Paleoenvironmental and paleobiological origins of coccolithophorid genus *Watznaueria* emergence during the late Aalenian–early Bajocian

Baptiste Suchéras-Marx*, Emanuela Mattioli, Fabienne Giraud, and Gilles Escarguel

Abstract.—The latest Aalenian–early Bajocian time interval (ca. 171-169 Ma) is marked by a global reorganization of oceanic plates with the Central Atlantic opening and the formation of the Pacific plate. This time interval is also marked by a global geochemical perturbation of $\delta^{13}C$ with a negative excursion at the Aalenian/Bajocian boundary and a positive excursion during the early Bajocian. Evolutionary diversifications of marine invertebrate taxa, namely ammonites, radiolarians, and coccolithophorids, are recorded at that time. Concerning coccolithophorids, this interval witnesses the diversification and expansion of the most successful Mesozoic genus: *Watznaueria*. In this study, we explore the potential environmental, ecological, and biological forcing at the origin of *Watznaueria* diversification and its effect on the coccolith assemblages through quantification of the absolute and relative abundances of calcareous nannofossils in two Middle Jurassic key sections: Cabo Mondego (Portugal) and Chaudon-Norante (France). In both sections, we find an increase in nannofossil absolute abundance and flux at the beginning of the lower Bajocian, coeval with an increase in absolute and relative abundances of *Watznaueria* spp., followed by a plateau in the middle and upper part of the lower Bajocian. The increase of *Watznaueria* spp. is synchronous with a decrease in relative abundance of other major coccolith taxa, whereas the absolute abundance of these species did not decrease. During the climatically driven early Bajocian eutrophication event, *Watznaueria* spp. integrated into the calcareous nannoplankton community in two successive evolutionary steps involving first *W. contracta* and *W. colaccicchii*, and second *W. britannica* and *W.* aff. *manivitiae*. Step 1 was driven by an increase in niche carrying capacities linked to the early Bajocian eutrophication. Step 2 was driven by specific adaptation of the newly evolved *Watznaueria* species to bloom in nutrient-rich environments not exploited before. These evolutionary events have initiated the 100-Myr reign of *Watznaueria* over the calcareous nannoplankton community.

Baptiste Suchéras-Marx. UMR CNRS 5276 LGL-TPE Université Claude Bernard Lyon 1, Ecole Normale Supérieure de Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne Cedex, France, and Université de Lyon, Université Jean Monnet and UMR-CNRS 6524, Laboratoire Magmas et Volcans, 23 rue du Dr Paul Michelon, 42023 Saint Etienne, France. *Present address: Aix-Marseille Université, CNRS, IRD, CEREGE UM34, 13545 Aix en Provence, France. E-mail: baptiste.sucheras@gmail.com, sucheras-marx@cerege.fr
Emanuela Mattioli and Gilles Escarguel. UMR CNRS 5276 LGL-TPE, Université Claude Bernard Lyon 1, Ecole Normale Supérieure de Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne Cedex, France
Fabienne Giraud. Université Grenoble Alpes, ISTerre, F-38041 Grenoble, France and CNRS, ISTerre, F-38041 Grenoble, France

Introduction

The Aalenian–Bajocian (Middle Jurassic, ca. 170 Ma) is known for many important geological features. The Ligurian-Piemontese Basin began its opening (Bill et al. 2001), the spreading rate of Central Atlantic Ocean intensified (Labails et al. 2010), and the Pacific plate started to evolve from the triple junction between the Izanagi, Farallon, and Phoenix plates (Nakanishi et al. 1992; Bartolini and Larson 2001) at the origin of a shift of strontium isotope toward unradiogenic values (data compiled by Jenkyns et al. [2002]). This new plate production is related to subduction on the border of the Pacific Superocean inducing volcanism (Yin et al. 1998; Pankhurst et al. 2000; Bartolini and Larson 2001). A bulk carbonate $\delta^{13}C$ negative perturbation was recorded in Italy (Bartolini et al. 1996), Spain (O'Dogherty et al. 2006), and Portugal (Suchéras-Marx et al. 2012). This negative excursion is also observed in $\delta^{13}C$ coal deposits of Yorkshire indicating input of ^{12}C into the

