



Spatial distribution patterns of calcareous nannofossils across the Callovian–Oxfordian transition in the French Subalpine Basin

Fabienne Giraud*, Bernard Courtinat, François Atrops

UMR 5125 PEPS, CNRS, France; Université Lyon 1, Campus de la Doua, Bâtiment Géode, 2 rue Raphaël Dubois, Lyon, F-69003, France

ARTICLE INFO

Article history:

Received 20 November 2008

Received in revised form 7 April 2009

Accepted 14 April 2009

Keywords:

Callovian–Oxfordian transition
calcareous nannofossils
French Subalpine Basin
proximal–distal transect
paleoproductivity

ABSTRACT

Callovian–Oxfordian calcareous nannofossils are documented from four sections distributed along a proximal–distal (slope to central basin) transect in the French Subalpine Basin (south-eastern France). The sections were dated and correlated using integrated ammonite, dinoflagellate and nannofossil biostratigraphies. The nannofossil assemblages are constantly dominated by *Watznaueria britannica*. However, significant spatial changes in nannofossil assemblage composition are recorded. Nannofossil assemblages recovered in slope and slope-to-basin transition sections are characterized by high abundances, lowest diversities, highest percentages of smallest-sized morphotypes of *W. britannica*, subordinated *W. britannica/manivittiae* (a morphotype described in this study), and are indicative of turbulent, unstable and/or eutrophic conditions. Towards the central part of the basin, as the nutrient content and turbulence declined and paleoenvironmental stability increased, the nannofossil assemblages become more diverse and characterized by lower relative abundances of *W. britannica* but higher contribution of larger morphotypes and higher relative abundances of *W. barnesiae/fossacincta*, *Biscutum dubium* and *Zeughrabdotus erectus*. These latter small coccoliths, markers of high surface-waters fertility for the Cretaceous, were probably not competitive with respect to smaller-sized *W. britannica* in unstable and eutrophic surface waters for the Jurassic. An increase in the surface water productivity is recorded both in proximal and distal sections at the Callovian–Oxfordian transition, and is demonstrated both by an increase in nannofossil total abundances and in the relative abundances of taxa adapted to high-trophic levels. Thermal minimum in surface waters, as indicated by an increase in the percentages of the cool-water nannofossil taxa, is associated to increased productivity. Further studies will be necessary to demonstrate whether surface-water productivity changes, already recorded in the eastern Paris Basin, were global.

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1. Introduction

The Middle–Late Jurassic transition is characterized by major climatic and paleoceanographic changes. An abrupt temperature fall is recorded at the Callovian–Oxfordian transition (Riboulleau et al., 1998; Abbink et al., 2001; Dromart et al., 2003; Lécuyer et al., 2003), followed by a long-term stepwise recovery (Dromart et al., 2003). During the climatic decline, atmospheric CO₂ levels could have dropped to values lower than 500 ppm V (350 ppm for the Late Callovian, 380 ppm for the Early Oxfordian; Yapps and Poths, 1996; Dromart et al., 2003; Louis-Schmid et al., 2007a). Important changes also occurred in the sedimentation pattern across the entire Tethys and peri-Tethyan regions, marked by the general absence of carbonate sediments and the lack of reef formations, reflecting a crisis in the carbonate production (Cecca et al., 2005). This is a period of reduced sedimentation, and very condensed series occurred (e.g., Norris and

Hallam, 1995; Dromart et al., 2003; Cecca et al., 2005). Some authors associated the extremely condensed series with marine transgression (Norris and Hallam, 1995); conversely, some others interpret condensation as the result of an abrupt sea-level fall that attained a minimum in the Late Callovian (*lamberti* ammonite zone, Dromart et al., 2003; Cecca et al., 2005). Whereas global perturbations occur at the Callovian–Oxfordian transition, paleoceanographic reconstitutions are limited because of poor biostratigraphic resolution of the majority of sections in the western Tethyan areas.

In modern oceans, spatial and vertical distribution patterns of calcareous nannoplankton are controlled by nutrient distribution and concentration, temperature and salinity (e.g., Winter et al., 1994; Brand, 1994). This phytoplanktonic group is commonly used as a paleoceanographic proxy. The potential for calcareous nannofossils to act as a paleoceanographic proxy in Mesozoic sediments is important (e.g., Lees et al., 2005), but despite major paleoenvironmental changes occurring at the Callovo–Oxfordian transition (i.e., global cooling), only one paper addresses calcareous nannofossils (Tremolada et al., 2006). This work evidenced enhanced surface-water productivity in the eastern Paris Basin during the cooling phase.

* Corresponding author. Tel.: +33 4 72 44 62 45; fax: +33 4 72 44 83 82.
E-mail address: Fabienne.Giraud@univ-lyon1.fr (F. Giraud).

Calcareous nannofossil quantitative analyses were carried out on samples from the French Subalpine Basin (Fig. 1). This basin presents a continuous spatial succession of different paleogeographical domains, from shelf to deep basin. Distal paleoenvironments are characterized by high sedimentation rates and, because of the presence of well-preserved ammonites, are well dated for the Callovian–Oxfordian transition. Spatial changes in the nannofossil abundance and assemblage composition were studied in four sections distributed along a proximal–distal transect across the Callovian–Oxfordian transition.

This study aims at the detection of the main paleoenvironmental factors influencing calcareous nannofossil distribution, such as nutrient supply, surface-water temperature, distance from the coast,

and general oceanic circulation in the French Subalpine Basin at the Callovian–Oxfordian transition, in order to ascertain:

- 1) whether the enhanced surface-water productivity is limited to the eastern Paris Basin, or whether it is recorded in the French Subalpine Basin;
- 2) whether or not the record of surface-water productivity changes depends on the position of the studied sections along a proximal–distal transect within the French Subalpine Basin.
- 3) if the cooling phase, associated with this increase in productivity, is recorded by nannofossil assemblages at a latitude setting below the eastern Paris Basin.

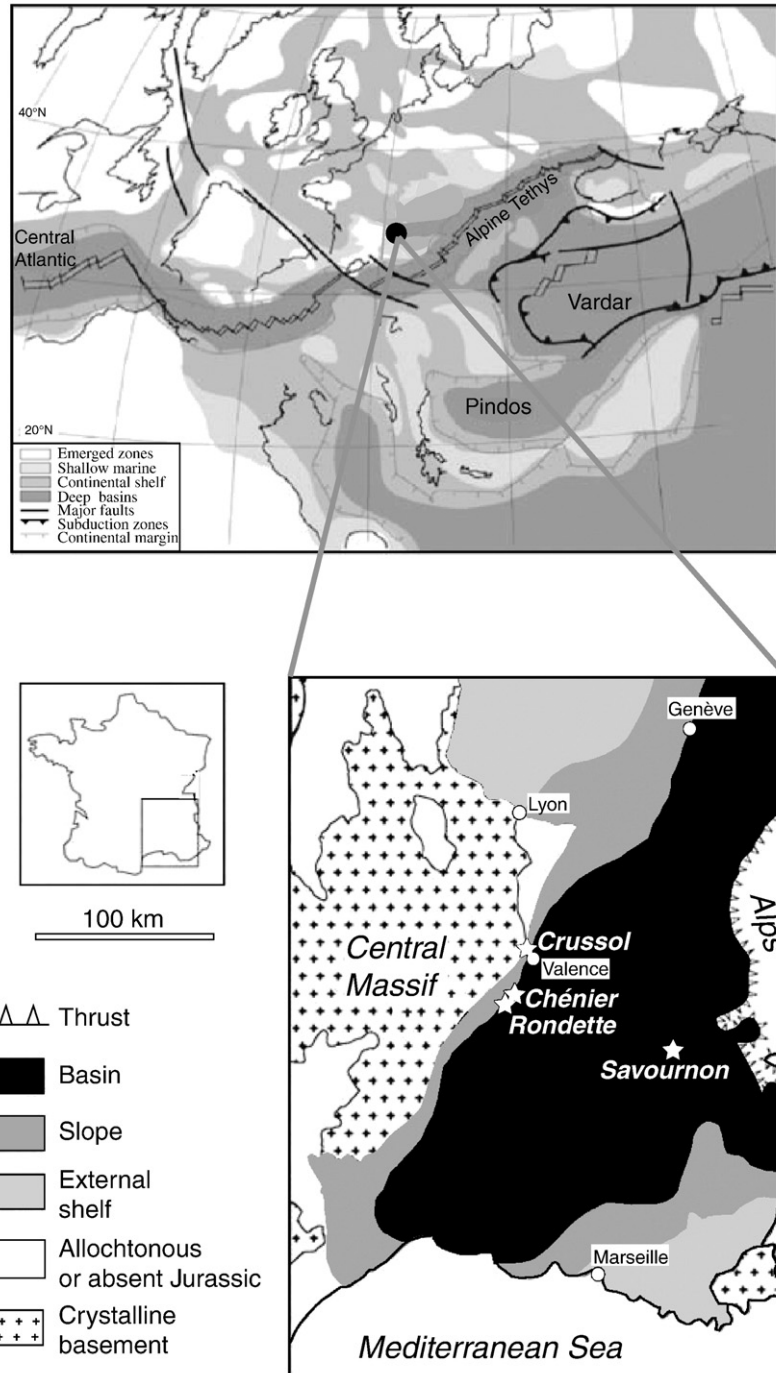


Fig. 1. Callovian–Oxfordian paleogeographic map (Stampfli et al., 2001) showing the location of the French Subalpine Basin and the paleogeographic setting of the studied sections. The paleogeography of the French Subalpine Basin is from Bouhamdi et al. (2000) and corresponds to the Middle Oxfordian.

