



## Diversity and morphological evolution of Jurassic belemnites from South Germany



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### ABSTRACT

Belemnites are extinct cephalopods whose evolutionary history is representative of successful adaptive radiations during the Mesozoic. Nevertheless, a detailed understanding of the dynamics and palaeoenvironmental drivers of this evolution is still lacking. In order to fill this gap, we analyze the diversity and morphological disparity of Jurassic rostra from South Germany, and compare these patterns with other Euro-Boreal trends. We show that, after an early apparition of few dissimilar groups during the Hettangian–Sinemurian interval, belemnites experienced four periods of diversification (i.e., Early Pliensbachian, Middle–Late Toarcian, Early Bajocian, and Oxfordian) marked by morphological disparifications of rostra towards forms potentially optimized for different hydrodynamic properties. These adaptive radiations were interrupted at regional scale by four biological crises corresponding to morphological bottlenecks (i.e., Pliensbachian–Toarcian, Aalenian, Late Bajocian, and Kimmeridgian). Most of them were morphoselective, except the Aalenian extinction, which could be related to a prominent sea level fall. By comparing our results to palaeoenvironmental data, we show that warm temperate seawater temperatures might have favoured the diversification of belemnites, potentially by accelerating their metabolic rates, the population turnovers, and the evolutionary rates on the long term. Conversely, cooling or hyperthermal events correspond with biological crises. Migrations towards refuge areas located in the Arctic and Mediterranean domains could have been key factors for rapid post-crisis recoveries. Finally, the available data suggest a trend towards increased streamlining of the rostrum through the Jurassic.

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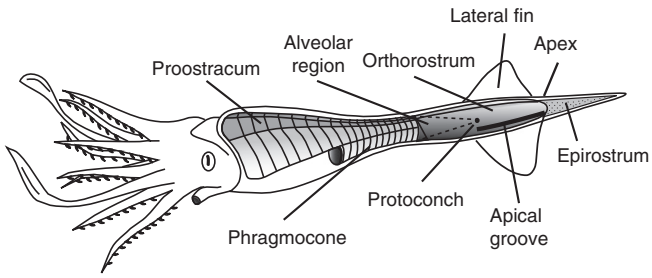
### 1. Introduction

Belemnites (Belemnitida order) are extinct cephalopods easily recognizable by the bullet shape of their calcitic rostra (Fig. 1), which are especially abundant in marine sediments of the Jurassic and Cretaceous. These organisms, considered as stem-group decabranchian coleoids (Doyle et al., 1994; Fuchs et al., 2015; Klug et al., 2016) (Fig. 1), composed a large part of the Mesozoic nekton and held a key position in the dynamics of trophic webs (i.e., as predators of small organisms and prey for marine reptiles and chondrichthyans; Massare, 1987; Doyle and MacDonald, 1993; Martill et al., 1994; Walker and Brett, 2002). According to their fossil record, these coleoids inhabited surface to deep waters of epicontinental domains, and were present at worldwide scale, both in the subtropical and polar areas (Stevens, 1963, 1965, 1971; Stevens and Clayton, 1971; Christensen, 1976; Doyle, 1987, 1994; Doyle et al., 1997; Christensen, 2002). In agreement with the regional distribution and the palaeoenvironmental differences in the taxonomic composition of most belemnite communities (Mutterlose

and Wiedenroth, 1998; Mariotti et al., 2012; Weis et al., 2012), recent geochemical analyses of rostra indicate that different species might have had different ecological preferences in terms of life depth, seawater temperature, or salinity (Dutton et al., 2007; McArthur et al., 2007; Dera et al., 2009; Rexford and Mutterlose, 2009; Mutterlose et al., 2010; Wierzbowski and Rogov, 2011; Li et al., 2012; Harazim et al., 2013; Stevens et al., 2014; Wierzbowski, 2015). Nevertheless, some eurytopic taxa likely migrated over several hundreds of kilometers and different depths during their lifetime (Christensen, 1997; Zakharov et al., 2006; Alsen and Mutterlose, 2009; Sørensen et al., 2015). According to Doguzhaeva et al. (2013), their colonization of deeper depths in the water column could rest on modifications of embryonic shell structures, preventing hatchlings from implosion in deeper waters. By this extraordinary profusion in diverse ecological niches at global scale, belemnites might therefore be excellent examples of a successful adaptive evolutionary radiation (sensu Neige et al., 2013) during the Mesozoic.

Over the last ten years, the taxonomical study of belemnites has shown a significant renewal partly boosted by the palaeoclimatic and palaeoenvironmental perspectives offered by oxygen and carbon isotope analyses of their rostra (Jenkyns et al., 2002; Mutterlose et al.,

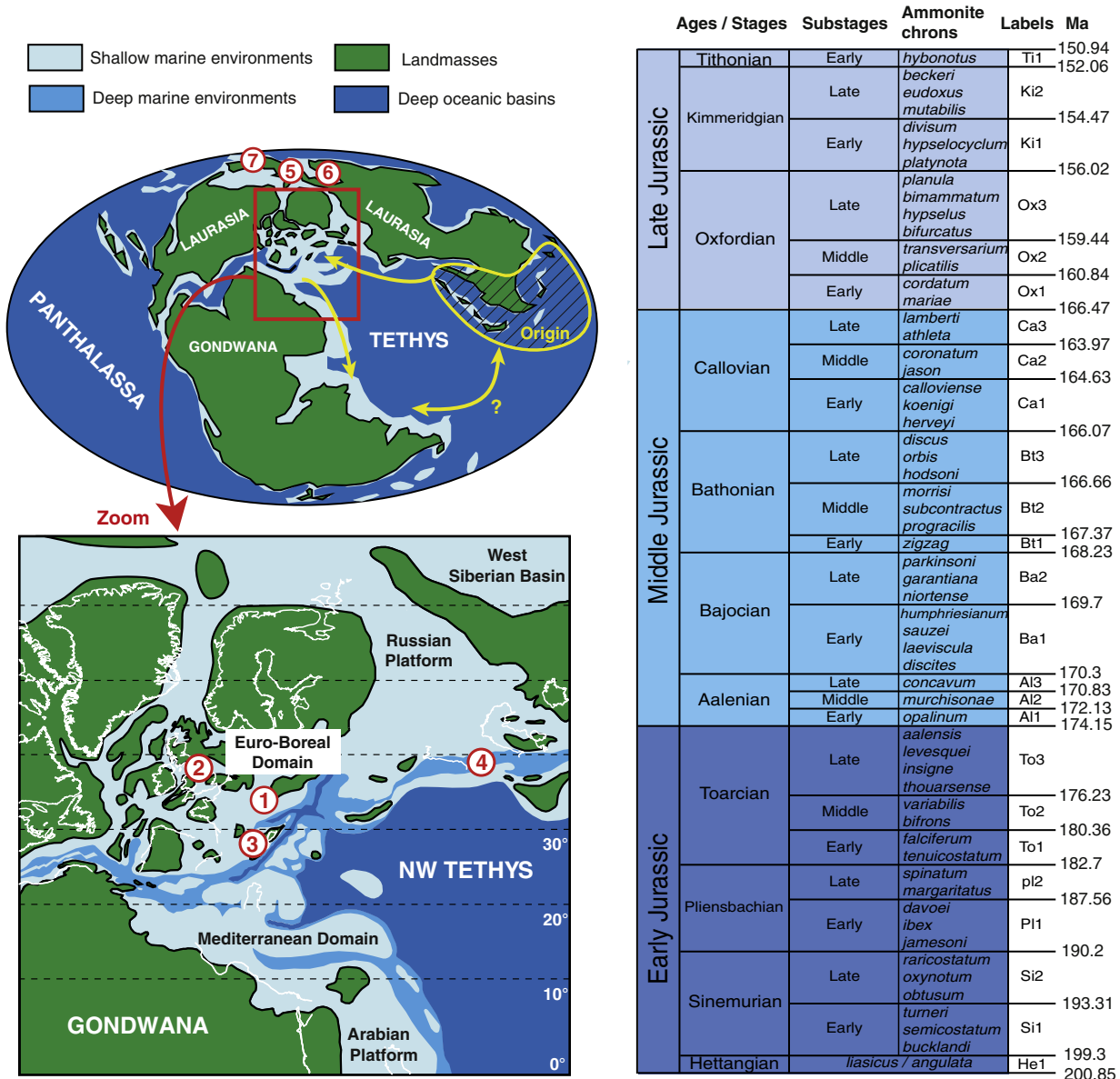
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**Fig. 1.** Reconstruction of a belemnite showing internal hard parts composing the endocoelate skeleton: proostracum, phragmocone, orthorostrum, and epirostrum. Modified from Spaeth (1975).

2010; Dera et al., 2011a; Bodin et al., 2015; Ullmann et al., 2015). Nevertheless, the origin, phylogeny, and macroevolutionary history of this group remain quite obscure and poorly constrained (Doyle et al.,

1994). Basically, recent palaeontological data suggest that: 1) the Belemnitida order likely originated in the Asian part of the Panthalassan domain during the Triassic (Iba et al., 2012) (Fig. 2); 2) it experienced a rapid radiation in the neritic domains of NW Tethyan and Gondwanan areas at the beginning of the Jurassic (Weis and Delsate, 2006; Iba et al., 2015b); 3) it was subject to several biological turnovers and palaeobiogeographical changes through the Jurassic–Cretaceous interval (Doyle, 1987; Doyle and Bennett, 1995; Christensen, 1997; Mutterlose, 1998), and 4) it disappeared at the K–T boundary in favour of modern coleoids (Iba et al., 2011). Nonetheless, only rarely studies have analyzed quantitatively the temporal variations of their diversity (Sachs and Nalnyaeva, 1975; Riegraf, 1981; Doyle and Bennett, 1995; Christensen, 1997; Dzyuba, 2013), and especially in the context of palaeoenvironmental, palaeoclimatic, and biotic crises recorded throughout the Mesozoic. More importantly, to our knowledge, their disparity in the Jurassic has not been quantitatively analyzed. Specific works focusing on short time intervals and regional contexts



**Fig. 2.** Palaeogeographic and chronostratigraphic contexts used in this study. The Jurassic stratigraphic scheme and the ages of substage boundaries are based on the GTS2012 (Gradstein et al., 2012), except for the Toarcian and Aalenian subdivisions, which respect the nomenclature of GFEJ (1997). The global map is a simplified Middle Jurassic map from Ron Blakey's website (<http://cpgeosystems.com>) and the NW Tethyan map corresponds to the Callovian map of Thierry et al. (2000) as modified by Dera et al. (2015). The palaeogeographic origin of Triassic belemnites is indicated (Iba et al., 2014), as well as possible migration pathways in the Early Jurassic. The areas discussed in this study are represented by numbers: 1, Swabo-Franconian Basin (southern Germany); 2, Great Britain; 3, Grands Causses Basin (southern France); 4, Caucasus; 5, Northern Siberia; 6, Western Siberia; 7, Eastern Siberia.

have yet shown that belemnites were especially sensitive to palaeoenvironmental stresses (e.g. anoxia, seawater acidification or temperature changes) and could represent good markers of biological crises (Harries and Little, 1999; Arkhipkin and Laptikhovskiy, 2012; Harazim et al., 2013; Pinard et al., 2014b; Ullmann et al., 2014).

Compared with Jurassic ammonites for which diversification, extinction, or palaeobiogeographical patterns are increasingly quantified by innovative methods (Dommergues et al., 1996; Sandoval et al., 2001; Dommergues et al., 2002; Gerber et al., 2007; Moynes and Neige, 2007; Neige et al., 2009; Dera et al., 2010, 2011b; Whiteside and Ward, 2011; Neige et al., 2013), a good understanding of long-term evolutionary trends is still lacking for belemnites. This is mainly because their rostra are difficult to identify at the species level. Indeed, morphological intraspecific variability, allometric growth, and dimorphism are very common (Stevens, 1965; Doyle, 1985), and anatomical characters useful for species identification often poorly preserved (e.g., grooves or apex). Moreover, most old systematic studies used qualitative descriptions of rostra and only rarely take intraspecific variation into account, such that synonymies are common and might distort the diversity estimates. By consequence, a thorough taxonomic reappraisal of specimens should be done using morphometric approaches in order to validate current species and untangle the temporal diversity patterns (compare De Baets et al., 2013). In this perspective, multivariate ordination methods describing the morphological disparity should be very promising (Roy and Foote, 1997), because they offer a suitable way to quantify the variability of forms without consideration of taxonomic or phylogenetic contexts (Foote, 1997). Already successfully applied to Jurassic ammonites (Dommergues et al., 1996; Dera et al., 2010; Simon et al., 2010, 2011) or modern coleoids (Neige, 2003), comparisons of diversity and disparity curves provide a robust framework for discussing genuine biological processes, assessing selective dynamics during crises, and minimizing taxonomic biases (Nardin et al., 2005).

In this study, we analyze for the first time the macroevolutionary dynamics of Jurassic belemnites by combining taxonomical and morphological approaches. We compiled a representative dataset including biostratigraphic, taxonomic, and morphometric information concerning 118 species present in the Euro-Boreal areas of NW Tethys. Diversity, extinction, origination, as well as morphological disparity curves are computed at a substage resolution and compared with Jurassic data from other marine domains. Here, we mainly focus on the Jurassic interval because: 1) it marks the radiation of belemnites in the NW Tethyan seas, and 2) by the abundance of recent palaeoenvironmental data concerning this period, it offers a continuous and suitable framework for discussing the influence of palaeoclimatic and eustatic constraints.

## 2. Material and methods

### 2.1. Data compilation

Our study is based on a panel of 118 Jurassic belemnite species (from the Hettangian to Early Tithonian) illustrated in the monograph of Schlegelmilch (1998). Although this compendium exclusively concerns species known from southern Germany (i.e., Swabian Alb and Franconian Alb, Fig. 2), it represents a synthetic work including the revisions of Schwegler (1961, 1962a, b, 1965, 1969, 1971) and Riegraf (1980, 1981) describing numerous Euro-Boreal taxa covering the Jurassic period with an ammonite biozone resolution. Similar datasets compiled by Schlegelmilch (1985, 1992, 1994) for ammonites have been successfully used to analyze disparity and diversity dynamics of Jurassic ammonites (Simon et al., 2010, 2011). The belemnite species presented in this monograph are relatively common in northern European basins and, to this date, this compilation is the only one which allows a continuous appraisal of Euro-Boreal diversity patterns for the whole Jurassic interval. Obviously, we expect that these regional data might not reflect the Mediterranean and Arctic belemnite communities because faunal segregation and endemism were frequent during the Jurassic (Doyle, 1994; Doyle

et al., 1997; Mariotti et al., 2012; Weis et al., 2012; Pinard et al., 2014b; Weis et al., 2015; Weis and Thuy, 2015). Additional comparisons with data from other basins will be necessary. Different types of information were used to build our database. We reported the taxonomic affiliation of each species according to the nomenclature of Schlegelmilch (1998), its maximal biostratigraphic range at the substage resolution, as well as morphometric data measured on the biggest, entire, figured specimen of each species (Supplementary data).

### 2.2. Morphometrics

Several measurements and ratios are generally used to describe the form of rostra and to discriminate specimens (Doyle, 1990; Schlegelmilch, 1998). Nevertheless, most metrics are specific to genera, so that they became not suitable to describe the overall variability of Jurassic species. In order to include all specificities of studied specimens, we introduce 14 morphological parameters describing the robustness and the external shape of rostra, as well as the number, position and relative length of grooves (Fig. 3). Thirteen of them are calculated from linear measurements taken on ventral (outline) and lateral (profile) views, whereas the last one is semi-quantitative.