0094-8373/15

atmospheric reservoir (Hesselbo et al. 2003). Meanwhile, leaf stomatal density results suggest an important increase in pCO$_2$ (Hesselbo et al. 2003). Together, these observations suggest an increase in volcanic activity. Following the Aalenian–Bajocian negative excursion, a δ^{13}C positive excursion is observed during the early Bajocian in Italy (Bartolini et al. 1996), Spain (O'Dogherty et al. 2006), Portugal (Suchéras-Marx et al. 2012), northern France (Brigaud et al. 2009), and southern France (Suchéras-Marx et al. 2013). This second event has not yet been observed in terrestrial material. It has been proposed that the δ^{13}C positive excursion of the early Bajocian is linked to an increase in oceanic primary productivity due to eutrophication caused by nutrient input (Bartolini et al. 1996; Bartolini and Cecca 1999).

In the same time interval, various paleontological changes are observed. The most striking change is a major turnover in ammonite fauna, in which the latest Aalenian–early Bajocian ammonites ancestors of the Middle and Late Jurassic faunas, replace typical Early Jurassic faunas (O'Dogherty et al. 2006). A parallel increase in radiolarian deposits is recorded in the Tethys Ocean, as well as a slight trend toward diversification, related to the increase in primary production during the δ^{13}C positive excursion (Bartolini et al. 1999). Eventually, calcareous nannofossils also diversified (Roth 1987; Mattioli and Erba 1999; Bown 2005). In the Mesozoic history of coccoliths, which are micrometric calcite platelets produced by planktic coccolithophorid algae, one highly successful genus, *Watznaueria*, appeared during the Toarcian (Early Jurassic, 183-174 Ma; Cobianchi et al. 1992; Mattioli 1996) and diversified during the Bajocian (170-168 Ma; Cobianchi et al. 1992; Mattioli and Erba 1999; Erba 2006; Tiraboschi and Erba 2010). *Watznaueria* species dominated the pelagic realm for ~70 Myr, from the Middle Jurassic until the end of the Early Cretaceous, and disappeared after the K/Pg boundary (Erba 2006; Bernaola and Monechi 2007). Nevertheless, this major evolutionary event within the most important Mesozoic pelagic carbonate producers in the oceans remains poorly documented in term of the dynamics of relative

and absolute abundances (most of the works published so far focused on nannofossil taxonomy and biostratigraphy [Cobianchi et al. 1992; Mattioli and Erba 1999; Tiraboschi and Erba 2010]) with some exceptions (Aguado et al. 2008; Suchéras-Marx et al. 2012).

In this study, we quantify absolute and relative abundance of calcareous nannofossils in the latest Aalenian–early Bajocian time interval in order to estimate the effect of *Watznaueria* diversification on the calcareous nannofossil assemblages and its relation to the δ^{13}C positive excursion of the early Bajocian. We focus on deposits from Cabo Mondego (Portugal), the Aalenian/Bajocian GSSP (Global Stratotype Section and Point; Pavia and Enay 1997), and Chaudon-Norante (SE France), the only early Bajocian time-calibrated section based on cyclostratigraphy (Suchéras-Marx et al. 2013).

Geological Settings

Cabo Mondego

The Cabo Mondego section is located in the Lusitanian Basin (Fig. 1), on the western Atlantic coast of Portugal, near Figueira da Foz. The succession is represented by marine deposits of Upper Toarcian to Kimmeridgian age (Ruget-Perrot 1961). Cabo Mondego is the Global Stratotype Section and Point (GSSP) for the Aalenian/Bajocian boundary (Pavia and Enay 1997) as well as the Auxiliary Stratotype Section and Point (ASSP) for the Bajocian/Bathonian boundary (Fernandez-Lopez et al. 2009). Numerous ammonites have been collected throughout the succession, allowing the establishment of a detailed biostratigraphical framework (Henriques et al. 1994).

