



Ammonite paleobiogeography during the Pliensbachian–Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions

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ABSTRACT

The Pliensbachian–Toarcian crisis (Early Jurassic) is one of the major Mesozoic paleoecological disturbances when ca. 20% of marine and continental families went extinct. Contemporaneously, profound paleobiogeographical changes occurred in most oceanic domains including a disruption of ammonite provincialism during the Early Toarcian. Here, we quantitatively reappraise the structure and evolution of paleobiogeographical patterns displayed by ammonite faunas before, during, and after the biological crisis, over a time-interval including 13 biochronozones. The high-resolution study presented here involves the use of hierarchical Cluster Analyses, non-metric Multi-Dimensional Scaling methods, and Bootstrap Spanning Network approaches that we apply to a large database including 772 ammonite species from 16 northwestern Tethyan and Arctic basins. Our results confirm a robust faunal dichotomy between Euro-Boreal and Mediterranean areas throughout the Pliensbachian, with the first emergence of an Arctic biome during the cooling regressive event of the Spinatum Zone. Whatever its complexity, Pliensbachian provincialism could be directly linked to paleogeographical barriers and to latitudinal paleoclimatic and paleoecological contrasts. During the Early Toarcian, this pattern was progressively lost, with northward expansions of Mediterranean ammonites during the Tenuicostatum Zone, followed by a strong interprovincial mixing during the Falciferum Zone. This faunal homogenization results from the combination of several parameters including a major sea-level rise facilitating basinal connections, a global warming event stretching the spatial range limits of southern taxa, and a mass extinction preferentially removing endemic species. Ammonite provincialism, although slightly different, was progressively re-established during the cooling regressive trend of the Middle Toarcian. These results therefore suggest a paramount influence of paleoclimatic, eustatic, and extinction constraints on the paleobiogeography of Early Jurassic ammonites, even if some threshold effects or independent biological factors may sporadically complicate the patterns.

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1. Introduction

First evidenced by Hallam (1961, 1967), the Pliensbachian–Toarcian crisis (183 Ma; Ogg et al., 2008) is now considered as one of the most severe extinction events of the Mesozoic. According to estimations, 15 to 20% of marine families and genera vanished during this episode (Rau and Sepkoski, 1984; Sepkoski, 1996). Whatever their life habits and their paleoecological affinities, most marine phyla were affected including ammonites, brachiopods, bivalves, belemnites, gastropods, corals, foraminifers, radiolarians, ostracods, and dinoflagellates (Hallam, 1987; Doyle and Bennett, 1995; Hori, 1997; Harries and Little, 1999; Aberhan and Fürsich, 2000; Vörös, 2002; Bucefalo Palliani and Riding, 2003; Cecca and Macchioni, 2004;

Herrero, 2008; Arias, 2009; Lathuilière and Marchal, 2009), as well as continental faunas (Benton, 1995; Caswell et al., 2009). Surprisingly, only calcareous nannofossils were apparently spared (Bown et al., 2004). This biological crisis mainly reflected in sharp drops in diversity levels and high turnover rates in Tethyan, Arctic, and Panthalassan seas during the Early Toarcian (Hallam, 1987; Aberhan, 1993; Hori, 1997; Nikitenko and Mickey, 2004; Ruban and Tyszka, 2005; Wignall et al., 2006; Zakharov et al., 2006). Moreover, this event coincides with bottlenecks in the morphological and scalar disparity of ammonites (Dommergues et al., 1996; Dera et al., 2010), and size reductions in microplankton and molluscan shells (Mattioli and Pittet, 2002, 2004; Morten and Twitchett, 2009). Recently, studies aiming at specifying its dynamics have revealed a longer-term process spanning about 6 Myr, with successive extinction pulses ranging from the Late Pliensbachian (Margaritatus Zone) to the Late Toarcian (Dispansum Zone) (Fig. 1) (Hallam, 1987; Little and Benton, 1995; Cecca and Macchioni, 2004; Wignall and Bond, 2008; Caswell et al., 2009; Dera et al., 2010). For the NW Tethyan and Arctic ammonite faunas, these successive events differed in terms of spatial and selective dynamics,

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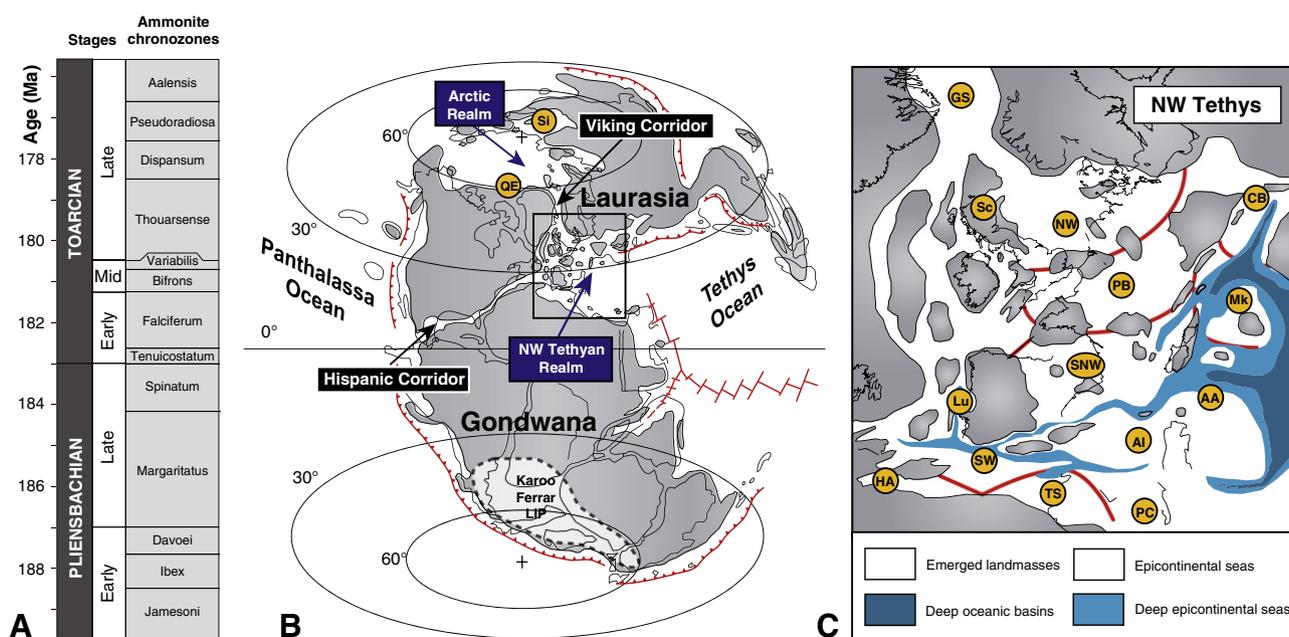


Fig. 1. Biostratigraphical and paleogeographical contexts of the Pliensbachian–Toarcian interval: A) succession of ammonite biochronozones (Page, 2003) and their relative ages (Ogg et al., 2008); B) global paleogeography; C) Paleogeographical details of the NW Tethyan domain. Si, Siberia; QE, Queen Elizabeth Islands; GS, Greenland–Spitsbergen; Sc, Scotland; NW, NW Europe; CB, Carpathian–Balkan areas; PB, Paris Basin *sensu lato*; Mk, Meksek (Hungary); SNW, South of NW Europe; Lu, Lusitanian Basin; AA, Austro- and southern Alpine regions; AI, Apennines–Ionian islands; PC, Peloritanean–Calabrian regions; TS, Tunisia–Sicilia; SW, SW Tethys (encompassing the Betic chains, Kabylias, and Middle Atlas); HA, Moroccan High Atlas. Maps are modified from Thierry et al. (2000) and Dera et al. (2009a).

probably owing to distinct kill mechanisms (Dera et al., 2010). Among them, volcanic events in the Karoo–Ferrar large igneous province, anoxia, regression, seawater acidification, disruption in food webs, or climate changes were suggested, acting either separately or in a combination of some events through time (Hallam, 1986, 1987; Hallam and Wignall, 1997, 1999; Pálffy and Smith, 2000; Wignall, 2001; Cecca and Macchioni, 2004; Wignall et al., 2005; Wignall and Bond, 2008; Mattioli et al., 2009; Dera et al., 2010; Gómez and Arias, 2010).