The measured dimensions correspond to the total preserved length of rostra ( $L_{max}$ ), as well as the heights and widths of apertural (H and W), alveolar ( $H_{alv}$  and  $W_{alv}$  at 1/4 of  $L_{max}$ ), median ( $H_{med}$  and  $W_{med}$  at 1/2 of  $L_{max}$ ), medio-apical ( $H_{map}$  and  $W_{map}$  at 3/4 of  $L_{max}$ ) and apical regions ( $H_{ap}$  and  $W_{ap}$  at 1/10 of  $L_{max}$ ). Moreover, we measured the length of ventral (V), ventro-lateral (VL), lateral (L), dorso-lateral (DL), and dorsal (D) grooves of rostra by assigning positive or negative signs according to their apical and/or alveolar positions, respectively. Grooves covering the total length of rostra or occupying central positions were arbitrarily considered as apical. These measurements were mainly done on orthorostra in order to exclude problems of palaeobiological interpretation of epistrostra (Doyle, 1985; Arkhipkin et al., 2015) (Fig. 1). After verifying that this has no major influence on disparity results, we only included *Youngibelus tubularis*, considered as a sexual dimorph of *Youngibelus trivialis* by Doyle (1985, 2003), for which we measured the total rostrum. From morphometrics, we calculated 14 morphological indices describing the form of ventral outlines and lateral profiles, as well as the relative length of grooves (Fig. 3):

- ROB is the robustness of rostra and corresponds to the ratio between the maximal length ( $L_{max}$ ) and the apertural width (W). It describes the general shape of rostra and the values discriminate stocky (~2), robust (~2 to ~10), or slender specimens ( $\geq 10$ ).
- $R_{ALV}$ ,  $R_{MALV}$ ,  $R_{MAP}$ , and  $R_{AP}$  indicate the relative inflation of outlines in the alveolar, medio-alveolar, medio-apical, and apical regions, respectively. Percentage values may be negative, positive, or equal to zero if the lateral flanks of rostra converge, diverge or remain parallel, respectively. Altogether, these parameters give a good estimate of conical, cylindrical, cylindrical, or hastate shapes and their intermediates.
- A represents the average apical angle of the outline (calculated in degrees) and basically discriminate sharp and obtuse apici. Values range from ~10° to ~90°. Note that mucronate apici are not considered here.
- $INF_{AP}$  is the apical inflation of profiles and measures the convergence of ventral and dorsal flanks in the apical region. Percentage values are generally close to  $R_{AP}$  when rostra are symmetrical but differ in asymmetric subhastate forms with ventral inflations.
- $G_D$ ,  $G_{DL}$ ,  $G_L$ ,  $G_{VL}$ , and  $G_V$  are the relative lengths of dorsal, dorso-lateral, lateral, ventro-lateral, and ventral grooves compared with the total length of rostra. The value of each index is null if the groove is lacking and reaches 100% if it covers the totality of the rostrum. Note that negative values indicate alveolar positions.
- COMP is a compression ratio and indicates the general shape of the alveolar aperture and/or cross-sections. The calculated values

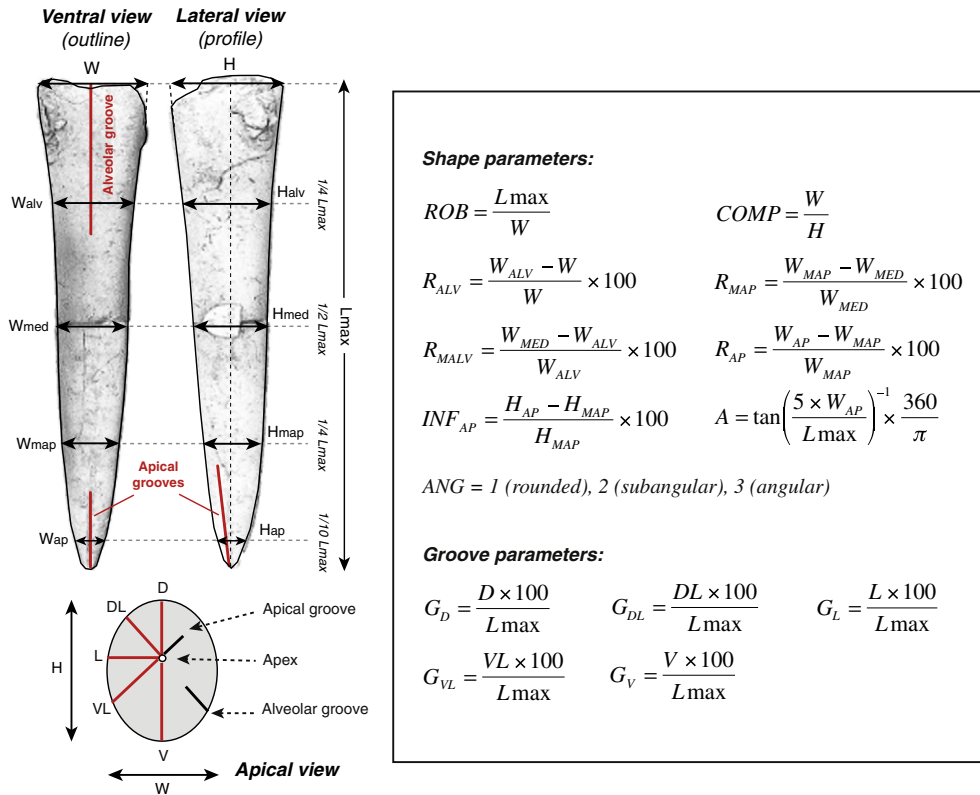


Fig. 3. Description of morphometrics measured on the apical, lateral and apical views of belemnite rostra and calculation of morphological (shape and groove) parameters.

may be inferior, equal or superior to one and refer to laterally compressed, regular, or flattened shapes, respectively.

- ANG refers to the angularity of cross-section contours. It is defined by discretised values ranging from 1 for smooth shapes to 3 for angular ones, with values of 2 for intermediate sub-angular shapes.

### 2.3. Diversity and morphological analyses

The diversity levels of belemnite genera and species were measured using different estimates to appraise the sampling biases inherent to our regional dataset. First, we calculated the total richness as the number of species and genera for the 25 substages of the Hettangian–Early Tithonian interval (Fig. 2). 1000 bootstraps were performed to evaluate the range of richness levels after random sampling (measured as percentiles). Once centered, these ranges were used as error estimates (Hammer and Harper, 2006). In complement, we analyzed the mean standing diversity as the average between the number of taxa crossing the bottom and top boundary of each interval (Foote, 2000; Caruthers et al., 2013). In order to test the influence of temporal inconsistency, diversity data were weighted by the duration of substages calculated from Gradstein et al. (2012) (Fig. 2). However, this latter approach is not ideal as it implies that time is the main control of diversity dynamics and favors a continuous extinction model – whereas extinctions typically occur in pulses (Foote, 2005). Finally, the relative diversity of each belemnite family was analyzed and the extinction and origination rates were measured using the van Valen metric (Foote, 2000; Caruthers et al., 2013), with and without time-standardization.

Compared with diversity estimates, variance-based disparity metrics are little affected by sample size and uneven fossil record (Butler et al., 2012). Parallel uses of morphological disparity and

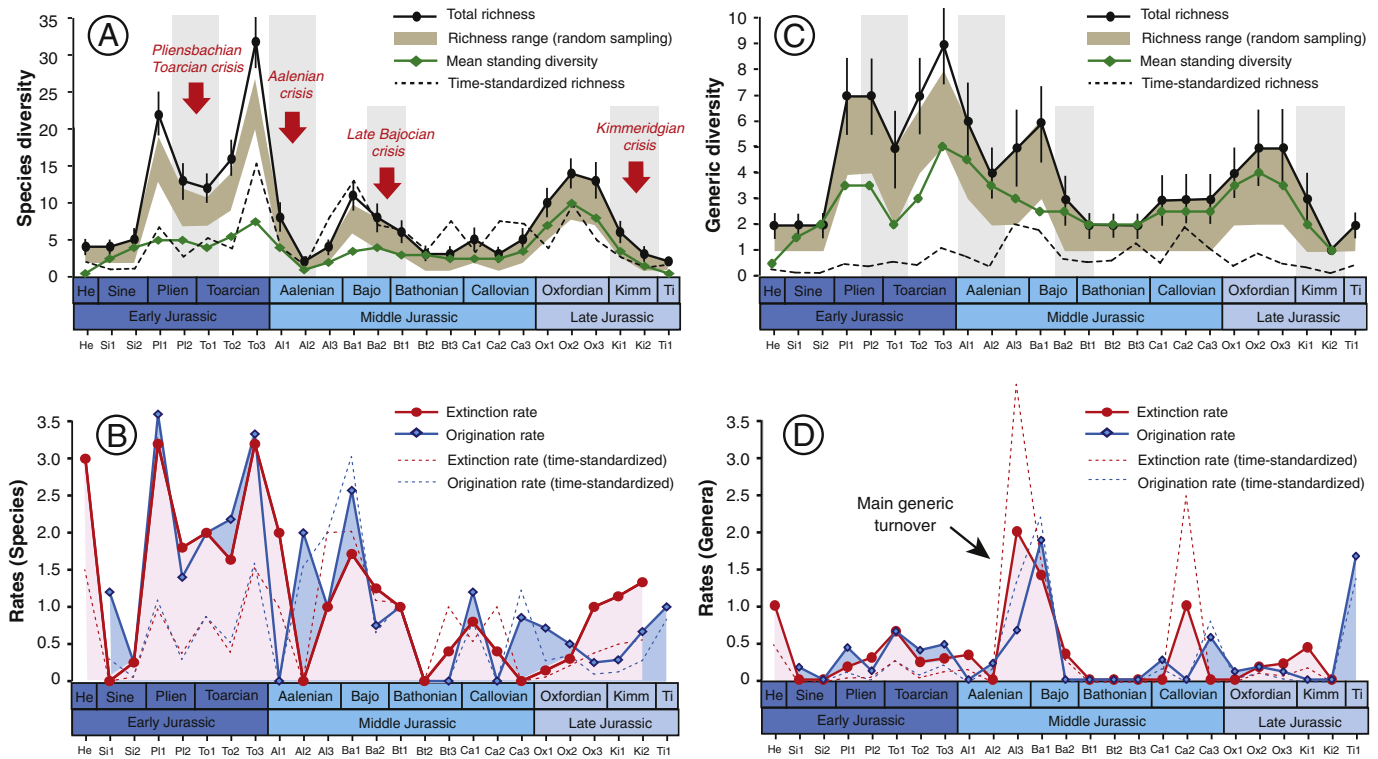
diversity curves appear therefore as a good means to better discriminate the influence of sampling or taxonomical biases. In order to analyze the morphological variability of species, we applied a principal component analysis to the data matrix including the 14 morphological parameters measured on the 118 species. By ordination method, we computed morphospaces (based on the four first principal components) in which the scores of all species are plotted to show the morphological differences between taxa. The results were divided in 25 substages to describe the morphological evolution of belemnite families through the 25 substages. We used the MDA Matlab package (Navarro, 2003) to analyze the morphospace occupation over time with conventional estimators, such as the PCO volume, the sum of variance, the mean pairwise distance, and the average occupation ranges on each principal component. All disparity metrics were corrected by using 1000 bootstraps and rarefaction procedures ( $n = 5$ ). In complement, we measured the partial disparity of belemnite families through time by following the method of Foote (1993).

## 3. Results

### 3.1. Evolution of diversity patterns

Whatever the taxonomical resolution (i.e., species or genus) and the metric used, the results show strong variations in the diversity of belemnites from South Germany through the Jurassic (Fig. 4). By considering the total richness estimates, it appears that the diversity levels remained low from the Hettangian to the Sinemurian and markedly rose during the Early Pliensbachian. In details, this radiation was linked to a massive diversification of Passaloteuthidae and the appearance of Hastitidae (Fig. 5a). From the Late Pliensbachian to the Early Toarcian, successive extinctions affected these two families and led to low diversity levels of species before and after the Pliensbachian–Toarcian boundary. Interestingly, this crisis might also be visible at the genus scale but it was seemingly delayed to the Early Toarcian (Fig. 4A,C).





**Fig. 4.** Estimates of Jurassic belemnite diversity patterns from South Germany according to different metrics and taxonomical scales (genus vs. species). The four main diversity crises are indicated with red arrows and grey bands. See Fig. 2 for age abbreviations.

This trend was reversed from the Middle to the Late Toarcian owing to the diversification of Acrocoelitidae originated during the crisis and the subsequent appearance of Salpingoteuthidae and Rhabdobelidae. Whatever the taxonomical scale, the diversity levels were maximal in this time interval but, throughout the Aalenian, an important drop occurred in response to low origination rates and higher extinction rates (Fig. 4A, B). This disturbance was accompanied by strong faunal turnovers (especially at the genus scale, Fig. 4D) marked by the disappearance of Rhabdobelidae and Salpingoteuthidae on the one hand, and the diversification of Cylindroteuthidae, Megateuthidae, and Belemnopseidae on the other (Fig. 5a). A third diversity peak occurred in the Early Bajocian, but the following disappearances of Megateuthidae and Cylindroteuthidae reduced the diversity levels from the Late Bajocian to the Late Callovian (more progressively for species than genera). Finally, the appearance of Duvaliidae drove a last Middle to Late Oxfordian diversity peak, which ended after their decline during the Kimmeridgian.

If mean standing diversity estimates are considered, the diversity fluctuations appear smoother (especially for species) and some potential crises and diversification events previously suggested disappear. At the species resolution, the main differences concern the lack of sharp diversity peaks during the Early Pliensbachian and the Early Bajocian. For genera, the patterns are more conservative, except for the Middle Jurassic during which the diversity levels gradually decline from the Late Toarcian to the Late Bathonian, without recognition of the Early Bajocian diversification. In comparison, the influence of time-standardization is more consequent. This is especially obvious at the genus resolution, as normalization tends to increase the richness levels during the Middle Jurassic and to enhance the extinction and origination rates during the Aalenian and Callovian. At the species level, the consequences appear less important, but we can note a rise of Middle Jurassic diversity estimates compared with the Early and Late Jurassic levels.

### 3.2. Evolution of disparity patterns

The morphospaces, namely PC1 vs. PC2 and PC3 vs. PC4, represent ~39% and 21% of the total variance supported by the data matrix (Fig. 6). In the first morphospace, PC1 indicates the general shape of belemnite rostra (i.e., conical, cylindrical, or hastate), whereas PC2 basically represents their robustness from slender to stocky rostra. The groove patterns are visualized along a diagonal gradient, in which the middle marks missing or small grooves, and the opposite corners indicate the presence of long grooves in apical (top left) or alveolar/lateral (bottom right) positions. The second graph mainly summarizes the angularity of flanks along PC3 and separate compressed, regular, and flattened rostra along PC4. The sharpening of apici is discriminated along a diagonal line ranging from smoother ones in the top right corner to sharper ones in the bottom left corner.

Fig. 7 summarizes the distribution of belemnite families and genera in the morphospace PC1 vs. PC2 through the 25 substages. In complement, we analyzed the temporal variations in morphological disparity (Fig. 8), the evolution of rostral forms (Fig. 9), and the relative contribution of belemnite groups to the overall morphological variability (Fig. 5b). Basically, all disparity estimates show the same trends, with both gradual increases from the Hettangian to the Early Pliensbachian and from the Late Callovian to the Early Kimmeridgian, and one sudden rise in the Late Toarcian (Fig. 8). Some peaks are linked to the co-occurrence of families with distinct morphologies (e.g., Acrocoelitidae, Salpingoteuthidae, and Rhabdobelidae during the Late Toarcian), whereas others reflect the predominance of one group with an important variability (e.g., Belemnopseidae during the Oxfordian and Kimmeridgian) (Figs. 5b and 7). In contrast, morphological bottlenecks occurred from the Early Pliensbachian to the Middle Toarcian, from the Late Toarcian to the Late Aalenian, at the Bajocian–Bathonian boundary, and during the Late Kimmeridgian–Tithonian interval.