2. Study area

2.1. Geological setting

The French Subalpine Basin belongs to the North Tethyan margin and was located between 30° and 35°N during the Middle–Upper Jurassic (Fig. 1). At the Callovian–Oxfordian transition, this basin recorded a major extensional tectonic phase, linked to the beginning of the Ligurian spreading (Lemoine and de Graciansky, 1988; de Graciansky et al., 1999). The expression of this extensional episode in the basin and its margin is a syndimentary block-faulting (Dardeau et al., 1988). From the Callovian–Oxfordian transition to the Early Cretaceous, there is a general subsidence from the western margin of the basin (Ardèche area) towards the east (Bonijoly et al., 1996). During the Callovo–Oxfordian, up to 1000 m of black marls ('Terres Noires' formation, Artru, 1972) was deposited throughout the basin (Debrand-Passard et al., 1984). The carbonate-mud export from the

platforms surrounding the basin (Fig. 1) was the principal source of carbonate for basinal sediments, whereas terrigenous inputs originated from the sub-marine erosion of the Hercynian basement and its Triassic sedimentary cover (Elmi, 1967, 1990).

The four selected sections are located on a proximal–distal transect. Three sections are located in the Ardèche area (western margin of the French Subalpine Basin; Fig. 1), and characterize the slope (Crussol section, Elmi, 1967) and slope-to-basin transition (Rondette section, Elmi, 1967 and (Chénier Ravine section, Elmi, 1967; Charbonnier et al., 2007). The fourth section (Savournon) is located in the central part of the French Subalpine Basin (Fig. 1) and corresponds to the deeper paleo-environment and thickest sedimentation of the 'Terres Noires' formation (Debrand-Passard et al., 1984). The four sections are characterized by a monotonous succession of marls, in which more or less regular, even nodular, limestones or argillaceous limestone beds are intercalated. Locally, as in the Chénier Ravine section, thin ferruginous levels are present in marls and limestones of the late Callovian age (Fig. 2).

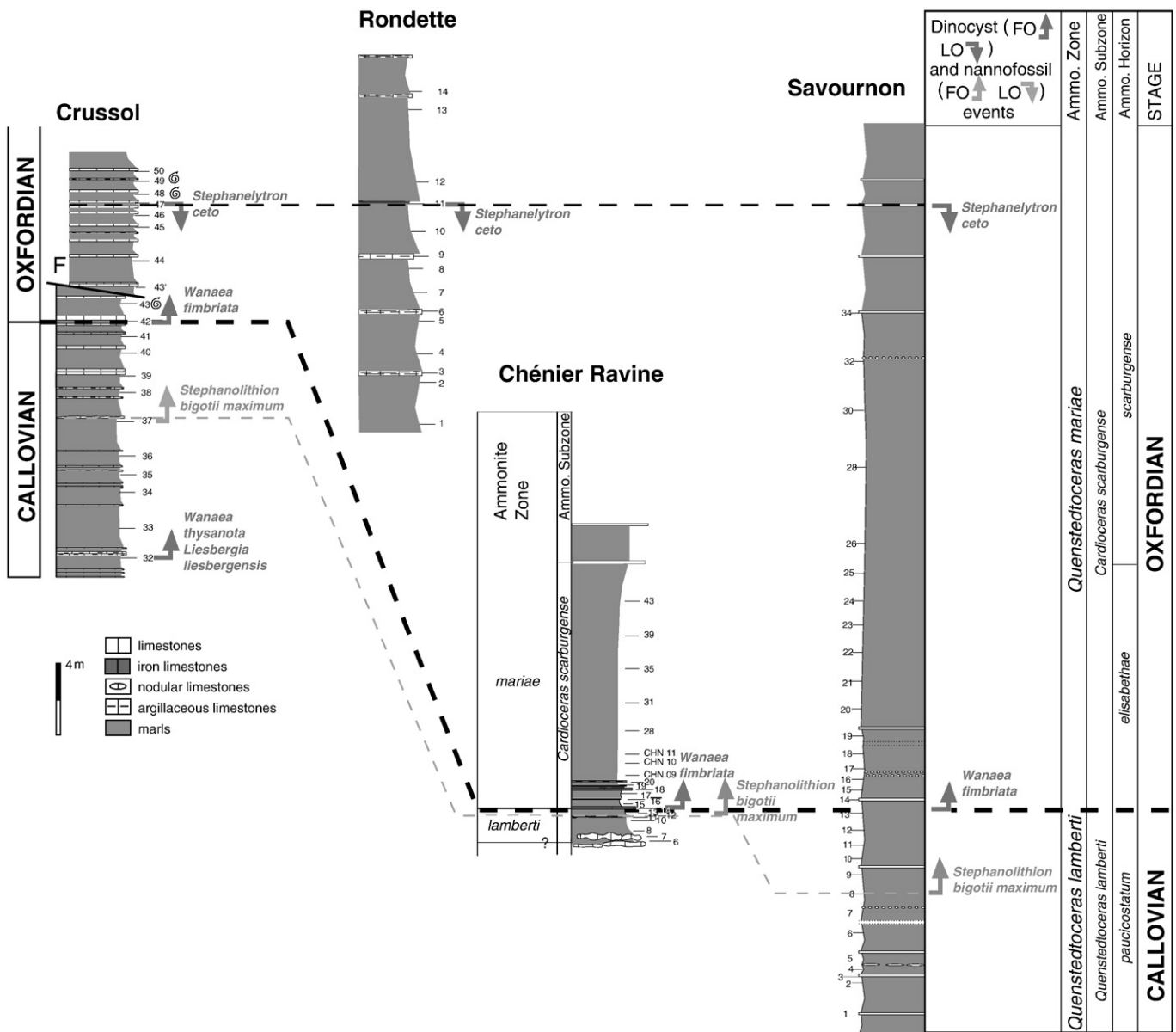


Fig. 2. Tentative correlation of the studied sections using ammonite biostratigraphy, calcareous nannofossils and dinoflagellate events. Ammonite biostratigraphy is after Elmi (1967) for the Chénier Ravine section and after Fortwengler and Marchand (in Groupe Français d'étude du Jurassique, 2000) for the Savournon section. Dinoflagellate events are after Courtinat (2006). Calcareous nannofossil events are from this work. Positions of samples selected for carbonate contents and calcareous nannofossil studies are indicated.

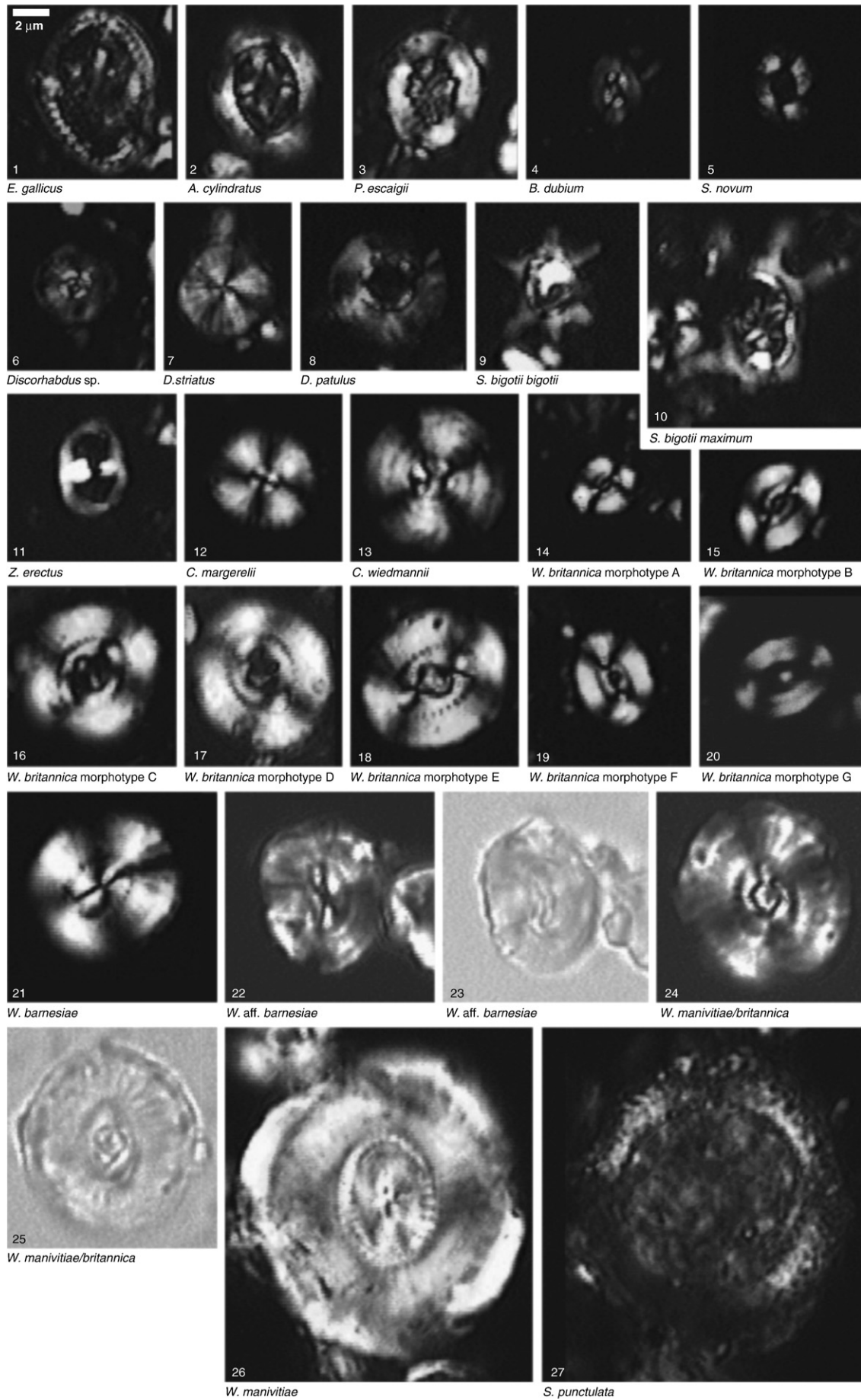


Fig. 4. Light microscope pictures of selected nannofossil species from the French Subalpine Basin.

polarizing microscope, at 1560× magnification, in order to find biostratigraphic markers. For the quantification of nannofossils, 300 specimens were counted in a variable number of fields of view on the smear slide in the richest samples. In the poorest samples, the specimens were counted following one or two longitudinal transverses. For each sample, the abundance of nannofossils per field of view is calculated by taking into account the number of fields of view necessary to count them and the density of material estimated on the smear slide, following the method of Pittet and Mattioli (2002). Relative abundance of each species was also calculated in each sample. The combination of semi-quantitative and relative abundances allows an accurate interpretation of nannofossil assemblage changes (Williams and Bralower, 1995). The taxonomy applied here follows the guidelines of Perch-Nielsen (1985) and Bown and Young (1997). The nannofossil assemblage composition is also described by means of species richness, the Shannon Diversity Index, and evenness, defined by Shannon and Weaver (1949). The nannofossil preservation was evaluated following the classes defined by Roth (1983).

