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# High-resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian ammonites (Cephalopoda)

GUILLAUME DERA*, PASCAL NEIGE, JEAN-LOUIS DOMMERGUES, EMMANUEL FARA, RÉMI LAFFONT & PIERRE PELLENARD

*Laboratoire Biogéosciences, CNRS–UMR 5561, Université de Bourgogne, 6 boulevard Gabriel, 21000, Dijon, France*

**Corresponding author (e-mail: guillaume.dera@u-bourgogne.fr)*

**Abstract:** The Pliensbachian–Toarcian interval was marked by major environmental disturbances and by a second-order mass extinction. Here, we reappraise the taxonomic, spatiotemporal and selective dynamics of extinctions over the whole interval, by analysing a high-resolution dataset of 772 ammonite species from NW Tethyan and Arctic domains. On average, 40–65% of ammonite species disappeared during each subchronozone, but higher extinction pulses (reaching 70–90%) prevailed from the Margaritatus to the Dispansum Chronozone. The main extinctions, corresponding to the Gibbosus, Pliensbachian–Toarcian boundary, Semicelatum, Bifrons–Variabilis, and Dispansum events, differed in their dynamics, suggesting episodes of ecological stress related to climate change, regression, disturbance in the carbon cycle or anoxia. The multi-pulsed volcanic activity in the Karoo–Ferrar province could well have triggered these ecological changes. In addition, ammonites experienced a morphological bottleneck during the Gibbosus event, 1 Ma before the Early Toarcian diversity collapse. Typically, drops in richness were related both to high extinctions and to declines in origination rates. This feature could result from strengthened ecological stresses related to the temporal overlap of environmental disturbances. After the Early Toarcian crisis, the recovery of ammonites was rapid (2 Ma) and probably influenced by a coeval marine transgression.

**Supplementary material:** Figures showing a comparison of extinction and origination patterns based on different datasets, and variations of the morphospace occupation are available at http://www.geolsoc.org.uk/SUP18381.

It is now widely assumed that the current erosion of biodiversity is a significant phenomenon in the Earth’s history, because of both its rapidity and the unequivocal role played by our species (Pimm *et al*. 1995; Myers & Knoll 2001; Novacek & Cleland 2001). Some biologists even regard it, perhaps prematurely, as a probable sixth major mass extinction event after the Late Ordovician, Late Devonian, Permian–Triassic, End Triassic, and Cretaceous–Tertiary events (Leakey & Lewin 1996; Pimm & Brooks 2000; Wake & Vredenburg 2008). Understanding the dynamics of past extinctions seems crucial if we are to put the attrition of biodiversity into perspective. Hence, since the pioneering work of Raup & Sepkoski (1982), many palaeontological studies, essentially focusing on mass extinctions, have investigated the environmental and biotic triggers of crises (Hallam & Wignall 1997, 1999; Wignall 2001; Twitchett 2006; Knoll *et al*. 2007), and studied differences and similarities in extinction and recovery patterns (Benton 1995; Erwin 1998; Foote 2000*b*, 2003, 2007; Bambach *et al*. 2004; Alroy 2008). These investigations have examined the effect of extinction selectivity on macroevolutionary patterns in relation to the geographical range, lifespan, morphology and ecology of taxa (McKinney 1997; Fara 2000; Jablonski 2001; Smith & Roy 2006; Payne & Finnegan 2007), the spatial dynamics of extinctions and recoveries (Jablonski 2002, 2005, 2008*b*), and the severity of events (Droser *et al*. 2000; McGhee *et al*. 2004).

Because a literal reading of the fossil record is not appropriate, many palaeontologists have identified and tried to take into account the biases inherent in the estimation of diversity (Foote 1994, 2000*a*, 2001; Peters 2006; Wang & Bush 2008). The consensus is that improvement is required in the spatiotemporal resolution of palaeontological studies, which are usually documented at the global scale and at the geological stage level. The resolution issue becomes crucial when addressing the precise timing of mass extinctions (Foote 2005). Is it a continuous signal through a given stratigraphic interval, a rapid pulsed event emerging from a background signal, or an addition of independent events? And if there are several events, what is their spatiotemporal distribution and can any periodicity be detected (Raup & Sepkoski 1984; Wang & Marshall 2004; Wang & Everson 2007; Alroy 2008)? These questions are essential to establish the link between extinction and recovery dynamics, as well as to explore the proximal causes of major extinction events (Erwin 1998, 2001).

On this topic, numerous studies with different degrees of taxonomic, stratigraphic and spatial resolution have focused on the Pliensbachian–Toarcian period (*c*. 190–175 Ma; Early Jurassic), which encompassed one of the most important marine crises of the Mesozoic (Sepkoski 1986). This event, the ‘Early Toarcian crisis’, affected groups such as ostracodes (Arias 2009), foraminifers (Wignall *et al*. 2006; Zakharov *et al*. 2006), microfossils (Bucefalo Palliani & Riding 2003; Mattioli *et al*. 2009), brachiopods (Vörös 2002), bivalves (Aberhan & Fürsich 2000; Aberhan & Baumiller 2003) and cnidarians (Lathuilière & Marchal 2009). Initially suggested as a regional Euro-Boreal episode linked to the Early Toarcian oceanic anoxic event (T-OAE) (Hallam 1986, 1987), numerous studies now regard it as a global biotic crisis, as it also prevailed in South America, Tibet and Siberia (Aberhan & Fürsich 2000; Wignall *et al*. 2006; Zakharov *et al*. 2006). A reappraisal by Little & Benton (1995) at the chronozone scale has also demonstrated that, although the most important drop in diversity occurred during the Early Toarcian crisis, many marine families vanished either before or after this interval. Moreover, the diversity patterns displayed by ammonites from the NW Tethys show that this drop in richness occurred in at least two major extinction events, at the Pliensbachian–Toarcian boundary (PTB) and during the Semicelatum Subchronozone (Macchioni & Cecca 2002; Cecca & Macchioni 2004).

Here we reappraise the spatiotemporal and selective dynamics of extinctions for the whole Pliensbachian–Toarcian interval at subchronozone resolution, by focusing on ammonites from the Tethyan and Arctic domains. We present a dataset of 772 ammonite species, including information about their biostratigraphic range at the subchronozone level, their palaeogeographical distribution within 17 areas, and their morphology using five geometric descriptors. We analyse the taxonomic, palaeogeographical and morphological patterns that together illustrate various facets of biodiversity (Rosenzweig 1995; Roy & Foote 1997), to address the following questions.

(1) What is the precise chronology of Pliensbachian–Toarcian extinctions? Is there a single pulsed event, a succession of distinct events, or a continuous process?

(2) Are there any differences in the spatial and morphoselective dynamics of extinctions, and do these data allow the identification of the kill mechanisms?

(3) What are the respective roles of extinction and origination processes in diversity collapses and recoveries?

## Material and methods

### *The Pliensbachian–Toarcian ammonite database*

Our study is founded on what we believe to be an exhaustive compendium of published (from 1789 to 2008) and properly illustrated Pliensbachian–Toarcian ammonites from the NW Tethyan and Arctic domains. This dataset (species list available upon request) includes a total of 772 species distributed in 179 genera that belong to the two representative groups of Early Jurassic ammonoid cephalopods: Psiloceratina (encompassing Ammonitina and Lytoceratina) and Phylloceratina.

The present work is confined to the study of NW Tethyan and Arctic areas, corresponding to two epicontinental domains separated by a narrow seaway called the 'Viking Corridor' (Fig. 1a). During the Pliensbachian–Toarcian interval, the Arctic Realm was not yet markedly differentiated but there was a significant contrast between the ammonite fauna from the Euro-boreal and Arctic regions on the one hand, and those from the Mediterranean areas on the other (Meister & Stampfli 2000; Zakharov *et al*. 2003). This provincialism was roughly delimited by a palaeogeographical barrier ranging from the Betic chains (southern Spain) to the Briançonnais ridge (Alps) (Dommergues *et al*. 2009). To emphasize the spatial patterns of diversity, the area under investigation was divided latitudinally and longitudinally into 17 units representing the main basins (Fig. 1b), and the occurrence of each species in these areas was recorded in the database. The dataset was updated for the Toarcian interval by new occurrence data from the Lusitanian Basin and the Moroccan High Atlas after fieldwork and identification of the fauna by the authors (P.N., J.-L.D. and G.D.). Importantly, we assume that, in the light of our extensive literature survey, the sampling and publication efforts were similar between the Euro-boreal and Mediterranean domains and between the Pliensbachian and Toarcian stages. For discussion, we will, however, keep in mind that a preservation bias potentially occurs, in relation to the local hiatus in Euro-boreal domains at the very beginning of the Early Toarcian (Guex *et al*. 2001; Macchioni 2002).