The studied part of the Cabo Mondego section extends from the latest Aalenian (Concavum ammonite zone) to the end of the lower Bajocian (base of the Humphriesianum ammonite zone) (Fernandez-Lopez et al. 1988). The early Bajocian is divided into four ammonite zones, namely Discites, Laeviuscula, Propinquans (formerly Sauzei zone), and Humphriesianum. Nannofossil zones ("Nanno. zone" in Figs. 3–6) follow Mattioli and Erba (1999), using the *W. britannica* occurrence for NTJ9 and
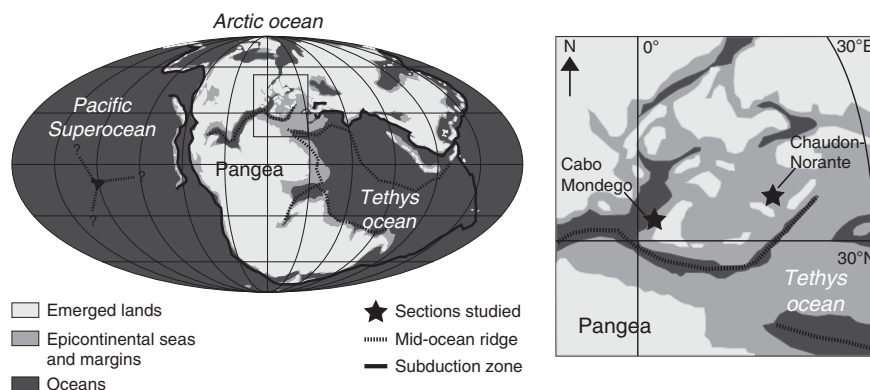
FIGURE 1. Paleogeographic distribution of oceans and lands during the Middle Jurassic (after Blakey 2008). On the left, a global view with subduction zones and mid-ocean ridges; on the right, focus on the western Tethys with the locations of Cabo Mondego in the Lusitanian Basin and Chaudon-Norante in the French Subalpine Basin.

W. manivitiae for NTJ10. The Aalenian NTJ8 zone is confirmed thanks to the presence of *W. contracta* since the base of the studied interval. The nannofossil zones proposed are partly in agreement with Henriques et al. (1994), the major difference being in the occurrence of *W. britannica* in the Aalenian in our observations whereas Henriques et al. (1994) observed it in the early Bajocian (Discites ammonite zone). The sedimentary succession consists of alternating marlstone and limestone (Fig. 2); the carbonate fraction is exclusively micritic or microsparitic calcite (Henriques et al. 1994; Canales and Henriques 2008). Abundant and diverse benthic foraminiferal assemblages were observed in the middle Aalenian–lower Bajocian limestone-marl alternations, suggesting a distal ramp paleoenvironment (Canales and Henriques 2013). The sediments corresponding to the Concavum (~5.5 m thick) and Discites (~7.2 m thick) ammonite zones are characterized by irregular nodular bedding but fairly regular alternations of ~20 cm argillaceous limestone and marlstone beds. The interval corresponding to the base of the Laeviuscula (~36 m thick) ammonite zone is limestone-dominated. At the base of the Propinquans (~32 m thick) ammonite zone, the argillaceous limestone beds become more regular and thicker in comparison to the base of the section through the Humphriesianum (~7 m) ammonite zone. From the Propinquans ammonite zone, the succession becomes limestone-dominated (Suchéras-Marx et al. 2012).

Chaudon-Norante

The Chaudon-Norante section is located in the Ravin de Coueste (Digne tectonic nappe, Southern Alps), which was emplaced during the Mio-Pliocene (Lemoine 1973; Gidon and Pairis 1992). It presents a continuous succession from the Toarcian (Early Jurassic) to the base of the Bathonian (Middle Jurassic). This section belongs to the French Subalpine Basin, which was bounded northward by the Jura platform, westward by the Central Massif and the Ardèche platform, and southward by the Provence platform (Fig. 1). The Chaudon-Norante succession is well exposed and the ammonite biostratigraphy for the Bajocian (Pavia 1973, 1983) has high temporal resolution. Nannofossil zones follow Mattioli and Erba (1999), using the *W. contracta* occurrence for NTJ8, *W. britannica* for NTJ9, and *W. manivitiae* for NTJ10. The nannofossil zones proposed here agree with Erba (1990).