4. Results

All nannofossil taxa encountered in this study are reported in Appendix A. Taxonomic remarks were added when needed. Some selected species are illustrated in Fig. 4. The entire nannofossil dataset is given as “supplementary material”.

4.1. Nannofossil biostratigraphy

Different species of the genus *Stephanolithion* are used as biostratigraphic markers for the Middle and Late Jurassic (Bown and Cooper, 1998). The first occurrence (FO) of the zonal marker *Stephanolithion bigotii maximum* is recognized within the *lamberti* ammonite zone (top of the zone) in both the Tethyan and Boreal Realms (Bown et al., 1988). The last occurrence (LO) of *Ansulaspheera helvetica* is roughly coincident with the FO of *S. bigotii maximum*, and both events have been correlated to the *lamberti* ammonite zone (Fig. 3) in NW Europe (Bown et al., 1988) and in SE France (de Kaenel et al., 1996). The LO of *S. bigotii maximum* is correlative to the top of the Early Oxfordian, but it is recorded in the *cordatum* ammonite zone in NW Europe (Bown et al., 1988) and in Switzerland (Liesberg section, de Kaenel et al., 1996), while this event falls within the underlying *mariae* ammonite zone in SE France, suggesting a diachroneity (de Kaenel et al., 1996; Fig. 3).

The FO of the zonal marker *S. bigotii maximum* is observed in the Savournon, Chénier Ravine, and Crussol sections (Fig. 2). Its FO lies within the *paucicostatum* horizon in the *lamberti* ammonite subzone and zone (Savournon section, Figs. 2 and 5). The FO of *S. bigotii maximum* predates that of the dinoflagellate cyst marker *W. fimbriata*

(Figs. 2 and 5). The LO of *A. helvetica* was not identified in the sections investigated.

4.2. Distribution of calcareous nannofossils at the Callovian–Oxfordian transition

In general, preservation is moderate, with moderately etched and/or overgrown nannofossil assemblages in the Crussol, Chénier Ravine and Savournon sections, with some samples showing slightly etched and overgrown nannofossils (see “Supplementary material data”). At the base of the Chénier Ravine section, samples 6 and 16 are barren of nannofossils, and samples 7, 11, 14, and 18 are poorly preserved with strongly etched and/or overgrowth assemblages. In the Rondette section, the preservation state of nannofossils is moderate (moderate etching and/or overgrowth) to good (slight etching and overgrowth).

The fluctuations in calcium carbonate content, calcareous nannofossil total abundance (specimens per field of view) and species richness, Shannon diversity and evenness are quite limited in amplitude in the four sections, except in the Chénier Ravine section (Figs. 6–9). However, highest nannofossil total abundances are recorded above the Callovian/Oxfordian boundary in the Crussol, Chénier Ravine and Savournon sections (Figs. 6, 8, 9).

For all of the sections, the nannofossil assemblages are mainly composed of *Watznaueria* spp. (Figs. 6–9), which represent more than 80%, and within the *Watznaueria* group, *W. britannica* is dominant, comprising between 45% and 88% of the group (Figs. 6–9). *Watznaueria britannica* presents seven morphotypes described in Giraud et al. (2006) and this study. Small-sized morphotypes (A + B) are always dominant. *Watznaueria barnesiae* and *W. fossacincta* are common; these two species are grouped, because they are believed to represent end-members of a morphological continuum (Lees et al., 2004, 2006; Bornemann and Mutterlose, 2006). Two other large *Watznaueria* morphotypes, frequent to common, are recognized in this study. The first one is named *W. manivittae/britannica*, and the second one is named *W. aff. barnesiae*. *Watznaueria manivittae* is rare to frequent in the assemblages. Other rare species of *Watznaueria* are grouped (“other *Watznaueria*” in Figs. 6–9). The other coccoliths contributing significantly to the assemblages are in decreasing order of abundance: *Cyclagelosphaera margerelii*, *Biscutum dubium*, *Discorhabdus* spp. (*Discorhabdus* sp., *D. striatus*, and *D. patulus*), *Zeugrhabdotus erectus* and the Axopodorhabdaceae, defined by Tremolada et al. (2006) as the A-group, which, in our sections, comprised the following taxa: *Axopodorhabdus* spp., *Etmorhabdus gallicus* and *Polypodorhabdus escaigii*. Nannofossils of incertae sedis *Schizosphaerella punctulata* are also present.

The relative abundance of *W. britannica* very slightly decreases throughout the succession of the Crussol section (Fig. 6), whereas it increases in the Chénier Ravine (Fig. 8) and is higher around the

AMMONITES			DINOCYSTS	NANNOFOSSILS
ZONES	SUBZONES	HORIZONS	(Courtinat, 2006)	SE France (this work)
<i>mariae</i>	<i>scarburgense</i>	<i>scarburgense</i>	← <i>Stephanolytron ceto</i>	EVENTS
		<i>elizabethae</i>		
<i>lamberti</i>	<i>lamberti</i>	<i>paucicostatum</i>	← <i>Wanaea fimbriata</i>	▲ <i>Stephanolithion bigotii maximum</i>
		<i>lamberti</i>		

Fig. 5. Dinocyst and calcareous nannofossil events recorded in the studied sections in south-eastern France and their calibration to the ammonite biostratigraphy for the Callovian–Oxfordian transition.

CRUSSOL

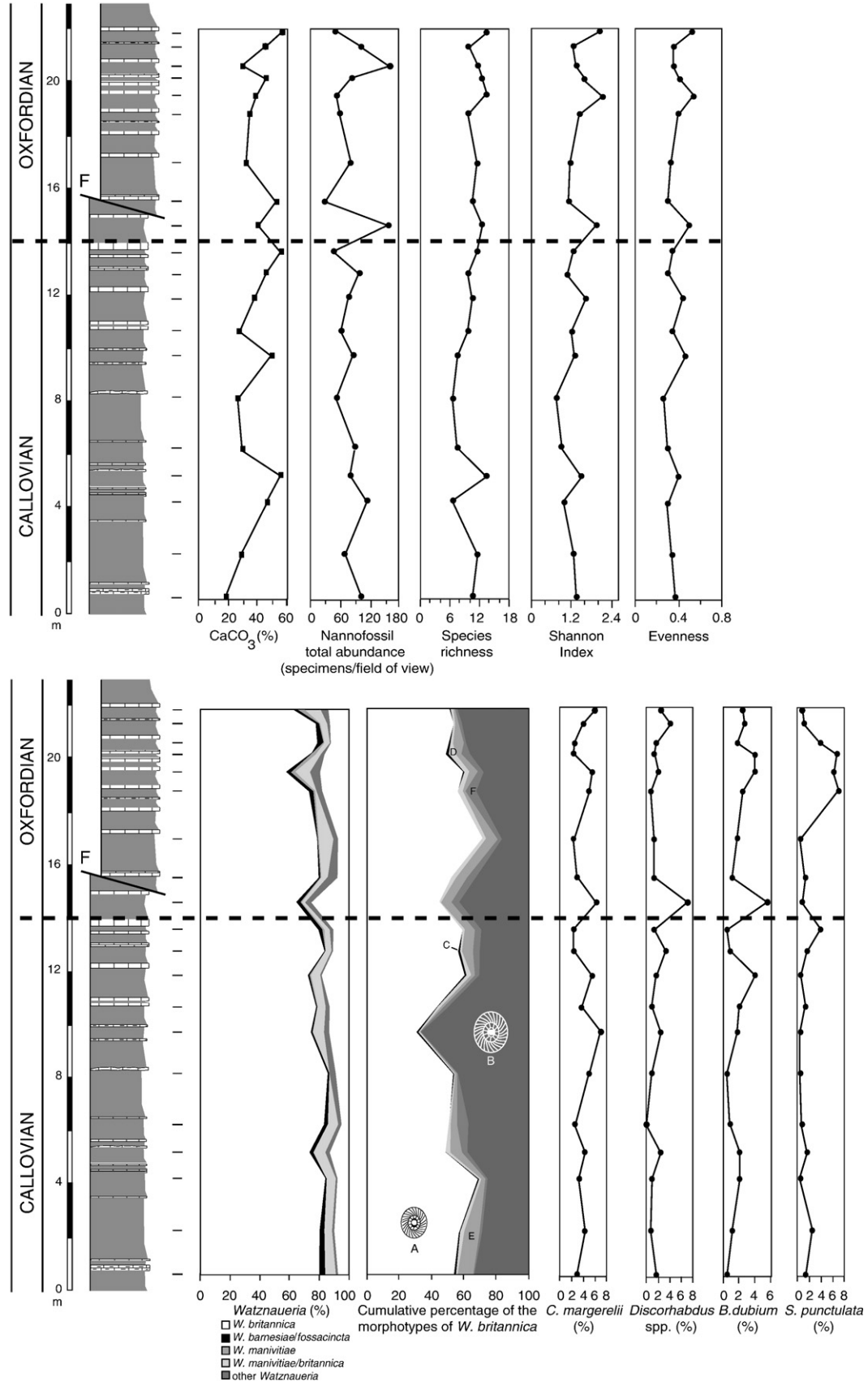


Fig. 6. Stratigraphic changes in calcium carbonate content, calcareous nannofossil total abundance (specimens per field of view), species richness, Shannon diversity, evenness and percentages of selected nannofossil taxa for the Crussol section.