In addition to taxonomic richness and morphological disparity estimators, it is widely accepted that paleobiogeographical parameters are key to understanding the evolution of biodiversity during past biological crises (Rosenzweig, 1995; Roy et al., 2001; Moyne et al., 2004; Brayard et al., 2005, 2006, 2007; Moyne and Neige, 2007; Jablonski, 2008; Bond and Wignall, 2009). On this topic, numerous studies have depicted modifications of paleobiogeographical patterns at the end of the Early Jurassic, associated with prominent changes in species distribution. For instance, a strong faunal provincialism was first empirically and then analytically evidenced in the NW Tethyan realm during the Pliensbachian, with a noticeable contrast between the Euro-Boreal and Mediterranean ammonites (Meister and Stampfli, 2000; Dommergues et al., 2009), ostracods (Arias and Whatley, 2005, 2009), belemnites (Doyle, 1994), bivalves (Hallam, 1977; Liu et al., 1998), brachiopods (Vörös, 1977, 1980; Manceñido, 2002; Vörös, 2005), and dinoflagellates (Bucefalo Palliani and Riding, 2003). Conversely, a dislocation of this paleobiogeographical pattern was suggested for the Early Toarcian, related to the extinction of endemic taxa at the onset of the biotic crisis (Aberhan and Fürsich, 1997; 2000) and northward expansions of Mediterranean faunas (Macchioni and Cecca, 2002; Cecca and Macchioni, 2004). However, the scope and causes of this disruption may be questioned because these paleobiogeographical patterns were mainly based on empirical data. To meaningfully depict faunal changes occurring before, during and after the crisis, quantitative analyses are necessary, based on data that are temporally and spatially well constrained.

In this article, we reappraise the structuring of paleobiogeographical patterns displayed by NW Tethyan and Arctic ammonites

throughout the Pliensbachian–Toarcian interval. To this purpose, we analyse the database recently published by Dera et al. (2010), which includes information on the biostratigraphical range and the paleogeographical distribution of 772 ammonite species within 16 basins. Provincialism and faunal networks are investigated for each ammonite biochronozon in order to address the following questions:

- (1) Is there a steady faunal dichotomy between the Euro-Boreal and Mediterranean provinces during the Pliensbachian?
- (2) Is there a robust disruption of this biogeographical pattern during the Early Toarcian? If yes, what are the dynamics of this event and what happened in its aftermath?
- (3) What are the paleoenvironmental and biological triggers of these changes?

2. Material and methods

2.1. The Pliensbachian–Toarcian ammonite dataset

Our study is based on an extensive synthesis of published (from 1789 to 2008) and properly illustrated Pliensbachian–Toarcian ammonites from the NW Tethyan and Arctic seas. This database has already been used by Dera et al. (2010) to characterize the dynamics of the Toarcian crisis. It contains a total of 772 species of 179 genera belonging to the two representative groups of Early Jurassic ammonoids, namely the Phylloceratina and Ammonitina (including the Lytoceratoidae *sensu* Hoffman 2010). The biostratigraphical scheme consisting of 13 ammonite biochronozones used in the present work is based on the updated Tethyan zonation defined by Page (2003) for NW Europe (Fig. 1A).

The present study is confined to the NW Tethyan and Arctic domains (Fig. 1B,C), which corresponded to two epicontinental seas separated by a narrow seaway named the “Viking Corridor” during the Early Jurassic (Ziegler, 1988). In order to accurately map the biogeographical patterns during each biochronozon, the studied domains were longitudinally and latitudinally divided into 16 spatial units corresponding to the main sedimentary basins, and the occurrence of each species was recorded in the database according

to these paleogeographic units. Importantly, this implies that the first and last appearance datum (FAD and LAD) for taxa cannot be considered for each basin, and that a given species could be virtually present in an area, even if it was not recorded in the field. Nevertheless, this does not affect the essential results of our analysis because, except for rare Phylloceratinae, most ammonite species have a short life-span which rarely exceeds the resolution of our study (*i.e.*, one ammonite biozone). In order to minimize potential biases related to the local incompleteness of the fossil record, only areas presenting at least five species were selected for each time-bin prior to analysis. For this reason, the Yukon area (Canada) which was considered in the work of Dera et al. (2010) was excluded from analyses. Note also that, owing to this sampling constraint, the number of basins from northern Europe was low during the last three chronozones of the Late Toarcian (*i.e.*, Dispansum, Pseudoradiosa, and Aalensis Zones) compared to the Mediterranean area. Consequently, this problem has to be taken into account in the interpretation of paleobiogeographical patterns for these three time-bins.

2.2. Paleobiogeographical analyses

For each chronozone, the incidence matrix of ammonite species was analysed. Similar to the approach used by Brayard et al. (2007, 2009), complementary mathematical methods were applied to characterize the provincialism and the robustness of faunal exchanges through time:

- (1) First, a hierarchical cluster analysis (hCA) was applied for each time-bin by using the software PAST (Hammer et al., 2001). This method groups localities according to their faunal similarity and differentiates large-scale provinces using dendrograms. Among the numerous available indices (Shi, 1993), we applied one of the most used in paleobiogeography, namely UPGMA aggregations (Unweighted Pair Group Method with Arithmetic mean) based on the Raup–Crick similarity coefficient (Hilton and Cleal, 2007; Cleal, 2008; Dommergues et al., 2009). This coefficient is well suited to comparing localities with different numbers of taxa because it uses a probabilistic “Monte-Carlo” approach which weights the data (Raup and Crick, 1979). One thousand bootstraps were performed to check the robustness of nodes identified on dendrograms.
- (2) The second approach corresponds to a NMDS analysis (Non-metric Multi-Dimensional Scaling) of the similarity matrix based on the Raup–Crick coefficient. This ordination method, performed using the software PAST (Hammer et al., 2001), allows the projection of localities in a two dimensional space where the distance between points illustrates the faunal similarity. This method is complementary to the hCA analysis because, in addition to showing the large-scale dichotomies between provinces, faunal connections between spatial units may be depicted by superposing minimum spanning trees. Multiple runs were performed for each time-bin in order to maximize the chance of capturing the global minimum of the objective function – multiple runs being: 25 successive computations starting from different random initial configurations of the ordinated space, which allow the iterative algorithm to potentially converge toward different NMDS projections, from which the one with the smallest stress-value is finally retained.
- (3) Finally, we used the Bootstrap Spanning Network method (BSN) developed by Brayard et al. (2007, 2009). This recent approach gives a simple, intuitively legible picture of the nested as well as gradational taxonomic similarity relationships, hence providing a good synthesis (and additional insights) between

hierarchical clustering and ordination in reduced space results. This method involves three distinct steps: i) building a faunal connection network between all spatial units by using the similarity matrix based on a Bray–Curtis distance (favouring the co-occurrence of species; Bray and Curtis, 1957); ii) testing the robustness of connections by measuring their bootstrap support values which are calculated by generating partial networks based on random subsamples of the data matrix; iii) deleting the weak connections (*i.e.*, bootstrap support values <50) in order to simplify the final network and maximize the product of bootstrap support values of remaining connections. Applied in superposition to paleobiogeographical maps, this analysis allows a robust appraisal of exchange ways, including faunal gradients or reticulated biogeographical structures showing strong species mixing.