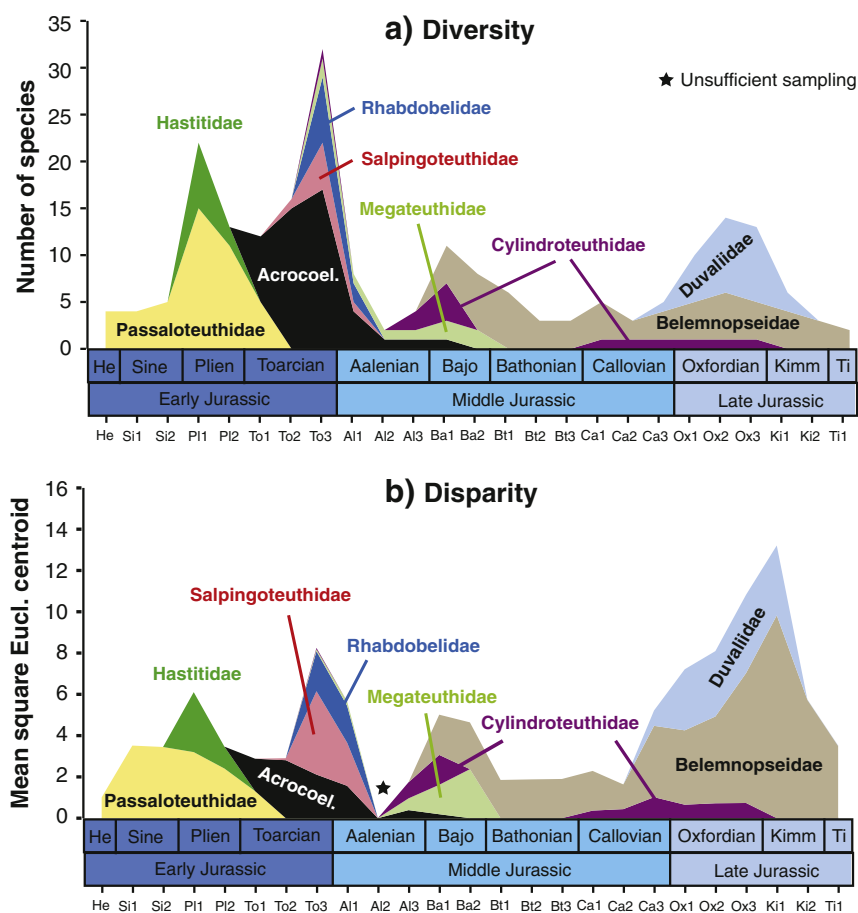


Fig. 5. Relative contribution of belemnite families to diversity (a) and disparity (b) levels through time. See Fig. 2 for age abbreviations.

### 3.3. Evolution of rostral forms

By analyzing the morphospace occupation patterns (Fig. 9), we demonstrate that the form of belemnite rostra markedly changed during the Jurassic:

- PC1 The belemnites produced a wide range of rostrum forms through the Early Jurassic (i.e., conical, hastate, and cylindrical), but they progressively became more hastate from the Middle to the Late Jurassic.
- PC2 On average, the Jurassic belemnites were robust but slender forms appeared through the Pliensbachian–Toarcian and Oxfordian–Kimmeridgian intervals. Stocky shapes also prevailed during the Oxfordian.
- PC3 While the Early Jurassic rostra had smoother apici and angular flanks, they progressively evolved towards streamlined shapes with sharp apici and smooth flanks during the Middle and Late Jurassic.
- PC4 The belemnite rostra gradually became more flattened through the Jurassic, except during the Oxfordian–Kimmeridgian interval when compressed rostra with smooth apici reappeared.

## 4. Belemnite diversity patterns from South Germany

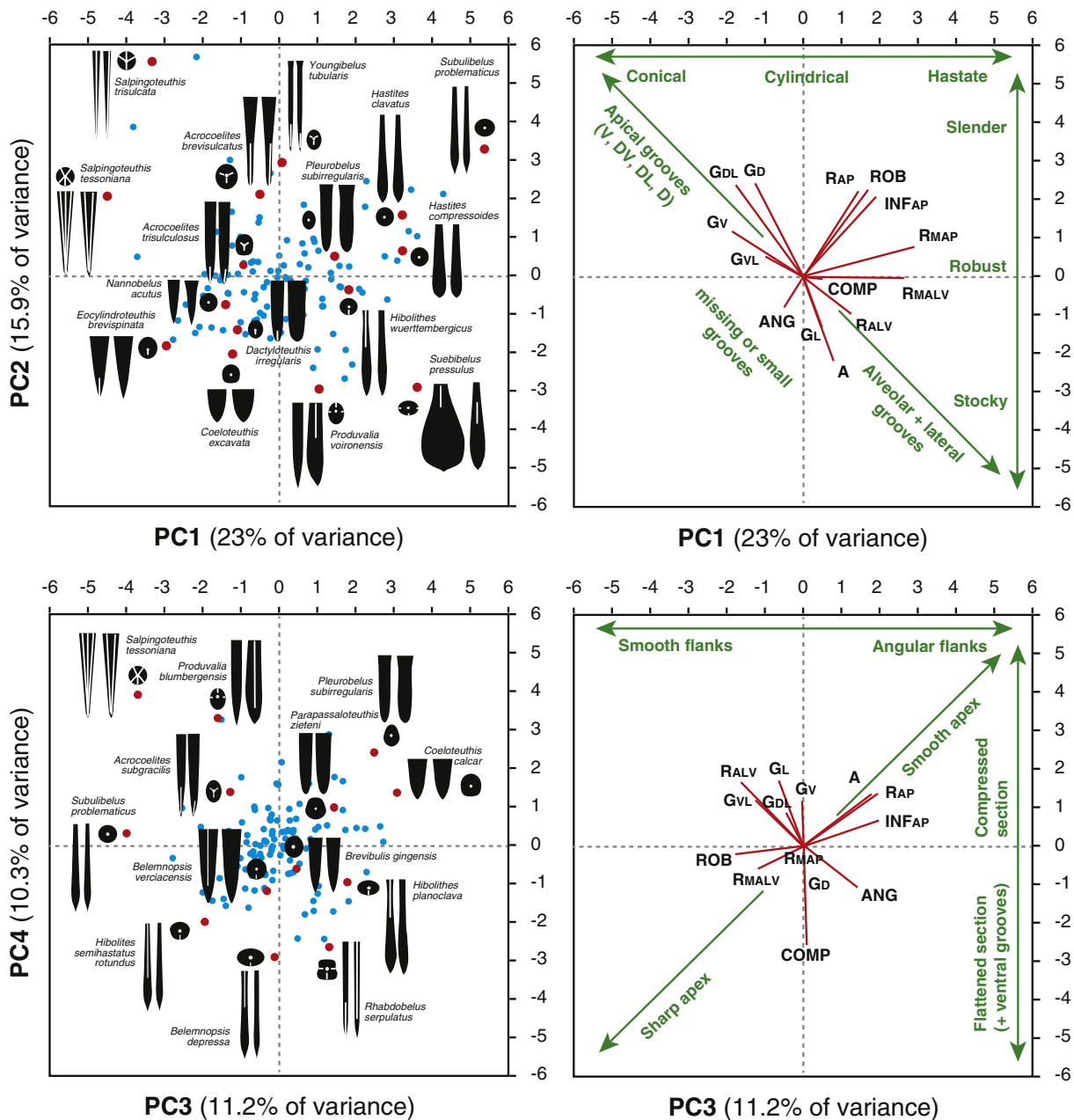
Riegraf (1981) as well as Doyle and Bennett (1995) already showed that the number of belemnite species in South Germany varied markedly through the successive stages of the Jurassic. Here, our reappraisal at the substage resolution specifies the results. As explained by Simon et al. (2010, 2011), this temporal scale is a good compromise

for depicting regional diversity/disparity patterns without major biases resulting from coarser or finer resolutions, such as excessive smoothing or background noise. When total richness levels are considered (Fig. 4A,C), four main diversity peaks are highlighted during the Early Pliensbachian, Late Toarcian, Early Bajocian, and Oxfordian, both at species and genus scales. Conversely, the Late Pliensbachian–Early Toarcian interval, Aalenian, Late Bajocian, and Kimmeridgian correspond to strong incisions of diversity levels, spanning either one or more substages. Importantly, the mean turnover of genera occurred at the Aalenian–Bajocian boundary (Fig. 4D).

It is evident that the regional fossil record from South Germany does not exactly represent the diversity patterns of belemnites prevailing at the Euro-Boreal scale. Beyond genuine evolutionary processes, it is possible that preservation biases, stratigraphic heterogeneities in sampling effort, and common causes (e.g., sea-level) driving both rock and fossil records have partly altered the expression of richness levels at local scale (Dunhill et al., 2012; Holland and Patzkowsky, 2015). For example, recent analyses of worldwide Jurassic benthic communities show that the Aalenian could be broadly undersampled compared with other stages (Kiessling et al., 2007), meaning that the depicted belemnite crisis would be artificially exaggerated. In addition, the choice of diversity metrics is of prime importance because methodological artefacts can affect the temporal trends (Foote, 2000). Appraising the potential biases is thus of prime importance before discussing any trend.

### 4.1. Quality of the belemnite fossil record

We assume that the sampling effort and the taxonomical biases (i.e., synonymy) should not heavily affect the long-term diversity patterns of belemnites, because the monograph of Schlegelmilch



**Fig. 6.** Morphospaces of Jurassic belemnite rostra built on the first principal components (i.e., PC1 vs. PC2 and PC3 vs. PC4) resulting from PCA. On the left, the morphospaces show the distribution of all species (blue dots) and representative forms of selected species (red dots) are drawn according to ventral (left), lateral (right), and apical views showing the position and the relative length of grooves. On the right, the morphological parameters structuring the distribution of species are plotted in the morphospaces. The correlation of parameters and the distribution of shapes indicate general morphological trends in the morphospace occupation (in green arrows).

(1998) synthesizes over forty years of fossil collecting in several regional outcrops and includes the major revisions of Schwegler (1961, 1962a,b, 1965, 1969, 1971) and Riegraf (1980, 1981). In South Germany, the stratigraphic record of marine Jurassic deposits does not present major hiatus at regional scale (Bayer and McGhee, 1986; DSK, 2002). However, the influence of temporal changes in lithology and palaeoenvironments cannot be neglected, because shifts from carbonate to siliciclastic rocks and/or proximal to distal marine contexts, may greatly impact the diversity patterns through preservation biases and palaeoecological partitioning of faunas (Peters, 2008; Holland and Patzkowsky, 2015). As belemnites are often considered inhabiting deeper, hemipelagic environments (Mutterlose et al., 2010), it would be expected that higher diversity levels correspond to deep shaly facies, which favour preservation

in return. However, this model is not fully coherent with data from South Germany and surrounding areas (e.g., Luxembourg and the UK) because belemnite rostra are commonly found in lagoonal carbonate facies of the Late Jurassic and conglomeratic and sandy littoral facies of the Aalenian (Weis and Mariotti, 2007; Stevens et al., 2014). The reason for this occurrence in shallow seas is that numerous belemnite species could have lived the major part of their life in deeper waters, but reached shallow ecosystems for reproducing then dying (Mutterlose et al., 2010). At least in some cases, there is indication that they might have even spent their entire life in these environments (e.g., inner shelf palaeoenvironments of the Nüßlingen Limestone; Stevens et al., 2014). In complement of the robust calcitic structure of rostra favouring their preservation (Saalen, 1989; Ullmann et al., 2015), this ability to occupy a wide range of

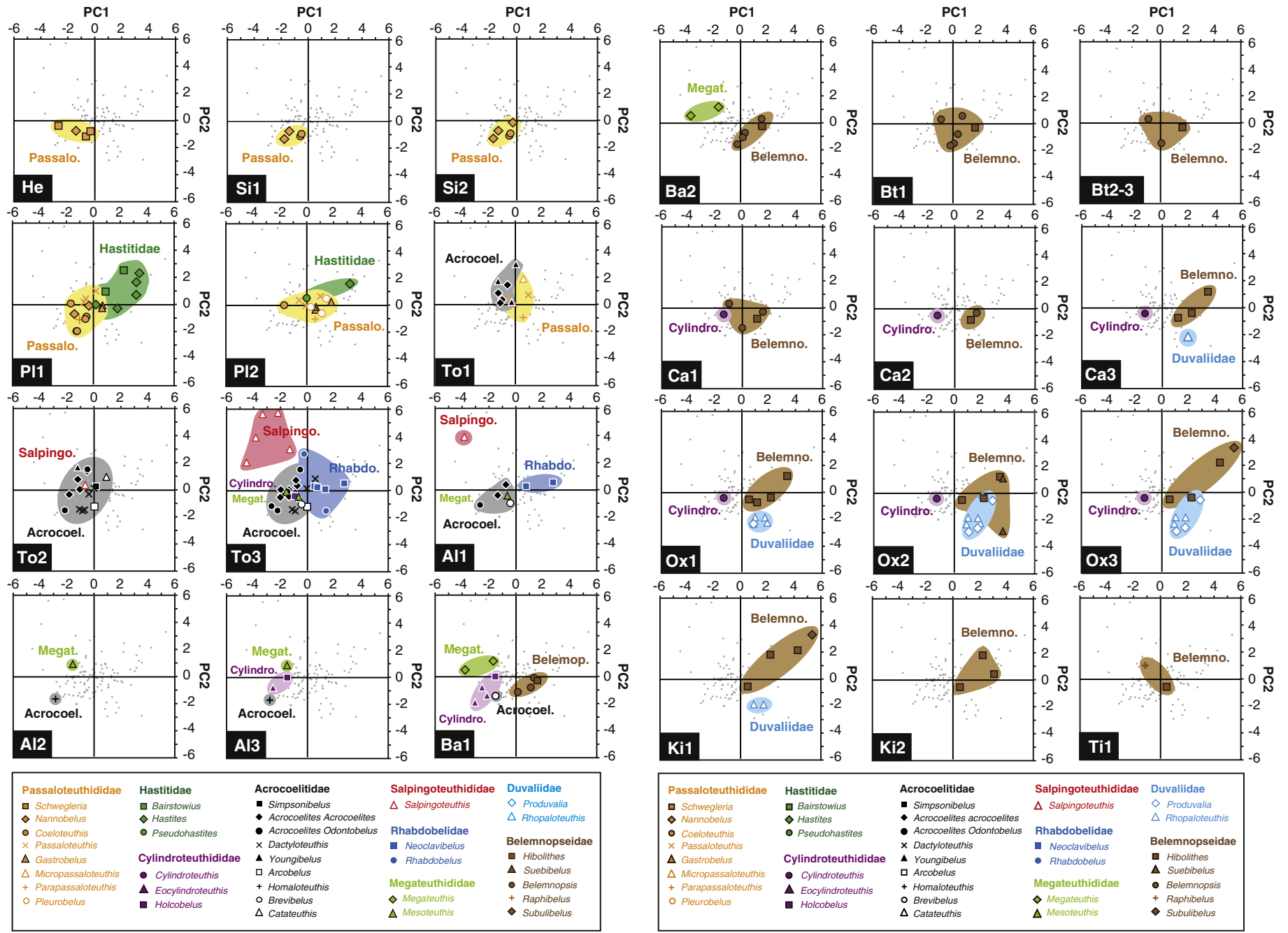
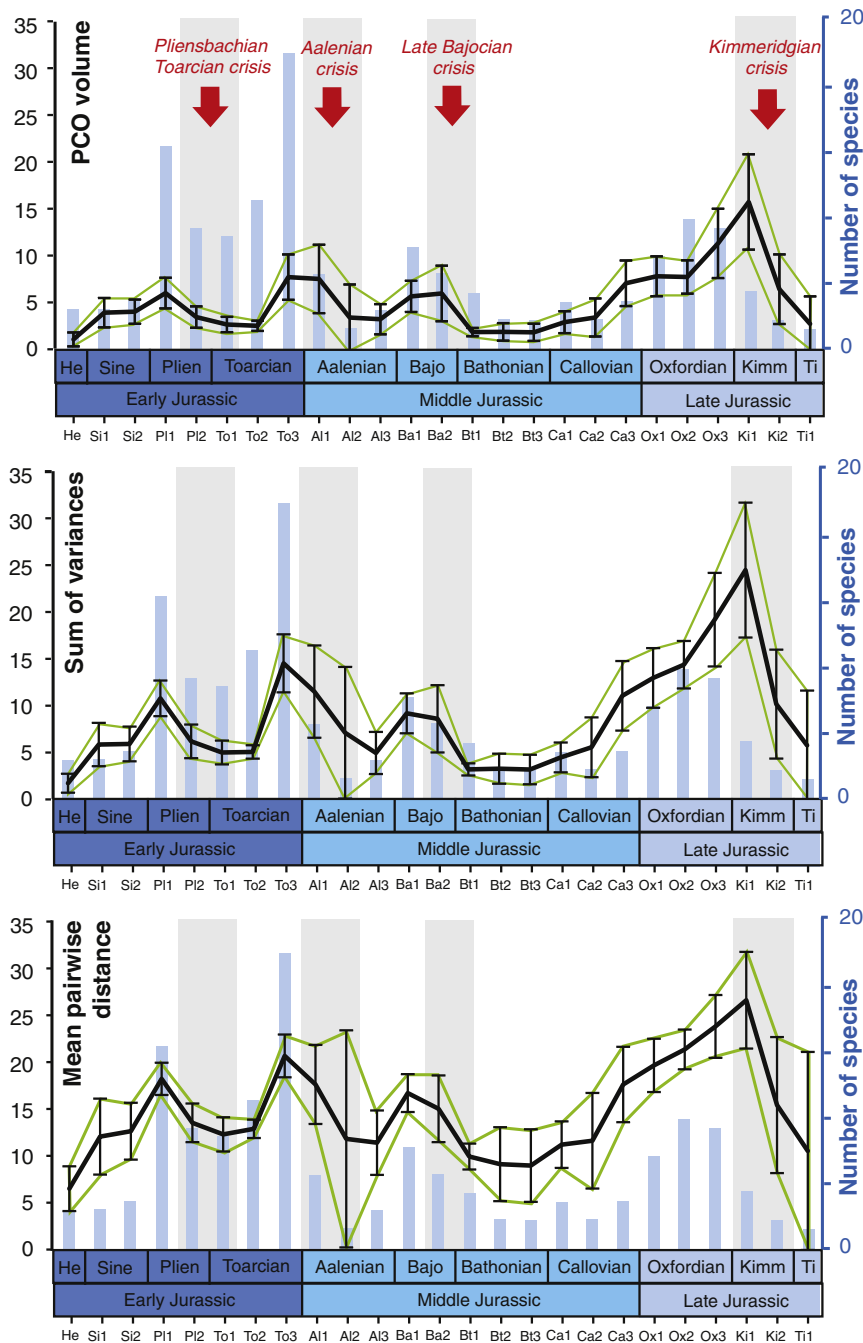


Fig. 7. Distribution of belemnite families and genera in the morphospace PC1 vs. PC2 through the 24 substages of the studied period. See Fig. 2 for age abbreviations.