The part of the section studied here extends from the end of the Aalenian to the end of the lower Bajocian. It is represented by decimetric hemipelagic marlstone-limestone alternations. The limestones are mainly wackestones to packstones with some bioclastic remains of *Bositra* (Bivalvia), radiolarians, rare benthic foraminifera, and rare siliceous sponge spicules (Pavia 1983). The top of the Aalenian is dated to the upper part of the Concavum ammonite zone. This 37.9-m-thick interval is composed of fairly regular marlstone-limestone alternations except for the uppermost part, which is

marl-dominated. The 131.1-m-thick lower Bajocian succession corresponds to four ammonite zones. From base to top, the Discites ammonite zone is dominated by marlstones, the Laeviuscula ammonite zone displays regular marlstone-limestone alternations, the Propinquans ammonite zone is limestone-dominated, and the Humphriesianum ammonite zone displays regular marlstone-limestone alternations (Suchéras-Marx et al. 2013).

Material and Methods

We quantified nannofossils (both coccoliths and the nannolith *Schizosphaerella*) in 41 samples from Cabo Mondego (collected in the field in 2004 by F. Giraud and E. Mattioli before the classification of this area as Natural Monument in 2007) and 50 samples from Chaudon-Norante. Sample preparation for absolute abundances per gram of rock used the random-settling method proposed by Beaufort (1991) and calibrated by Geisen et al. (1999), consisting of a suspension of 20 to 30 mg of rock powder mixed with water settled for 24 h on a cover slide. Once cover slides were dry, they were glued to a microscope slide using eukitt®. Usually 300 nannofossils were counted, using a Zeiss optical microscope with a ×1000 magnification. In poor samples, at least 100 coccoliths were counted in a slide in order to reach reliable relative abundance estimations at the genus level. Unfortunately, eight samples from Cabo Mondego and six samples from Chaudon-Norante were too poor and were excluded from the relative abundance data set. The preservation of coccoliths was estimated on a scale from 1 (very poor preservation) to 6 (excellent preservation; modified from Bown and Young 1998). Criteria chosen for this scale are mainly based on dissolution and overgrowth patterns, preservation of the crystallographic organization, and preservation of the central area.

We used the counts to calculate absolute abundance of each sample; this represents the number of specimens per gram of rock (Geisen et al. 1999). Relative abundance of the nannolith *Schizosphaerella* was calculated with respect to the whole nannofossil assemblage, whereas relative abundances of coccolith species (including *Watznaueria* species) were calculated with respect to the coccolith assemblage only. We derived confidence limits of the sample relative abundances from their underlying binomial distributions by using the algorithm of Beaudoin et al. (2007a,b). Given a type I error rate $\alpha = 0.05$, these limits define the 95% confidence intervals associated with each sample's relative abundance, that is, the range of percentage values within which there is a probability of $1 - \alpha = 95\%$ of finding the unknown true (parametric) percentage. Eventually, nannofossil fluxes in number of nannofossils per m^2 per year were calculated from ammonite zone durations based on Suchéras-Marx et al. (2013) or Gradstein et al. (2012; only for the Aalenian part of Cabo Mondego). Only the genera of calcareous nannofossils representing >5% of the assemblage in more than ten samples (and >90% of all identified nannofossils when considered together) are presented in the results.