3. Results

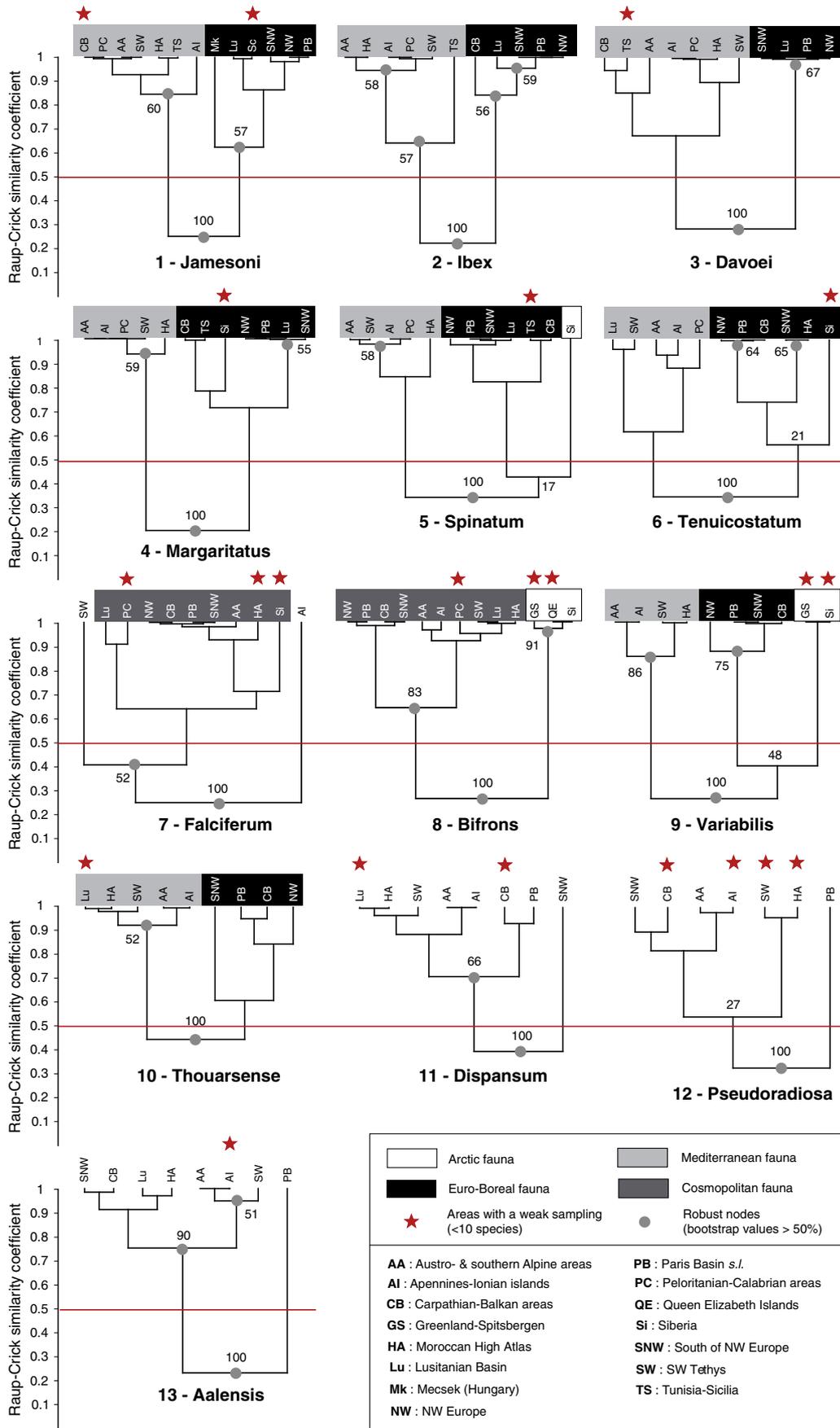
3.1. Hierarchical cluster analyses

The dendrograms resulting from hCA analyses allow a first appraisal of provincialism patterns through the studied interval (Fig. 2). In order to be consistent, large-scale paleobiogeographical units are defined by choosing a threshold of 50% of similarity between faunas (*i.e.*, Raup–Crick coefficient = 0.5). During the Early Pliensbachian (*i.e.*, Jamesoni, Ibex, and Davoei Zones), we note a strong faunal dichotomy between basins from the northern (Mk, Lu, Sc, SNW, NW, PB) and southern (PC, AA, SW, HA, TS, AI) margins of the NW Tethys, illustrating the Euro-Boreal vs. Mediterranean provincialism (see Fig. 1 for abbreviations). Only the Carpathian–Balkan domain (CB) displays fluctuating faunal affinities for this time interval. The main latitudinal dichotomy is maintained during the Late Pliensbachian but slight changes may be highlighted: 1) the Tunisian–Sicilian area (TS) is included in the Euro-Boreal group (NW, PB, Lu, SNW, CB); 2) the Siberian area (Si) seems to progressively depart from the Euro-Boreal cluster during the Spinatum Zone (despite the low bootstrap value of nodes). During the Tenuicostum Zone (Early Toarcian), two main groups are evidenced by the dendrogram but the Siberian area (Si) returns to the Euro-Boreal cluster whereas the Lusitanian Basin (Lu) is merged to the Mediterranean group. During the Falciferum Zone, most spatial units show high faunal similarities (>0.5) disturbing the major dichotomy. Only the Apennine–Ionian regions (AI) and the south of NW Europe (SNW) appear different. A distinct Arctic biota (GS, QE, Si) reappears during the Bifrons Zone, and in parallel, the northern and southern basins are progressively differentiated (in spite of high similarity values), before to be distinct during the subsequent Variabilis Zone. Importantly, the Lusitanian Basin (Lu) still remains in the Mediterranean cluster. Finally, we note a strong dichotomy between the Euro-Boreal and Mediterranean ammonites during the Thouarsense Zone. Owing to the poor sampling of northern basins, results are more difficult to interpret for the three last biochronozones of the Late Toarcian. Nevertheless, it seems that southern basins are generally clustered and that the Paris Basin (PB) is often isolated.

3.2. Non-metric multi-dimensional scaling

The results displayed by NMDS analyses are fairly concordant with those displayed by the hCA analyses (Fig. 3). Two main clusters presenting a steady latitudinal segregation are evidenced during the Early Pliensbachian. From the Margaritatus Zone to the Spinatum Zone, the major dichotomy is maintained but the Tunisian–Sicilian area (TS)

Fig. 2. Dendrograms resulting from hierarchical cluster analyses (hCA) computed for successive ammonite biochronozones of the Pliensbachian–Toarcian interval. Red lines indicate a faunal similarity of 50% and discriminate large-scale provinces represented by different colors (except for the three last time-bins). Numbers represent the robustness of main nodes after 1000 bootstraps.



get closer to the Mediterranean group and the Siberian area becomes progressively distinct from the Euro-Boreal cluster in the NMDS space. It is also noteworthy that, in spite of their distant positions, the Carpathian–Balkan (CB) and Tunisian–Sicilian (TS) regions could act as possible relays between the Euro-Boreal and Mediterranean provinces throughout the Pliensbachian. Nevertheless, as this result may be influenced by the local prevalence of cosmopolitan species, this link will be reappraised with BSN analyses which are more suitable to detect robust faunal networks. During the Tenuicostatum Zone, two main groups are still identified but noticeable changes take place, with the progressive merging of Siberia (Si) and High Atlas (HA) into the Euro-Boreal domain, and the convergence of Lusitanian faunas to Mediterranean ones. During the Falciferum Zone, the chief dichotomy disappears and some areas such as the south-western and the Apennines–Ionian domains (SW and AI) become very isolated. In spite of slight latitudinal segregations, all NW Tethyan basins are still clustered during the Bifrons Zone but those from the Arctic realm show a clear separation (GS, Si, QE). The triple provincialism reappears during the Variabilis Zone and the Euro-Boreal vs. Mediterranean dichotomy is maintained at the very beginning of the Late Toarcian (Thouarsense Zone). Finally, this contrast is less distinct during the last three time-bins.

3.3. Bootstrap spanning networks

From the Jamesoni to the Davoei Zones, the configuration of faunal networks confirms the main segregation between the Euro-Boreal and Mediterranean domains, with a robust and constant exchange route located in the Austro- and southern Alpine areas (Fig. 4). Surprisingly, the Carpathian–Balkan region is often connected to the Mediterranean network but these links are not very robust. Interestingly, the organization of faunal networks latitudinally fluctuates through the Early Pliensbachian. The results show looped connection patterns to the north (e.g., between NW, SNW, PB) and gradational exchanges to the south (e.g., PC, TS, HA) during the Jamesoni and Davoei Zones, and conversely during the Ibex Zone. Throughout the Late Pliensbachian, the provincialism is maintained and characterized by a strong mixing in the Mediterranean domain (e.g., between SW, PC, AI, AA) and by gradual exchanges in the Euro-Boreal one. Nevertheless, the Siberian area (Si) is progressively disconnected from the Euro-Boreal domain between the Margaritatus Zone and the Spinatum Zone. Although the main biogeographical contrast persists during the Tenuicostatum Zone, new interprovincial exchange ways located in the western part of the studied area (i.e., between Lu and SW and between HA and SNW) are made evident by BSN analyses. The main structural changes occur during the Falciferum Zone, with strengthened exchanges between Arctic and Euro-Boreal domains on the one hand (e.g., Si and CB), and between Euro-Boreal and Mediterranean areas on the other (e.g., between AA, SNW, PB). The interprovincial mixing is still high during the subsequent Bifrons Zone but it is noteworthy that the Lusitanian connection disappears in the western part of the studied area. During the Variabilis Zone, exchanges decrease and the Arctic biota previously close to the Euro-Boreal one is clearly differentiated. Finally, the paleobiogeographical patterns fluctuate during the Late Toarcian marked by new faunal exchange ways in the SNW (especially during the Thouarsense and Dispansum Zones).