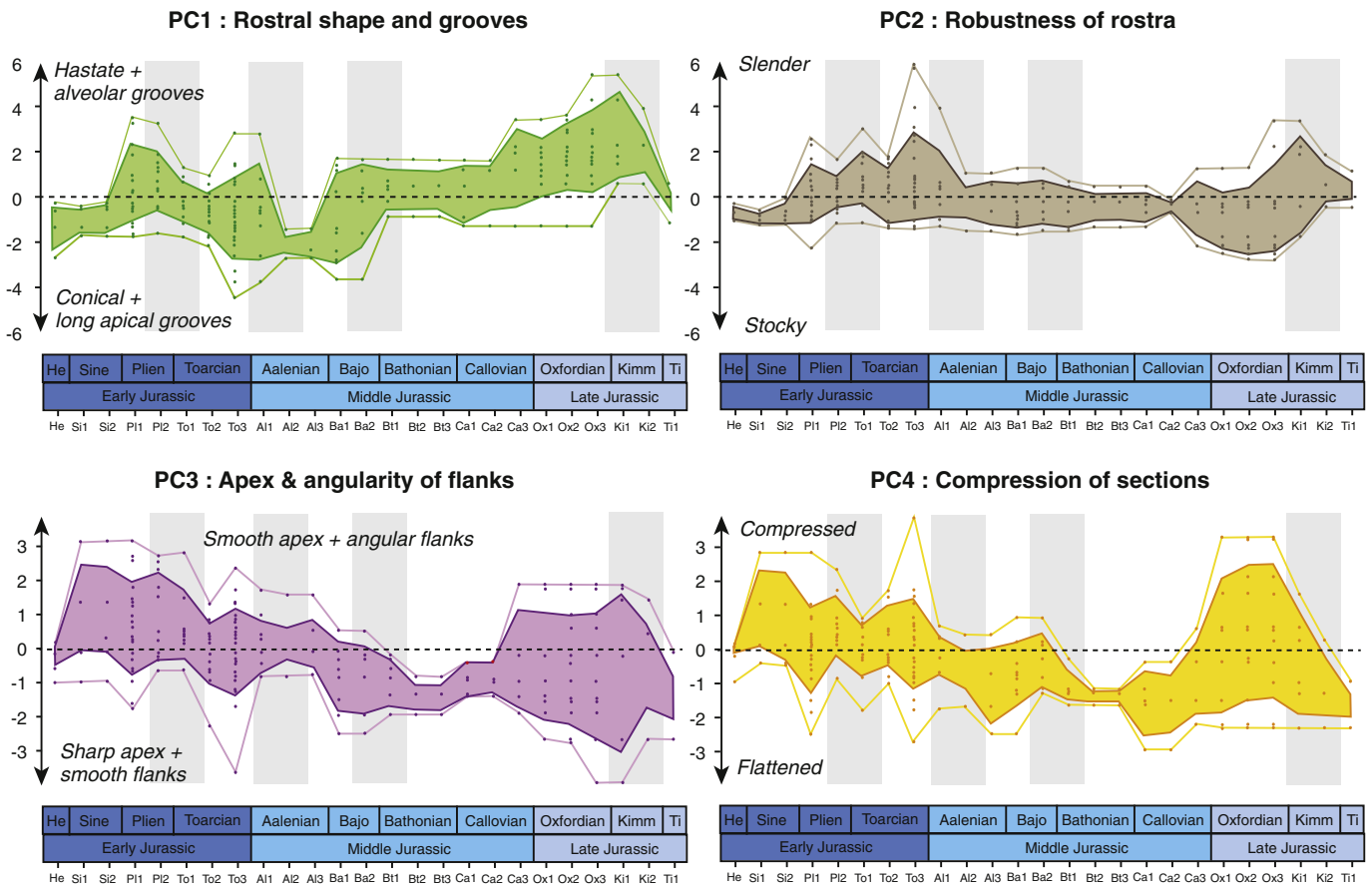


**Fig. 8.** Evolution of disparity levels through time (expressed by PCO volume, sum of variance, mean pairwise distance in the morphospace). Error bars are computed after 1000 bootstraps and rarefaction procedures ( $n = 5$ ). For comparison, the number of species and the four main diversity crises are also indicated with blue bars and red arrows. See Fig. 2 for age abbreviations.

environments (and facies) is quite positive if we expect to have a continuous fossil record whatever the lithology. However, this calls for careful interpretation of diversity results because the variability of ecological tolerances and behaviours of belemnite taxa could distort the faunal composition and richness levels through time at regional scale (Mutterlose and Wiedenroth, 1998). Despite these considerations, we consider that the belemnite fossil record from South Germany might be the most suitable for appraising general biodiversity patterns because similar analyses of regional ammonite faunas with similar collection efforts match broader diversity variations depicted at Euro-Boreal scale (Moyné and Neige, 2007; Simon et al., 2010, 2011).

#### 4.2. Reliability of diversity metrics

Whatever the taxonomical resolution, standardizing the richness levels by interval durations amplifies the Middle Jurassic diversity estimates on the one hand, and minimizes the diversity peaks of the Early and Late Jurassic on the other. Nevertheless, this normalization precludes direct comparisons of peak magnitudes through time because the temporal calibration of the Jurassic is still not fully reliable (Gradstein et al., 2012). Uncertainties on radio-isotopic dates and interpolated numerical ages of stage boundaries range from  $\pm 1$  to  $\pm 1.4$  Myr for the Middle Jurassic, against  $\pm 0.2$  to  $\pm 1$  Myr for the Early and Late Jurassic. This range of uncertainty is very



**Fig. 9.** Morphospace occupation patterns according to each principal component. Thin lines represent the maximal and minimal values of specimens through time. Coloured envelopes represent the average boundaries of occupation patterns after 1000 bootstraps and rarefaction procedures ( $n = 5$ ). Dots correspond to the scores of each specimen and grey bands depict the main diversity drops. See Fig. 2 for age abbreviations.

problematic when considering the average durations of studied sub-stages, which are in the same order of magnitude (Gradstein et al., 2012). Recent cyclostratigraphic works even suggest that the Middle Jurassic could be longer of 2 to 3 Myr than currently accepted (Suchéras-Marx et al., 2013; Martinez and Dera, 2015), with the consequence of exaggerating the standardized diversity estimates. In addition, time-normalization can introduce a negative correlation between calculated rates and interval durations (Foote, 1994), and it assumes that the magnitude of extinction and origination rates is time dependent, which is not necessarily true (Raup and Sepkoski, 1984; Foote, 2005). For these reasons, we prefer to avoid any interpretation of time-standardized metrics.

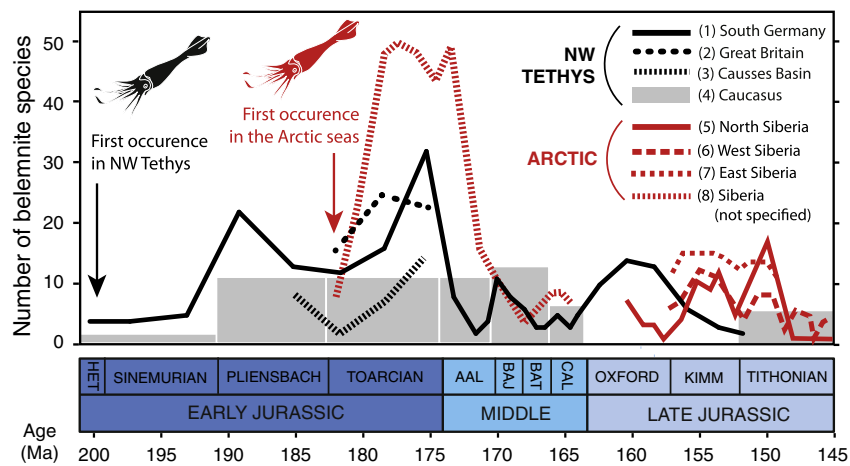
Compatible with the short longevity of most belemnite species (i.e., 0.5 to 2 ammonite chrons) (Doyle and Bennett, 1995), the discrepancies between the total richness estimates and the mean standing diversity curves highlight a possible influence of singletons (i.e., taxa confined to a single interval) on the raw temporal trends. The consequences are major because this suggests that the Early Pliensbachian and Early Bajocian diversity peaks could include regional artefacts depending either on the occurrence of short-lived endemic taxa, temporal migrations, or regional appearance/disappearances of species. In a similar way, the magnitude of Pliensbachian–Toarcian and Aalenian depletions in the total richness could be exaggerated. From available regional data, it is therefore difficult to conclude whether the depicted rises and falls in diversity reflect genuine macroevolutionary processes prevailing at the entire Euro-Boreal scale, or regional diversity patterns influenced by regional constraints. Appraising the macroevolutionary dynamics of Euro-Boreal belemnites requires both complete revisions and analyses of palaeontological data from several European basins,

but this is beyond the scope of this study. Nevertheless, it is worth mentioning that recent compilations of all European belemnite faunas and their analysis at the biozone scale display very similar results for the Hettangian–Aalenian interval (Pinard et al., 2014a). Moreover, sub-polar data from Siberia support our regional results (Meledina et al., 2005), except for the Middle and Late Jurassic when a strong faunal provincialism obscured the supra-regional trends (Sachs and Nalinyaeva, 1975; Dzyuba, 2013) (Fig. 10). In consequence, we suggest that the main diversity peaks and biotic crises recorded in South Germany can at least be regarded as robust Euro-Boreal events, except the Early Pliensbachian and Early Bajocian diversifications, which remain to be confirmed at broader spatial scale.

**5. Spatio-temporal dynamics of diversity**

*5.1. Early Jurassic events*

After a 10-Myr-long stagnation of diversity levels after their arrival in NW Tethys, the belemnites experienced their first diversification during the Early Pliensbachian. In several localities from western and central Europe, this radiation marked a rapid change in faunal communities marked by replacements of small Hettangian and Sinemurian taxa (e.g., *Schwegleria*, *Nannobelus*, and *Coeloteuthis*) by numerous bigger species belonging to the genera *Passaloteuthis*, *Hastites*, or *Gastrobelus* (Doyle, 1987, 1994; Riegraf, 2000; Weis and Thuy, 2015). However it is currently difficult to assess if this corresponds to a global event because, with the exception of Japan and Tibet (Iba et al., 2015a, b), Pre-Toarcian belemnites have not yet been found in other domains such as the Arctic seas (i.e., Siberia) or eastern and southern Panthalassa



**Fig. 10.** Comparison of belemnite diversity levels measured in the Swabo-Franconian Basin (this study) with literature data compiled from Great Britain (Doyle, 1990, 1992), Grands Causses Basin (Pinard et al., 2014b), Caucasus (Ruban, 2007), and Siberia (Sachs and Nalnyaeva, 1975; Meledina et al., 2005; Dzyuba, 2013; Zakharov et al., 2014). The numbers ascribed to geographic areas refer to the locations indicated on Fig. 2.

(i.e., South America, NW Zealand) (Stevens, 1965; Doyle, 1994; Doyle et al., 1997). Moreover, Iba et al. (2014) recently showed that the Sinemurian belemnites from Japan completely differed from European families, attesting an obvious provincialism between the Tethyan and Panthalassan areas. As a consequence, the first major radiation of Jurassic belemnites may be considered as a regional or NW Tethyan event, which affected homogeneous faunas across the European basins (Doyle, 1994; Weis and Thuy, 2015).

Evidences for a worldwide drop of belemnite diversity levels during the Late Pliensbachian are currently lacking and call for further investigation, especially if genera are not affected (Fig. 4C). Nevertheless, this regional decline is compatible with the precursor events of the multiphased Pliensbachian–Toarcian crisis having affected various organisms at global scale (Dera et al., 2010; Caruthers et al., 2013), namely the “*valdani*” and “*gibbosus*” extinction events. Comparatively, data from southern France and Great Britain indicate that the subsequent Early Toarcian extinction event and the Late Toarcian recovery of belemnites were more widespread features in the Euro-Boreal basins (Doyle, 1990; Harries and Little, 1999; Pinard et al., 2014a, b). In the Mediterranean domains, the Toarcian species became rare and most groups did not reappear before the Middle Aalenian (Sanders et al., 2015; Weis et al., 2015). As for other marine organisms (Hallam, 1987; Little and Benton, 1995; Caswell et al., 2009; Dera et al., 2010; Caruthers et al., 2013), this might suggest that the Pliensbachian–Toarcian crisis of belemnites recorded in South Germany could have been worldwide in extent, and paced by successive extinction pulses.

Compared with NW Tethyan ammonites, which achieved their rediversification during the Middle Toarcian (Dera et al., 2010), the main recovery phase of belemnites was delayed to the Late Toarcian in the southern German basins. Nevertheless, data from Siberia and Great Britain show that the diversification was faster (i.e., Middle Toarcian) and twice more prolific towards high latitudes (Sachs and Nalnyaeva, 1975; Doyle, 1990, 1992; Meledina et al., 2005) (Fig. 10). Atypically, this would suppose an inverted latitudinal diversity gradient opposed to the classical conception of subtropical “hotspots” observed for modern coleoids (Rosa et al., 2008) or Toarcian ammonites (Macchioni and Cecca, 2002; Dera et al., 2010, 2011b). However, it is possible that the spatial distribution of belemnites was more influenced by salinity and oxygenation constraints than temperature (Doyle, 1987; Harazim et al., 2013; Ullmann et al., 2014).

To date, the origin of this Arctic faunal burst remains speculative. By accepting that the Siberian taxa defined by Sachs and Nalnyaeva (1975) are all valid, Doyle (1987) proposed that this flourishing Arctic diversity could result from northward migrations of NW Tethyan groups, which regionally survived during the Early Toarcian crisis (e.g., *Passaloteuthis*,

*Nannobelus*, *Acrocoelites*, *Clastoteuthis*, and *Holcobelus*), and their rapid evolution into new endemic genera (e.g., *Lenobelus*, *Pseudodicoelites*, and *Rarobelus*) (Sachs and Nalnyaeva, 1975; Meledina et al., 2005; Dzyuba et al., 2015). This diversification could have been facilitated by the environmental partitioning of Siberian domains (Zakharov et al., 2003), as well as new ecological opportunities in these boreal “refuge” areas marked by more clement conditions in terms of seawater temperature, oxygenation, food availability, competition, and predation.