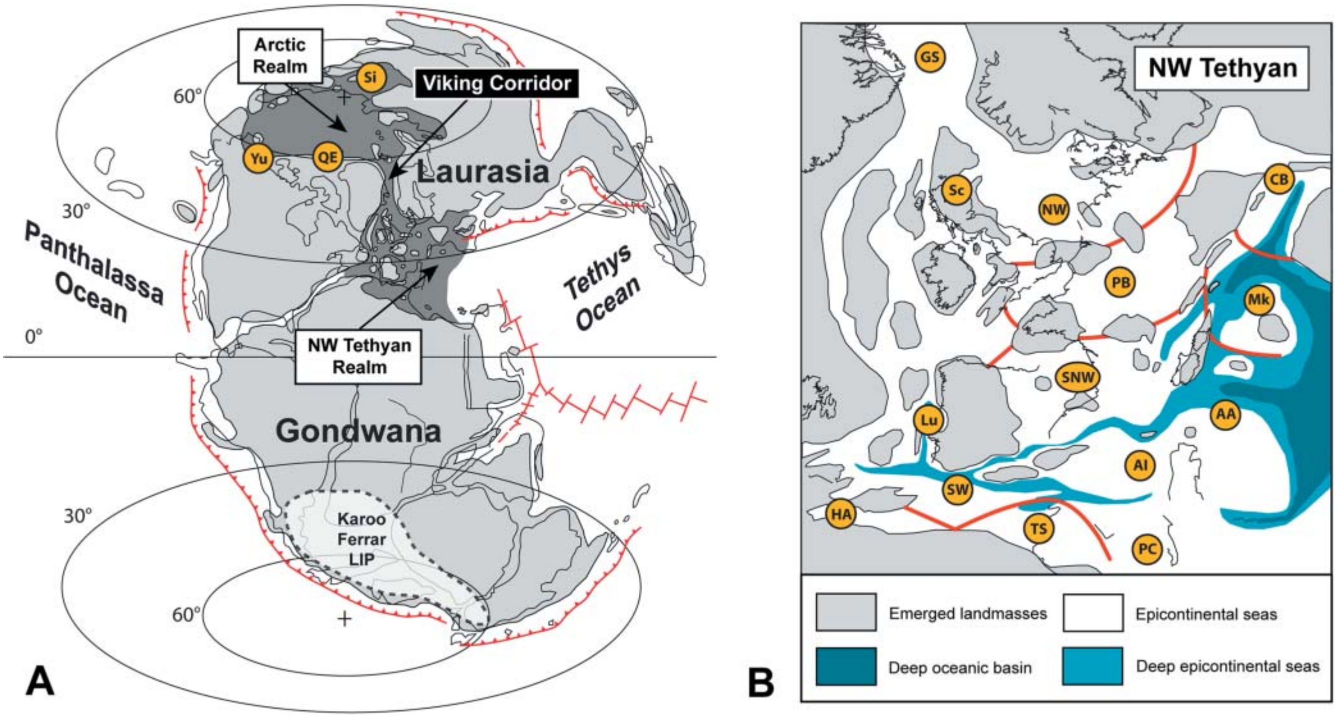


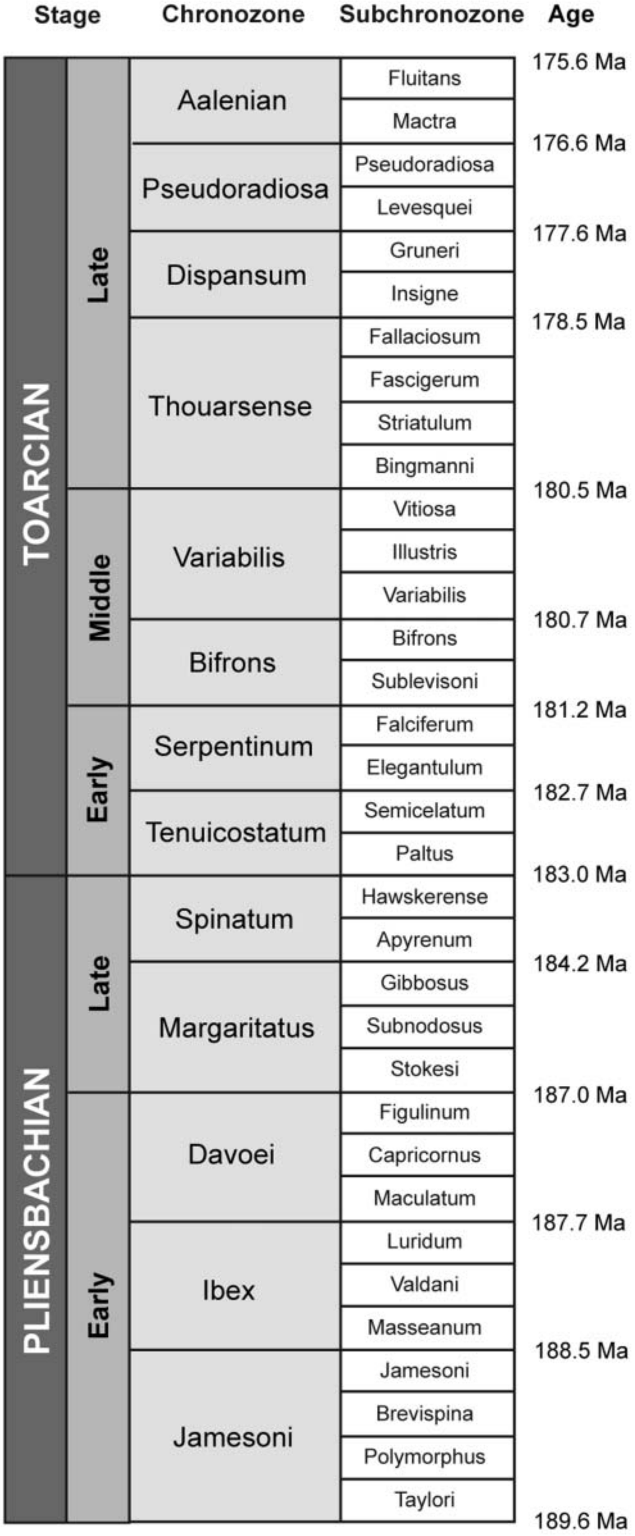
**Fig. 1.** Representations of the Pliensbachian–Toarcian palaeogeographical context at (**a**) global and (**b**) NW Tethyan scale. Si, Siberian Platform; QE, Queen Elizabeth Island; Yu, Yukon; GS, Greenland–Spitsbergen; Sc, Scotland; NW, NW Europe; CB, Carpathians–Balkans; PB, Paris Basin *sensu lato*; Mk, Mecsek; SNW, southern NW Europe; Lu, Lusitanian Basin; AA, Austro- and southern Alpine regions; AI, Apennines–Ionian islands; PC, Peloritanian–Calabrian regions; TS, Tunisia–Sicilia; SW, SW Tethys (encompassing Betic chains, Kabylia and Middle Atlas); HA, Moroccan High Atlas. The Karoo–Ferrar Large Igneous Province is indicated. Maps are modified from Thierry *et al*. (2000) and Dera *et al*. (2009*b*).

The biostratigraphic framework chosen in the present work corresponds to the updated Tethyan biozonation defined by Page (2003) for NW Europe. The interval studied is therefore subdivided into 13 ammonite chronozones and 34 subchronozones (Fig. 2). This biostratigraphic scheme was subsequently converted into absolute time intervals using the numerical ages of chronozone boundaries reported by Gradstein *et al.* (2004). Except for the Late Pliensbachian–Middle Toarcian interval, few studies have documented the duration of subchronozones (McArthur *et al.* 2000; Suan *et al.* 2008*b*). When unavailable, we approximated this by dividing the length of a chronozone by the number of corresponding subdivisions (supposing an equal duration of subchronozones within a given chronozone). At the subchronozone scale, this implies an average resolution of 0.4 ± 0.2 Ma over the 14 Ma of the Pliensbachian–Toarcian interval. As far as possible, we reported the stratigraphic range of ammonite species according to the 13 chronozones and the 34 subchronozones, by considering their first and last appearance at Tethyan and Arctic scales. However, because of the scarcity of some local biostratigraphic information, and difficulty in correlation, data for about 10% of species were lacking at the subchronozone level but available at the chronozone scale. The treatment of such cases is detailed below.

The morphology of each species was described using five morphometric parameters measured on entire adult shells (Fig. 3), thus obviating ontogenetic considerations (Gerber *et al.* 2008). The characters retained correspond to the whorl expansion rate (W), the umbilical expansion rate (D), and the whorl shape (S). They represent the basic theoretical parameters defined by Raup & Michelson (1965), which may be related to the buoyancy, swimming velocity, and manoeuvrability of the shell. They are widely applied to characterize the morphological evolution of ammonoids through time (e.g. Dommergues *et al.* 1996; Neige *et al.* 2001; McGowan 2004; Saunders *et al.* 2008), as well as to explore the spectrum of possible coiled geometries in theoretical morphospaces (McGhee 1999; Dera *et al.* 2008). The other morphometric indices correspond to the relative whorl width (RW) and the aperture overlap (AH) (Dommergues *et al.* 1996).