4. Discussion

4.1. Evolution of ammonite paleobiogeography

4.1.1. The Pliensbachian provincialism

The results of hCA, NMDS, and BSN analyses are quite concordant and allow an objective characterization of paleobiogeographical patterns through the studied interval (Fig. 5). In agreement with

numerous works presenting descriptions and analyses of ammonite biogeography during the Early Jurassic (see Dommergues et al., 2009 for a review), a significant faunal contrast is confirmed between the Mediterranean and Euro-Boreal domains during the Early Pliensbachian (Fig. 5A), with an apparent frontier ranging from the Betic range (southern Spain) to the Briançonnais ridge (Alps). Interestingly enough, this latitudinal partitioning is roughly similar for brachiopods (Vörös, 1977, 1980), ostracods (Arias and Whatley, 2005, 2009), and bivalves (Hallam, 1977; Liu et al., 1998). This concordance between organisms which are physiologically and phylogenetically unrelated and of markedly differing modes of life suggests common regional paleobiogeographical constraints (see below). Typically, the Euro-Boreal domain was mostly dominated by representatives of the Phricodoceratidae, Polymorphytidae, and Liparoceratidea, whereas the Eoderoceratida and Harpoceratinae prevailed in southern regions during the Early Pliensbachian (Meister and Stampfli, 2000). Beyond these distinctive compositions, Dommergues et al. (2009) also showed that species richness estimates were twice as high for the Mediterranean domain, probably related to high levels of endemism (Dommergues and El Hariri, 2002). Nevertheless, both provinces underwent a similar drop in ammonite diversity during the Davoei Zone, the causes of which still remain debated (Dommergues et al., 2009; Dera et al., 2010). In addition, a robust faunal connection is emphasized in the Austro- and southern Alpine areas, allowing interprovincial exchanges and biostratigraphical correlations at the NW Tethyan scale (Dommergues and Meister, 1991). These results corroborate those of Dommergues et al. (2009), although the latter authors also identified a second faunal relay in the Pontic region (not considered in our study). Notwithstanding these potential links, ammonite faunal exchanges remained restricted at this time with few northward expansions of Mediterranean Phylloceratidae, Juraphyllitidae, and Lycoceratidae (Dommergues and Meister, 1991; Meister and Stampfli, 2000). Besides, sporadic occurrences of these epicontinental taxa in Dobrogea (Romania) and Kotel Klippe (Bulgaria), associated with regionally low endemism levels (Dommergues et al., 1987a), could explain the brief and fluctuating Mediterranean affinities of the Carpathian–Balkan region during the Early Pliensbachian (Meister and Stampfli, 2000).

During the Late Pliensbachian, the ammonite diversity gradient and the main faunal dichotomy remained globally unchanged (Smith and Tipper, 1986) (Fig. 5B,C). Except the Euro-Boreal affinity of the distant Tunisian–Sicilian area, which appears to have originated from sampling biases, the unique difference concerns the definitive merging of the Carpathian–Balkan regions to the Euro-Boreal province, probably due to the prominent radiation of Euro-Boreal Amaltheidae (*Amaltheus* and *Pleuroceras*) in all northern and some southern basins (e.g., Apennines and Subbetic chains) (Enay and Mangold, 1982; Meister, 1988; Meister and Stampfli, 2000; Smith et al., 2001). By contrast, the Arieticeratinae and Harpoceratinae were prevalent in the southern basins (Dommergues and Meister, 1991; Meister and Stampfli, 2000), leading to a strong faunal homogeneity in the Mediterranean domain. Most important, we also note that the Siberian ammonite species, closely similar to the Euro-Boreal ones during the Margaritatus Zone, differentiated during the subsequent Spinatum Zone owing to a strong endemism of members of the Amaltheidae (Meledina and Shurygin, 2001; Meledina et al., 2005). As empirically suggested by Zakharov et al. (2003), this episode therefore marks the first faunal differentiation of the Arctic province. Consequently, our results statistically contradict hypotheses based on ammonite genera, which suggested a first emergence of the Arctic biome during the Middle Jurassic (Dommergues, 1994; Westermann, 2000; Zakharov et al., 2002).

4.1.2. Disruption during the crisis

As previously suggested by empirical studies focusing on the distribution of ammonite faunas in Europe and North Africa (Enay and Mangold, 1982; Cariou et al., 1985; Mouterde and Elmi, 1991; Macchioni and Cecca, 2002; Cecca and Macchioni, 2004), our analyses

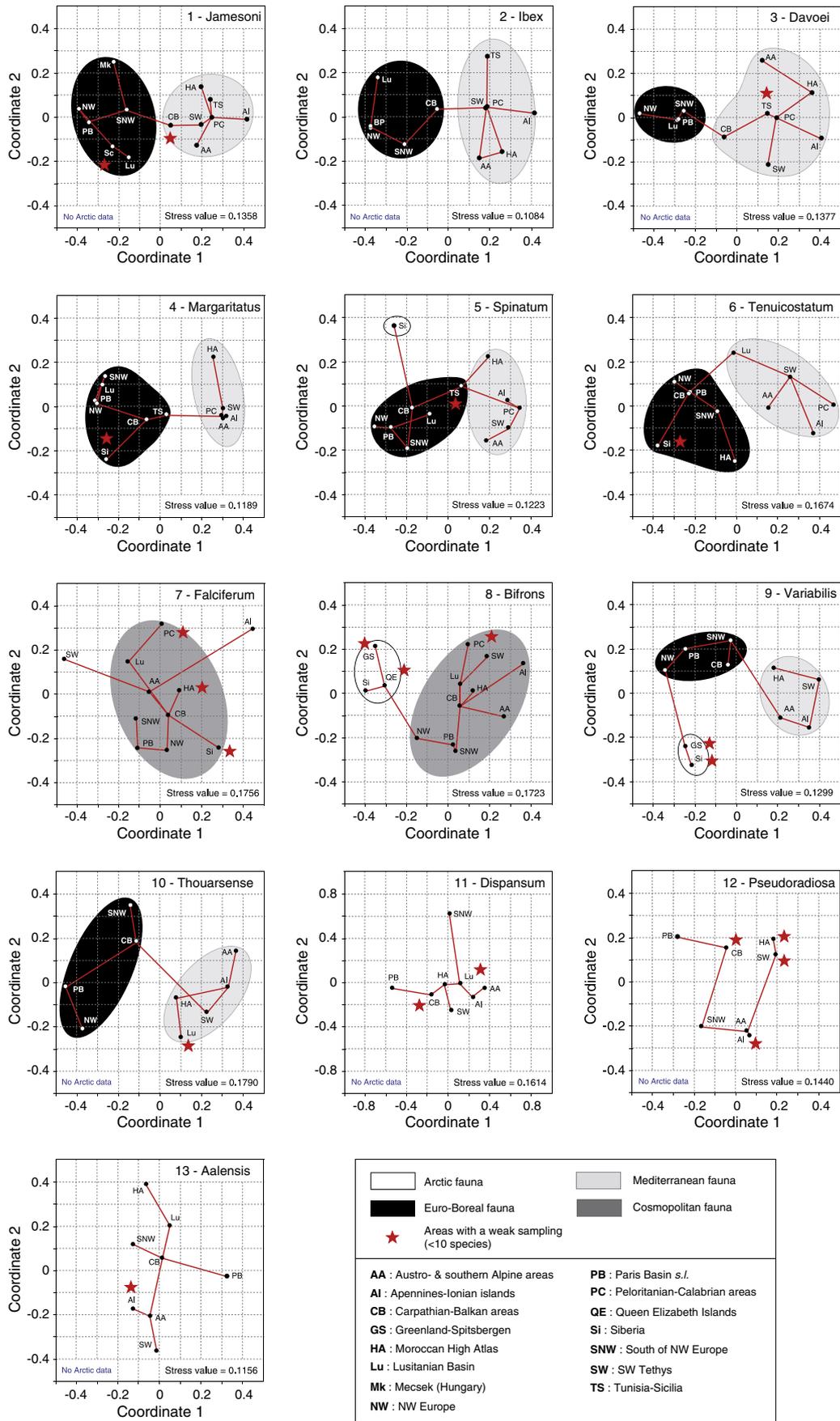


Fig. 3. Projections of spatial units in NMDS spaces (Non metric Multi-Dimensional Scaling) in which faunal networks are computed using minimum spanning trees. Colors are similar to those used in Fig. 2.