## 5.2. Middle and Late Jurassic events

As previously shown by Doyle and Bennett (1995), the most important disruption in the evolutionary dynamics of belemnites occurred throughout the Aalenian. It ended at the Aalenian–Bajocian boundary with a profound turnover of Jurassic families, likely accounting for the initiation of a profound provincialism between the NW Tethyan and Arctic belemnite faunas (Doyle, 1987). In the Swabo-Franconian basins, this biotic crisis started with a sudden interruption of origination processes and massive extinctions of Toarcian Acrocoelitidae, Salpingoteuthidae, and Rhabdobelidae at the Toarcian–Aalenian boundary (Figs. 4 and 5). Although delayed by one substage (i.e., Middle Aalenian), a strong incision of diversity levels also occurred in the Siberian basins (Sachs and Nalnyaeva, 1975; Meledina et al., 2005) (Fig. 10), which would indicate profound disturbances in the belemnite communities at the North hemisphere scale. This biotic crisis is compatible with the low diversity levels of European ammonites at the Toarcian–Aalenian boundary and their high turnover rates at the Aalenian–Bajocian transition (Sandoval et al., 2001; Moyne and Neige, 2007). Nevertheless, the status of this Aalenian crisis is still a matter of debate because analyses of Jurassic benthic faunas performed at stage resolution show that numerous groups survived without apparent changes in the structure of communities (Kiesling et al., 2007). This discordance between the evolutionary dynamics of benthic and pelagic organisms could be a key for understanding the Aalenian crisis but, prior to any conclusion, benthic diversity patterns should be reappraised at a substage resolution. Indeed, analysis of ammonite faunas shows that the Aalenian diversity drop is completely smoothed when stage-scale diversity patterns are considered (Yacobucci, 2005).

Contrary to the Arctic diversity levels, which declined until the Bathonian, a prolific and rapid recovery happened in South Germany during the Early Bajocian, before declining again from the Late Bajocian to the Callovian (as in Caucasus; Ruban, 2007). Interestingly, this ephemeral rediversification seems to have been partly boosted by the return and the evolution of Belemnopseidae having previously deserted the NW Tethyan basins for refuge areas

during the Toarcian (Weis et al., 2015). To our knowledge, this Early Bajocian diversity peak of belemnites has not been described elsewhere, but it was synchronous to a major diversification of NW Tethyan ammonites, radiolarians, and coccolithophorids (see Suchéras-Marx et al., 2015; and references herein). As it also corresponds to profound palaeoenvironmental changes characterized by the recovery of reefal ecosystems and carbonate production in the Euro-Boreal seas (Leinfelder et al., 2002; Lathuilière and Marchal, 2009; Brigaud et al., 2014), we consider this peak as a regional event interrupting a monotonous Middle Jurassic diversity. The short duration of this diversification episode (Early–Middle Bajocian) and the following extinction remain intriguing. O’Dogherthy et al. (2006) linked a similar crisis recorded in the ammonite communities (i.e., namely the *niortense* event; Moyné and Neige, 2007) to a general fall of NW Tethyan productivity levels manifested by  $\delta^{13}\text{C}$  decreases. It is possible that belemnites were similarly affected.

Compared with the homogenous trends depicted during the Early Jurassic and the Aalenian, the palaeontological data from Russia show that the macroevolutionary dynamics of Euro-Boreal and Arctic belemnites was more heterogeneous, even opposite, from the Bajocian to the Tithonian (Fig. 10). Whereas data from South Germany indicate an Oxfordian diversification followed by a progressive collapse during the Kimmeridgian, those from Siberia display a net diversity fall through the Oxfordian (Zakharov et al., 2014), followed by regional rises in the number of species from the Kimmeridgian to the Early Tithonian (Dzyuba, 2013). These opposite patterns of biodiversity are here highlighted for the first time, and it is likely that they reflect diversity dynamics of two independent evolutionary histories constrained by different palaeoecological constraints. In agreement, Doyle (1987) noted that a strong provincialism prevailed between the Euro-Boreal and Arctic belemnite communities from the Middle to the Late Jurassic. The origin of these faunal segregations and decoupled evolutionary histories remains obscure, but it could be anchored in the aftermath of the supra-regional Aalenian crisis, because temporal obstructions of the marine pathway connecting the two domains (i.e., Viking Corridor) are known to have strongly decreased the faunal exchanges at this time (Nikitenko et al., 2006; Korte et al., 2015).

**6. Morphological evolution of belemnite rostra**

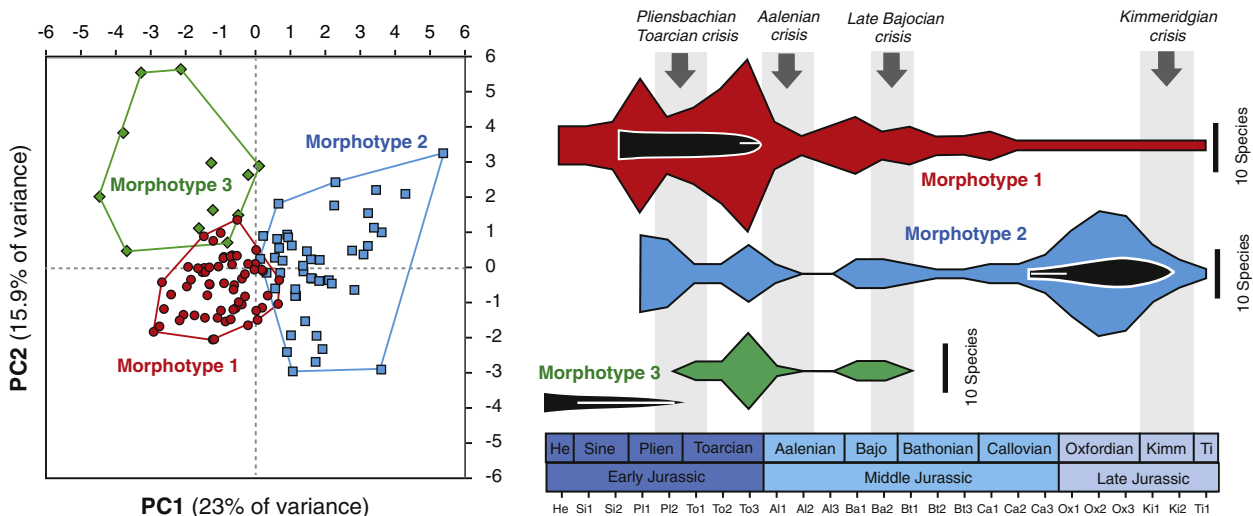
The morphospace occupation patterns show that the belemnite rostra had a great variability of forms (Fig. 6), which markedly varied through time (Figs. 7 and 8). On average, the Jurassic rostra were robust,

cylindrical to cylindrical, and had small grooves, but many groups without apparent phylogenetic links (Schlegelmilch, 1998) successively experienced evolution towards hastate, conical, slender or stocky shapes (Figs. 7 and 9). Whatever the estimators used, the resulting disparity levels broadly match the diversity trends (Fig. 8), but a detailed comparison allows us to specify the selective dynamics of main events previously discussed (Fig. 11).

**6.1. Disparification, morphological bottlenecks, and selective extinctions**

The temporal differences in the rise of diversity and disparity levels show that the first radiation of NW Tethyan belemnites was a two-step process (Figs. 5 and 8). This is explicit when detailing the evolutionary history of first Passaloteuthidae, which rapidly explored various rostral forms (morphotype 1: robust cylindrical shapes with apical grooves; Fig. 11) with few species in the Sinemurian, before producing an efficient taxonomical diversification with similar shapes during the Early Pliensbachian (Fig. 5b). As described in numerous studies (Foote, 1997; Hughes et al., 2013; Oyston et al., 2015), the temporal discrepancy between morphological and taxonomical diversifications is frequent in the early history of clades, and it can be explained in two complementary ways: 1) ecological opportunities (and thus morphological adaptation) are usually more important in the early history of groups, while they gradually disappear through ecological saturation of environments; and 2) developmental pathways are much less canalized by genetic legacy in the early evolution of clades. However, the low disparity of Passaloteuthidae was balanced by the rapid diversification and disparification of Hastitidae (Fig. 5), which initiated a new kind of slender hastate morphology (morphotype 2) during the Early Pliensbachian (Fig. 11). As previously described in other contexts (Foote, 1997; Losos and Miles, 2002; Neige et al., 2013), this morphological diversification could mark an adaptive radiation driven by new ecological opportunities.

The Pliensbachian–Toarcian crisis marked the first morphological bottleneck in the evolution of belemnites, with a preferential extinction of outlying shapes in the morphospace (Fig. 7). In details, this was manifested by two successive extinction events marked by distinct morphoselective dynamics. The first one occurred during the Late Pliensbachian, when morphotype 1 preferentially vanished compared to morphotype 2 (Fig. 11). Then, species with hastate rostra were further affected during the Early Toarcian event. In parallel, new belemnites characterized by longer and more conical rostra (morphotype 3) appeared for the first time. The reasons for these dynamics remain obscure



**Fig. 11.** Categorization and diversity of belemnite morphotypes through time. The three morphological groups are based on a K-clustering method ( $n = 3$ ) using the fourth first principal components. The main diversity crises are indicated with arrows and grey bands. Representative rostra of each morphotype are represented. See Fig. 2 for age abbreviations.



but, in agreement with isotopic analyses reporting coeval changes in belemnite life habits (Ullmann et al., 2014), it is possible that the prominent warming and anoxic events of the Pliensbachian–Toarcian boundary selected forms adapted to different water depth ranges or environments. When optimal conditions reappeared in the Middle and Late Toarcian, each morphotype rediversified (Fig. 11), which led to the highest disparity levels of the Early Jurassic (Fig. 8). Similarly to ammonites displaying common patterns in the Middle Toarcian (Dera et al., 2010; Neige et al., 2013), the recovery of belemnites and their morphological exploration could be linked to a rapid colonization of vacated ecological niches.

Like the previous one, the major Aalenian crisis was characterized by a significant drop in the morphological disparity of belemnite rostra from the Late Toarcian to the Late Aalenian (Fig. 5). However, it was non-selective (i.e., random extinction; Roy and Foote, 1997), because taxa vanished independently of their morphology (Fig. 11). Only few species belonging to Megateuthidae and Acrocoelitidae (i.e., morphotype 1) survived at regional scale. These patterns contrast with the macroevolutionary dynamics of NW Tethyan ammonites (Neige et al., 2001), for which no morphological bottleneck was highlighted during this interval. The random selective dynamics of the crisis might therefore suggest a profound disturbance in the belemnite communities (if sampling or collection biases can be ruled out), independently of their ecological affinities.

After the Aalenian crisis, the recovery of belemnites was marked by a diversification of new dominant groups (e.g., Cylindroteuthidae, Megateuthidae, and Belemnopseidae) exhibiting morphotypes similar to previous extinct ones (Figs. 5 and 11). However, confidence intervals remain too high for attesting a significant disparification event during the Early Bajocian (Fig. 8). On the other hand, a significant drop in disparity prevailed at the Bajocian–Bathonian boundary, whereas the diversity levels from South Germany declined more gradually from the Early Bajocian to the Middle Bathonian. As first suggested by Villier and Korn (2004), this further indicates that disparity patterns may be reliable markers of the very beginning of a biological crisis, whereas regional richness patterns are sometimes less relevant. Interestingly, this new crisis was selective against morphotypes 2 and 3 (Fig. 11). The cause of this selection remains unknown, but it is likely that the palaeoenvironmental conditions became unsuitable for at least some groups which went extinct (i.e., Megateuthidae with morphotypes 3) or temporarily left the Swabian–Fraconian basins (i.e., Cylindroteuthidae) during the Bathonian.

The last disparification of Jurassic belemnites occurred during the Oxfordian diversification marking the evolutionary success of hastate rostra (morphotypes 2) (Fig. 11). Although new Duvaliidae represented the most diversified group, this episode was especially linked to a morphological explosion of Belemnopseidae, whose disparity was previously low. This rapid burst of new rostral shapes could imply an adaptive radiation of this group (sensu Neige et al., 2013). However, this major disparification was interrupted by the Kimmeridgian crisis, which produced a last morphological bottleneck from the Late Kimmeridgian to the Early Tithonian. As during the Early Toarcian, the hastate shapes were further affected, and it is possible that a major anoxic event drove this selective dynamics (Tribovillard et al., 2012).

## 6.2. Morphofunctional adaptations

It is tempting to attribute the great morphological variability of belemnite rostra and the recurrent morphoselective patterns to different ecological and/or morphofunctional constraints through time. Recently, geochemical analyses (i.e.,  $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ , Mg/Ca) performed on belemnite rostra have highlighted singular ecological differences in term of seawater temperature or life depth according to species (McArthur et al., 2007; Wierzbowski and Joachimski, 2007; Dera et al., 2009; Wierzbowski and Joachimski, 2009; Mutterlose et al., 2010; Wierzbowski and Rogov, 2011; Li et al., 2012; Harazim et al., 2013; Stevens et al., 2014; Ullmann et al., 2014;

Wierzbowski, 2015). However, some geochemical analyses are not without controversy (see Mutterlose et al. 2010) and might in some cases be compounded by late ontogenetic migrations (e.g., Alberti et al., 2012), vital effects (e.g., Harazim et al. 2013) or diagenetic alterations (e.g., Ullmann et al. 2015). Basically, belemnites are supposed to have inhabited a wide range of ecological niches ranging from shallow coastal domains (Stevens et al., 2014) to the top of the thermocline (i.e., 50 to 250 m; Mutterlose et al., 2010), and even migrated vertically at 600–1000 m depths (Zakharov et al., 2006, 2011). Nonetheless, no clear bathymetric relation to rostrum morphology has been proven to this date. Rare anatomical evidences suggest that most belemnites were active predators and good swimmers (Reitner and Urlichs, 1983; Riegraf and Hauff, 1983; Klug et al., 2010, 2016). Some authors hypothesized that taxa with short and robust rostra could be nekto-benthic, while forms with laterally compressed rostra like *Duvalia* may have even had a bottom-dwelling lifestyle in analogy with considerations for extant coleoids (Packard, 1972; Mutterlose et al., 2010; Arkhipkin et al., 2015). It is however hard to tie pelagic organisms to a particular environment or depth based on shell shape alone (Ritterbush et al., 2014).

In analogy with recent studies on ammonoids (Tendler et al., 2015), rostral forms can never be fully optimized for a single function because of trade-offs between different tasks, including hydrodynamics, economy of shell material and growth. However, swimming constraints are often considered, perhaps prematurely, as the most relevant as the streamlining of rostra is generally regarded as an “emergency adaptation” favouring quick propulsive backward escapes in front of predators (Seilacher, 1968; Seilacher and Weisenauer, 1978). As for modern coleoids (Stevens, 1965; Johnson et al., 1972; O’Dor, 1988; Chamberlain, 1993; Monks et al., 1996; Hewitt et al., 1999; Bartol et al., 2001; Arkhipkin et al., 2015), the form of rostra, the position of fins or muscles, as well as the size of phragmocones could directly influence their maneuverability, buoyancy, drag, swimming velocity or equilibrium constraints, each of them potentially giving advantages in term of fitness and evolutionary success. For instance, the hydrodynamic models of Hoener (1965) suggest that the drag coefficient (i.e., summarizing the force opposed to motion) should decrease as the robustness (ROB) and the apical angle (A) of rostra decrease, while the apical inflation (INFap) increases and the apex becomes smoother. In other words, the metabolic cost credited to rapid escape movements, already high for modern squids (O’Dor and Webber, 1986; Wells and Clarke, 1996), might have been more expensive for stocky conical forms than slender hastate ones. Conversely, it might be expected that small conical rostra had further maneuverability, which is another prerequisite to escape predators more successfully.

By following the Parento optimality concept recently applied to ammonite shells (Tendler et al., 2015), these different hydrodynamic properties might suggest that, combined to modifications of phragmocones, fins, and other soft parts (Klug et al., 2016), the rostral morphotypes could be evolutionary tradeoffs towards one or more specific tasks. The exact identification of respective tasks is beyond the goal of this study, but it is possible that the outlying rostral forms of the morphospace correspond to specialized taxa optimized for singular swimming behaviours. For example, it is arguable that the Jurassic species with slender hastate rostra (morphotype 2) were very fast swimmers. Furthermore, it is likely that most of them inhabited deep waters, as they massively disappeared during the bottom anoxic events of the Early Toarcian and Kimmeridgian. To the opposite, the poor hydrodynamic properties of conical rostra with long apical grooves (morphotype 3) suggest that the relative species (e.g., *Salpingoteuthis*) were potentially more adapted to maneuverability. This adaptation could imply slow motions in turbulent surface waters, which are compatible with the presence of long robust fins favouring stability. Finally, the hydrological properties of stocky to robust cylindrical and cylindrical rostra (morphotype 1) remain more enigmatic, in part

because the relative species inhabited various environments and some of them possessed epirostra (Reitner and Urlichs, 1983; Mutterlose et al., 2010; Ullmann et al., 2014; Arkhipkin et al., 2015). Hypothetically, their intermediate properties in terms of maneuverability and velocity could suggest a large spectrum of behaviours potentially implying spatial or vertical migrations over long distances.