RONDELETTE

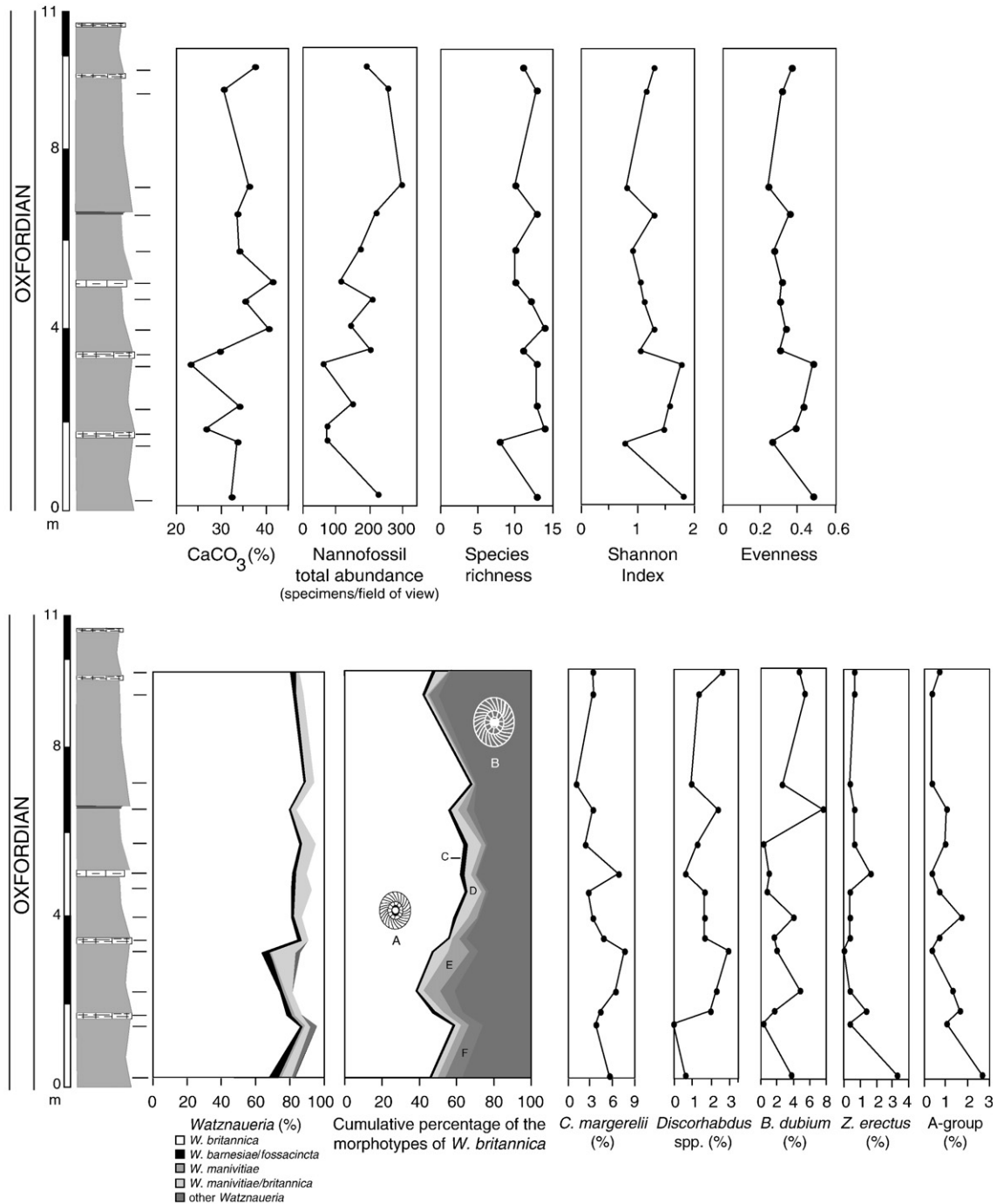


Fig. 7. Stratigraphic changes in calcium carbonate content, calcareous nannofossil total abundance (specimens per field of view), species richness, Shannon diversity, evenness and percentages of selected nannofossil taxa for the Rondette section.

Callovian/Oxfordian boundary in the Savournon section (Fig. 9). The contribution of large-sized specimens of *W. britannica* (in particular Morphotypes D and E) increases after the Callovian/Oxfordian boundary only in the Chénier Ravine section (Fig. 8). Across the Callovian–Oxfordian boundary, the relative abundance of *W. barnesiae/fossacincta* decreases (Figs. 6, 8, 9). For all of the successions, the *C. margerelii* percentage generally decreases in the Early Oxfordian time (Figs. 6–9). In the rest of the assemblage, *Discorhabdus* spp., *B. dubium* present their highest relative abundances either below the Callovian/Oxfordian boundary

(Savournon section, Fig. 9) or above it (Crussol and Chénier Ravine sections, Figs. 6 and 8). *Z. erectus* presents its highest percentage below (Savournon section, Fig. 9) or above the boundary (Chénier Ravine section, Fig. 8). The A-group presents its highest relative abundance above the boundary (Chénier Ravine and Savournon sections, Figs. 8 and 9). Higher percentages of *S. punctulata* are recorded in the Early Oxfordian than in the Late Callovian in the Crussol section (Fig. 6).

We have compared the mean nannofossil abundances, assemblage compositions and carbonate content between the different sections

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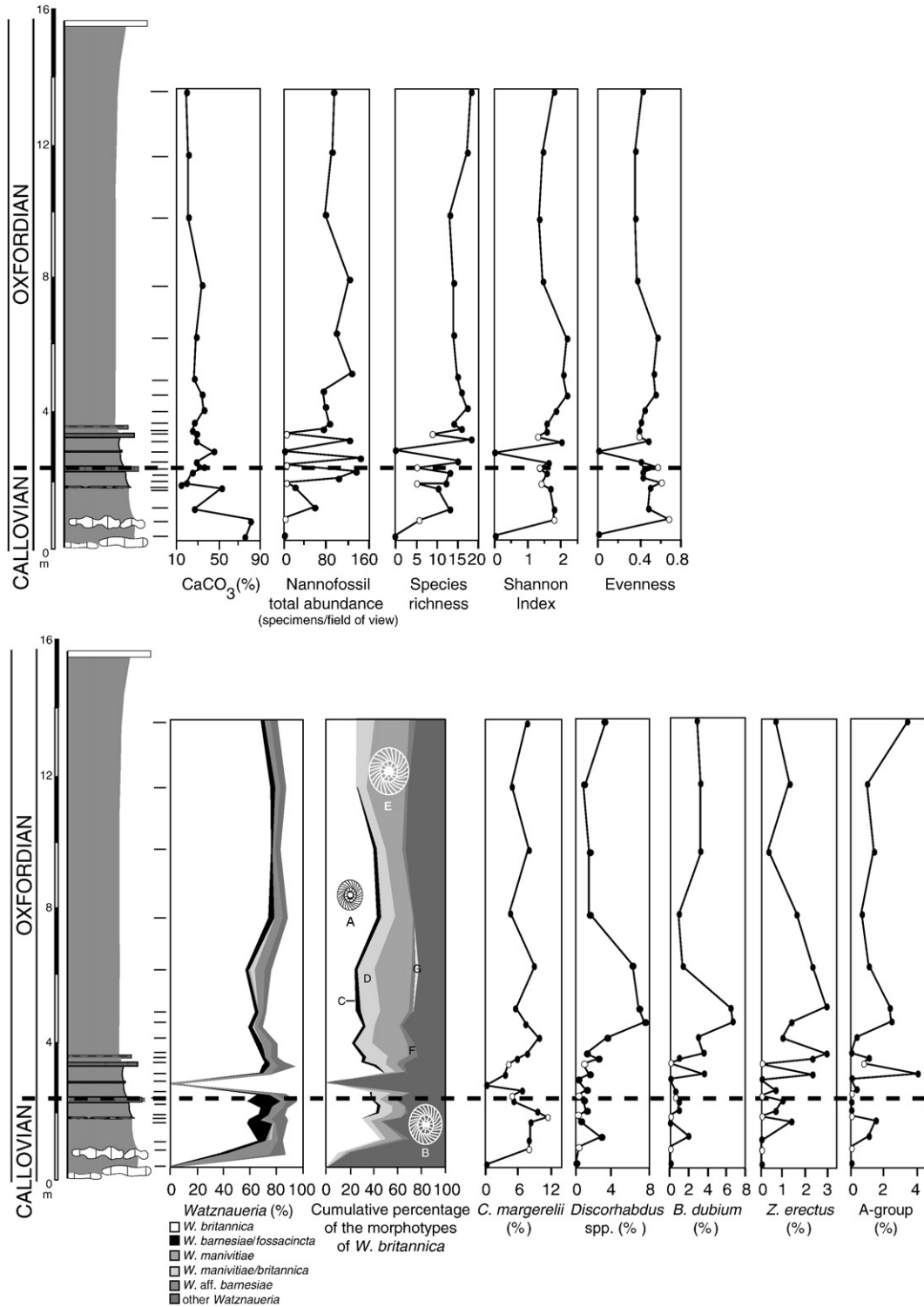


Fig. 8. Stratigraphic changes in calcium carbonate content, calcareous nanofossil total abundance (specimens per field of view), species richness, Shannon diversity, evenness and percentages of selected nanofossil taxa for the Chénier Ravine section. The white circles correspond to poorly preserved samples (strongly etched and/or overgrown).