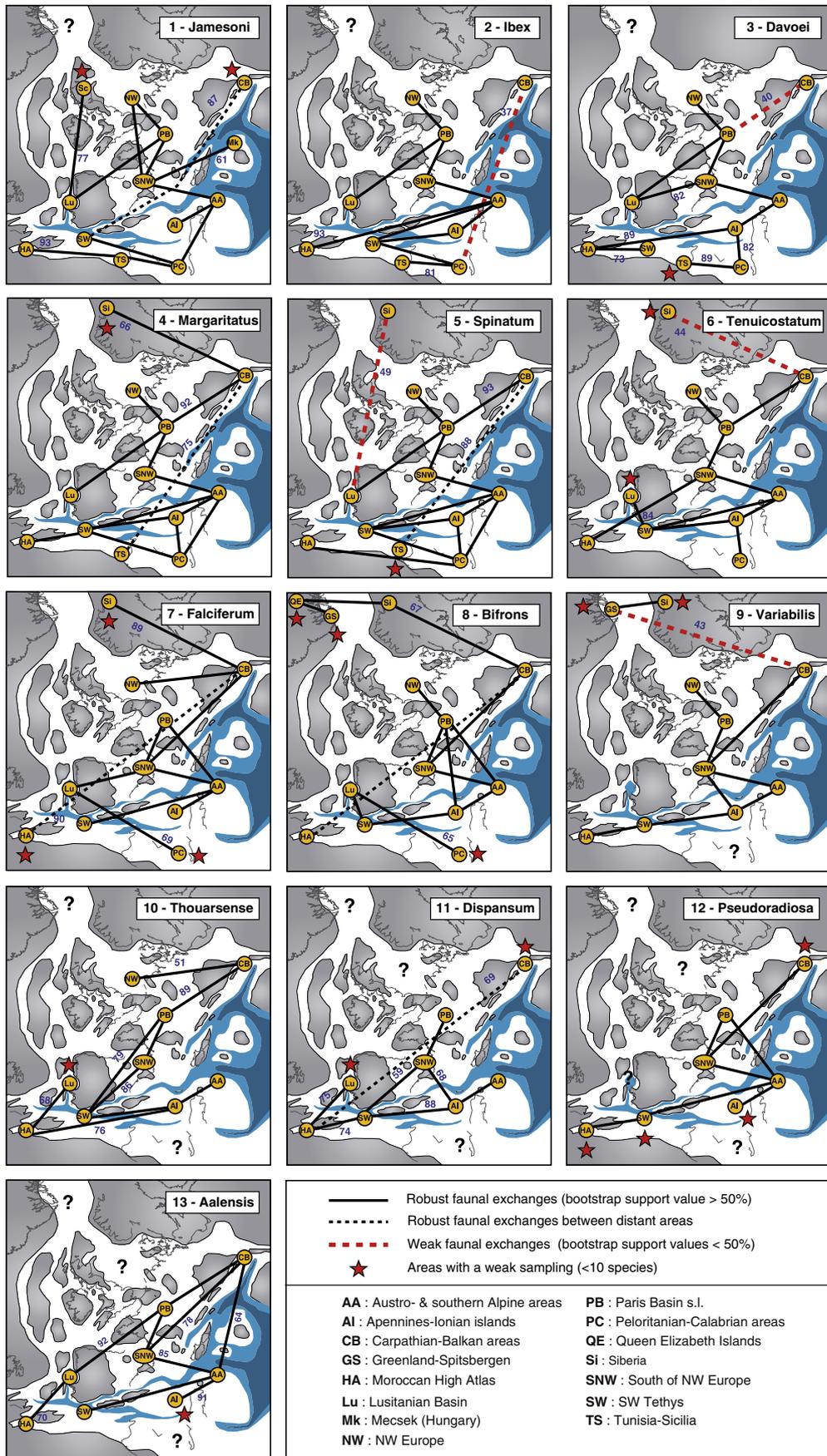


Fig. 4. Maps representing the Bootstrap Spanning Networks computed for the 13 ammonite biochronozones of the Pliensbachian–Toarcian interval. Numbers represent the bootstrap support values for each link (100% if not specified). Note that Siberia (Si) is located in the Arctic domain but is voluntarily positioned in the northern part of the NW Tethyan map.

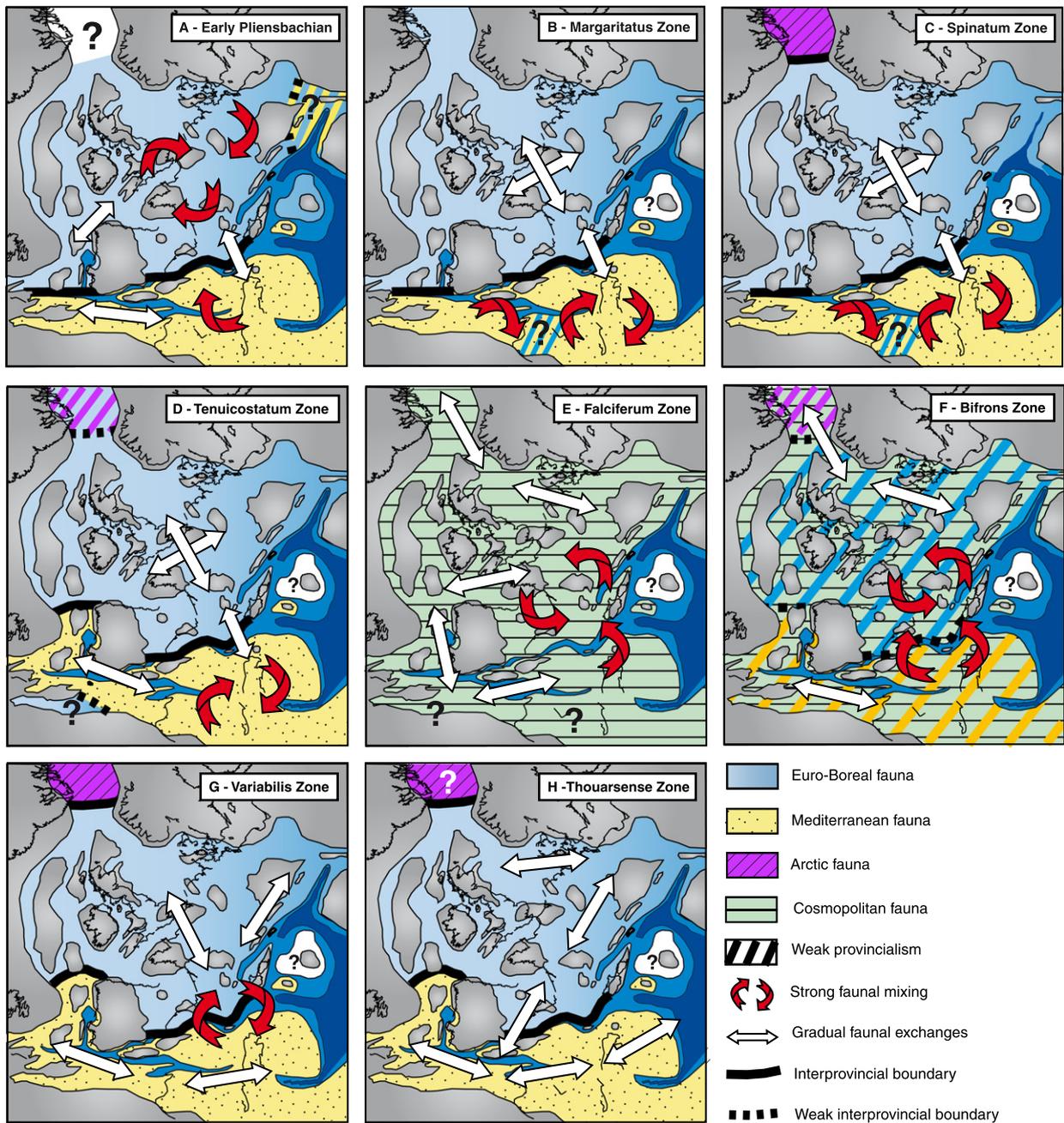


Fig. 5. Interpretative maps detailing the evolution of ammonite paleobiogeographical patterns during the Pliensbachian–Toarcian interval. Owing to the similarity of results, only one map named “Early Pliensbachian” is presented for the Jamesoni, Ibex, and Davoei Zones. Data corresponding to the Dispansum, Pseudoradiosa, and Aalensis Zones are not represented owing to the insufficient sampling (especially in the northern areas).

emphasize a progressive disappearance of the triple provincialism (Arctic vs. Euro-Boreal vs. Mediterranean) at the beginning of the Toarcian. During the Tenuicostatum Zone (Fig. 5D), the NW Tethyan faunal partitioning was still present but its western boundary shifted northward as a consequence of the incipient merging of the Lusitanian Basin to the Mediterranean province. According to Mouterde and Ruget (1975) as well as Macchioni and Cecca (2002), northward propagations of Mediterranean Harpoceratinae and Dactyloceratidae (e.g. *Lioceratoides* and *Eodactylites*) could explain this southern affinity. At the same time, higher latitudes underwent a similar change in ammonite paleobiogeography marked by a progressive homogenization between the Arctic and Euro-Boreal faunas (shown by the hCA and NMDS analyses). This disruption is coherent with

faunal events recorded by other marine groups, including poleward movements of Euro-Boreal foraminifers and ostracods (Zakharov et al., 2006; Nikitenko, 2008), as well as the first incursion of belemnites (before solely present in Europe) into Siberian basins (Doyle, 1987, 1994). Nevertheless, patterns emerging from the BSN analysis slightly moderate this conclusion, because the presence of a few endemic ammonite species belonging to the genera *Arctomercaticeras* and *Kedonoceras* could support the persistence of a tenuous provincialism in the Arctic seas.