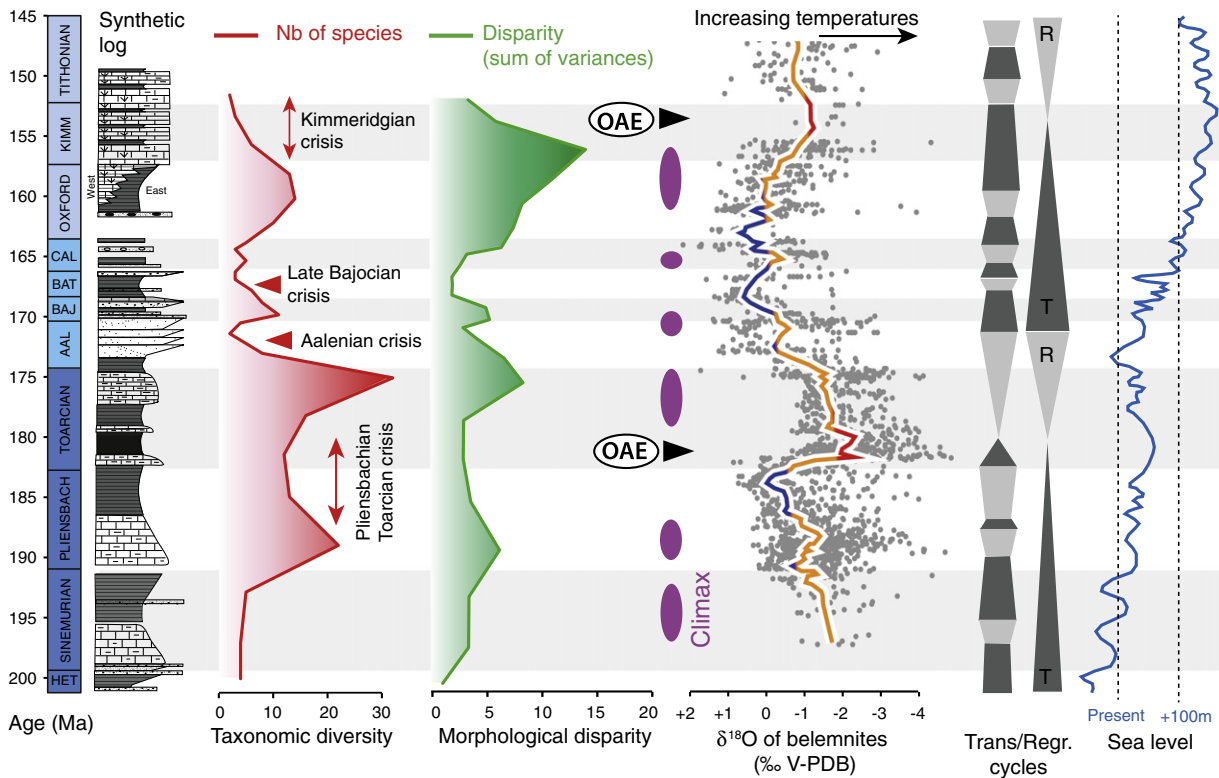
Beyond the successful ecomorphological exploration of belemnites, it is worth mentioning that their rostra were more and more hastate during the Middle to the Late Jurassic. Initially subangular and regular during the Early Jurassic, the flanks of rostra also became progressively smoother and flattened (or compressed) through time (Fig. 9). By following the hydrodynamic models of Hoener (1965), this gradual evolution seen in most belemnite groups could indicate a progressive optimization of the rostrum for increased swimming velocity and energy efficiency. In the context of the Mesozoic Marine Revolution (Vermeij, 1977), it is possible that such pattern reflects a progressive rise in the selective pressure exerted by marine predators (e.g., marine reptiles, chondrichthyans) and a stronger competition forcing belemnites to be faster and energetically more efficient through time. This escalation model, in which the evolution of prey (through acquisition of defensive traits) is controlled by the coeval evolution of predators (Vermeij, 1987, 2008), could be incidentally reflected by reciprocally low diversity levels of belemnites and marine reptiles during the Middle Jurassic (Bardet, 1995; Thorne et al., 2011) (Fig. 12). Further proof is still needed to confirm this hypothesis, but if true, this means that, beyond defensive aspects, morphological traits favouring escape strategy could also form important components of this theory. Note that various other factors, which might or might not also represent advantages against increased predation and competition (e.g., those related to economy of shell material and growth) are hard to assess due to the limited available data for belemnites on this matter. Some authors have argued that some belemnites might have lived longer than others

(Dunca et al., 2006; Wierzbowski and Joachimski, 2009; Wierzbowski, 2013), while others have demonstrated complex mechanisms of biomineralization in at least some taxa (Bandel and Spaeth, 1988; Arkhipkin et al., 2015). More data are therefore necessary to better understand the biology of these organisms before consistent predictions related with those factors can even be formulated.

### 7. Influence of palaeoenvironmental factors

#### 7.1. Palaeoclimatic constraints

By analyzing the evolution of  $\delta^{18}\text{O}$  values from NW Tethys (Dera et al., 2011a), it appears that seawater temperature was an important driver of belemnite diversification during the Jurassic (Fig. 12). Indeed, the main radiation phases coincide with warm temperate periods such as the Early Pliensbachian, Middle–Late Toarcian, Early Bajocian, and Middle–Late Oxfordian. Conversely, the main biotic crises correspond either to cold episodes (i.e., Late Pliensbachian, Aalenian, Bathonian, and Callovian–Oxfordian transition) or hyperthermal events (i.e., Early Toarcian and Kimmeridgian) coeval with suboxic to euxinic conditions in the Euro–Boreal basins (Tribouillard et al., 2012). However, estimating accurately the best temperature range is not straightforward as the palaeothermometry equations rest on seawater  $\delta^{18}\text{O}$  values (Anderson and Arthur, 1983), which fluctuated through time in response to changes in ice volume and freshwater supplies (Dera et al., 2011a). By assuming seawater  $\delta^{18}\text{O}$  values between  $-1$  and  $0\%$ , the most favourable temperatures would have broadly ranged from  $12$  to  $25\text{ }^\circ\text{C}$ . As observed for modern squids (Pecl and Jackson, 2008; Hoving et al., 2013), these temperate to warm conditions might have increased the turnover of belemnite populations because elevated temperatures accelerate the metabolism, growth rate and sexual maturity of individuals, while shortening their life spans. Consequently, it is



**Fig. 12.** Evolution of belemnite diversity, disparity, and size patterns compared with palaeoenvironmental signals of the Jurassic. Purple symbols indicate the warm temperate climax periods favouring the diversification of belemnites.

Synthetic log of Jurassic deposits from South Germany is modified from Bayer and McGhee (1986) and Schmid et al. (2005). Evolution of seawater temperatures based on the NW Tethyan  $\delta^{18}\text{O}$  datasets is modified from Dera et al. (2011a) and Martinez and Dera (2015). Main global oceanic anoxic events (i.e., Early Toarcian and Late Jurassic) are from Jenkyns (1988) and Nozaki et al. (2013). Transgressive and regressive cycles are from Hardenbol et al. (1998). Sea-level curve is from Ruban (2015).

possible that, in association with other factors, warm periods were more favourable to faster population dynamics and potentially higher diversification rates on the long term.

Most coleoids require important oxygen and food supplies to ensure extremely fast growth rates and efficient propulsion (O'Dor and Webber, 1986; Wells and Clarke, 1996). The pitfall of this fast life mode is that too elevated temperatures might cause rapid and extreme proliferations of mature specimens with faster metabolisms requiring both more food and more oxygen (Pecl and Jackson, 2008). In addition, warming and acidification of the surface ocean may also create a ceiling that might preclude cephalopods from entering more shallow waters, while the expanding hypoxic zone will increase the depth below which they cannot penetrate, reducing the habitable depth range of species (Rosa and Seibel, 2008; Pörtner et al., 2011; Melzner et al., 2013). Hence, combined effects associating size reductions of available habitable zones, rises of physiological constraints, deteriorations of population dynamics, and destabilizations of ecological resources could potentially explain why the belemnites massively disappeared during the hyperthermal and anoxic conditions of the Early Toarcian and Kimmeridgian.

On the opposite, too cold seawater temperatures might also have been harmful for most NW Tethyan belemnites because this implies a considerable energetic cost for survival. This hypothesis could partly explain the strong extinction events during the Late Pliensbachian and Middle Jurassic cold snaps (Dera et al., 2011a; Korte et al., 2015). Through successive generations, these adverse conditions might have selected specimens with slower metabolisms, leading to long-lived specimens with delayed maturity reducing the turnover of populations (Pecl and Jackson, 2008). As observed in modern communities, this shift in evolutionary dynamics could potentially account for the lower diversification rates of belemnites during these cold periods. However, further studies are necessary to confirm if predications based on trends observed within single species or genera on annual to decadal time-scales (Pecl and Jackson, 2008; Hoving et al., 2013), also hold up on longer macroevolutionary time-scales.

The only ways to withstand rapid adverse climate changes were latitudinal migrations towards refuge areas acting as diversity pools for recovery after biotic crises. Because their diversity levels generally counterbalanced the Euro-Boreal trends (Dzyuba, 2013; Weis et al., 2015), we suggest that the Arctic and Mediterranean basins could have played this role for the survival of Euro-Boreal belemnites during hyperthermal and cold events, respectively.

## 7.2. Eustatic influences

In complement to palaeoclimatic changes, the sea level fluctuations could be additional drivers of the macroevolutionary dynamics of Euro-Boreal belemnites. The main reason is that the shallowing/deepening of basins modulates the potential of diversification and adaptation in new bathymetrical niches (Dzyuba, 2013). Moreover, it is likely that sea-level changes have directly affected the surface and access to shallow spawning grounds, as well as preservation potential (discussed above). Regarding our results, this straightforward model is however difficult to confirm for the long-term transgressions of the Early and Late Jurassic (Hallam, 2001; Haq and Al-Qahtani, 2005; Ruban, 2015) (Fig. 12), because repeated palaeoclimatic disturbances likely altered the gradual process of ecological diversification. Nevertheless, the influence of eustatic changes could have been more significant during the major regressions of the Late Pliensbachian and Aalenian (Hallam, 2001), which coincide with transient cooling events previously discussed (Price, 2010; Suan et al., 2010; Dera et al., 2011a; Korte et al., 2015) (Fig. 12). Due to a lithospheric updoming in the North Sea region, the Aalenian regression is known to have been especially important at regional scale, as it caused extended emersions and numerous basinal restrictions (Korte et al., 2015). This prominent sea level fall can therefore be considered as a supplementary trigger of the Aalenian

crisis, as it considerably reduced the volume of deep and intermediate habitats in the northern basins, and restricted the migration of belemnites towards more suitable seawater conditions.

## 8. Conclusions

We analyzed the diversity and morphological disparity of Jurassic belemnites from the Swabo-Franconian basin at a substage resolution. By comparing our results with trends from other palaeobiogeographical domains and palaeoenvironmental data, the following points are highlighted:

1. After a long quiescence from the Hettangian to the Sinemurian, the evolution of Euro-Boreal belemnites was boosted by four periods of taxonomical diversification coupled with disparification of rostra (i.e., Early Pliensbachian, Late Toarcian, Early Bajocian, and Oxfordian).
2. Four diversity drops manifested by morphological bottlenecks punctuated the evolution of Euro-Boreal belemnites during the Pliensbachian–Toarcian interval, Aalenian, Late Bajocian, and Kimmeridgian. Most extinction episodes were morphoselective, except the Aalenian crisis.
3. Comparisons with Siberian data show that the Pliensbachian–Toarcian crisis, the Middle–Late Toarcian recovery and the Aalenian extinction remain distinguishable at supra-regional scale. The other events can merely be considered as regional because comparative data are lacking or opposite. We suggest that the Arctic domain could have been a refuge area during the Toarcian and Kimmeridgian hyperthermal events.
4. Our results highlight a strong morphological variability of rostra, in which each morphotype represents an evolutionary trade-off towards specific tasks combining velocity, maneuverability, buoyancy, drag, or equilibrium constraints. The trend towards smoother and hastate rostra could indicate increases of hydrodynamic properties throughout the Jurassic, potentially mirroring rises in predation and competition during the Mesozoic Marine Revolution.
5. The episodes of belemnite diversification were mainly favoured by warm seawater temperatures potentially allowing fast metabolic rates and rapid population turnovers. Conversely, cooling or hyperthermal events triggered biological crises probably through direct physiological impacts or destabilizations of ecosystems. The major Aalenian crisis was amplified by a strong regression in the Euro-Boreal domain.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.05.029>.

## References

- Alberti, M., Fürsich, F.T., Pandey, D.K., Ramkumar, M., 2012. Stable isotope analyses of belemnites from the Kachchh Basin, western India: paleoclimatic implications for the Middle to Late Jurassic transition. *Facies* 58 (2), 261–278.
- Alsen, P., Mutterlose, J., 2009. The Early Cretaceous of the North-East Greenland: a crossroads of belemnite migration. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280 (1–2), 168–182.
- Anderson, T.F., Arthur, M.A., 1983. Stable isotopes of oxygen and carbon and their application to sedimentologic and paleoenvironmental problems. In: Arthur, M.A., Anderson, T.F., Kaplan, I.R., Veizer, J., Land, L.S. (Eds.), *Stable Isotopes in Sedimentary Geology*. SEPM Short Course, Tulsa, pp. 1–151.