### *Data analysis*

As a first step, we analysed the broad-scale variations of species and genus richness over the 34 subchronozones of the Pliensbachian–Toarcian interval. To resolve the problem of taxa poorly constrained at the subchronozone scale, three approaches were used: (1) an inclusive method that validates the occurrence of poorly constrained species for all subchronozones composing an occupied chronozone; (2) an exclusive method that disregards these species; (3) a probabilistic method that assigns an occurrence probability to them for each subchronozone and whose value is inversely proportional to the number of subchronozones in a given chronozone (Sepkoski 1990). These three methods are expected to capture maximal, minimal, and weighted measures of richness fluctuations at the subzone level. To assess the robustness of these variations, we also calculated richness after removing geographical and stratigraphic singletons (i.e. taxa respectively confined to a single area and to a single subchronozone). In addition, richness was calculated separately for boundary-crossers (i.e. taxa whose presence is confirmed in two consecutive time bins (for discussion, see Carr & Kitchell 1980; Foote 2000*a*; Alroy *et al.* 2001; Fara 2004). The influence of unequal sampling was explored with sample-based rarefaction curves using the software Past (Hammer *et al.* 2001). This technique can be used to standardize richness using the same number of samples for all time intervals (Tipper 1979).



| Stage | | Chronozone | Subchronozone | Age |
|---|---|---|---|---|
| TOARCIAN | Late | Aalenian | Fluitans | 175.6 Ma |
| | | | Mactra | |
| | | Pseudoradiosa | Pseudoradiosa | 176.6 Ma |
| | | | Levesquei | |
| | | Dispansum | Gruneri | 177.6 Ma |
| | | | Insigne | |
| | | Thouarsense | Fallaciosum | 178.5 Ma |
| | | | Fascigerum | |
| | | | Striatulum | |
| | | | Bingmanni | |
| | Middle | Variabilis | Vitiosa | 180.5 Ma |
| | | | Illustris | |
| | | | Variabilis | |
| | | Bifrons | Bifrons | 180.7 Ma |
| | | | Sublevisoni | |
| | Early | Serpentinum | Falciferum | 181.2 Ma |
| | | | Elegantulum | |
| | | Tenuicostatum | Semicelatum | 182.7 Ma |
| | | | Paltus | |
| PLIENSBACHIAN | Late | Spinatum | Hawskerense | 183.0 Ma |
| | | | Apyrenum | |
| | | Margaritatus | Gibbosus | 184.2 Ma |
| | | | Subnodosus | |
| | | | Stokesi | |
| | Early | Davoei | Figulinum | 187.0 Ma |
| | | | Capricornus | |
| | | | Maculatum | |
| | | Ibex | Luridum | 187.7 Ma |
| | | | Valdani | |
| | | | Masseanum | |
| | | Jamesoni | Jamesoni | 188.5 Ma |
| | | | Brevispina | |
| | | | Polymorphus | |
| | | | Taylori | |
| | | | | 189.6 Ma |

**Fig. 2.** Biostratigraphic framework used in this work. Zonations are from Page (2003). Numerical ages of chronozone boundaries are from Gradstein *et al.* (2004).

Subsequently, we estimated the extinction and origination rates for each subchronozone at global and local scales by using

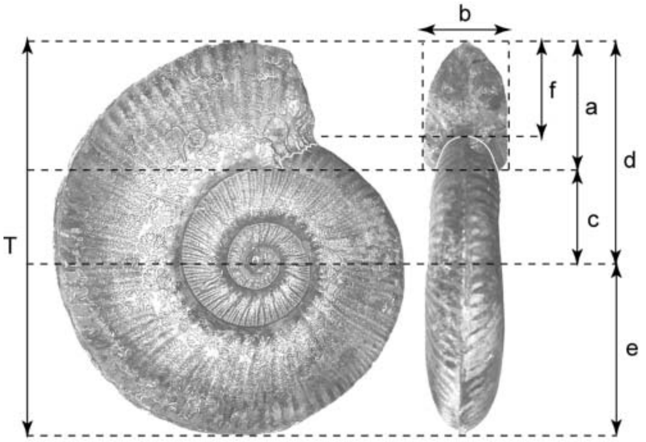


**Fig. 3.** Morphometric measurements of ammonite shells. The five derived shape ratios used in this study are: D = c/d; S = b/a; W = $(d/e)^2$; RW = b/T; AH = f/a.

exclusive subsets. Among the numerous metrics that have been applied to palaeontological data (Foote 1994, 2000*a*), we used proportional rates: the ratios between the number of disappearing or originating species and the standing diversity in a given time interval. However, because proportional rates may reach high values when diversity is low (Benton 1995), extinction and origination metrics were standardized using 10 000 bootstraps and rarefaction procedures taking the lowest richness value as a standard (performed on Matlab®). The rates were not standardized by the duration of intervals for three reasons: (1) the actual duration of the subchronozones is poorly constrained; (2) normalization would assume that the magnitude of extinction and origination processes is time dependent, which is not necessarily true (Raup & Sepkoski 1984; Foote 2005); (3) this standardization generally introduces a negative correlation between calculated rates and interval durations (Foote 1994).

Finally, we analysed disparity variations (i.e. the morphological component of biodiversity; Roy & Foote 1997) throughout the Pliensbachian–Toarcian interval using multivariate statistics. A principal component analysis (PCA) was conducted on the morphometric data matrix to produce, using ordination methods, a morphospace in which overall shell variability is represented. To evaluate the impact of extinction events on different forms, we subsequently separated the species into four main morphotypes by applying a hierarchical cluster analysis to factorial scores (UPGMA aggregation using Euclidian distances; see Dommergues *et al.* 1996). Finally, using the MDA Matlab® package (Navarro 2003), we analysed morphospace occupation over time with conventional estimators, such as the sum of variances, the volume of the convex hull, the mean pairwise distance, and the minima and maxima of each component, using 10 000 bootstraps and rarefaction procedures.

## Results

### *Richness patterns*

Figure 4 presents richness patterns obtained from different metrics at the species and genus levels. Degrading the apparent diversity signal by ruling out singletons or by considering boundary-crossers alone permits a good appraisal of the components forming the variations in richness. Although the generic signal is generally flatter, the fluctuations in genus and species richness are similar over time. We assume that these results are

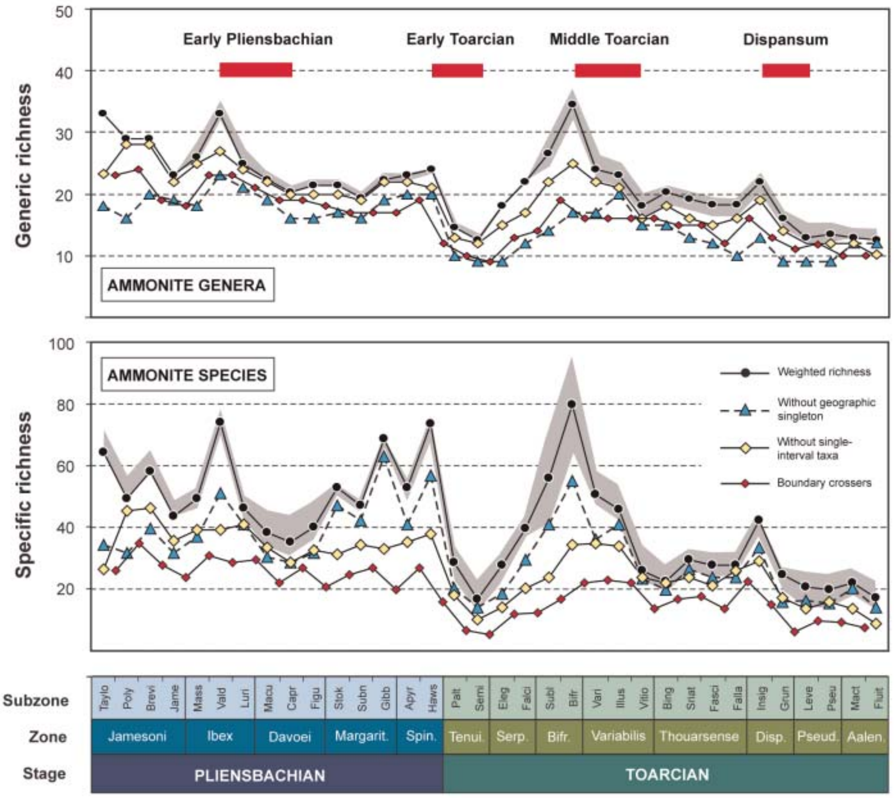


**Fig. 4.** Specific and generic richness of ammonites throughout the Pliensbachian–Toarcian interval. Bands surrounding the weighted diversity curves represent maximal and minimal estimations of richness. Main richness drops are indicated by grey/red lines.

not sampling dependent because rarefied patterns (not shown here) are strongly similar.