Results

At Cabo Mondego, 50 nannofossil species have been identified (partly presented in Fig. 2). The main genera are, starting from the most abundant: *Watznaueria*, *Schizosphaerella*, *Discorhabdus*, *Similiscutum*, *Biscutum*, *Carinolithus*, and *Lotharingius*. At Chaudon-Norante, 44 different species of nannofossils have been identified. The main genera are, starting from the most abundant: *Watznaueria*, *Similiscutum*, *Lotharingius*, *Discorhabdus*, *Biscutum*, *Carinolithus*, and *Schizosphaerella*. Despite the slight difference in total species observed between the two sections, the assemblages are remarkably similar. The preservation of nannofossils in both sections is better in marlstones than in limestones (see counting charts in Supplementary Materials). At Cabo Mondego, preservation in limestones is poor to moderate, whereas it is moderate in marlstones, with some samples showing a good preservation. There is no stratigraphic influence on the preservation; samples with poor to moderate preservation are found all along the section. At Chaudon-Norante, preservation is poor to moderate (but mostly moderate) in limestones; in marlstones it is moderate to moderate-good. Here, also, there is no stratigraphic pattern in preservation,
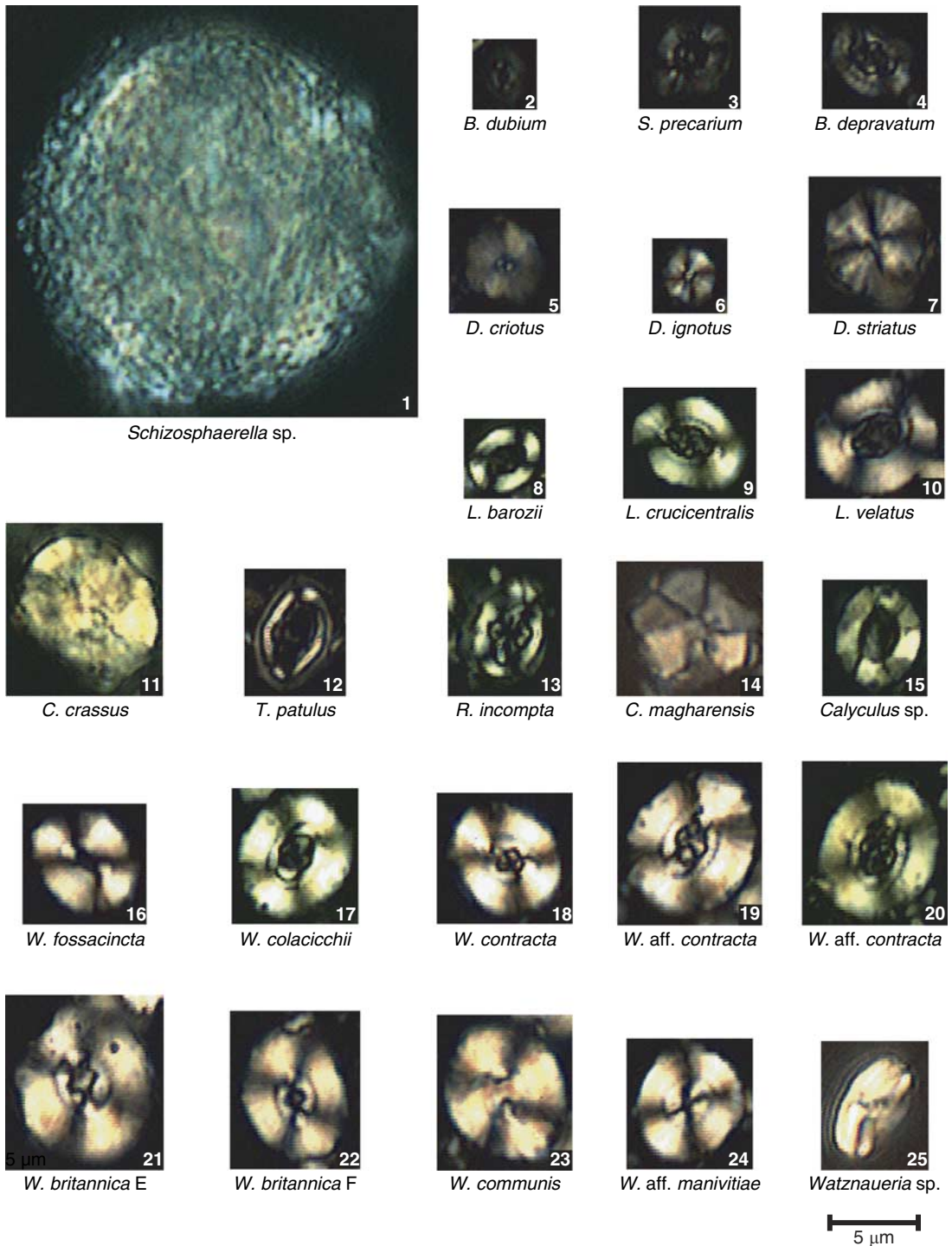
FIGURE 2. Calcareous nannofossils photographs from Cabo-Mondego (CM) and Chaudon-Norante (CN) under cross-polarized light.
1. *Schizosphaerella* sp. CM67; 2. *Biscutum dubium* CM26; 3. *Similiscutum precarium* CM17; 4. *Biscutum depravatum* CM62; 5. *Discorhabdus criotus* CM62; 6. *Discorhabdus ignotus* CM26; 7. *Discorhabdus striatus* CM26; 8. *Lotharingius barozii* CN420; 9. *Lotharingius crucicentralis* CN220; 10. *Lotharingius velatus* CM62; 11. *Crepidolithus crassus* CN380; 12. *Tubirhabdus patulus* CM60 (large specimen); 13. *Retecapsa incompta* CN1680; 14. *Carinolithus magharensis* CM26; 15. *Calyculus* sp. CN260; 16. *Watznaueria fossacincta* CM62; 17. *Watznaueria colacicchii* CN200; 18. *Watznaueria contracta* CM26; 19. *Watznaueria* aff. *contracta* CM17; 20. *Watznaueria* aff. *contracta* CN550; 21. *Watznaueria britannica* E CM60; 22. *Watznaueria britannica* F CM62; 23. *Watznaueria communis* CM62 (large specimen); 24. *Watznaueria* aff. *manivitiae* CM60; 25. *Watznaueria* sp. lateral view CM26.