- Arkhipkin, A.I., Laptikhovskiy, V.V., 2012. Impact of ocean acidification on plankton larvae as a cause of mass extinctions in ammonites and belemnites. *Neues Jb. Geol. Paläontol. Abh.* 266 (1), 39–50.
- Arkhipkin, A.I., Weis, R., Mariotti, N., Shcherbich, Z., 2015. 'Tailed' cephalopods. *J. Molluscan Stud.* 81 (3), 345–355.
- Bandel, K., Spaeth, C., 1988. Structural differences in the ontogeny of some belemnite rostra. In: Wiedmann, J., Kullmann, J. (Eds.), *Cephalopods – Present and Past*, Stuttgart, pp. 247–271.
- Bardet, N., 1995. Evolution et extinction des reptiles marins au cours du Mésozoïque. *Palaeovertebrata* 24 (3–4), 177–283.
- Bartol, I.K., Patterson, M.R., Mann, R., 2001. Swimming mechanics and behavior of the shallow-water brief squid *Lolliguncula brevis*. *J. Exp. Biol.* 204, 3655–3682.
- Bayer, U., McGhee, G.R., 1986. Cyclic patterns in the Paleozoic and Mesozoic: implications for time scale calibrations. *Paleoceanography* 1 (4), 383–402.
- Bodin, S., Meissner, P., Janssen, N.M.M., Steuber, T., Mutterlose, J., 2015. Large igneous provinces and organic carbon burial: controls on global temperature and continental weathering during the Early Cretaceous. *Glob. Planet. Chang.* 133, 238–253.
- Brigaud, B., Vincent, B., Carpentier, C., Robin, C., Guillocheau, F., Yven, B., Huret, E., 2014. Growth and demise of the Jurassic carbonate platform in the intracratonic Paris Basin (France): interplay of climate change, eustasy and tectonics. *Mar. Pet. Geol.* 53, 3–29.
- Butler, R.J., Brusatte, S.L., Andres, B., Benson, R.B.J., 2012. How do geological sampling biases affect studies of morphological evolution in deep time? A case study of pterosaur (Reptilia: Archosauria) disparity. *Evolution* 66 (1), 147–162.
- Caruthers, A.H., Smith, P.L., Gröcke, D.R., 2013. The Pliensbachian–Toarcian (Early Jurassic) extinction, a global multi-phased event. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 386, 104–118.
- Caswell, B.A., Coe, A.L., Cohen, A.S., 2009. New range data for marine invertebrate species across the early Toarcian (Early Jurassic) mass extinction. *J. Geol. Soc.* 166, 859–872.
- Chamberlain, J.A.J., 1993. Locomotion in ancient seas: constraint and opportunity in cephalopod adaptive design. *Gebios* 15, 49–61.
- Christensen, W.K., 1976. Palaeobiogeography of the late Cretaceous belemnites of Europe. *Paläontol. Z.* 50 (3), 113–129.
- Christensen, W.K., 1997. Palaeobiogeography and migration in the Late Cretaceous belemnite family Belemnitellidae. *Acta Palaeontol. Pol.* 42 (4), 457–495.
- Christensen, W.K., 2002. Palaeobiology, phylogeny and palaeobiogeography of belemnoids and related coleoids. *Berliner Paläobiologische Abhandlungen* Vol. 1, pp. 18–21.
- De Baets, K., Klug, C., Monnet, C., 2013. Intraspecific variability through ontogeny in early ammonoids. *Paleobiology* 39 (1), 75–94.
- Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P., Joachimski, M.M., Durllet, C., 2011a. Climatic ups and downs in a disturbed Jurassic world. *Geology* 39, 215–218.
- Dera, G., Neige, P., Dommergues, J.L., Brayard, A., 2011b. Ammonite paleobiogeography during the Pliensbachian–Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. *Glob. Planet. Chang.* 78, 92–105.
- Dera, G., Neige, P., Dommergues, J.-L., Fara, E., Laffont, R., Pellenard, P., 2010. High-resolution dynamics of Early Jurassic marine extinctions: the case of Pliensbachian–Toarcian ammonites (Cephalopoda). *J. Geol. Soc.* 167 (1), 21–33.
- Dera, G., Prunier, J., Smith, P.L., Haggart, J.W., Popov, E., Guzhov, A., Rogov, M., Delsate, D., Thies, D., Cuny, G., Pucéat, E., Charbonnier, G., Bayon, G., 2015. Nd isotope constraints on ocean circulation, paleoclimate, and continental drainage during the Jurassic breakup of Pangea. *Gondwana Res.* 27 (4), 1599–1615.
- Dera, G., Pucéat, E., Pellenard, P., Neige, P., Delsate, D., Joachimski, M.M., Reisberg, L., Martinez, M., 2009. Water mass exchange and variations in seawater temperature in the NW Tethys during the Early Jurassic: evidence from neodymium and oxygen isotopes of fish teeth and belemnites. *Earth Planet. Sci. Lett.* 286 (1–2), 198–207.
- Doguzhaeva, L.A., Weis, R., Delsate, D., Mariotti, N., 2013. Embryonic shell structure of Early-Middle Jurassic belemnites, and its significance for belemnite expansion and diversification in the Jurassic. *Lethaia* 47 (1), 49–65.
- Dommergues, J.L., Laurin, B., Meister, C., 1996. Evolution of ammonoid morphospace during the Early Jurassic radiation. *Paleobiology* 22 (2), 219–240.
- Dommergues, J.L., Montuire, S., Neige, P., 2002. Size patterns through time: the case of the Early Jurassic ammonite radiation. *Paleobiology* 28, 423–434.
- Doyle, P., 1985. Sexual dimorphism in the belemnite *Youngibelus* from the Lower Jurassic of Yorkshire. *Paleontology* 28 (1), 133–146.
- Doyle, P., 1987. Lower Jurassic–Lower Cretaceous belemnite biogeography and the development of the Mesozoic Boreal Realm. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 61, 237–254.
- Doyle, P., 1990. The British Toarcian (Lower Jurassic) belemnites. Part 1. Monograph of the Palaeontographical Society Vol. 144, pp. 1–49.
- Doyle, P., 1992. The British Toarcian (Lower Jurassic) belemnites. Part 2. Monograph of the Palaeontographical Society Vol. 144, pp. 50–79.
- Doyle, P., 1994. Aspects of the distribution of Lower Jurassic belemnites. *Palaeopelagos Spec. Publ.* 1, 109–121.
- Doyle, P., 2003. Type belemnites of Simpson's fossils of the Yorkshire Lias. *Proc. Yorks. Geol. Soc.* 54 (3), 147–184.
- Doyle, P., Bennett, M.R., 1995. Belemnites in biostratigraphy. *Palaeontology* 38 (4), 815–829.
- Doyle, P., Donovan, D.T., Nixon, M., 1994. Phylogeny and systematics of the Coleoidea. University of Kansas Paleontological Contributions Vol. 5, pp. 1–15.
- Doyle, P., Kelly, S.R.A., Pirrie, D., Riccardi, A.C., 1997. Jurassic belemnite distribution patterns: implications of new data from Antarctica and Argentina. *Alcheringa* 21 (3), 219–228.
- Doyle, P., MacDonald, D.I.M., 1993. Belemnite battlefields. *Lethaia* 26 (1), 65–80.
- DSK (Deutsche Stratigraphische Kommission), 2002. Stratigraphische Tabelle von Deutschland 2002. Deutsche Stratigraphische Kommission, Potsdam.
- Dunca, E., Doguzhaeva, L.A., Schöne, B.R., van de Schootbrugge, B., 2006. Growth patterns in rostra of the Middle Jurassic belemnite *Megateuthis giganteus*: controlled by the moon? *Acta Univ. Carol. Geol.* 49, 107–117.
- Dunhill, A.M., Benton, M.J., Twitchett, R.J., Newell, A.J., 2012. Completeness of the fossil record and the validity of sampling proxies at outcrop level. *Palaeontology* 55 (6), 1155–1175.
- Dutton, A., Huber, B.T., Lohmann, K.C., Zinmeister, W.J., 2007. High-resolution stable isotope profiles of dimitobelid belemnite: implications for paleodepth habitat and Late Maastrichtian climate seasonality. *PALAIOS* 22 (6), 642–650.
- Dzyuba, O.S., 2013. Belemnites in the Jurassic–Cretaceous boundary interval of the Maurya and Yatriya River sections, Western Siberia: biostratigraphic significance and dynamics of taxonomic diversity. *Stratigr. Geol. Correl.* 21 (2), 189–214.
- Dzyuba, O.S., Weis, R., Nalynayeva, T.I., Riegraf, W., 2015. *Rarobelus* nom. nov. from the boreal Toarcian–Aalenian and its systematic position (Belemnitida, Belemnitina, Megateuthididae). *Neues Jb. Geol. Paläontol. Abh.* 275 (3), 305–315.
- Footo, M., 1993. Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19, 403–419.
- Footo, M., 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology* 20, 424–444.
- Footo, M., 1997. The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* 28, 129–152.
- Footo, M., 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology supplement* 26, 74–102.
- Footo, M., 2005. Pulsed origination and extinction in the marine realm. *Paleobiology* 31 (1), 6–20.
- Fuchs, D., Iba, Y., Tischlinger, H., Keupp, H., Klug, C., 2015. The locomotion system of Mesozoic Coleoidea (Cephalopoda) and its phylogenetic significance. *Lethaia* <http://dx.doi.org/10.1111/let.12155>.
- Gerber, S., Neige, P., Eble, G.J., 2007. Combining ontogenetic and evolutionary scales of morphological disparity: a study of early Jurassic ammonites. *Evol. Dev.* 9 (5), 472–482.
- GFEJ (Groupe Français d'Etude du Jurassique), 1997. Biostratigraphie du Jurassique Ouest-Européen et Méditerranéen. *Bull. Centre Rech. Elf Explor. Prod. Mém.* 17 (Pau, 440 pp.).
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M., 2012. The Geologic Time Scale 2012, 2. Elsevier BV, Amsterdam.
- Hallam, A., 1987. Radiations and extinctions in relation to environmental change in the marine Jurassic of north west Europe. *Paleobiology* 13, 152–168.
- Hallam, A., 2001. A review of broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 167 (1–2), 23–37.
- Hammer, O., Harper, D., 2006. *Paleontological Data-Analysis*. Blackwell Publishing, Massachusetts.
- Haq, B.U., Al-Qahtani, A.M., 2005. Phanerozoic cycles of sea-level change on the Arabian Platform. *GeoArabia* 10, 127–160.
- Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2013. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian–Toarcian). *Sedimentology* 60 (2), 359–390.
- Hardenbol, J., Thierry, J., Farley, M.B., de Graciansky, P.-C., Vail, P.R., 1998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. In: de Graciansky, P.-C., Hardenbol, J., Jacquin, T., Vail, P.R. (Eds.), *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins*. Special publication. Society for Sedimentary Geology, pp. 3–13.
- Harries, P.J., Little, C.T.S., 1999. The early Toarcian (Early Jurassic) and the Cenomanian–Turonian (Late Cretaceous) mass extinctions: similarities and contrasts. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154, 39–66.
- Hewitt, R.A., Westermann, G.E.G., Judd, R.L., 1999. Buoyancy calculations and ecology of Callovian (Jurassic) cylindroteuthid belemnites. *Neues Jb. Geol. Paläontol. Abh.* 211 (1/2), 89–112.
- Hoener, S.F., 1965. *Fluid Dynamic Drag: Practical Information on Aerodynamic Drag and Hydrodynamic Resistance*. self published, Midland Park, NJ.
- Holland, S.M., Patzkowski, M.E., 2015. The stratigraphy of mass extinction. *Palaeontology* 58 (5), 903–924.
- Hoving, H.J.T., et al., 2013. Extreme plasticity in life history strategy allows a migratory predator (jumbo squid) to cope with a changing climate. *Glob. Chang. Biol.* 19, 2089–2103.
- Hughes, M., Gerber, S., Wills, M.A., 2013. Clades reach highest morphological disparity early in their evolution. *PNAS* 110 (34), 13875–13879.
- Iba, Y., Mutterlose, J., Tanabe, K., Sano, S.-I., Misaki, A., Terabe, K., 2011. Belemnite extinction and the origin of modern cephalopods 35 m.y. prior to the Cretaceous–Paleogene event. *Geology* 39, 483–486.
- Iba, Y., Sano, S.-I., Goto, M., 2015a. Large belemnites were already common in the Early Jurassic – new evidence from Central Japan. *Paleontol. Res.* 19 (1), 21–25.
- Iba, Y., Sano, S.-I., Mutterlose, J., 2014. The early evolutionary history of belemnites: new data from Japan. *PLoS One* 9 (5), e95632.
- Iba, Y., Sano, S.-I., Mutterlose, J., Kondo, Y., 2012. Belemnites originated in the Triassic – a new look at an old group. *Geology* 40, 911–914.
- Iba, Y., Sano, S.-I., Rao, X., Fuchs, D., Chen, T., Weis, R., Sha, J., 2015b. Early Jurassic belemnites from Gondwana margin of the Southern Hemisphere – Sinemurian record from South Tibet. *Gondwana Res.* 28 (2), 882–887.
- Jenkyns, H.C., 1988. The Early Toarcian (Jurassic) anoxic event – stratigraphy, sedimentary, and geochemical evidence. *Am. J. Sci.* 288 (2), 101–151.
- Jenkyns, H.C., Jones, C.E., Grocke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. *J. Geol. Soc.* 159, 351–378.