Initially, a long-term decrease in ammonite richness is emphasized throughout the Early Pliensbachian, with a sudden bloom of short-lived species during the Valdani Subchronozone. The offset between weighted and singleton-free curves indicates a strong proportion (one-half to one-third) of endemic and rare taxa during that interval, progressively decreasing during the Davoei Chronozone. Subsequently, a step-by-step escalation in richness, reaching its maximum at the end of the Late Pliensbachian, is recorded at the species level. When the datasets with boundary-crossers or without single-interval taxa are considered, diversity remains constant and considerably lower, involving a diversification made up of a progressive bloom of short-lived species. Additionally, the poor influence of geographical singletons shows that more widespread species prevailed during the Late Pliensbachian.

The Pliensbachian–Toarcian boundary corresponds to a drastic drop in diversity, whatever the metrics and taxonomic levels used. The minimal richness (fewer than 20 species) is reached during the Semicelatum Subchronozone. From the Serpentinum Chronozone onwards, all metrics display a reversed trend characterized by a gradual but rapid rise in richness, marking a maximum during the Bifrons Chronozone. This pulse of diversification allows the ammonite richness to reach levels similar to or higher than those preceding the Early Toarcian crisis. Furthermore, the strong offsets between weighted and singleton-free curves demonstrate the influence of short-lived and endemic taxa on Tethyan–Arctic patterns. During the Variabilis Chronozone, a sharp decrease in richness is evidenced by all metrics, except for boundary-crossers. It is also worth noting that a slight richness drop is recorded during the Dispansum Chronozone, and that the signal seems to be mostly made up of long-lived fauna throughout the Late Toarcian.

### *Extinction and origination patterns*

During the Pliensbachian–Toarcian interval, extinction rates fluctuate markedly, and display slightly different patterns for species and genera (Fig. 5). At the species level, the extinction curve has a discontinuous bell-shaped pattern centred on the Pliensbachian–Toarcian boundary, followed by a peak during the Dispansum Chronozone. In detail, high extinction pulses (70–90%) are recorded during the Gibbosus, Hawskerense, Paltus, Semicelatum, Insigne, Gruneri, and Mactra Subchronozones. At the genus level, the most intense events (extinction rates reaching 50%) correspond to rapid and significant extinction peaks during the Hawskerense and Bifrons Subchronozones, and to a lesser extent during the Brevispina, Falciferum, and Insigne Subchronozones. After removing singletons, the extinction pulses generally persist at both taxonomic scales. Among these lethal episodes, we will focus on five main events markedly evidenced at local scales (Fig. 6), and corresponding to drops in (or low levels of) morphological disparity (see below). For convenience, these five extinction pulses are here chronologically named the Gibbosus, PTB (Hawskerense and Paltus Subchronozones), Semicelatum, Bifrons–Variabilis, and Dispansum (Insigne and Gruneri Subchronozones) events. Remarkably, these extinction pulses differ in their palaeogeographical dynamics (Fig. 6). Whereas the PTB and Dispansum events prevailed at least at the Tethyan scale (also in the Arctic domain for the PTB), the Mediterranean fauna would have been more affected during the Gibbosus event. Conversely, the Semicelatum event was more prominent in Euroboreal domains and could have lasted until the Elegantulum Subchronozone. The geographical pattern of extinctions was not investigated at the genus scale for the Bifrons–Variabilis event, but it displays spatially homogeneous dynamics at the species level.

Origination rate values are relatively low during the Early Pliensbachian, but display a pulse during the Ibex Chronozone, followed by a drastic drop during the Davoei Chronozone (Fig. 5). Throughout the Late Pliensbachian, origination rates increase and stay relatively high at the species level, but decrease during the PTB event (especially at the specific level), and remain moderate during the Semicelatum event (<20% for genera). Whatever the taxonomic scale, this trend is subsequently reversed by an origination pulse from the Serpentinum to the Bifrons Chronozone, followed by a drastic decline during the Variabilis Chronozone. Finally, the Late Toarcian origination rates stay relatively low, but are marked by a rapid rise during the Levesquei Subchronozone for species, and a drastic decrease during the Dispansum Chronozone for genera.

### *Morphological disparity patterns*

The PCA allows the overall variability expressed by ammonite shells to be summarized according to new variables (principal components; PCs) synthesizing the raw morphological parameters. The morphospace built on the two first PCs resulting from the PCA represents about 80% of the total variance supported by the data matrix (Fig. 7). PC1 chiefly represents the degree of involution, and PC2 mainly differentiates between depressed and compressed shells. Using a hierarchical cluster analysis, the Pliensbachian–Toarcian ammonites may be categorized according to four main morphotypes (Fig. 7b): M1, cadi-planorbicone (e.g. Phricodoceratidae or some depressed Dactylioceratidae); M2, oxy-discocone (e.g. Phylloceratinae); M3, disco-spherocone (e.g. Liparoceratidae or Paroniceratinae); M4, serpenticone to oxy-platycone (e.g. Dactylioceratinae, Grammoceratinae or Dumortieriinae).

By analysing the disparity patterns through time, significant variations are observed (Fig. 8a). These results remain similar whatever the disparity estimator used. Global morphological variability is high and stable from the Jamesoni to the Margaritatus Chronozone, decreases from the Spinatum to the onset of the Serpentinum Chronozone (except in the Arctic domain), rises rapidly during the Bifrons Chronozone, drops significantly during the Variabilis Chronozone, and finally remains low during the Late Toarcian. Globally, the bottlenecks appear chiefly related to the decline of Psiloceratina with depressed whorls and involute geometries. Conversely, the morphological variability introduced by evolute and compressed Phylloceratina seems less influenced.

Remarkably, the five main extinction events do not homogeneously affect the different morphotypes (Fig. 8b). During the Gibbosus event, morphotypes M4 and M3 are slightly diminished whereas oxycone shapes are not affected. The disappearance of rare, depressed M1 morphologies leads to a drop in disparity. All morphotypes decrease in the PTB event, and the depletion altering groups M2 and M3 accentuates the decrease in disparity. The subsequent post-crisis diversification was not synchronous among the morphotypes. Whereas M4 quickly blooms through the Serpentinum Chronozone, the richness of depressed forms M3 and M1 does not markedly rise before the Bifrons Chronozone. During the Bifrons–Variabilis event, the considerable loss of disparity corresponds to a progressive extinction of M1 and to a gradual decrease in M4. As is the case during the Gibbosus event, morphotype M2 is apparently not affected. Finally, only