The Falciferum Zone marks the onset of the provincialism disruption, with a strong homogenization of all Tethyan and Arctic ammonite species (Fig. 5E). These results contradict the empirical observations of Mouterde and Elmi (1991) who suggested a dislocation

solely recorded at the family level. According to the BSN analysis, this event was characterized by a multiplication of interprovincial faunal networks, both westward and eastward, and marked by a proliferation of cosmopolitan taxa that originated in the Mediterranean domain (Macchioni and Cecca, 2002). Similar mixing events and northward expansions of southern taxa have been recently demonstrated for other marine organisms, including ostracods (Arias and Whatley, 2005), bivalves (Damborenea, 2002), and brachiopods belonging to the Koninckinidae (Vörös, 2002). These changes were not restricted to the NW Tethyan and Arctic domains, as contemporaneous events were also evidenced in several oceanic domains. This includes incursions of equatorial ammonites such as Arabian–Madagascan Bouleiceratidae into Mediterranean basins (Rulleau et al., 2003), poleward extensions of bivalve biochores in the southern hemisphere (Damborenea, 2002), and migrations of Andean bivalves in the NW Tethys through the Hispanic Corridor (Aberhan, 2001, 2002). Independently of the prominent mass extinction, the Early Toarcian therefore corresponds to a period of worldwide paleobiogeographical disturbance affecting most marine organisms. Surprisingly, the only exception concerns the belemnite faunas, which came completely differentiated (Arctic vs. Euro-Boreal vs. Mediterranean) during this episode (Doyle, 1987, 1994).

4.1.3. The post-crisis recovery

In parallel with a rapid recovery of ammonite diversity levels (Dera et al., 2010), the Middle Toarcian marks a progressive resurgence of provincial patterns. During the Bifrons Zone (Fig. 5F), the NW Tethyan ammonite species were still poorly differentiated because a significant interprovincial mixing prevailed on the eastern margins. Most of genera belonging to the Dactyloceratinae, Harpoceratinae and Hildoceratinae were cosmopolitan. The rare exceptions concerned the Zugodactylites and Septimaniceras which were restricted to the Euro-Boreal basins, and the Mercaticeras, Leukadelia, and Nejdia which were typical of Mediterranean domains (Mouterde and Elmi, 1991). Nevertheless, the deletion of western connections through the Lusitanian Basin would have created a weak latitudinal faunal gradient at the species level. At higher latitudes, species from Greenland, Siberia, and Queen Elizabeth Islands were still similar to the Euro-Boreal ones according to the BSN analyses (less so than during the Falciferum Zone), but already distinct according to the hCA and NMDS results. This could suggest a weak provincialism, notably characterized by the presence of endemic *Omolonoceras*.

During the Variabilis Zone (Fig. 5G), the triple partitioning of species (*i.e.*, Arctic vs. Euro-Boreal vs. Mediterranean) was completely re-established, in spite of severe extinction pulses recorded at both species and genus levels (Dera et al. 2010). These results therefore corroborate previous interpretations of Mouterde and Elmi (1991), who mentioned the prevalence of *Haugia* and *Pseudolioceras* in the Euro-Boreal domains. Also, we note that the interprovincial boundary shifted northward as the result of the definitive merging of the Lusitanian Basin to the Mediterranean province. This partitioning was maintained during the subsequent Thouarsense Zone (Late Toarcian) (Fig. 5H), but in contrast to previous paleobiogeographical patterns, the main interprovincial network moved to the Betic chains (southern Spain).

During the last biochronozones of the Toarcian, the paleobiogeographical patterns are slightly obscured because available data are scarcer (Figs. 2–4). Nevertheless, it appears likely that, despite a strong interprovincial mixing, a weak provincialism occurred during the Dispansum and Pseudoradosa Zones, with a differentiation of *Pseudolioceras* in the Arctic domains, *Phlyseogrammoceras* and *Hudlestonia* in the Euro-Boreal domains, and *Cagliceras* and *Geczyeras* in the southern areas (Mouterde and Elmi 1991). Finally, a multiplication of interprovincial exchange routes could suggest a new disruption during the Aalensis Zone, but this hypothesis needs to be confirmed using a better sampling.

4.2. Factors constraining the faunal segregation

4.2.1. Paleogeography

The faunal partitioning displayed by Pliensbachian ammonites is quite intriguing and its origin has been widely discussed (see Dommergues et al., 2009 for a review). The principal control is the paleogeography of the NW Tethyan realm, which consisted of epicontinental basins separated by emerged lands and very shallow areas to the south of the Euro-Boreal domain (Dommergues, 1982; Cariou et al., 1985; Dercourt et al., 1985; Dommergues et al., 1987b; Dommergues and Meister, 1991; Meister and Stampfli, 2000). The efficiency of this latitudinal threshold would be intrinsically related to tectonic events and eustatic changes, so that it could have constituted a full physical barrier during regressive sequences or a faunal filter during sea-level highstands. In contrast, alternative paleogeographical reconstructions suggest a large and deep marine trough (Thierry et al., 2000), preventing for instance massive expansions of brachiopods from Mediterranean microplates (Vörös, 1993, 2005). However, this second hypothesis fails to explain the segregation of supposed hemipelagic organisms such as ammonites.

Toward higher latitudes, the narrow and latitudinally-elongated Viking Corridor probably regulated the mixing between Arctic and Euro-Boreal ammonites (Smith et al., 2001) (Fig. 1). Since its opening in the Sinemurian (Doré, 1991), faunal exchanges continuously occurred but their magnitude was weighted by sea-level fluctuations and current directions (Bjerrum et al., 2001). As a consequence, periods of low sea level such as the Late Pliensbachian were probably favourable to stronger segregations between the Arctic and Euro-Boreal domains. Nevertheless, other exchange routes cannot be excluded. For instance, recent discoveries of Euro-Boreal *Amaltheus* in Iran and Japan would suggest sporadic circum-Laurasian exchanges by Asian margins (Seyed-Emami et al., 2008; Nakada et al., 2010). In contrast, we exclude broad circum-American connections because faunal assemblages from Pacific terranes suggest latitudinal faunal gradients in the Panthalassa Ocean marked by poorly diversified Euro-Boreal ammonites in Stikinia and Quesniella, and dominant Tethyan species in Wrangelia (Smith et al., 2001). In addition, we presume that even if the Hispanic Corridor was intermittently active since the Late Sinemurian–Early Pliensbachian interval (Fig. 1) (Aberhan, 2001, 2002; Venturi et al., 2006; Dera et al., 2009b), this epicontinental seaway was certainly too shallow for allowing massive movements of hemipelagic organisms such as ammonites. Accordingly, Moyne et al. (2004) suggest that the first important migration events through this corridor occurred during the Middle Jurassic.

During the Toarcian, the paleogeographical constraints remained roughly similar, except in the Lusitanian Basin where major tectonic events occurred at the beginning of the Tenuicostatium Zone (Duarte, 1997). As a consequence, we suggest that uplifts could have stopped (or reduced) the dispersal of Euro-Boreal ammonites by western routes and could partly explain the higher latitudinal position of the provincial boundary during the Toarcian (Fig. 5D,G,H). Nevertheless, it is not excluded that such local constraints occurred earlier because Dommergues and El Hariri (2002) and Reggiani et al. (2010) noted that the Mediterranean ammonites and calcareous nannofossils were already abundant in the Lusitanian Basin since the Spinatum Zone (Late Pliensbachian). This may indicate that the isolation of the Lusitanian Basin from Euro-Boreal domains was progressive and probably related to successive events.