- Johnson, W., Soden, P.D., Trueman, E.R., 1972. A study in jet propulsion: an analysis of the motion of squid, *Loligo vulgaris*. *J. Exp. Biol.* 56, 155–165.
- Kiessling, W., Aberhan, M., Brennes, B., Wagner, P.J., 2007. Extinction trajectories of benthic organisms across the Triassic–Jurassic boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 244 (1–4), 201–222.
- Klug, C., Schweigert, G., Fuchs, D., Dietl, G., 2010. First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany). *Lethaia* 43 (4), 445–456.
- Klug, C., Schweigert, G., Fuchs, D., Kruta, I., Tischlinger, H., 2016. Adaptations to squid-style high-speed swimming in Jurassic belemnites. *Biol. Lett.* 12 (1), 201550877.
- Korte, C., Hesselbo, S.P., Ullmann, C.V., Dietl, G., Ruhl, M., Schweigert, G., Thibault, N., 2015. Jurassic climate mode governed by ocean gateway. *Nat. Commun.* 6, 10015.
- Lathuilière, B., Marchal, D., 2009. Extinction, survival and recovery of corals from the Triassic to Middle Jurassic time. *Terra Nova* 21 (1), 57–66.
- Leinfelder, R.R., Schmid, D.U., Nose, M., Werner, W., 2002. Jurassic reef patterns – the expression of a changing globe. *SEPM Spec. Publ.* 72, 465–520.
- Li, Q., McArthur, J.M., Atkinson, T.C., 2012. Lower Jurassic belemnites as indicators of palaeo-temperatures. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 315–316, 38–45.
- Little, C.T.S., Benton, M.J., 1995. Early Jurassic mass extinction: a global long-term event. *Geology* 23 (6), 495–498.
- Losos, J.B., Miles, D.B., 2002. Testing the hypothesis that a clade has adaptively radiated: iguanid lizard clades as a case study. *Am. Nat.* 160, 147–157.
- Macchioni, F., Cecca, F., 2002. Biodiversity and biogeography of middle–late liassic ammonoids: implications for the early Toarcian mass extinction. *Geobios* 35 (Supplement 1), 165–175.
- Mariotti, N., Weis, R., Di Cencio, A., Clément, A., De Baets, K., 2012. New records of early Middle Jurassic belemnites in the French Subalpine Basin and their paleobiogeographic significance. *Geobios* 45, 99–108.
- Martill, D.M., Taylor, M.A., Duff, K.L., Riding, J.B., Bown, P.R., 1994. The trophic structure of the biota of the peterborough Member, Oxford Clay Formation (Jurassic), UK. *J. Geol. Soc.* 151 (1), 173–194.
- Martinez, M., Dera, G., 2015. Orbital pacing of carbon fluxes by a ~9-My eccentricity cycle during the Mesozoic. *PNAS* 112 (41), 12604–12609.
- Massare, J.A., 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vertebr. Paleontol.* 7 (2), 121–137.
- McArthur, J.M., Doyle, P., Leng, M.J., Reeves, K., Williams, C.T., Garcia-Sanchez, R., Howarth, R.J., 2007. Testing palaeo-environmental proxies in Jurassic belemnites: Mg/Ca, Sr/Ca, Na/Ca,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ . *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252 (3–4), 464–480.
- Meledina, S.V., Shurygin, B.N., Dzyuba, O.S., 2005. Stages in developments of molluscs, paleobiogeography of boreal seas in the Early–Middle Jurassic and zonal scales in Siberia. *Geol. Geofiz.* 46 (3), 239–255 (in Russian).
- Melzner, F., Thomsen, J., Koeve, W., Oeschlies, A., Gutowska, M., Bange, H., Hansen, H., Körtzinger, A., 2013. Future ocean acidification will be amplified by hypoxia in coastal habitats. *Mar. Biol.* 160 (8), 1875–1888.
- Monks, N., Hardwick, J.D., Gale, A.S., 1996. The function of the belemnite guard. *Paläontol. Z.* 70 (3–4), 425–431.
- Moyné, S., Neige, P., 2007. The space–time relationship of taxonomic diversity and morphological disparity in the Middle Jurassic ammonite radiation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 248 (1–2), 82–95.
- Mutterlose, J., 1998. The Barremian–Aptian turnover of biota in the northwestern Europe: evidence from belemnites. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 144 (1), 161–173.
- Mutterlose, J., Malkoc, M., Schouten, S., Sinnighe Damsté, J.S., Forster, A., 2010. Tex86 and stable  $\delta^{18}\text{O}$  paleothermometry of early Cretaceous sediments: implications for belemnite ecology and paleotemperature proxy application. *Earth Planet. Sci. Lett.* 298 (3–4), 286–298.
- Mutterlose, J., Wiedenroth, K., 1998. Early Cretaceous (Valanginian–Hauterivian) belemnites from western Morocco: stratigraphy and palaeoecology. *Cretac. Res.* 29 (5–6), 814–829.
- Nardin, E., Rouget, I., Neige, P., 2005. Tendencies in paleontological practice when defining species, and consequences on biodiversity studies. *Geology* 33 (12), 969–972.
- Navarro, N., 2003. MDA: a MATLAB-based program for morphospace-disparity analysis. *Comput. Geosci.* 29 (5), 655–664.
- Neige, P., 2003. Spatial patterns of disparity and diversity of the Recent cuttlefishes (Cephalopoda) across the Old World. *J. Biogeogr.* 30 (8), 1125–1137.
- Neige, P., Brayard, A., Gerber, S., Rouget, I., 2009. Ammonoids (Mollusca, Cephalopoda): recent advances and contributions to evolutionary paleobiology. *C.R. Palevol* 8 (2–3), 167–178.
- Neige, P., Dera, G., Dommergues, J.L., 2013. Adaptive radiation in the fossil record: a case study among Jurassic ammonoids. *Palaeontol.* 56 (6), 1247–1261.
- Neige, P., Elmi, S., Rulleau, L., 2001. Crisis – what crisis? Quantification of the morphological disparity of ammonites at the Lias–Dogger boundary. *Bull. Soc. Geol. Fr.* 172 (2), 257–264.
- Nikitenko, B., Shurygin, B., Mickey, M., 2006. High resolution stratigraphy of the Lower Jurassic and Aalenian of Arctic regions as the basis for detailed palaeobiogeographic reconstructions. *Nor. J. Geol.* 88, 267–278.
- Nozaki, T., Kato, Y., Suzuki, K., 2013. Late Jurassic ocean anoxic event: evidence from voluminous sulphide deposition and preservation in the Panthalassa. *Sci. Rep.* 3, 1889.
- O'Dogherty, L., Sandoval, J., Bartolini, A., Bruchez, S., Bill, M., Guex, J., 2006. Carbon-isotope stratigraphy and ammonite faunal turnover for the Middle Jurassic in the Southern Iberian palaeomargin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239 (3–4), 311–333.
- O'Dor, R.K., 1988. The forces acting on swimming squid. *J. Exp. Biol.* 137, 421–442.
- O'Dor, R.K., Webber, D.M., 1986. The constraints on cephalopods: why squid aren't fish. *Can. J. Zool.* 64 (8), 1591–1605.
- Oyston, J.W., Hughes, M., Wagner, P.J., Gerber, S., Wills, M.A., 2015. What limits the morphological disparity of clades. *Interface Focus* 5, 20150042.
- Packard, A., 1972. Cephalopods and fish: the limits of convergence. *Biol. Rev.* 47, 241–307.
- Pecl, G.T., Jackson, G.D., 2008. The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Rev. Fish Biol. Fish.* 18, 373–385.
- Peters, S.E., 2008. Environmental determinants of extinction selectivity in the fossil record. *Nature* 454, 626–629.
- Pinard, J.-D., Neige, P., Weis, R., Fara, E., 2014a. Diversity and palaeobiogeography of belemnites during the Early Jurassic. In: Klug, C., Fuchs, D. (Eds.), 9th International Symposium, Cephalopods – Present and Past in Combination with the 5th International Symposium Coleoid Cephalopods Through Time, Zürich.
- Pinard, J.-D., Weis, R., Neige, P., Mariotti, N., Di Cencio, A., 2014b. Belemnites from the Upper Pliensbachian and the Toarcian (Lower Jurassic) of Tournadous (Causses, France). *Neues Jb. Geol. Paläontol. Abh.* 273 (2), 155–177.
- Pörtner, H.-O., Gutowska, M., Ishimatsu, A., Lucassen, M., Melzner, F., Seibel, B.A., 2011. Effects of ocean acidification on nektonic organisms. In: Gattuso, J.-P., Hansson, L. (Eds.), *Ocean Acidification*. Oxford University Press, Oxford, pp. 154–175.
- Price, G.D., 2010. Carbon-isotope stratigraphy and temperature change during the Early–Middle Jurassic (Toarcian–Aalenian), Raasay, Scotland, UK. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 285 (3–4), 255–263.
- Raup, D.M., Sepkoski, J.J., 1984. Periodicity of extinctions in the geological past. *PNAS* 81, 801–805.
- Reitner, J., Urlichs, M., 1983. Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Südwestdeutschlands. *Neues Jb. Geol. Paläontol. Abh.* 165, 450–465.
- Rexford, A., Mutterlose, J., 2009. The role of biogeography and ecology on the isotope signature of cuttlefishes (Cephalopoda, Sepiidae) and the impact on belemnite studies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 284, 153–163.
- Riegraf, W., 1980. Revision der Belemniten des Schwäbischen Jura, Teil 7. *Palaeontogr. A* 169, 128–208.
- Riegraf, W., 1981. Revision der Belemniten des Schwäbischen Jura, Teil 8. *Palaeontogr. A* 173, 64–139.
- Riegraf, W., 2000. The belemnites described by Baron Ernst Friedrich von Schlotheim (1764–1833). *Paläontol. Z.* 74 (3), 281–303.
- Riegraf, W., Hauff, R., 1983. Belemnitenfunde mit Weichkörper, Fangarmen und Gladius aus dem Untertoarcium (Posidonienschiefer) und Unteraalenium (Opalinuston) Südwestdeutschlands. *Neues Jb. Geol. Paläontol. Abh.* 165 (3), 466–483.
- Ritterbush, K.A., Hoffman, R., Lukeneder, A., De Baets, K., 2014. Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. *J. Zool.* 292, 229–241.
- Rosa, R., Dierksen, H.M., Gonzales, L., Seibel, B.A., 2008. Ecological biogeography of cephalopod molluscs in the Atlantic: historical and contemporary causes of coastal diversity patterns. *Glob. Ecol. Biogeogr.* 17, 600–610.
- Rosa, R., Seibel, B.A., 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *PNAS* 105 (52), 20776–20780.
- Roy, K., Foote, M., 1997. Morphological approaches to measuring biodiversity. *Trends Ecol. Evol.* 12 (7), 277–281.
- Ruban, D.A., 2007. Jurassic transgressions and regressions in the Caucasus (northern Neotethys Ocean) and their influences on the marine biodiversity. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 251, 422–436.
- Ruban, D.A., 2015. Mesozoic long-term eustatic cycles and their uncertain hierarchy. *Geosci. Front.* 6, 503–511.
- Sachs, V.N., Nalynayeva, T.I., 1975. The Early and Middle Jurassic belemnites of the North of the USSR, Megateuthinae and Pseudodicoelinitinae. *Transactions of the Institute of Geology and Geophysics*, 239. Nauka, Moscow.
- Saalen, G., 1989. Diagenesis and construction of the Belemnite rostrum. *Palaeontology* 32 (4), 765–798.
- Sanders, M.T., Bardin, J., Benzaggagh, M., Cecca, F., 2015. Early Toarcian (Jurassic) belemnites from northeastern Gondwana (South Riffian ridges, Morocco). *Paläontol. Z.* 89, 51–62.
- Sandoval, J., O'Dogherty, L., Guex, J., 2001. Evolutionary rates of Jurassic ammonites in relation to sea-level fluctuations. *PALAIOS* 16 (4), 311–335.
- Schlegelmilch, R., 1985. Die Ammoniten des süddeutschen Doggers. Gustav Fischer, Stuttgart & New York.
- Schlegelmilch, R., 1992. Die Ammoniten des Süddeutschen Lias. Gustav Fischer, Jena & New York, Stuttgart.
- Schlegelmilch, R., 1994. Die Ammoniten des Süddeutschen Malms. Gustav Fischer, Stuttgart, Jena & New York.
- Schlegelmilch, R., 1998. Die Belemniten des Süddeutschen Jura. Gustav Fischer Verlag, Stuttgart (155 pp.).
- Schmid, D.U., Leinfelder, R.R., Schweigert, G., 2005. Stratigraphy and palaeoenvironments of the Upper Jurassic of Southern Germany – a review. *Zitteliana* 26, 31–41.
- Schwegler, E., 1961. Revision der Belemniten des Schwäbischen Jura, Teil 1. *Palaeontogr. A* 116, 59–103.
- Schwegler, E., 1962a. Revision der Belemniten des Schwäbischen Jura, Teil 2. *Palaeontogr. A* 118, 1–22.
- Schwegler, E., 1962b. Revision der Belemniten des Schwäbischen Jura, Teil 3. *Palaeontogr. A* 120, 121–164.
- Schwegler, E., 1965. Revision der Belemniten des Schwäbischen Jura, Teil 4. *Palaeontogr. A* 124, 75–115.
- Schwegler, E., 1969. Revision der Belemniten des Schwäbischen Jura, Teil 5. *Palaeontogr. A* 132, 179–219.
- Schwegler, E., 1971. Revision der Belemniten des Schwäbischen Jura, Teil 6. *Palaeontogr. A* 138, 81–129.
- Seilacher, A., 1968. Swimming habits of belemnites – recorded by boring barnacles. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 4, 279–285.
- Seilacher, A., Weisenauer, E., 1978. Preservational and adaptational history of belemnites. *Neues Jb. Geol. Paläontol. Abh.* 157, 145–149.

- Simon, M.S., Korn, D., Koenemann, S., 2010. Disparity fluctuations in Jurassic ammonoids by means of conch geometry. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 292 (3–4), 520–531.
- Simon, M.S., Korn, D., Koenemann, S., 2011. Temporal pattern in disparity and diversity of the Jurassic ammonoids of southern Germany. *Fossil Rec.* 14 (1), 77–94.
- Sørensen, A.M., Ullmann, C.V., Thibault, N., Korte, C., 2015. Geochemical signatures of the early Campanian belemnite *Belemnelloccamax mammillatus* from the Kristianstad Basin in Scania, Sweden. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 433, 191–200.
- Spaeth, C., 1975. Zur Frage der Schwimmverhältnisse bei Belemniten in Abhängigkeit vom Primärgefüge der Hartteile. *Paläontol. Z.* 49, 321–331.
- Stevens, G.R., 1963. Faunal realms in Jurassic and Cretaceous belemnites. *Geol. Mag.* 100 (6), 481–497.
- Stevens, G.R., 1965. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific Region. *Paleontol. Bull.* 36, 1–283.
- Stevens, G.R., 1971. Relationship of isotopic temperatures and faunal realms to Jurassic–Cretaceous paleogeography, particularly of the South-west Pacific. *J. R. Soc. N. Z.* 1 (2), 145–158.
- Stevens, G.R., Clayton, R.N., 1971. Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. *N. Z. J. Geol. Geophys.* 14 (4), 829–897.
- Stevens, K., Mutterlose, J., Schweigert, G., 2014. Belemnite ecology and the environment of the Nusplingen Plattenkalk (Late Jurassic, southern Germany): evidence from stable isotope data. *Lethaia* 4 (512–523).
- Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. *Earth Planet. Sci. Lett.* 290, 448–458.
- Suchéras-Marx, B., Giraud, F., V., F., Pittet, B., Lécuyer, C., Olivero, D., Mattioli, E., 2013. Duration of the Early Bajocian and the associated  $\delta^{13}\text{C}$  positive excursion based on cyclostratigraphy. *J. Geol. Soc.* 170, 107–118.
- Suchéras-Marx, B., Mattioli, E., Giraud, F., Escarguel, G., 2015. Paleoenvironmental and paleobiological origins of coccolithophorid genus *Watznaueria* emergence during the late Aalenian–early Bajocian. *Paleobiology* 41 (3), 415–435.
- Tendler, A., Mayo, A., Alon, U., 2015. Evolutionary tradeoffs, Pareto optimality and the morphology of ammonite shells. *BMC Syst. Biol.* 9, 1–12.
- Thierry, J., Barrier, E., et al., 2000. Middle Callovian. In: Dercourt, J., et al. (Eds.), *Atlas Peri-Tethys, Paleogeographical Maps Paris*, p. 9.
- Thorne, P.M., Ruta, M., Benton, M.J., 2011. Resetting the evolution of marine reptiles at the Triassic–Jurassic boundary. *PNAS* 108, 8339–8344.
- Tribouillard, N., Algeo, T.J., Baudin, F., Riboulleau, A., 2012. Analysis of marine environmental conditions based on molybdenum–uranium covariation – applications to Mesozoic paleoceanography. *Chem. Geol.* 324–325, 46–58.
- Ullmann, C.V., Frei, R., Korte, C., Hesselbo, S.P., 2015. Chemical and isotopic architecture of the belemnite rostrum. *Geochim. Cosmochim. Acta* 159, 231–243.
- Ullmann, C.V., Thibault, N., Ruhl, M., Hesselbo, S.P., Korte, C., 2014. Effect of a Jurassic oceanic anoxic event on belemnite ecology and evolution. *Proc. Natl. Acad. Sci.* 111 (28), 10073–10076.
- Vermeij, G.J., 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3 (3), 245–258.
- Vermeij, G.J., 1987. *Evolution and Escalation – An Ecological History of Life*. Princeton University Press, Princeton.
- Vermeij, G.J., 2008. Escalation and its role in Jurassic biotic history. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 263 (1–2), 3–8.
- Villier, L., Korn, D., 2004. Morphological disparity of ammonoids and the mark of Permian mass extinctions. *Science* 306 (5694), 264–266.
- Walker, S.E., Brett, C.E., 2002. Post-paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontol. Soc. Pap.* 8, 119–194.
- Weis, R., Delsate, D., 2006. The earliest belemnites: new records from the Hettangian of Belgium and Luxembourg. *Acta Univ. Carol. Geol.* 49 (1), 181–184.
- Weis, R., Mariotti, N., 2007. A belemnite fauna from the Aalenian–Bajocian boundary beds of the Grand Duchy of Luxembourg (NE Paris Basin). *Boll. Soc. Paleontol. Ital.* 46 (2–3), 149–174.
- Weis, R., Mariotti, N., Di Cencio, A., 2015. Systematics and evolutionary implications of Early Jurassic belemnites from the Peri-Mediterranean Tethys. *Paläontol. Z.* 89 (4), 729–747.
- Weis, R., Mariotti, N., Riegraf, W., 2012. The belemnite family Holcobelidae (Coleoidea) in the European Jurassic: systematics, biostratigraphy, palaeobiogeography and evolutionary trends. *Palaeodiversity* 5, 13–49.
- Weis, R., Thuy, B., 2015. A Sinemurian–Pliensbachian belemnite assemblage from the Glashenbach Gorge (Northern Calcareous Alps, Austria). *Ann. Naturhist. Mus. Wien* 117, 101–114.
- Wells, M.J., Clarke, A., 1996. Energetics: the costs of living and reproducing for an individual cephalopod. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 351, 1083–1104.
- Whiteside, J.H., Ward, P.D., 2011. Ammonoid diversity and disparity track episodes of chaotic carbon cycling during the early Mesozoic. *Geology* 39 (2), 99–102.
- Wierzbowski, H., 2013. Life span and growth rate of Middle Jurassic mesohibolitid belemnites deduced from rostrum microincrements. *Volumina Jurassica* 11, 1–18.
- Wierzbowski, H., 2015. Seawater temperatures and carbon isotope variations in central European basins at the Middle–Late Jurassic transition (Late Callovian–Early Kimmeridgian). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 506–523.
- Wierzbowski, H., Joachimski, M., 2007. Reconstruction of late Bajocian–Bathonian marine palaeoenvironments using carbon and oxygen isotope ratios of calcareous fossils from the Polish Jura Chain (central Poland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 254 (3–4), 523–540.
- Wierzbowski, H., Joachimski, M.M., 2009. Stable isotopes, elemental distribution, and growth rings of belemnites belemnite rostra: proxies for belemnite life habitat. *PALAIOS* 24 (6), 377–386.
- Wierzbowski, H., Rogov, M.A., 2011. Reconstructing the palaeoenvironment of the Middle Russian Sea during the Middle–Late Jurassic transition using stable isotope ratios of cephalopod shells and variations in faunal assemblages. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299 (1–2), 250–264.
- Yacobucci, M.M., 2005. Multifractal and white noise evolutionary dynamics in Jurassic–Cretaceous Ammonoidea. *Geology* 33 (2), 97–100.
- Zakharov, V.A., Meledina, S.V., Shurygin, B.N., 2003. Paleobiocoheres of Jurassic boreal basins. *Russ. Geol. Geophys.* 44 (7), 664–675.
- Zakharov, V.A., Rogov, M.A., Dzyuba, O.S., Zak, K., Košťák, M., Pruner, P., Skupien, P., Chadima, M., Mazuch, M., Nikitenko, B.L., 2014. Palaeoenvironments and palaeoceanography changes across the Jurassic/Cretaceous boundary in the Arctic realm: case study of the Nordvik section (north Siberia, Russia). *Polar Res.* 33, 19714.
- Zakharov, Y.D., Shigeta, Y., Nagendra, R., Safronov, P.P., Smyshlyayeva, O.P., Popov, A.M., Velivetskaya, T.A., Afanasyeva, T.B., 2011. Cretaceous climate oscillations in the southern palaeolatitudes: new stable isotope evidence from India and Madagascar. *Cretac. Res.* 32, 623–645.
- Zakharov, Y.D., Shigeta, Y., Smyshlyayeva, O.P., Popov, A.M., Ignatiev, A.V., 2006. Relationship between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of the recent *Nautilus* and brachiopod shells in the wild and the problem of reconstruction of fossil cephalopod habitat. *Geosci. J.* 10 (3), 331–345.