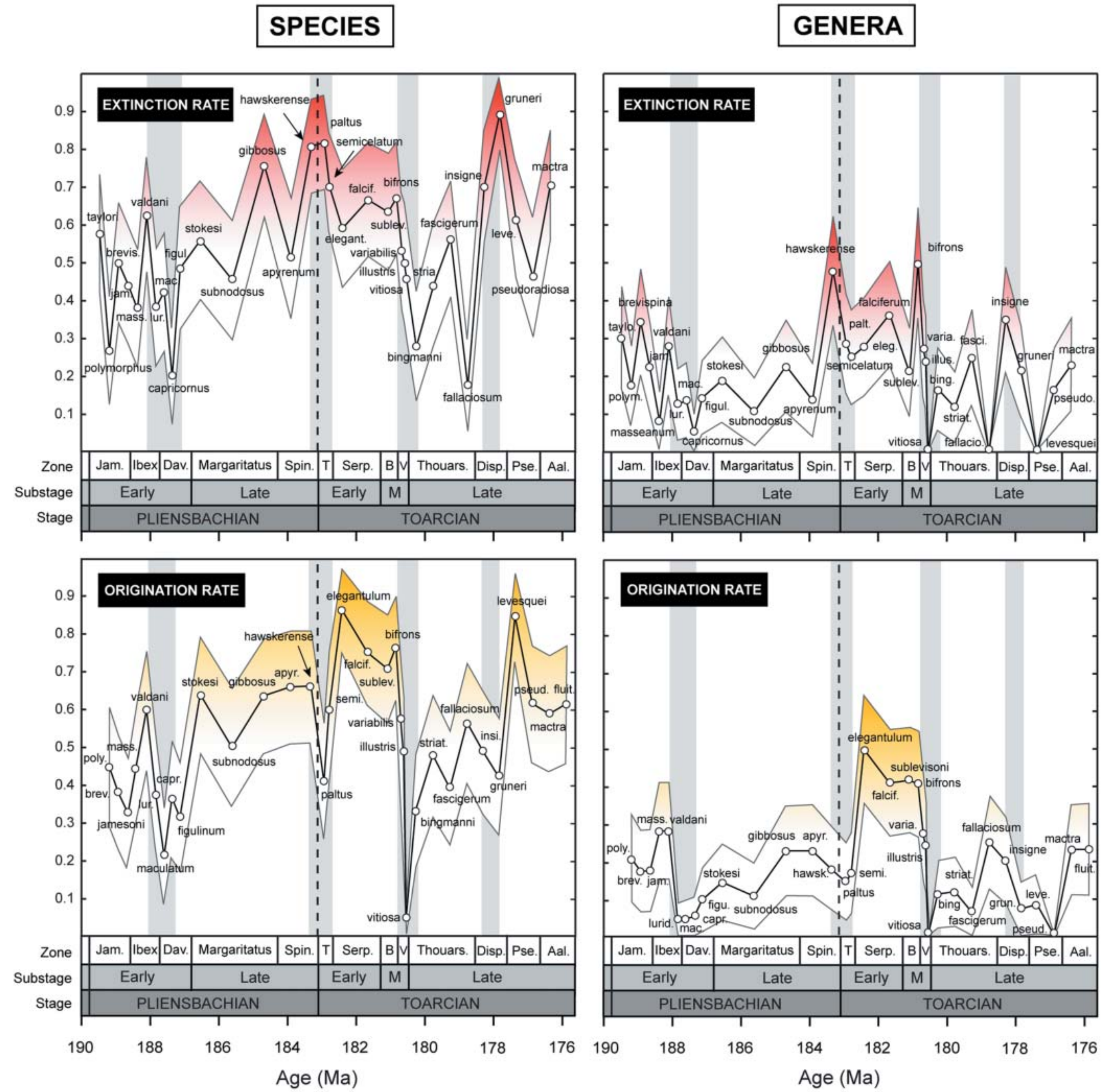


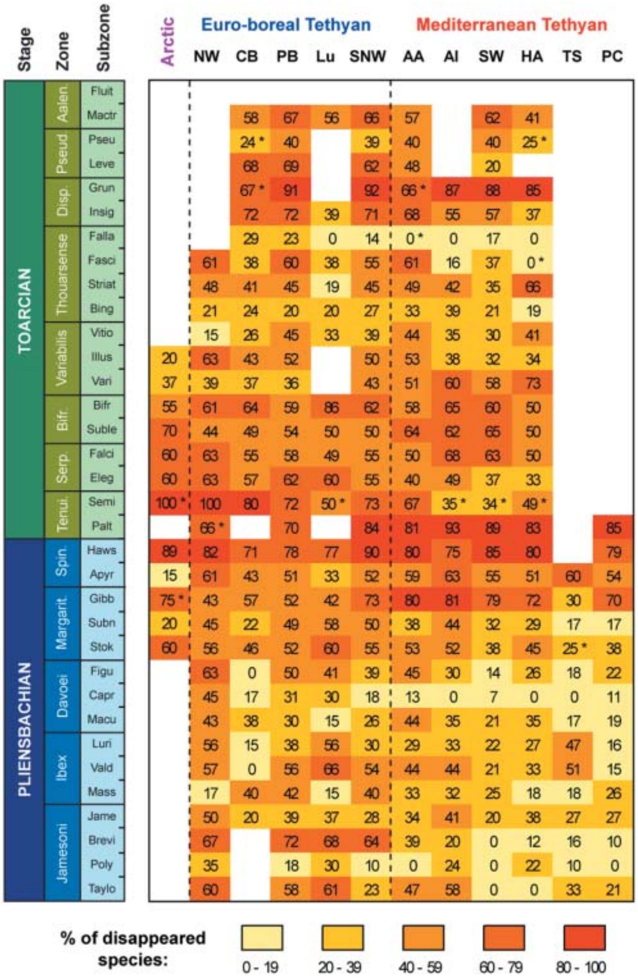
**Fig. 5.** Variations of extinction and origination rates at specific and generic levels against numerical ages. Bands surrounding apparent rates are ±1 standard deviation, as determined from 10 000 bootstraps and rarefaction procedures using the lowest richness value as a standard. The name of each subchronozone is indicated. Grey bands indicate intervals characterized by considerable drops in ammonite richness (see Fig. 4).

species belonging to M3, previously diversified at the onset of the chronozone, were affected by the Dispansum event.

## Discussion

### *Multiple extinction pulses during the Pliensbachian–Toarcian interval*

On average, 40–65% of species and 10–30% of ammonite genera disappeared during each subchronozone (400 ± 200 ka) of the Pliensbachian–Toarcian interval. Compared with other organisms such as bivalves, whose species duration reached 4–8 Ma during the Early Jurassic (Hallam 1987; Aberhan & Fürsich 2000), these extinction rates appear particularly high, but are in agreement with the volatility displayed by cephalopods throughout the Phanerozoic (Wiedmann & Kullmann 1996). Indeed, cephalopods and more especially ammonites are usually recognized as one of the groups most susceptible to both background and mass extinctions (Wang & Bush 2008). This feature suggests that high turnover rates in ammonite populations may represent relevant indicators of weak palaeoecological stresses that could not be evidenced by less extinction-prone



| Stage | Zone | Subzone | Arctic | Euro-boreal Tethyan | | | | | Mediterranean Tethyan | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | NW | CB | PB | Lu | SNW | AA | AI | SW | HA | TS | PC |
| TOARCIAN | Aalen. | Fluit | | | | | | | | | | | | |
| | | Mactr | | | 58 | 67 | 56 | 66 | 57 | | 62 | 41 | | |
| | Pseud. | Pseu | | | 24 * | 40 | | 39 | 40 | | 40 | 25 * | | |
| | | Leve | | | 68 | 69 | | 62 | 48 | | 20 | | | |
| | Disp. | Grun | | | 67 * | 91 | | 92 | 66 * | 87 | 88 | 85 | | |
| | | Insig | | | 72 | 72 | 39 | 71 | 68 | 55 | 57 | 37 | | |
| | Thouarsense | Falla | | | 29 | 23 | 0 | 14 | 0 * | 0 | 17 | 0 | | |
| | | Fasci | | 61 | 38 | 60 | 38 | 55 | 61 | 16 | 37 | 0 * | | |
| | | Striat | | 48 | 41 | 45 | 19 | 45 | 49 | 42 | 35 | 66 | | |
| | | Bing | | 21 | 24 | 20 | 20 | 27 | 33 | 39 | 21 | 19 | | |
| | Variabilis | Vitio | | 15 | 26 | 45 | 33 | 39 | 44 | 35 | 30 | 41 | | |
| | | Illus | 20 | 63 | 43 | 52 | | 50 | 53 | 38 | 32 | 34 | | |
| | | Vari | 37 | 39 | 37 | 36 | | 43 | 51 | 60 | 58 | 73 | | |
| | Bifr. | Bifr | 55 | 61 | 64 | 59 | 86 | 62 | 58 | 65 | 60 | 50 | | |
| | | Suble | 70 | 44 | 49 | 54 | 50 | 50 | 64 | 62 | 65 | 50 | | |
| | Serp. | Falci | 60 | 63 | 55 | 58 | 49 | 55 | 50 | 68 | 63 | 50 | | |
| | | Eleg | 60 | 63 | 57 | 62 | 60 | 55 | 40 | 49 | 37 | 33 | | |
| | Tenui. | Semi | 100 * | 100 | 80 | 72 | 50 * | 73 | 67 | 35 * | 34 * | 49 * | | |
| | | Palt | | 66 * | | 70 | | 84 | 81 | 93 | 89 | 83 | | 85 |
| PLIENSBACHIAN | Spin. | Haws | 89 | 82 | 71 | 78 | 77 | 90 | 80 | 75 | 85 | 80 | | 79 |
| | | Apyr | 15 | 61 | 43 | 51 | 33 | 52 | 59 | 63 | 55 | 51 | 60 | 54 |
| | Margarit. | Gibb | 75 * | 43 | 57 | 52 | 42 | 73 | 80 | 81 | 79 | 72 | 30 | 70 |
| | | Subn | 20 | 45 | 22 | 49 | 58 | 50 | 38 | 44 | 32 | 29 | 17 | 17 |
| | | Stok | 60 | 56 | 46 | 52 | 60 | 55 | 53 | 52 | 38 | 45 | 25 * | 38 |
| | Davoei | Figu | | 63 | 0 | 50 | 41 | 39 | 45 | 30 | 14 | 26 | 18 | 22 |
| | | Capr | | 45 | 17 | 31 | 30 | 18 | 13 | 0 | 7 | 0 | 0 | 11 |
| | | Macu | | 43 | 38 | 30 | 15 | 26 | 44 | 35 | 21 | 35 | 17 | 19 |
| | Ibex | Luri | | 56 | 15 | 38 | 56 | 30 | 29 | 33 | 22 | 27 | 47 | 16 |
| | | Vald | | 57 | 0 | 56 | 66 | 54 | 44 | 44 | 21 | 33 | 51 | 15 |
| | | Mass | | 17 | 40 | 42 | 15 | 40 | 33 | 32 | 25 | 18 | 18 | 26 |
| | Jamesoni | Jame | | 50 | 20 | 39 | 37 | 28 | 34 | 41 | 20 | 38 | 27 | 27 |
| | | Brevi | | 67 | | 72 | 68 | 64 | 39 | 20 | 0 | 12 | 16 | 10 |
| | | Poly | | 35 | | 18 | 30 | 10 | 0 | 24 | 0 | 22 | 10 | 0 |
| | | Taylo | | 60 | | 58 | 61 | 23 | 47 | 58 | 0 | 0 | 33 | 21 |