except for marlstone-limestone alternations. Overall, nannofossil preservation is very similar at Cabo Mondego and Chaudon-Norante, thus allowing a direct comparison between the two sections.

Nannofossil Absolute Abundances and Fluxes

In Figure 3, nannofossil absolute abundance and flux are presented, as well as absolute abundance for *Schizosphaerella* spp., *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. for Cabo Mondego. Nannofossil absolute abundance shows the lowest values in the Aalenian part of the section, with values between 10^6 and 10^7 nannofossils/g. The nannofossil absolute abundance gradually increases from the Discites ammonite zone up to a maximum of ~10^9 nannofossils/g in the middle of the Laeviuscula ammonite zone. Then, except for two low values at the end of the Laeviuscula ammonite zone and at the beginning of the Propinquans ammonite zone, the nannofossil absolute abundance remains high and mostly fluctuates between 10^8 and 10^9 nannofossils/g. The estimated nannofossil flux shows exactly the same trend as absolute abundance, with the lowest Aalenian values ranging between 10^8 and 10^9 nannofossils/m^2/year and the highest values exceeding 10^{11} nannofossils/m^2/yr in the middle of the Laeviuscula ammonite zone.

Schizosphaerella spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. absolute abundances show the same trend, with a decrease from the base of the section to minimal values at the Aalenian/Bajocian boundary, followed by an increase ending in the middle part of the Discites ammonite zone. Then, the absolute abundances fluctuate between the middle Discites ammonite zone values and values from the beginning of the section. After the main increase, only a few samples show values comparable to the Aalenian/Bajocian minimum. On average, *Schizosphaerella* spp., *Discorhabdus* spp., and *Biscutum* spp. + *Similiscutum* spp. have comparable absolute abundances whereas *Lotharingius* spp. and *Carinolithus* spp. have lower absolute abundances. *Watznaueria* spp.

absolute abundance increases from the base of the section until the middle of the Laeviuscula ammonite zone. Then, absolute abundances remain high and fluctuate between 8×10^7 and 10^9 nannofossils/g. Overall, the *Watznaueria* spp. absolute abundance curve is very similar to the nannofossil absolute abundance curve.

The nannofossil absolute abundance at Chaudon-Norante (Fig. 4) increases from the Aalenian until the upper part of the Discites ammonite zone. Then there is a decrease in the Laeviuscula ammonite zone and a return to high absolute abundance at the beginning of the Propinquans ammonite zone. Within the Propinquans ammonite zone, there is a small decrease and a return to high values at the Propinquans/Humphriesianum ammonite zones boundary. The nannofossil flux has exactly the same trend as the nannofossil absolute abundance.

