species (Boomer and Whatley 1992; Whatley et al. 1994; Arias and Whatley 2004). Without interference from competitors, these species rapidly reproduce and augment their populations exponentially. *Cytherella* and *Cytherelloidea* could display the kind of r-strategy that allowed these organisms to take full advantage of stressed and disturbed habitats. When nutrient levels become insufficient to sustain this growth they declined, therefore, opening niches to the ecologic generalists.

Improving stable environmental conditions, increasing competition, niche development, and restoration of well-stratified water masses were again available for the specialized K-strategists. Ecological generalists, which can tolerate large-scale environmental changes, could displace the opportunists species. The reestablishment of highly diverse and mature assemblages (mainly formed by large cytheroids, such as *Kinkelinella* or *Ektyphocythere*) would represent full recovery of the ecological succession after a major environmental perturbation. Disaster specialists and opportunist taxa become rare during ecosystem recovery.

This ostracod mass extinction shows the typical sequence of events in a mass extinction episode (Harries and Kauffman 1990; Harries 1993), which is initiated by an extinction phase during which diversity falls rapidly (generalists), followed by a survival or lag phase of minimal diversity (disaster opportunists), and then a recovery phase of rapid diversity increase (ecological generalists).

Aberhan and Fürsich (1997, 2000) explained the bivalve P–T turnover by a combined paleoceanographical–ecological model that involved sea-level changes, anoxia, environmental stress, species-area effects, and competition. It is difficult to believe that these changes in diversity can be explained by only one local paleoenvironmental change. Although it is often difficult to prove that an effect has a single cause, most authors consider that this extinction episode resulted from changes in climate conditions induced by terrestrial processes, such as extensive volcanic activity, for example the Karoo–Ferrar (Duncan et al. 1997; Pálfy and Smith 2000; Pálfy et al. 2002), large-scale methane dissociation driven by massive astronomical forcing (Hesselbo et al. 2000; Beerling et al. 2002; Jenkyns 2003; Kemp et al. 2005), or some large paleoceanographic change as a result of the opening of the Hispanic Corridor (Arias, 2006, 2007).

However, the most promising cited causes have been major sea-level changes, anoxia, and oceanic changes (Hallam 1986, 1987, 1988, 2001; Hallam and Wignall 1997, 1999; Jenkyns 1988; Arias 2006, 2007).

The sea-level changes seem to be more doubtful, because during the interval of mass extinction, sea level changed cyclically, but crisis continued during both transgression and regression. On the other hand, the peak of mass extinction in the global record is related to the maximum of transgressions (Haq et al. 1987; Hallam, 1987, 1988, 2001; Little and Benton 1995; Hallam and Wignall 1999; Harries and Little 1999; Pálfy and Smith 2000), whereas the early Toarcian in northeast Spain was a time of a major marine regression (Gómez and Goy 2005), reaching its maximum at the beginning of the *Serpentinus* Zone, early Toarcian (Fig. 2).

Detailed estimates of the influence of anoxia on extinction of Ostracoda are not achievable in northeast Spain, where no typical black shale deposition episode took place during the early Toarcian in the Cordillera Ibérica (Gómez and Goy 2005). Thus the development of anoxic conditions as a factor controlling Ostracoda mass extinction in northeast Spain cannot be re-evaluated.

Nevertheless, the Spanish record gives another opportunity to analyze the causes of a possible massive extinction event in the light of a recent paleoceanographic scenario by

Arias (2006, 2007). Changes in oceanic circulation related to the opening of the Hispanic Corridor have also been proposed for the P–T ostracod extinction episode. The Hispanic Corridor was an emergent seaway between eastern Panthalassa and western Tethys oceans, and that temporal opening coincided with the P–T mass extinction. An earlier study of a simple ocean model showed that a western ocean current flowed in this strait since some 196 million years ago (Arias 2006, 2007), allowing warm Tethyan waters to flow into the Panthalassa Ocean, diminishing the warm water flux into the European Epicontinental Sea (EES). This modification of the amount of oceanic heat transport to northwestern EES areas would have generated a decrease of the sea-surface temperature from the tropics to the temperate zones during the early Toarcian.

Despite earlier reports (Hesselbo et al. 2000; Jenkyns 2003), there is some evidence for cooling associated with the early Toarcian event (van de Schootbrugge et al. 2005; Arias 2006, 2007). If the P–T event was associated with a period of global cooling, this change in temperature could particularly have favoured ostracod species that were well adapted to cold temperate water conditions and would have been particularly harsh on those that were not. The P–T boundary event, as was mentioned previously, appears to have come down especially hard on large Healdioidea. Healdioidea, typical tropical ostracod fauna, could have had smaller populations with greater area requirements, and as a result, they could have been more sensitive to habitat loss or fragmentation. Moreover, their temperature requirements (they could have preferred warm-water conditions, see Casier et al. 2000) and low rates of population growth could have made them slow to recover from sudden changes of temperature. Subsequently, this ostracod extinction episode could have originated from a global cooling event.

Conclusions

One diversification episode of ostracod faunas, followed by a diversity decline and finally a new recovery episode, are documented in northeast Spain basins during the Pliensbachian–Toarcian transition. The most dramatic faunal turnover occurred in the early Toarcian (in the *Serpentinus* Zone), when diverse ostracod assemblages experienced a severe extinction. Similar diversity changes have been reported from coeval biota in other Boreal and Tethyan regions and for other fossil groups.

The ostracod assemblages of the Spanish sections show the alternating numerical dominance of the Polycopidae, Cytherellidae, Healdioidea, Bairdioidea, Cypridoidea, and Cytheroidea. In particular, it should be noted that the Metacopina became the most common component in assemblages throughout the Pliensbachian. During the P–T boundary transition, minor changes in the composition of ostracod assemblages took place. The major faunal turnover is seen subsequently, in the *Semicelatum–Strangewaysi* subzones transition (*Tenuicostatum–Serpentinus* transition), with the last occurrence of nine species of Healdioidea and the first appearance of the most common cytheroid species of the genus *Kinkelinella.* These cytheroid species and *Cytherella toarcensis* and *Liasina lanceolata* are well represented throughout the *T–S* interval, although with important fluctuations in their abundance, showing apparently cyclic relationships between them. Therefore, during this change, Cypridoidea and Cytherellidae are important elements and are even better represented than Cytheroidea. Nevertheless, these components then almost disappear from the succession, when the Cytheroidea become dominant in the *Falcifer* and *Sublevisoni* subzones (*Serpentinus* Zone). The *Strangewaysi* and *Falcifer* subzones (*Serpentinus–Bifrons* zones) transition represents the most significant renewal period, with the Healdioidea extinction and the replacement of Cypridoidea and Cytherellidae by Cytheroidea, which became dominant, making up 90% of the total fauna in the early Toarcian.

Such benthos collapse was obviously related to environmental stress factors operating globally through the late Pliensbachian to the early Toarcian (anoxia, sea-level changes, climate cooling). Although this study provides important results on paleoecological processes around the P–T boundary, it has no direct indication of the cause(s) of the mass extinction.

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