(Table 1). For the Chénier Ravine and Savournon sections, samples displaying strongly etched and/or overgrown nanofossils were not taken into account to calculate the mean values.

A progressive slope-to-central basin differentiation in the nanofossil assemblage composition was recorded. From the proximal sections to the more distal one, there is 1) an increase in nanofossil species richness, diversity and evenness (Table 1), and

relative abundance of *W. barnesiae/fossacincta* and of small coccoliths (*B. dubium*, *Discorhabdus* spp., *Zeughrabdotus erectus*, Figs. 6–10); 2) a general decrease of calcium carbonate content and in the relative abundance of *W. britannica*, in particular, of the small morphotypes, *W. manivittiae/britannica*, *W. manivittiae*, *S. punctulata* (Table 1, Figs. 6–10). The Rondette section located at the slope–basin transition presents the highest mean nanofossil total abundance

SAVOURNON

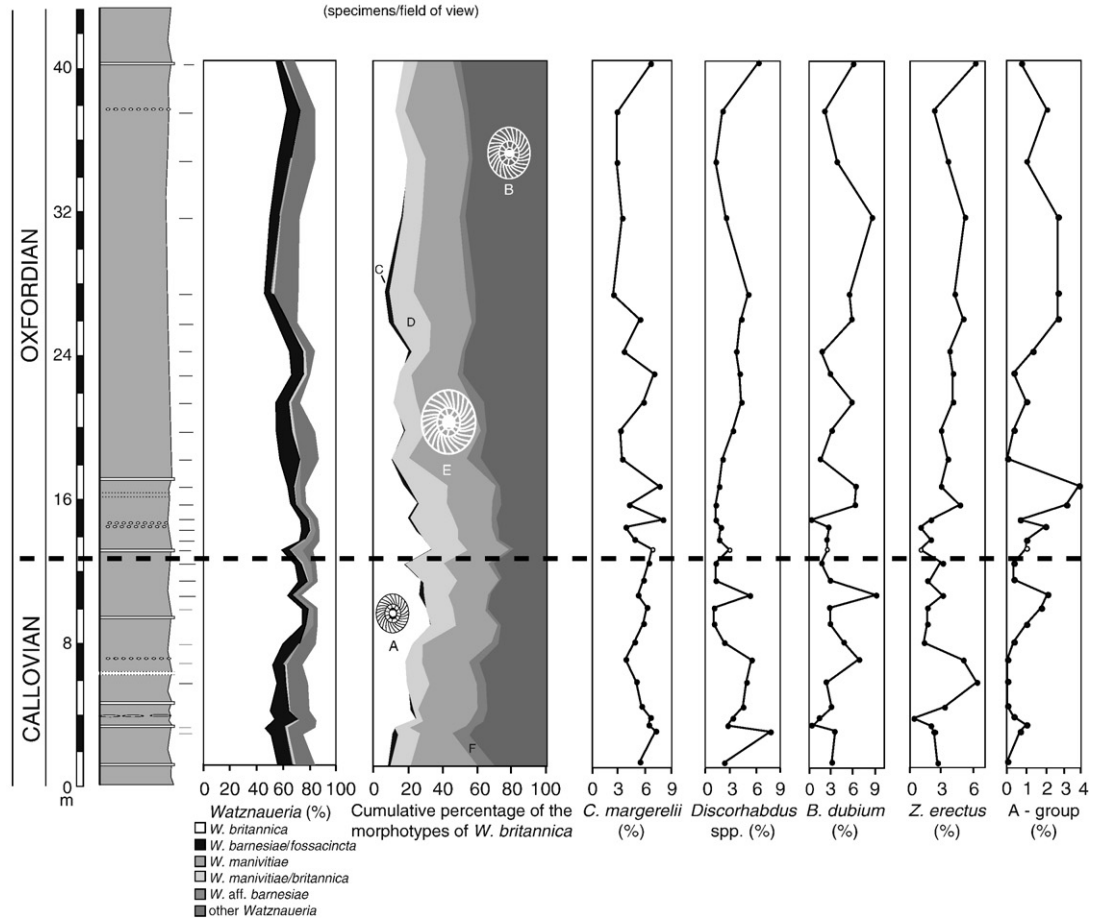
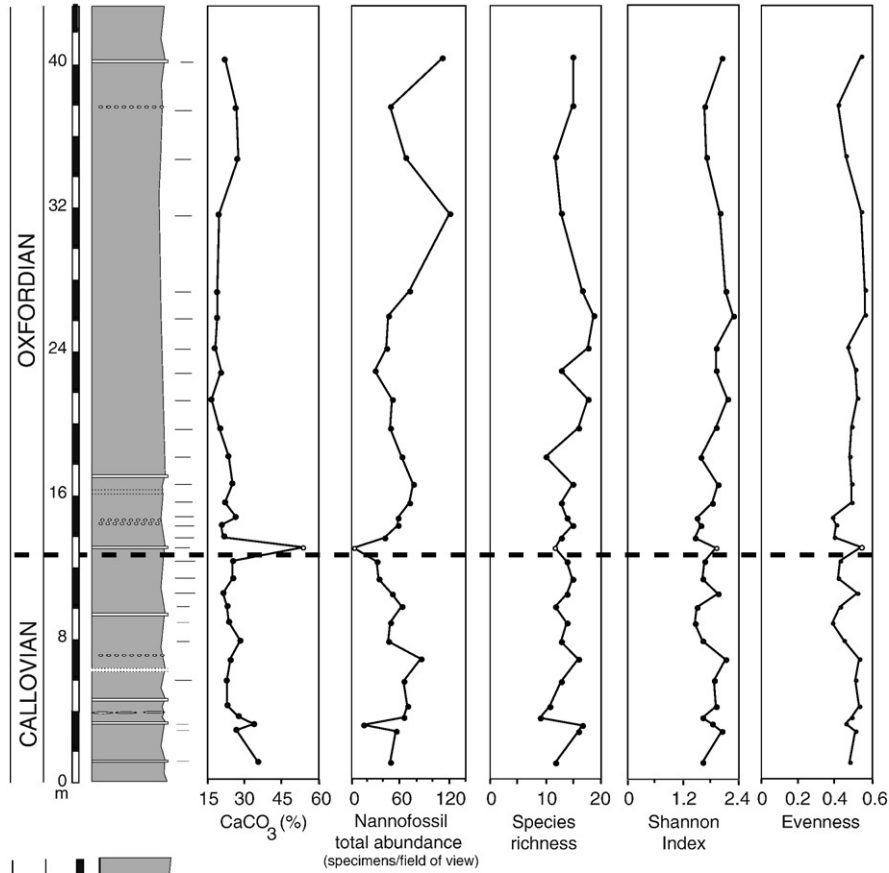


Table 1

Mean values of nannofossil total abundance (specimens per field of view), species richness, Shannon diversity, evenness and calcium carbonate content for the Crussol, Rondette, Chénier Ravine and Savournon sections at the Callovian–Oxfordian transition.

	Crussol	Rondette	Chénier Ravine	Savournon
Nannofossil total abundance (specimens per field of view)	78	188	92	57
Species richness	12	11	14	14
Shannon Index	1.33	1.24	1.71	1.8
Evenness	0.37	0.35	0.45	0.48
CaCO ₃ (%)	40	33.6	28	23

and the lowest diversity (Table 1), and the highest relative abundance of *W. britannica* represented mainly by small morphotypes (Figs. 7 and 10).

5. Discussion

5.1. Calcareous nannofossil preservation

In the French Subalpine Basin, nannofossil assemblages are dominated by *W. britannica*. This dominance is also indicated by the Shannon index comprised between 1.24 (Rondette section) and 1.8 (Savournon section), which correspond to low-diversity values (Frontier and Pichod-Viale, 1998). Nannofossil assemblages corresponding to the Bajocian–Tithonian interval are dominated worldwide by the genus *Watznaueria* (Bown et al., 1988; Bown and Cooper, 1998). The *Watznaueria* group, because of its robust morphology (thick placolith with a closed or slightly opened central area), is considered to be more resistant to dissolution than other coeval nannofossils (Roth and Bowdler, 1981). As the dominance of *Watznaueria* is recognized in poorly preserved assemblages of oceanic sites (Roth, 1983) as well as in pristinely preserved assemblages of open-ocean environments (Lees et al., 2006), this dominance is not regarded as a consequence of selective diagenesis. Conversely, *Biscutum*, *Z. erectus*, *Discorhabdus*, and *Stephanolithion* are delicate taxa, considered to be very susceptible to dissolution (Hill, 1975; Thierstein, 1980; Roth, 1981, 1983), and an increase in diagenetic overprint may imply a decrease in their relative abundances.