4.2.2. Paleoenvironmental discrepancies

As an alternative hypothesis, paleoecological differences between Euro-Boreal and Mediterranean domains have often been invoked to explain the faunal patterns of the Pliensbachian (Hallam, 1972; Enay and Mangold, 1982; Alméras and Elmi, 1993; Vörös, 2005; Arias, 2007; Dommergues et al., 2009). Typically, the Euro-Boreal area was dominated by shallow silled basins surrounded by numerous

archipelagos (Thierry et al., 2000). Recent sedimentary and geochemical studies show that these marine paleoenvironments were strongly influenced by basinal restrictions favouring anoxic events, recurrent freshwater influxes from deltaic systems, incursions of boreal currents, and important nutrient inputs (Saalen et al., 1996; Wignall et al., 2005; McArthur et al., 2008; Dera et al., 2009b). In contrast, the Mediterranean domain was physically more stable and characterized by open-marine paleoenvironments influenced by warm and nutrient-rich surface water flows from the Tethyan Ocean (Dera et al., 2009b; Reggiani et al., 2010). These conditions were especially suitable for the development of carbonate platforms and the emergence of rich tropical biomes (Dommergues et al., 2009).

As suggested by Hallam (1972), these latitudinal differences in environmental stability, substrate, and food availability probably drove the regional distribution of benthic faunas in the NW Tethyan seas. For example, Hallam (1972) noted that the Early Jurassic gastropods were more abundant in the Mediterranean domain owing to the presence of reef paleoenvironments. In contrast to other epibenthic mollusc groups, bivalve populations prevailed in the Euro-Boreal areas because of their supposedly better resistance to adverse ecological conditions (Hallam, 1972). Such a paleoenvironmental control may be active for Jurassic ammonites. Indeed, it is usually accepted that some morphological groups (and consequently some taxa) occupied certain habitats and distinct depths (Tintant et al., 1982; Elmi and Alm eras, 1984; Marchand, 1984; Westermann, 1996), so that little disturbances in ecosystems could have triggered extinction pulses in different communities during the Pliensbachian–Toarcian interval (Dera et al., 2010). The propensity of high- and mid-latitude basins to be affected by stressing conditions (especially during climate change) could therefore explain the lower taxonomic richness of ammonites in the Arctic and Euro-Boreal basins compared to the Mediterranean domain. In addition, it is obvious that, independent of paleoenvironmental factors, intrinsic biological parameters such as trophic chains, interspecific competition, or population dynamics were also of prime importance in structuring the diversity and the latitudinal distribution of ammonite faunas (Dommergues et al. 2009).

4.2.3. Paleocenic circulations

As mentioned above, the direction of surface seawater flows would have been markedly different between the Euro-boreal and Mediterranean domains, so that it could constitute a secondary physical barrier preventing massive exchanges between the two marine domains. Recent hypotheses based on both phytoplankton assemblages and neodymium isotope data suggest prevailing southward directed boreal currents in the first domain and opposite southeasterly Tethyan oceanic currents in the second one (van de Schootbrugge et al., 2005; Dera et al., 2009b; Reggiani et al., 2010). The evolution of these parameters would have been especially important for the propagation and segregation of small-sized and planktic fossils such as calcareous nannofossils and ostracods (Arias, 2007; Reggiani et al., 2010). Regarding the similar mode of life of ammonites during their early developmental stages (Shigeta, 1993), we presume that changes in surface currents cannot be excluded to explain some dispersal events. Nevertheless, improvements in Early Jurassic paleocenic models (implying GCM simulations) are required to more confidently reconstruct their influence.

4.2.4. Paleoclimatic gradients

First mentioned in the pioneering works of Neumayr (1883), latitudinal temperature gradients are often regarded as essential to the development of large-scale provincialism and biodiversity gradients in both past (Brayard et al., 2004, 2005; Cecca et al., 2005a,b; Brayard et al., 2006; 2007; Cecca, 2009) and modern cephalopod communities (Nesis, 2003; Rosa et al., 2008). However, most authors have questioned the influence of this parameter during the Early Jurassic (Hallam, 1972; Doyle, 1987; Dommergues and

Meister, 1991; Doyle, 1994; Dommergues et al., 2009): it was generally suspected that, in a greenhouse context, paleoclimatic conditions were globally warmer, with reduced thermal differences between equatorial and polar areas (Hallam, 1985; Frakes et al., 1992). Conversely, recent data based on paleobotany, sedimentary indices, clay mineralogy, modelling experiments, and oxygen isotope analyses reveal a strong division of climatic zones during the Early Jurassic (Chandler et al., 1992; McArthur et al., 2000; Rees et al., 2000; Bailey et al., 2003; Wignall, 2005; Dera et al., 2009a,b). Warm and semiarid conditions prevailed in the Mediterranean domain, whereas the Euro-Boreal area was characterized by a subtropical humid climate affected by seasonal megamonsoons leading to frequent northerly freshwater influxes. At higher latitudes, cold to temperate conditions and the possible formation of partial ice caps have been suggested for the Late Pliensbachian because of glendonite (cold water carbonates) occurrences in Siberia and high oxygen isotope values (Price, 1999; Suan et al., 2010; Dera et al., 2011). In the light of these recent data, the latitudinal partitioning of temperature and freshwater influxes should therefore be considered when trying to explain some episodes of ammonite provincialism during the Early Jurassic.

4.3. Triggers of paleobiogeographical changes

Most authors assume that eustatic fluctuations have actively shaped paleobiogeographical and macroevolutionary patterns of ammonites by isolating proximal populations during regressive sequences and promoting interbasinal connections and faunal exchanges during transgressions (Enay, 1980; Neige et al., 1997; O'Dogherty et al., 2000; Sandoval et al., 2001; Dommergues and El Hariri, 2002; Bourillot et al., 2008). Nevertheless, paleoclimatic parameters are also decisive because, as mentioned above and in numerous studies (Ross et al., 1992; Wiese and Voigt, 2002; Jansson, 2003; Brayard et al., 2005; Cecca et al., 2005a,b; Brayard et al., 2006), expansions and shifts in climatic belts may lead to displacements of ammonite faunas toward new suitable regions. Because paleoclimatic gradients are generally contrasted during cool periods and more homogeneous during warm episodes (IPCC, 2007), the evolution of the average temperature of Earth may induce considerable changes in paleobiogeography by expanding or reducing the spatial range of species. Actually, this straightforward model is verified in the light of current global warming, with poleward migrations of marine and continental species of about 6 km per decade during the last century (Parmesan and Yohe, 2003).

Beyond these paleoenvironmental triggers, the impact of extinction pulses cannot ever be excluded. As suggested by Aberhan and F rsich (1997, 2000), the rapid disappearance of provincial species theoretically facilitates invasions and proliferation of cosmopolitan taxa in vacated niches.

These different examples show that paleobiogeographical changes are complex processes in which the role of each paleoenvironmental and biotic factor is difficult to disentangle because of their interrelations. We suggest, however, that paleoclimatic changes were of prime importance because they exerted a strong influence on both the regional emergence of lethal anoxic conditions and glacio-eustatic variations during the studied period (Saalen et al., 1996; McArthur et al., 2008; Suan et al., 2010). Climate changes may therefore be considered as direct physical constraints moving, expanding, or reducing the spatial range of paleoecological niches inhabited by ammonite populations whereas eustatic and extinction events rather act as secondary factors regulating or facilitating the dispersal of organisms.

4.3.1. Impacts of cooling events and regressive sequences

In order to better understand the mechanisms underlying changes in ammonite provincialism, we compare the paleobiogeographical patterns with ammonite diversity fluctuations, transgressive/ regressive cycles, and oxygen isotope data ($\delta^{18}\text{O}$) depicting changes in