**% of disappeared species:** 0 - 19 | 20 - 39 | 40 - 59 | 60 - 79 | 80 - 100

**Fig. 6.** Spatiotemporal extinction patterns of ammonite species in Arctic, Euro-boreal, and Mediterranean domains. (See Fig. 1 for abbreviations.) Asterisks indicate rates calculated using a reduced fossil record (five or fewer species).

organisms. In addition, the analysis of disparity patterns complements the taxonomic patterns, as the morphological pathway of ammonoids generally shows bottlenecks during severe extinctions (McGowan 2004; Villier & Korn 2004; Klug *et al*. 2005; Saunders *et al*. 2008).

In agreement with Little & Benton (1995), our high-resolution study shows that, although the most drastic drop in ammonite richness occurred during the Early Toarcian, the higher extinction rates prevailed during a protracted stratigraphic interval, ranging from the end of the Margaritatus Chronozone to the Bifrons Chronozone (i.e. about 4 Ma). Additionally, a belated event is apparent during the Dispansum Chronozone. The strongly fluctuating extinction rates recorded at both regional and basinal scales indicate a discontinuous process, characterized by a series of distinct pulsed extinctions, successively corresponding to the Gibbosus, PTB, Semicelatum, Bifrons–Variabilis, and Dispansum events. Independently of taxonomic patterns, these self-contained episodes are also confirmed by coeval decreases in (and low levels of) morphological disparity, and by differences in their morphoselective and spatial dynamics (Fig. 9).

Interestingly, these five main extinction pulses are recorded at different taxonomic levels (Fig. 5). As the extinction risk of a genus is partly related to the spatial range, diversity, and ecological variability of its constituent species, we expect this feature to be linked to temporal inconstancies in the extrapolation of emerging properties between biological scales (Jablonski 2005, 2008*a*). For example, if during a given interval most genera are composed of a small number of endemic and stenotopic species (e.g. during the Bifrons Chronozone), they are likely to present a higher extinction risk. Under this assumption, these high extinction pulses must be regarded with the same consideration whatever the biological scale.

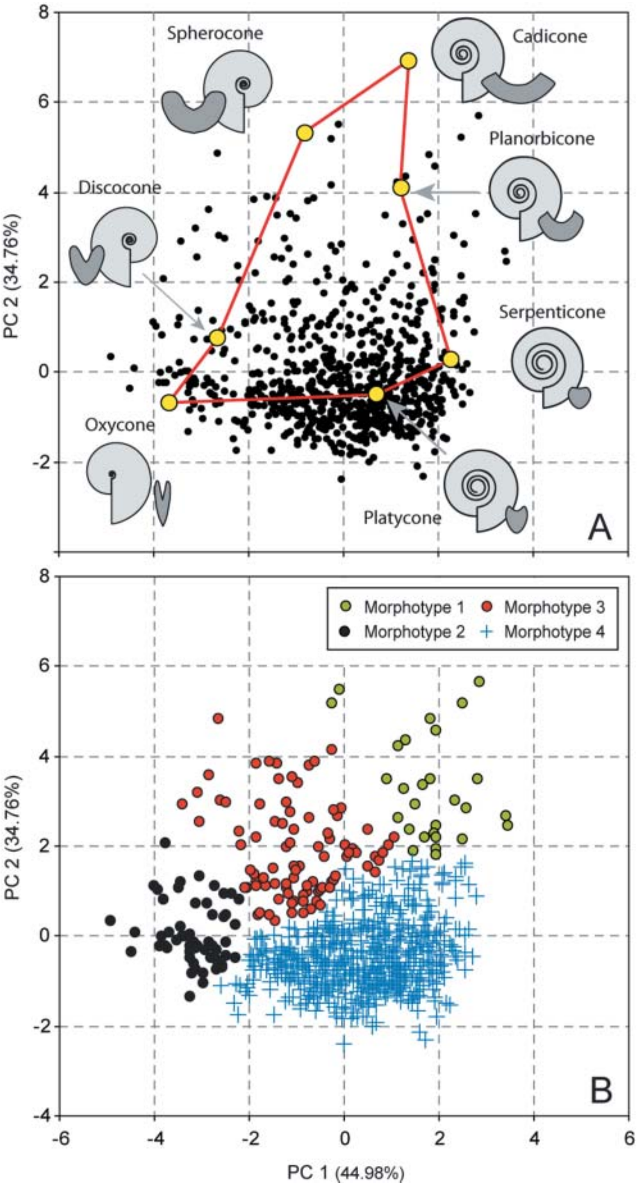


**Fig. 7.** Morphospace of Pliensbachian–Toarcian ammonites constructed from a principal component analysis. (**a**) The characteristic shell morphologies defined by Westermann (1996) are added for comparison. (**b**) The morphospace is divided according to four principal groups defined from a hierarchical clustering analysis.

The evidence of multi-pulsed extinction patterns obviously has many palaeoecological implications, as it suggests a disturbed period characterized by a succession of environmental and biotic stresses. The latter can correspond either to recurring ‘press’ disturbances (e.g. eustatic change, climate change or volcanism) or to ‘pulsed’ mechanisms (e.g. anoxia or meteor impact). The

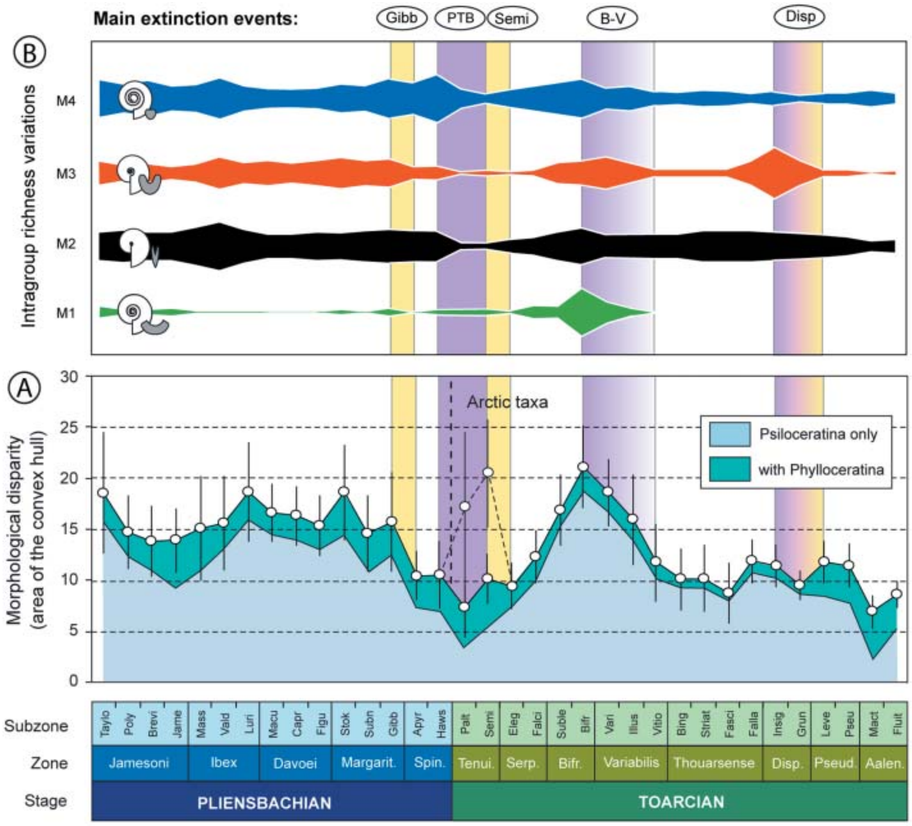


**Fig. 8.** Impacts of the five main extinction events on the morphological patterns. (**a**) Morphological disparity in ammonites measured as the area of the convex hull. Error bars are generated by bootstrapping (1000 replicates) and rarefaction procedures. Results are presented both by considering all Early Jurassic ammonoids and by removing Phylloceratina. (**b**) Standardized intragroup richness variations expressed as percentages of the maximal richness of each group. Light/yellow bands indicate extinctions counterbalanced by high origination rates; dark/purple bands indicate extinctions followed by a drop in origination rates.

press disturbances alter biodiversity by placing multigenerational stress on ecosystems whereas pulsed disturbances correspond to sudden and catastrophic events (Arens & West 2008). Nevertheless, it is crucial to specify the dynamics of extinction events to decipher the nature and number of potential causes. Here, as the main extinctions of the interval under study differ in their taxonomic, spatial, and morphoselective patterns, we suppose that different environmental or biotic factors prevail.