Preservation state can control nannofossil abundance, species richness, and relative abundance of some species. Preservation of nannofossils also depends on the lithology and is generally lower in limestones than in marls due to increasing diagenesis in limestone (Roth and Thierstein, 1972). Four classes of preservation are recognized in the investigated sections (see “Supplementary Material data”). Class 1: SE and/or SO (strong etching and/or overgrowth); class 2: ME–MO (moderate etching and overgrowth); class 3: ME–SO or SE–MO (moderate etching–slight overgrowth or slight etching–moderate overgrowth); class 4: sE–sO (slight etching and overgrowth). We have statistically tested for each section, the recognized effects of the different classes of preservation on nannofossil total abundance, species richness, relative abundance of delicate taxa (*B. dubium* + *Discorhabdus* spp. + *S. bigotii* + *Z. erectus*), and CaCO₃ content (Fig. 11). Higher mean nannofossil total abundance, species richness and relative abundance of delicate taxa are recorded in samples presenting a preservation class 3 or 4. Samples with a high mean CaCO₃ percentage are poorly preserved (class 1). However, only two sections (Chénier Ravine and Savournon) present statistically significant differences for means of some parameters between the different classes of preservation (Fig. 11b and d). In the Chénier Ravine section, the mean nannofossil total abundance and species richness

are statistically different only between class 1 of preservation (poor preservation) and the other classes, whereas for the relative abundance of delicate taxa, differences are significant only between class 1 and class 4 (good preservation) of preservation (Fig. 11b). In the Savournon section, the nannofossil total abundance presents significant different mean values only between class 1 and class 4 of preservation, whereas the mean calcium carbonate content is statistically different between class 1 and the other classes of preservation (Fig. 11d).

We can therefore conclude that a strong diagenetic alteration affects the nannofossil composition in poorly preserved samples (class 1 of preservation) observed in the Chénier Ravine and Savournon sections. In the other samples of the four sections, characterized by moderately to well-preserved assemblages (classes 2–4 of preservation), nannofossils are only moderately affected by diagenesis and may reflect original assemblage composition. In order to avoid a bias by preservation, the poorly preserved samples corresponding to class 1 of preservation (4 samples in the Chénier Ravine section and 1 sample in the Savournon section) are not taken into consideration in the paleoenvironmental reconstitutions.

5.2. Calcareous nannofossil paleoecological affinities and paleoenvironmental conditions at the Callovian–Oxfordian transition in the French Subalpine Basin

The paleoecological significances of the discussed calcareous nannofossil taxa are summarized in Table 2.

The small-sized specimens of *W. britannica* (Morphotypes A + B) are characteristic of nannofossil assemblages of low species richness, diversity and evenness encountered in the Crussol and the Rondette sections (Table 1, Figs. 6, 7, 10). This could be indicative of unstable environmental conditions where nutrients are used by a small number of dominant taxa (Watkins, 1989). The contribution of the largest morphotypes (D + E) is maximal in the more distal section (Savournon), characterized by the highest diversity (Figs. 9 and 10 and Table 1). These observations suggest that small-sized morphotypes of *W. britannica* were tolerant to unstable and fluctuating conditions and can be considered as meso-eutrophic, whereas large-sized morphotypes were adapted to stable, and more oligotrophic environmental conditions.

In more proximal and carbonate-rich section of Crussol, frequent *S. punctulata* are observed and associated with rare *W. manivitiae*. Crussol is located in proximity to carbonate platforms lying on the submerged French Central Massif (Elmi, 1967, 1990). This could explain the higher percentage of *S. punctulata* in this section than in the other ones.

The paleoecological affinities of *W. manivitiae/britannica* are still unclear. Significant variations in the relative abundances of this taxon are recorded between proximal and distal settings. High relative abundances of *W. manivitiae/britannica* are recorded both in the proximal setting and in the Rondette section and are associated with the lowest diversities and high relative abundance of small-sized *W. britannica*. This could suggest a preference for proximal paleoenvironments and/or high productivity in surface waters.

The highest relative abundance of *W. barnesiae/fossacincta* and of small coccoliths (*B. dubium*, *Z. erectus* and *Discorhabdus* spp.) are recorded in the more distal section of Savournon, characterized by more diverse assemblages and lowest percentages of *W. britannica* with respect to the other sections (Table 1 and Fig. 10). Eutrophic conditions in surface waters are thus unlikely for this section. In the Middle and Late Jurassic, species of *Watznaueria* are dominant and could be, similarly to the small-sized *W. britannica*, indicative of trophic levels higher than *Z. erectus* and *Biscutum* spp., markers of

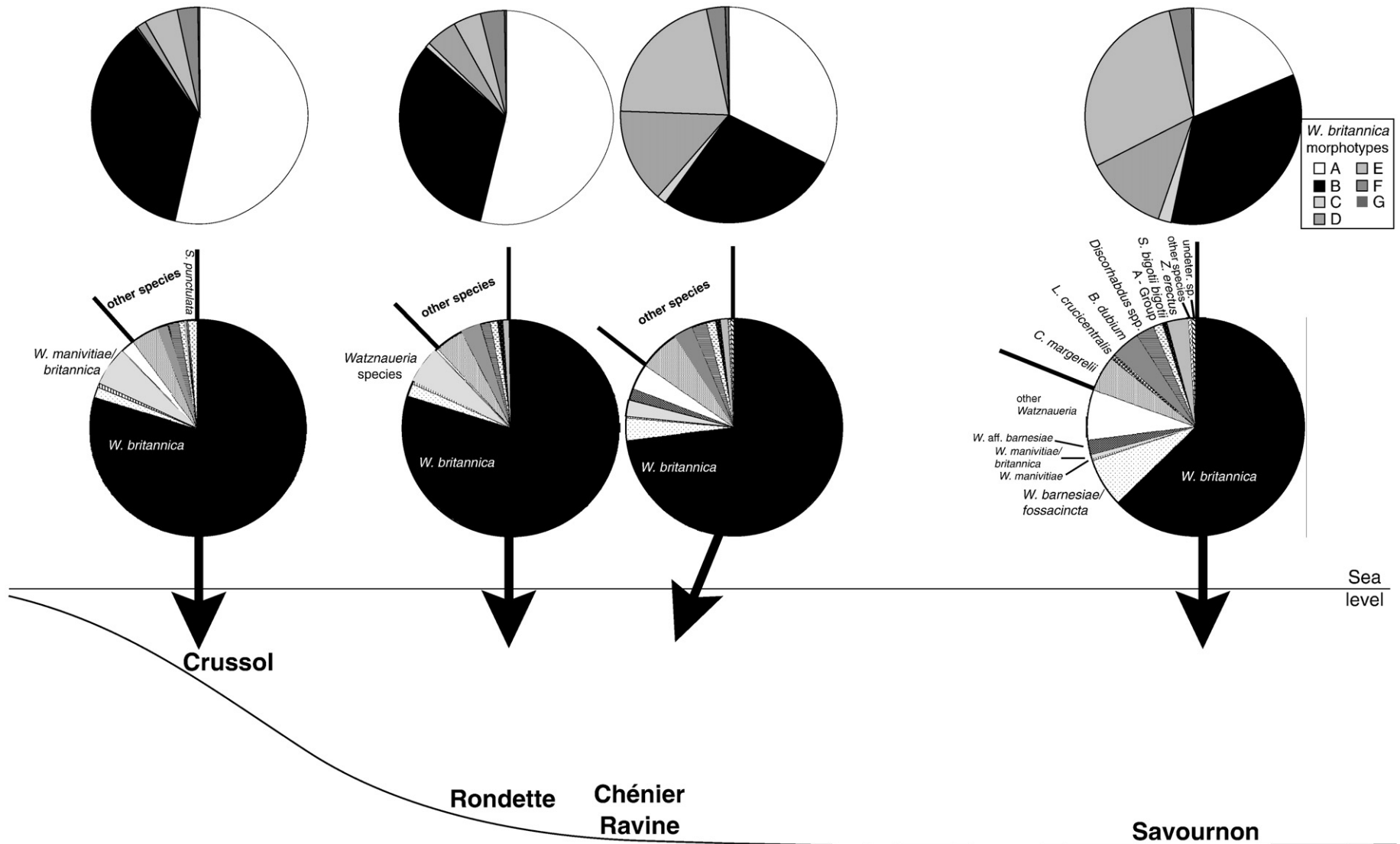


Fig. 10. Pie-charts showing the average compositions of calcareous nannofossil assemblages and of different morphotypes of *Watznaueria britannica* within the *W. britannica* group, across the Callovian–Oxfordian transition along a proximal–distal transect in the French Subalpine basin.