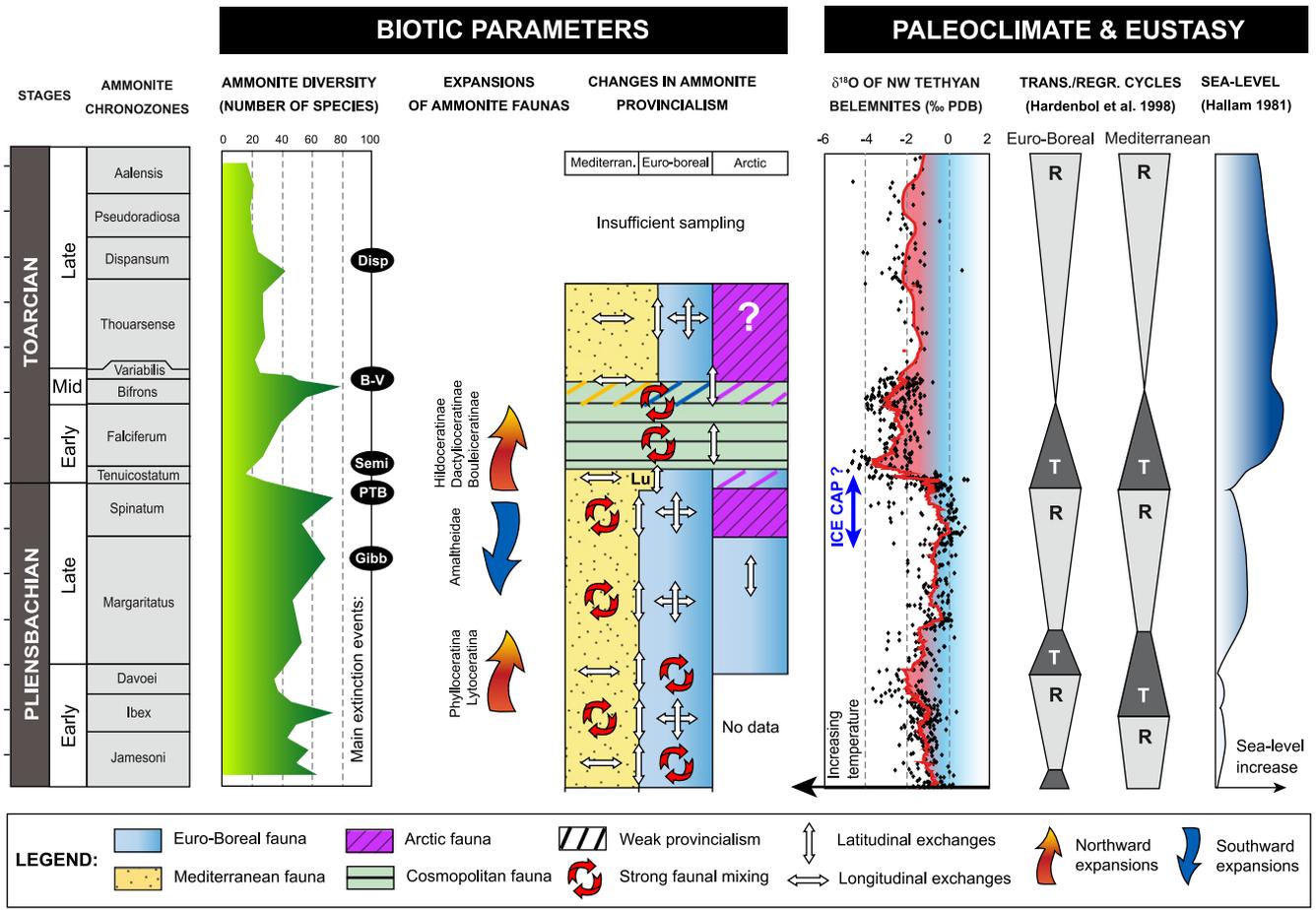


Fig. 6. Correlations between paleobiogeographical patterns, ammonite diversity levels, paleoclimatic proxies, and sea-level changes during the Pliensbachian–Toarcian interval. Variations in ammonite species richness from Dera et al. (2010). Belemnite $\delta^{18}\text{O}$ data from the synthesis of Dera et al. (2009a). Transgressive–regressive cycles and sea-level changes respectively from Hallam (1981) and Hardenbol et al. (1998). Lu indicates the merging of the Lusitanian Basin to the Mediterranean realm. See the main text for further details concerning the spatial movements of ammonite faunas. Gibb, Gibbosus Subzone; PTB, Pliensbachian–Toarcian boundary; Semi, Semicelatum Subzone; B–V, Bifrons–Variabilis Zones; Disp, Dispsansum Zone.

seawater temperature (Fig. 6). It is noteworthy that the first emergence of Arctic ammonite faunas occurred during a sea-level fall, at the onset of a drastic cooling event evident during the Spinatum Zone (Bailey et al., 2003; Rosales et al., 2004; van de Schootbrugge et al., 2005; Dera et al., 2009b; Suan et al., 2010). Conceivably, we suggest that cooler conditions would have strengthened climatic contrasts between high and mid-latitudes, initiated glacio-eustatic regressions isolating proximal basins, and finally allowed the creation of regional biotopes favouring the proliferation of distinctive faunas. Also, coeval ammonite radiations in independent biomes was likely responsible for the high diversity levels recorded during the Late Pliensbachian (Dera et al., 2010). Similarly, this climatic-eustatic model appears to explain the paleoecological recovery reflected in biogeographical patterns during the Middle–Late Toarcian, as a drop in temperature and an incipient regression occurred at the end of the Bifrons Zone (Dera et al., 2009b). Nevertheless, it is intriguing that this provincial pattern was re-established during a period of low diversity related to the Bifrons–Variabilis extinction pulse (Dera et al., 2010).

4.3.2. Roles of warming events, transgressive sequences, and extinctions

As suggested by Macchioni and Cecca (2002) and Cecca and Macchioni (2004), the main disruption in ammonite provincialism could have been directly related to a drastic rise in seawater temperature (5 to 7 °C) during the Early Toarcian (McArthur et al.,

2000; Bailey et al., 2003; Rosales et al., 2004; van de Schootbrugge et al., 2005; Gómez et al., 2008; Suan et al., 2008; Dera et al., 2009b). Similar to short episodes described during the Early Triassic (Brayard et al., 2005, 2006, 2007), we postulate that this global warming event, coupled with an attenuation in latitudinal climatic contrasts, could have gradually expanded the spatial range of thermophile species during the Tenuicostatum Zone and then totally disrupted provincialism by strong interprovincial exchanges during the thermal high of the Falciferum Zone. Naturally, the contemporaneous marine transgression and mass extinction were of prime importance, facilitating interbasinal networks and vacating ecological niches occupied by endemic species such as the Euro-Boreal Amaltheidae (Hallam, 1987; Cecca and Macchioni, 2004).

In contrast to the Early Toarcian event, it is surprising that, despite a strong drop in endemism levels (Dommergues and El Hariri, 2002), the slight warming event and the transgressive trend recorded during Davoei Zone had no affect on paleobiogeographical patterns (Dommergues et al., 2009). Even if some northward incursions of Mediterranean species occurred in the Euro-Boreal domain (Meister and Stampfli, 2000; Dommergues et al., 2001), they likely remained insufficient and too restricted to disturb the main paleobiogeographical dichotomy. This difference could potentially stem from threshold effects related to insufficient amplitude in temperature and sea level variations. Alternatively, the lack of major extinction pulses during the Early Pliensbachian could have been significant.

5. Conclusions

The paleobiogeographical patterns of ammonite occurrences in the NW Tethyan and Arctic seas were quantitatively investigated by applying hCA, NMDS, and BSN analyses for the 13 chronozones of the Pliensbachian–Toarcian interval. By combining the results, several conclusions can be drawn:

(1) A robust faunal dichotomy (Euro-boreal vs. Mediterranean) is confirmed throughout the Pliensbachian with a boundary ranging from the Briançonnais ridge (Alps) to the Subbetic chains (southern Spain). Nevertheless, a restricted interprovincial mixing area is evident in the Austro- and southern Alpine region. Paleogeographical barriers, paleoenvironmental differences, and strong climatic gradients account for this faunal partitioning. In addition, the Arctic species were fully differentiated during the Spinatum Zone, at the onset of a cooling event and a sea-level fall.

(2) During the Early Toarcian, the paleobiogeographical pattern was disrupted in two steps, with northward expansions of Mediterranean species to the Lusitanian Basin during the Tenuicostatum Zone, and faunal homogenizations linked to strong interprovincial exchanges during the Falciferum Zone. These events were related to a major marine transgression allowing better connections between basins, to a rise in temperature stretching the spatial range of southern species, and to selective extinctions in endemic taxa.

(3) The triple provincialism was progressively re-established during the Middle Toarcian, and conserved at the beginning of the Late Toarcian. The interprovincial boundary was slightly different because the Lusitanian Basin was definitively merged to the Mediterranean domain. As during the Pliensbachian, this segregation was related to sea level falls and temperature decreases after the Bifrons Zone.

(4) By comparing our results with available diversity estimates, oxygen isotope data, and eustatic curves, it appears that paleoclimatic changes, sea-level fluctuations, and extinction events explain most of the paleobiogeographical patterns displayed by ammonites during the studied period. These constraints are interrelated but act at different levels: i) paleoclimatic changes physically drive the displacements, expansions, or reductions of paleoecological niches inhabited by ammonite populations; ii) sea-level variations regulate the basinal connections which modulate the dispersion or the segregation of faunas; iii) extinction events remove endemic species and facilitate the invasion and the proliferation of cosmopolitan taxa in vacated domains. Nevertheless, slight divergences occurred during the Davoei Zone. This suggests that other parameters such as intrinsic population dynamics, interspecies competitions, threshold effects in paleoenvironmental changes, or complex interactions between all paleoenvironmental constraints could have complicated the paleobiogeographical dynamics.

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