### *Kill mechanisms and extinction triggers*

The Gibbosus extinction was marked both by the disappearance of Liparoceratidae, Phricodoceratidae, and Cymbitidae, and by the first step in the Pliensbachian–Toarcian morphological bottleneck related to the disappearance of some cadi-planorbicone and disco-spherocone forms (M1 and M3). Its impact was mainly regional, as it predominantly affected ammonites from Mediterranean domains (e.g. *Arieticeras*, *Leptaleoceras* and *Reynesoceras*). This feature is supported by extinctions of Mediterranean brachiopods between the Margaritatus and Spinatum Chronozones (Vörös 2002). It is tempting to relate this event to contemporaneous methane releases recently evidenced by a negative $\delta^{13}$C excursion (van de Schootbrugge *et al*. 2008) or to the very beginning of volcanism in the Karoo–Ferrar province (Pálfy & Smith 2000). However, these mechanisms imply global disturbances that fail to explain the regional pattern. Alternatively, we suggest that, as at the Sinemurian–Pliensbachian transition (Meister *et al*. 2006), the extinction of tropical fauna could result from a strong cooling of seawater at the end of the Late Pliensbachian (Dera *et al*. 2009*a*,*b*). Tropical taxa being generally more extinction-prone than temperate species (Jablonski 1991), they could have been directly affected by the temperature decrease and/or the competition with Euro-Boreal Amaltheidae expanding southwards (Meister & Stampfli 2000).

The PTB event corresponds to the disappearance of Amaltheidae and some Hildoceratidae. It appears as one of the most severe because it occurred at the global scale, affected all ammonite morphologies, and prevailed at different taxonomic levels. These features therefore suggest global mechanisms that disturbed most habitats. However, as this crisis occurred at the end of a global regressive cycle, the sedimentary hiatus present in the Euro-boreal context during the Paltus Subchronozone could have exaggerated the amplitude of this extinction (Guex *et al*. 2001; Sandoval *et al*. 2001; Macchioni 2002). The PTB event was coeval with reversals in $\delta^{18}$O and $^{87}$Sr/$^{86}$Sr curves (Dera *et al*. 2009*a*), suggesting drastic climate variations that could have disrupted ammonite provincialism (Macchioni & Cecca 2002; Cecca & Macchioni 2004). Rapid disturbances are also reported in the carbon cycle, marking a decrease in carbonate production (Hesselbo *et al*. 2007; Suan *et al*. 2008*a*). Potentially, these different mechanisms may account for the PTB event and their combined actions could explain its severity.

The Semicelatum extinction is generally regarded as a global event, which mostly concerned benthic and nektobenthic organisms (Hallam 1987; Little & Benton 1995; Harries & Little 1999; Aberhan & Baumiller 2003). If ammonite morphology is related to ecology, as suggested by Westermann (1996), this selective dynamics seems validated because the diversification of suspected vertical migrant morphologies (M1 and M3) is delayed compared with those of planktonic hemipelagic shapes (M4) such as serpenticone Dactylioceratidae (Fig. 8). This trait would emphasize the prevalence of critical conditions in bottom waters, and could confirm the influence of a global or at least regional anoxia (T-OAE) (Jenkyns & Clayton 1997; McArthur *et al*. 2008), itself related to releases of greenhouse gas, warming, and

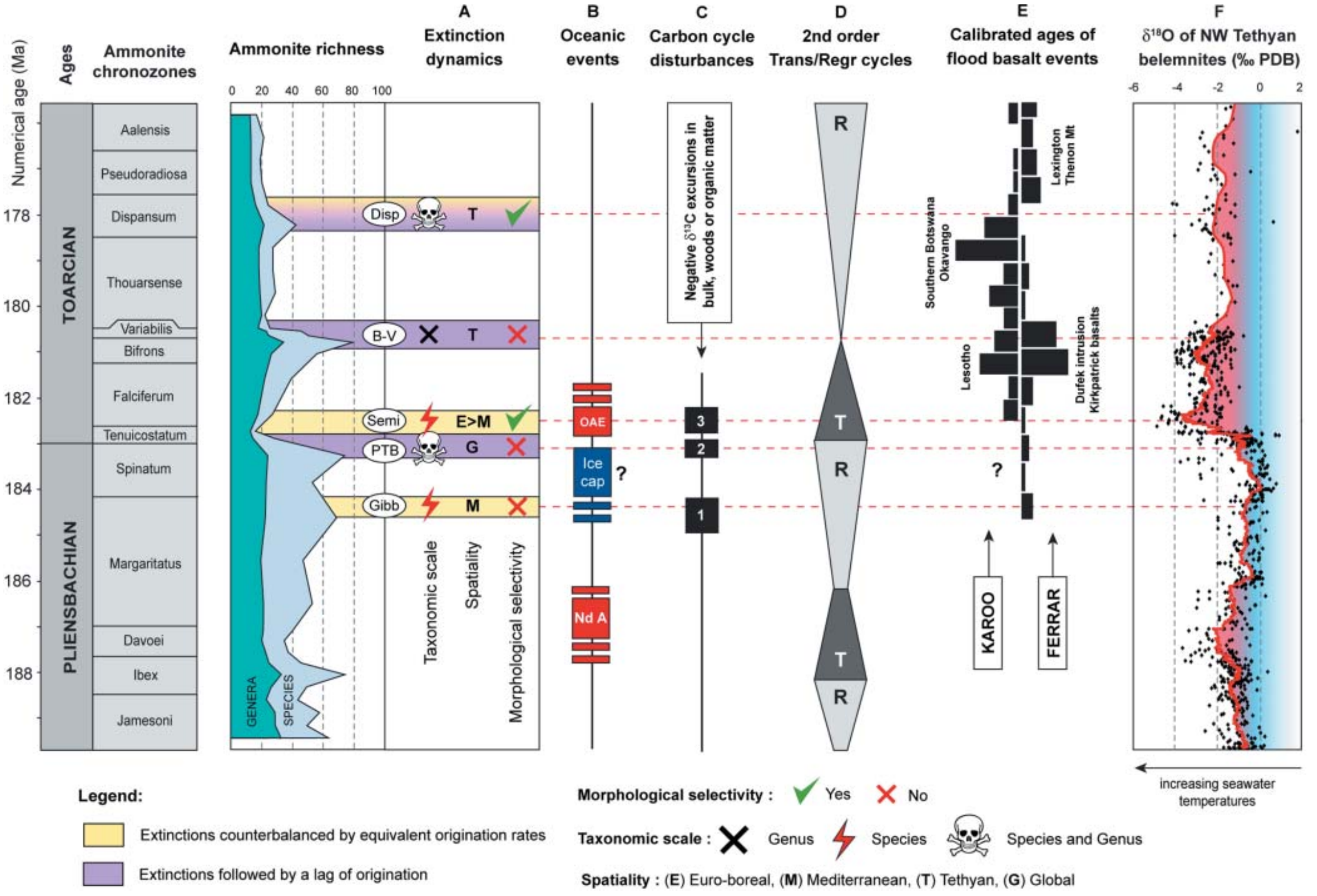


**Fig. 9.** (**a**) Taxonomic, spatial, and morphoselective dynamics of extinction events. Relationships between diversity patterns, main extinction events, and palaeoenvironmental changes throughout the Pliensbachian–Toarcian interval; (**b**) OAE corresponds to the Early Toarcian anoxic event (Jenkyns & Clayton 1997) and NdA indicates the Pliensbachian Tethyan circulation change (Dera *et al*. 2009b); (**c**) the three negative $\delta^{13}$C excursions are reported from Hesselbo *et al*. (2007) and van de Schootbrugge *et al*. (2008); (**d**) transgressive or regressive facies cycles observed in Mediterranean contexts (Hardenbol *et al*. 1998); (**e**) cumulative dating of flood basalt events in the Karoo–Ferrar province, based on data from Jourdan *et al*. (2007) for the Karoo, and Riley & Knight (2001) for the Ferrar; (**f**) $\delta^{18}$O curve representing seawater temperatures variations (modified from Dera *et al*. 2009*a*).

sea-level rises. As suggested by Macchioni & Cecca (2002) or Wignall *et al*. (2005), the T-OAE could have been longer and more lethal in Euro-boreal domains because of basinal restrictions, which could explain the high extinction rates recorded in northern domains. Alternatively, biostratigraphic correlation discrepancies between the Euro-boreal and Mediterranean areas could discredit the expanded expression of this extinction in Euro-boreal areas (Sabatino *et al*. 2009).