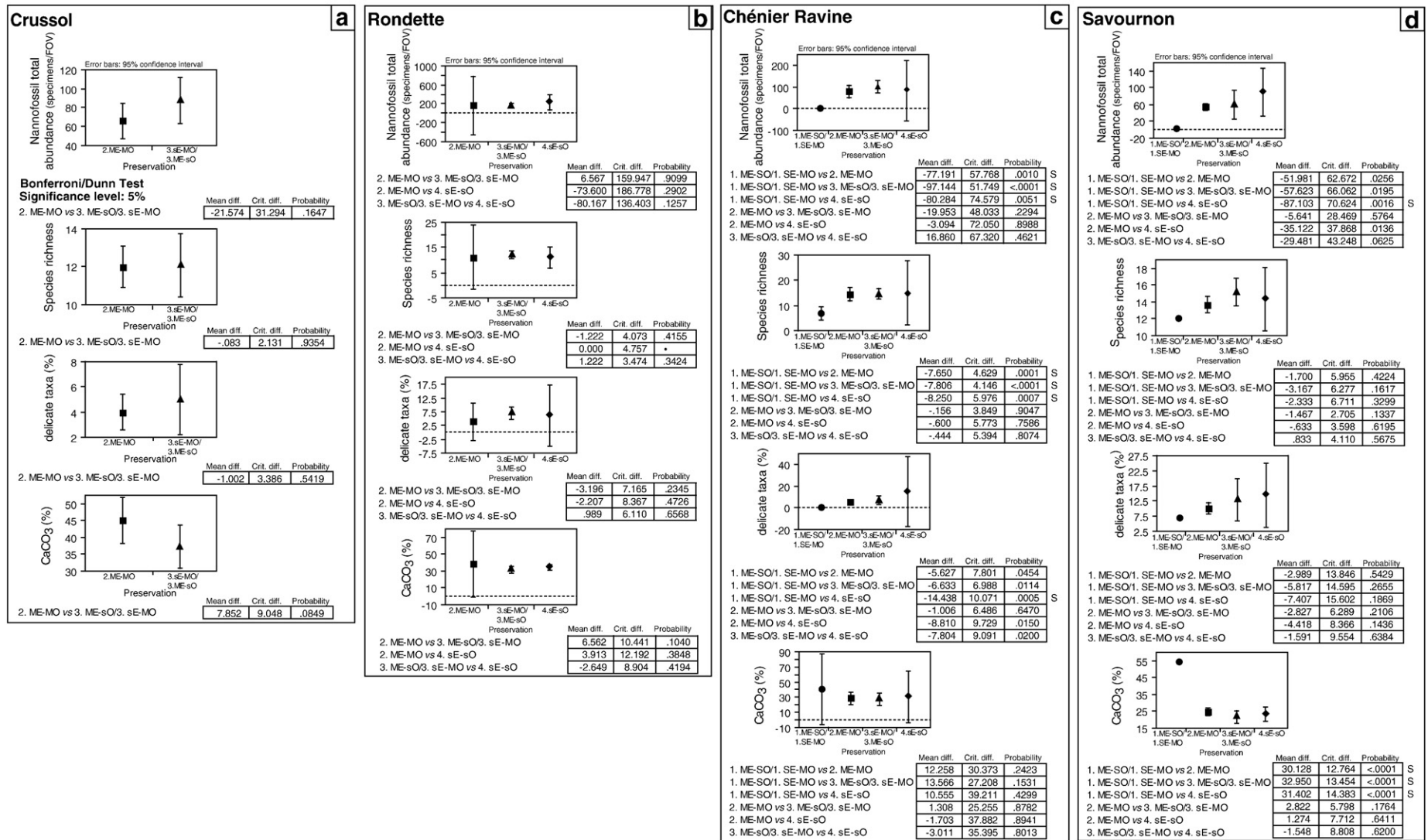


Fig. 11. a–d. Mean nannofossil total abundance (specimens per field of view), mean species richness, mean relative abundance of delicate taxa (*B. dubium* + *Discorhabdus* spp. + *Stephanolithion* + *Z. erectus*) and mean calcium carbonate content for different classes of preservation for a) the Crussol section, b) the Rondette section, c) the Chénier Ravine section, and d) the Savournon section. The different classes of preservation for nannofossil assemblages are: 1. SE and/or SO, 2. ME-MO, 3. sE-MO or ME-sO, 4. sE-sO with SE: strongly etched, SO: strongly overgrown, ME: moderately etched, MO: moderately overgrown, sE: slightly etched, sO: slightly overgrown. In order to estimate the significance of the observed differences between the different classes of preservation, a Bonferroni/Dunn test is applied. It allows comparison of the calculated means for datasets with different sizes (here, the highly variable number of samples showing different preservation states). Statistically significant differences (S) are observed at *p* (probability) < 0.0083 for the Chénier and Savournon sections. Eighty-six samples are considered in this analysis.

Table 2
Paleoecological significance of selected nannofossil taxa.

Nannoplankton paleoecological indices	Nutrient concentration	Ecological strategy	Paleoceanography
<i>Watznaueria britannica</i> Small morphotypes Large morphotypes	High mesotrophic ¹ Meso-eutrophic ^{4,5,6} Oligotrophic ^{4,5,6} Mesotrophic ^{this study}	r-selected ^{2,3}	Very unstable conditions ^{this study}
<i>Watznaueria barnesiae</i>	Oligotrophic ^{7,8,9,10} Mesotrophic ¹ Oligotrophic ¹	Eurytopic ^{11,12,13} r-selected ^{3,12}	Warm surface waters ^{4,14} Unstable conditions ^{this study} Oceanic sites of upwelling/shelf areas with storm mixing ^{8,15,16} Cooler surface waters ^{8,17}
<i>Watznaueria manivittiae</i> <i>Watznaueria manivittiae/britannica</i> <i>Biscutum</i> spp., <i>Z. erectus</i>	Eutrophic ^{8,15,16}		
<i>Discorhabdus</i> spp. A-group <i>Schizosphaerella punctulata</i>	Meso-eutrophic ^{18,19,20,21,22} Meso-eutrophic ⁵ Oligotrophic with sporadic pulse of nutrients ²³		Cooler surface waters ⁵ Warm surface waters of shallow basins close to carbonate platforms ²⁴

Data from 1: Pittet and Mattioli (2002); 2: Walsworth-Bell (2000); 3: Lees et al. (2005); 4: Olivier et al. (2004); 5: Tremolada et al. (2006); 6: Giraud et al. (2006); 7: Roth (1986); 8: Roth and Krumbach (1986); 9: Roth (1989); 10: Erba et al. (1992); 11: Mutterlose (1991); 12: Street and Bown (2000); 13: Lees et al. (2004); 14: Bartolini et al. (2003); 15: Roth (1981); 16: Roth and Bowdler (1981); 17: Mutterlose and Kessels (2000); 18: Premoli Silva et al. (1989); 19: Erba (1991); 20: Coccioni et al. (1992); 21: Herrle (2003); 22: Giraud et al. (2003); 23: Mattioli and Pittet (2004); 24: Mattioli (2006).

high-fertility surface waters for the Cretaceous period (see Table 2). Lees et al. (2006) have observed in the Kimmeridge Clay Formation that abundance peaks of *Z. erectus* and *Biscutum* spp. only occur during the switchovers between two intervals dominated by watznaueriaceans. Walsworth-Bell (2000) has observed in the Oxford Clay Formation (Middle Callovian–Early Oxfordian) an increase in the relative abundance of *Biscutum* spp. and *Z. erectus* associated with an increase in the species diversity and a decrease in the relative abundance of *W. britannica*. Our data corroborated these latter observations. In the Callovian–Oxfordian marine paleoenvironments of the French Subalpine Basin, when trophic levels in surface waters become very high (such as in the Rondette section), *Z. erectus* and

B. dubium are probably not competitive for nutrients with respect to small morphotypes of *W. britannica*.

The large abundance of small-sized *W. britannica* associated with low coccolith diversities, frequent *S. punctulata* and very low percentages of *W. manivittiae*, suggests that paleoenvironmental conditions in proximal setting were unstable, with variable nutrient levels (Fig. 12). Sporadic increases in nutrients associated with higher carbonate and/or terrigenous input probably caused higher turbidity in the water column and unstable paleoenvironmental conditions. In the slope–basin transition setting, higher percentages of *W. britannica* that are largely represented by small morphotypes associated with the lowest diversities, are indicators of unstable surface waters (Fig. 12).

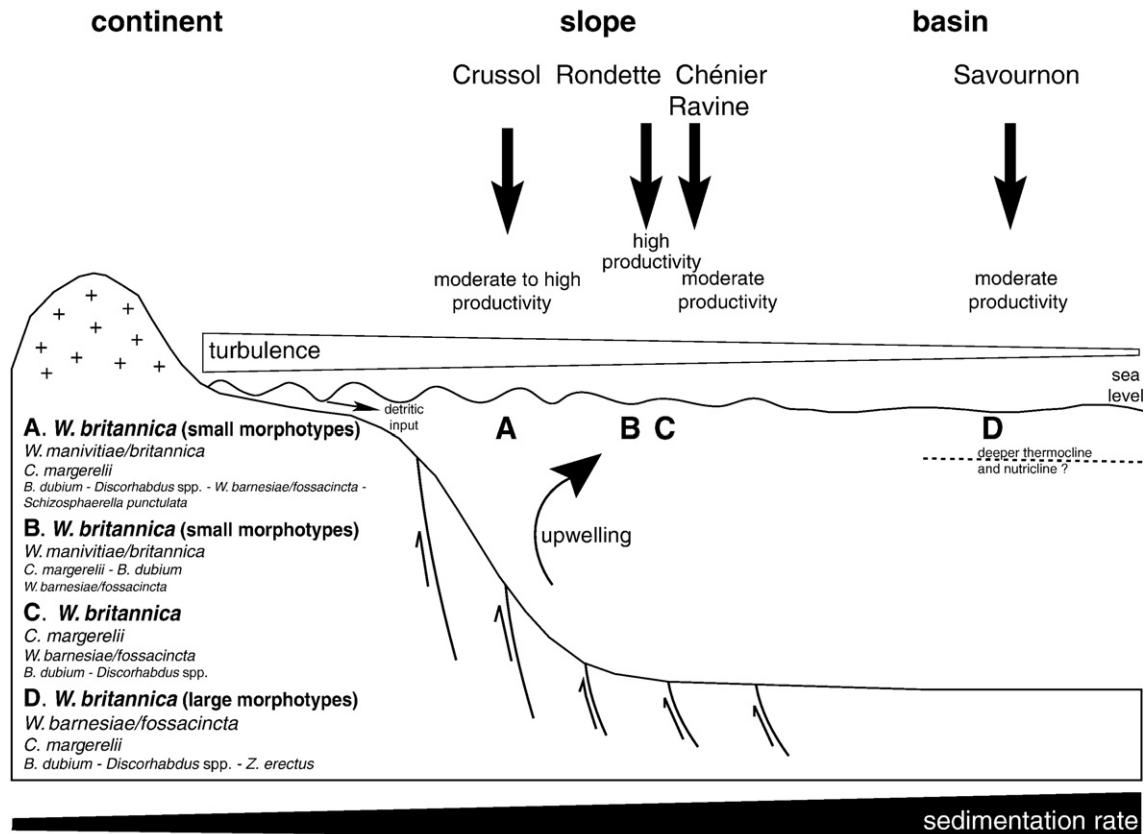


Fig. 12. Changes in paleoenvironmental conditions from proximal to distal settings within the French Subalpine Basin at the Callovian–Oxfordian transition.