At Chaudon-Norante, *Schizosphaerella* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. increase until the upper part of the Discites ammonite zone, except for a high value in the Aalenian for *Carinolithus* spp. Both *Schizosphaerella* spp. and the major coccolith genera show absolute abundances lower at Chaudon-Norante than at Cabo Mondego, except for *Biscutum* spp. + *Similiscutum* spp. For *Watznaueria* spp., there is a rising trend from the base of the section until the upper part of the Discites ammonite zone.

Relative Abundance of Most Relevant Nannofossil Genera

Figure 3 shows the relative abundance of *Schizosphaerella* spp. with respect to the whole nannofossil assemblage at Cabo Mondego, as well as relative abundances of *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. with respect to the coccolith assemblage. *Schizosphaerella* spp. relative abundance decreases from the Aalenian to lower Bajocian except for one sample at the base of the Laeviuscula ammonite zone and three samples at the top of the section. *Watznaueria* spp. relative abundance gradually increases from the base of the section until the upper part of
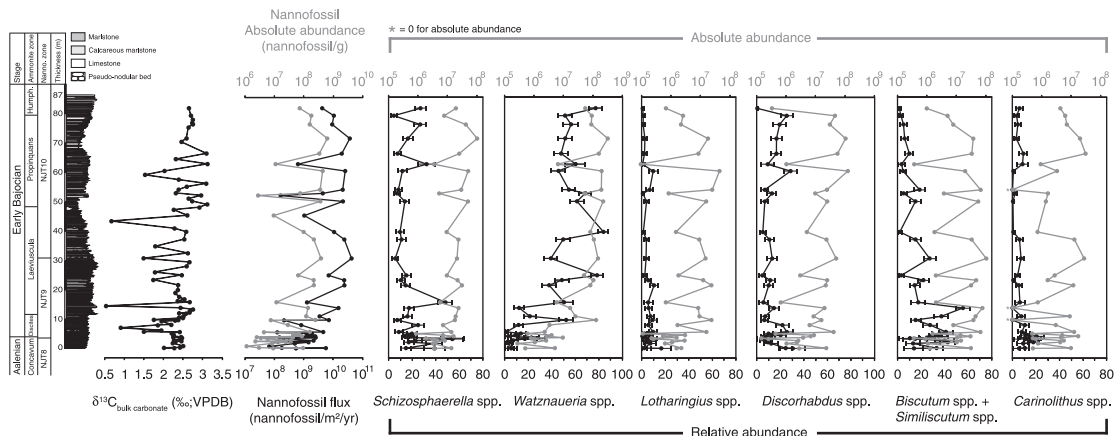
Nannofossil
Absolute abundance
(nannofossil/g)

✳ = 0 for absolute abundance

Absolute abundance

$\delta^{13}C_{bulk\,carbonate}$ (‰;VPDB)   Nannofossil flux (nannofossil/m²/yr)   *Schizosphaerella* spp.   *Watznaueria* spp.   *Lotharingius* spp.   *Discorhabdus* spp.   *Biscutum* spp. + *Similiscutum* spp.   *Carinolithus* spp.