Recognized by O'Dogherty *et al*. (2000) at the species scale, the Bifrons–Variabilis extinction is more obvious at the genus level in our study. It was at least Tethyan in extent, affected many endemic ammonite genera, and was not specifically morphoselective because most forms vanished, except the M2 shapes mainly represented by Phylloceratinae. The Dactylioceratidae and Hildoceratidae characterized by depressed shells (cadi-planorbicone M1) were particularly affected by this event and were totally extinct at the end of the Variabilis Chronozone (Bécaud *et al*. 2005). Because it occurred at the onset of a sea-level fall, this extinction was related to an incipient reduction of epicontinental environments during the Variabilis Zone (Sandoval *et al*. 2001). This model seems convincing, as it could explain the collapse of numerous epeiric Psiloceratinae and the persistence of oxycone Phylloceratinae (M2) generally related to open marine environments (Westermann 1996). However, a cooling at the very end of the Bifrons Chronozone and simultaneous volcanic events in the Karoo–Ferrar area could have partly strengthened this biotic crisis (Jourdan *et al*. 2007; Dera *et al*. 2009b) (Fig. 9).

To our knowledge, the Dispansum extinction has never been addressed as such in the literature, probably because it was not followed by a significant drop in diversity. However, Hallam (1987) showed important turnovers among marine organisms during the Late Toarcian. This period was marked by a decline of the Grammoceratinae and Paroniceratinae, whereas the Hammatoceratinae and Lytoceratina bloomed (Bourillot *et al*. 2008). This episode concerned at least the Tethyan areas and was morphoselective in the sense that M3 was most affected. The causes of this turnover remain speculative because palaeoenvironmental and geochemical studies are scarce for the Late Toarcian. This event could be related to carbon cycle or climate disturbances linked to volcanic activity at the onset of the Dispansum Chronozone (Gómez *et al*. 2008).

Hence, the extinction pulses that occurred throughout the interval studied could result from a series of palaeoenvironmental stresses caused by climate change, sea-level fluctuation, oceanic disturbances, or variations in geochemical cycles. At the same time, coupled biotic factors such as rises in parasitism during warming could perhaps have strengthened extinction processes (Brooks & Hoberg 2007). Based on an apparent synchronism, Pálfy & Smith (2000) suggested that these environmental changes could have been triggered by volcanic activity in the Karoo–Ferrar province (Fig. 9). Interestingly, the recognition of consecutive pulsed eruptions in the Karoo area (Jourdan *et al.* 2007) and a slight diachronism with the Ferrar activity (Riley & Knight 2001) could explain the rhythm of ecological changes and associated extinctions. However, further dating of volcanic pulses together with the refinement of chronozone ages remain crucial to test for this causal relationship.

### Role of extinctions and originations in diversity patterns

Importantly, our results show that the main extinction pulses are not systematically associated with the significant drops in richness that occurred during the Early Pliensbachian, the Early Toarcian, the Middle Toarcian and the Dispansum Chronozone (Figs 4 and 5). For example, the first major extinctions of ammonite species during the Gibbosus Subchronozone were matched by high origination rates, leading to elevated richness levels during the subsequent Spinatum Chronozone. However, it is worth noting that this first event initiated the morphological bottleneck, 1 Ma before the Early Toarcian crisis. This suggests that disparity patterns may be reliable indicators of the very beginning of a biotic crisis, whereas richness patterns may be less relevant (Villier & Korn 2004).

On the other hand, the severe drops in richness during the interval studied generally result from the combination of high extinction pulses followed by sharp breaks in origination rates, leading to unbalanced replacements of fauna (Fig. 6). This is particularly obvious for the Early and Middle Toarcian diversity drops. Interestingly, these features appear frequent in past crises because, as discussed by Foote (2000*b*), variations in origination rates mainly shaped diversity patterns after the Palaeozoic. Also, Bambach *et al.* (2004) proposed that only three mass extinctions (i.e. Late Ordovician, Permian–Triassic, and Late Cretaceous) exclusively resulted from elevated extinction rates. For the others, drops in origination rates contributed more strongly to severe diversity collapses. As an aside, our study corroborates these observations at high biostratigraphic resolution. Following the conceptual framework of the press–pulse theory (Arens & West 2008), we suggest that the extinction peaks and associated origination drops could be related to strengthened effects of multigenerational and sudden ecological stresses. Potentially, the temporal overlap of several palaeoenvironmental disturbances (e.g. during the Early Toarcian crisis) could account for this process.

Recently analysed by Dommergues *et al.* (2009), the diversity drop occurring at the end of the Early Pliensbachian is markedly related to a break in origination processes during the Davoei Chronozone, and to a lesser extent to a slight extinction pulse during the Valdani Subchronozone (Fig. 5). In addition, it coincides with a long-term reduction in endemism that is significant during the Davoei Chronozone (Dommergues & El Hariri 2002). Hence, we suppose that this drop corresponds to a phylogenetic impoverishment linked to the disappearance of endemic taxa. This trait could result from sporadic northward invasions by Mediterranean fauna (Dommergues & Meister 1991), potentially connected to changes in oceanic circulation (Dera *et al.* 2009*b*).

### Recovery after the Early Toarcian crisis

The disappearance of bottom anoxic conditions at the end of the Semicelatum–Exaratum Subchronozones is generally regarded as the onset of a pulsed and rapid diversification of surviving fauna and crisis progenitors (Harries & Little 1999). Also, our data show that 85% of species and 50% of ammonite genera are new during the subsequent Elegantulum Subchronozone. According to recent cyclostratigraphic refinements for the duration of the Early Toarcian (Suan *et al.* 2008*b*), high ammonite richness and disparity levels were regained during the Bifrons Chronozone, 1.5–2 Ma after the beginning of the Early Toarcian crisis. The delay was of similar length for nektobenthic belemnites (Little & Benton 1995), but was 7–8 Ma for bivalves, which did not expand before the development of carbonate platforms in the Middle Jurassic (Hallam 1996; Aberhan & Fürsich 2000). Following the ecomorphological model of Westermann (1996), the substantial bloom of cadi-planorbicone and disco-spherocone morphotypes (M1 and M3) could reflect a rapid diversification of demersal or bottom-dwelling ammonites (e.g. *Transicoeloceras*, *Catacoeloceras*, *Nodicoeloceras*, *Frechellia*). As suggested by Sandoval *et al.* (2001), this feature could confirm that the fast recovery of cephalopods might be linked to a rapid colonization of new neritic and deep environments formed during the Early–Middle Toarcian transgression. Hence, the different rates of recovery observed between cephalopods and bivalves seem to be mainly related to the lag time necessary for the reappearance of optimal conditions for each group. However, for all fauna, the delay in recovery after the Early Toarcian crisis is globally comparable with the delays estimated for other mass extinctions, which vary from 2 to 10 Ma depending on taxonomic and geographical scales (Erwin 1998; Krug & Patzkowsky 2007; Alroy 2008). These results suggest that biotic recoveries are complex processes, and that simple extrapolations between the magnitude of extinctions and the rate of recovery must be avoided (Erwin 2001).

## Conclusion

Taxonomic, palaeogeographical and morphological extinction patterns in NW Tethyan and Arctic ammonites have been investigated at the subchronozone resolution over the 14 Ma spanning the Pliensbachian–Toarcian interval. The results show that, on average, 40–65% of ammonite species and 10–30% of genera went extinct every 400 ± 200 ka, therefore confirming the fossil cephalopods as one of the groups most sensitive to both background and mass extinctions. However, elevated extinction pulses (i.e. 70–90% of disappearances for species and 50% for genera) are recognized over a time interval ranging from the end of the Margaritatus to the Dispansum Chronozone (*c.* 6 Ma). These consecutive extinctions, corresponding to the Gibbosus, PTB (Pliensbachian–Toarcian boundary), Semicelatum, Bifrons–Variabilis, and Dispansum episodes, differed in their taxonomic, geographical and morphoselective dynamics. This suggests a chain of distinct ecological stresses related to climate change, sea-level fall, anoxia and disturbances in the carbon cycle. It is likely that the multi-pulsed volcanic activity in the Karoo–Ferrar province was the distal trigger of these environmental changes and associated extinctions.

It is worth noting that the morphological pathway of ammonites experienced a bottleneck after the Gibbosus event, whereas the diversity collapse was delayed to the Pliensbachian–Toarcian boundary (1 Ma later), owing to high origination rates during the Spinatum Chronozone. Typically, the main richness drops for the interval studied were related to the combination of strong extinction processes and decreases in origination rates. Following the press–pulse theory, we suggest that these features could result from strengthened ecological stresses related to the temporal overlap of environmental disturbances. After the Early Toarcian biotic collapse, the recovery of ammonite richness levels was rather rapid (*c.* 2 Ma), and was probably influenced by a coeval marine transgression that generated new habitats.

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