Towards the distal settings, more stable paleoecological conditions (more open paleoenvironment) for the coccolithophorid population (highest diversities) occurred, and the nannofossil assemblages are characterized by a higher contribution of large morphotypes of *W. britannica* and the highest percentages of *W. barnesiae/fossacincta*. Higher percentages of *Z. erectus* and *B. dubium* are also recorded, indicating that surface waters were rather mesotrophic than oligotrophic (Fig. 12). In the modern ocean, distal settings are generally characterized by oligotrophic conditions in surface waters due to a more or less permanent stratification of the water column (Winter et al., 1994). This suggests that the thermocline was too unstable to allow a permanent stratification of the water column in the central part of the French Subalpine Basin (Fig. 12). A progressive decrease in temperatures passing from the more proximal, shallower setting to more distal and deeper areas could also explain the observed increase in the relative abundances of these two taxa. This is also in agreement with the higher contribution of the A-group (which are interpreted to be more adapted to cooler surface-waters; Tremolada et al., 2006) in the distal settings (Figs. 8–10).

Changes in nannofossil total abundances from proximal to distal sections can be related to a variable sedimentation rate. In fact, a high sedimentary flux (carbonate or siliciclastic) from shallower areas towards the basin dilutes the (para)autochthonous pelagic rain that is essentially formed by nanoplankton. The correlations between Crussol, Chénier Ravine and Savournon sections show a higher sedimentation rate in the Savournon section than in the other sections (Fig. 2). This could explain the lowest mean total abundance recorded in the Savournon section among the four compared sections. In the Rondette section, the total abundance is considerably higher than in the other settings (Figs. 6–9). Because of the short analyzed succession, it is not possible to compare its sedimentation rate with the other sections. As there is no sedimentological evidence of very condensed deposits in the Rondette section, the highest total abundances recorded could thus be the result of a high primary productivity related to intensified nutrient recycling in surface waters because of storms or upwelling rather than a reduced accumulation rate.

The slight increase in nannofossil total abundance recorded for the successions at the Callovian–Oxfordian transition is interpreted as a slight increase in nanoplankton primary production. Increasing nannofossil total abundance is not the result of reduced accumulation rate. On the contrary, there is a strong increase in the sedimentation rate in the Early Oxfordian in the French Subalpine Basin (Fortwengler et al., 1997). Maximum percentages of small coccoliths (*Biscutum* spp., *Z. erectus*, and the A-group) across the Callovian/Oxfordian boundary are also indicative of enhanced primary productivity and thermal minimum in surface waters. Colour banding is recognized in the Early Oxfordian ‘Terres Noires’ Formation and attributed to periodic monsoon-type climates (Tribovillard, 1989). Increased precipitation and runoff under contrasting seasonal climatic conditions (monsoon-type) lead to eutrophication of marine surface waters in the French Subalpine Basin. High primary productivity is also supported by the C-isotope record from another section located in the central part of the French Subalpine Basin (Trescléoux section), showing an increase in bulk carbonate carbon isotope values ($\delta^{13}\text{C}_{\text{carb}}$) in the Early Oxfordian ‘Terres Noires’ Formation (Louis-Schmid et al., 2007b). The dominance of *W. britannica*, with a high contribution of small-sized specimens recorded in the investigated sections, could be indicative of higher surface-water fertility in the French Subalpine Basin than those of the eastern Paris Basin, where *W. barnesiae/fossacincta* is dominant (Tremolada et al., 2006).

6. Conclusions

Integrated ammonite, dinoflagellate cyst and nannofossil biostratigraphies allowed good correlation of four sections located on a proximal–distal transect in the French Subalpine Basin and dated to

the Callovian–Oxfordian. The FO of the nannofossil zonal marker, *S. bigotii maximum*, is recognized in three sections and lies within the ammonite *paucicostatum* horizon (*lamberti* subzone and zone). Complementary new nannofossil data are presented in this work.

Despite the dominance of *W. britannica*, a slope-to-basin differentiation in nannofossil assemblage is recognized. It is related to a decrease in nutrient concentration, turbulence and environmental instability towards the central part of the basin. Slope setting is characterized by low-diversity assemblage with dominant small-sized *W. britannica*, subordinated *W. manivittiae/britannica* (a morphotype described in this study) and frequent *S. punctulata*. Central basinal setting is characterized by more diverse assemblages associated with lower percentages of *W. britannica*, but a higher contribution of large morphotypes and higher percentages of *W. barnesiae/fossacincta* and small coccoliths (*B. dubium* and *Z. erectus*). These coccoliths, indicators of high surface-waters fertility for the Cretaceous, were probably not competitive with respect to small-sized morphotypes of *W. britannica* in unstable and eutrophic surface waters for the Jurassic.

At the Callovian–Oxfordian transition, an increase in surface-water productivity is recorded both in proximal and distal sections and is demonstrated by both an increase in nannofossil total abundances and in the percentages of taxa adapted to high-trophic levels (as already shown by Tremolada et al., 2006 in the eastern Paris Basin). This event is also coincident in the French Subalpine Basin with a cooling of surface waters as indicated by an increase in the relative abundance of cool-water taxa. Further studies will be necessary to demonstrate whether the increase in productivity is a global event.

Acknowledgements

We would like to thank Paula Desvignes (Lyon) for smear slides preparation and calcimetric analyses. We are extremely grateful to Stéphane Guillot, Emanuela Mattioli and Bernard Pittet for stimulating discussions. The thoughtful suggestions of two anonymous reviewers and the editor helped to improve the manuscript. This work is a contribution to the team project ‘Quantification of productivities and transfers in the Mesozoic’ of the CNRS-UMR 5125 ‘Paléoenvironnements et Paléobiosphère’, Lyon.

Appendix A

List of species cited in the text, figures and dataset (“supplementary material”)

Axopodorhabdus cylindratus (Noël, 1965) Wind and Wise in Wise and Wind, 1977 (Fig. 4.2)

Biscutum dubium (Noël, 1965) Grün in Grün et al., 1974 (Fig. 4.4)

Crepidolithus crassus (Deflandre, 1954) Noël, 1965

C. perforata (Medd, 1979) Grün and Zweili, 1980

Cyclagelosphaera margerelii (Noël, 1965) (Fig. 4.12)

C. wiedmannii Reale and Monechi, 1994 (Fig. 4.13)

D. patulus (Deflandre in Deflandre and Fert, 1954) Noël, 1965 (Fig. 4.8)

D. striatus Moshkovitz and Ehrlich, 1976 (Fig. 4.7)

Discorhabdus sp. (Fig. 4.6)

Description: a species of *Discorhabdus* with a circular to subcircular outline, ranging from 3 to 4.5 μm . Coccoliths are composed of at least 20 radial, non-imbricate elements. The central area is open and variable in size. In crossed-nicols, the inner ring is brighter than the rim as in *D. criotus*, but the presence of another birefringent central element cycle suggests the presence of a small inner spine.

Ethmorhabdus gallicus Noël, 1965 (Fig. 4.1)

Lotharingius crucicentralis (Medd, 1971) Grün and Zweili, 1980

L. hauffii Grün and Zweili in Grün et al., 1974

L. velatus Bown and Cooper, 1989

Polypodorhabdus escaigii Noël, 1965 (Fig. 4.3)

Similiscutum novum (Goy, 1979) Mattioli et al., 2004 (Fig. 4.5)

Stephanolithon bigotii Deflandre, 1939 ssp. *bigotii* (Fig. 4.9)
S. bigotii Deflandre, 1939 ssp. *maximum* Medd, 1979 (Fig. 4.10)
Triscutum expansus (Medd, 1979) Dockerill, 1987
Tubirhabdus patulus Rood et al., 1973
Watznaueria barnesiae (Black, 1959) Perch-Nielsen, 1968 (Fig. 4.21)
Watznaueria aff. *barnesiae* (Fig. 4.22–23)

Description: large elliptical to subcircular coccoliths. In crossed-nicols, *W.* aff. *barnesiae* shows yellow colors. It is very similar in general structure (included the central area) to *W. barnesiae*, but the coccolith size is larger (diameter 7–9 µm) and the birefringence is higher, but lower than *W. manivitiae*.

Remarks: The high birefringence could be due to recrystallisation. *W. britannica* (Stradner, 1963) Reinhardt, 1964 (Fig. 4.14–20)

Remarks: The different morphotypes A–F described in Giraud et al. (2006) are present in the assemblages. Another morphotype, called G, presents a very large central area spanned by a small bridge with a button-shaped, is recognized.

W. communis Reinhardt, 1964

W. fossacincta (Black, 1971) Bown in Bown and Cooper, 1989

W. manivitiae Bukry, 1973 (Fig. 4.26)

W. manivitiae/britannica (Fig. 4.24–25)

Description: a large (diameter >8 µm) and highly birefringent *Watznaueria* with a large external cycle. The central area is small and spanned by a bridge with a button-shaped (characteristic of *W. britannica*). It is very similar in morphology to *W. manivitiae*.

W. ovata Bukry, 1969

Watznaueria sp. 3 (Erba, 1990)

Watznaueria sp. 4 (Erba, 1990)

Zeughrabdodus embergeri (Noël, 1958) Perch-Nielsen, 1984

Z. erectus (Deflandre in Deflandre and Fert, 1954) Reinhardt, 1965 (Fig. 4.11)

Incertae sedis

Schizosphaerella punctulata Deflandre and Dangeard, 1938 (Fig. 4.27)

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2009.04.004.

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