Relative abundance

FIGURE 3.   The Cabo Mondego section showing the $\delta^{13}C$ (Suchéras-Marx et al. 2012), nannofossil absolute abundance (gray), and nannofossil flux (black) based on time estimation of early Bajocian ammonite zones (Suchéras-Marx et al. 2013); *Schizosphaerella* spp. absolute (gray) and relative (black) abundances in the nannofossil assemblage; *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp.; and *Carinolithus* spp. absolute (gray) and relative (black) abundances in the coccolith assemblage. Ammonite biostratigraphy is based on Fernandez-Lopez et al. (1988) and nannofossil biostratigraphy derived from this study.
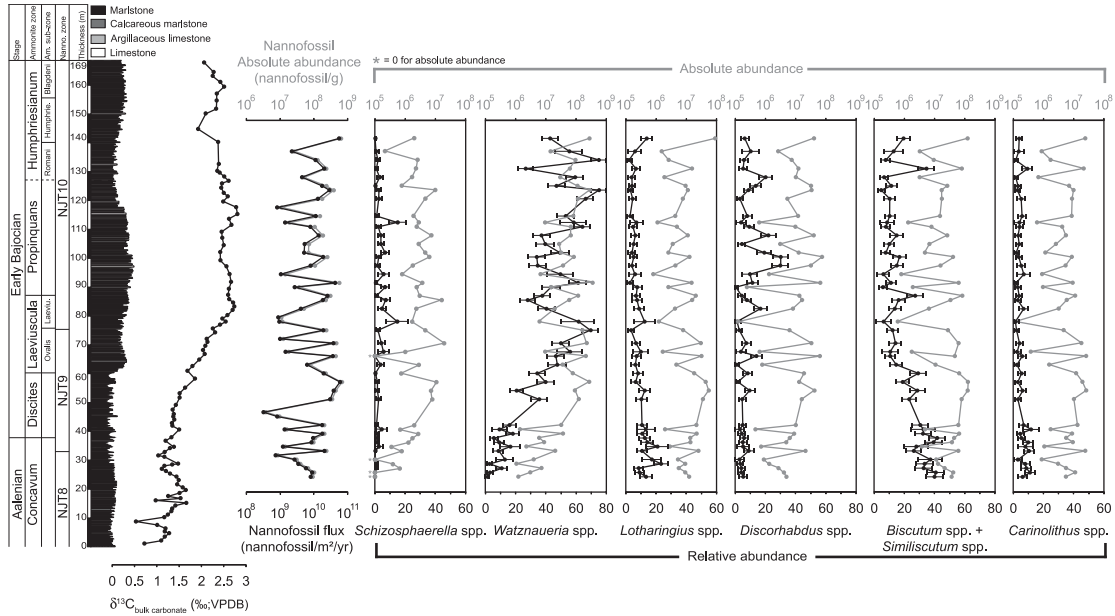
FIGURE 4.   The Chaudon-Norante section. Details as in Figure 3. Ammonite biostratigraphy is based on Pavia (1983) and nannofossil biostratigraphy derived from this study.

the Laeviuscula ammonite zone, with maximum values around 80%. Then it decreases and stabilizes between 50% and 60%. The percentages of *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. decreases, with minimum values in the middle to the upper part of the Laeviuscula ammonite zone. On average, *Biscutum* spp. + *Similiscutum* spp. are more abundant than *Lotharingius* spp., *Discorhabdus* spp., and *Carinolithus* spp.

At Chaudon-Norante (Fig. 4), the relative abundance of *Schizosphaerella* spp. remains low except for a few samples around 20% in the upper part of the Laeviuscula ammonite zone and in the upper part of the Propinquans ammonite zone. The increasing trend of *Watznaueria* spp. relative abundance is similar to the rise observed at Cabo Mondego, ending in the middle part of the Laeviuscula ammonite zone. A decreasing trend is observed (except for the last four samples at the top of Chaudon-Norante) for *Lotharingius* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. at Chaudon-Norante as well as at Cabo Mondego. Contrary to Cabo Mondego, the relative abundance of *Schizosphaerella* spp. in the upper part of the Laeviuscula ammonite zone is higher than that of *Discorhabdus* spp. in the lower part of Propinquans ammonite zone. On average, *Biscutum* spp. + *Similiscutum* spp. are more abundant than *Lotharingius* spp., *Discorhabdus* spp., and *Carinolithus* spp.

Absolute and Relative Abundance of Most Abundant *Watznaueria* Species

Figure 5 presents the absolute abundances of *W. colacicchii*, *W. contracta*, *W.* aff. *contracta*, *W. britannica*, and *W.* aff. *manivitiae* and their relative abundances in the coccolith assemblage of Cabo Mondego. Absolute abundances of *W. colacicchii* and *W. contracta* increase in the Aalenian and Discites ammonite zone up to a maximum between the end of the Discites ammonite zone and the beginning of the Laeviuscula ammonite zone. Then, a slight decrease is observed. The same pattern is observed for *W.* aff. *contracta*, except for the highest values reached in the Laeviuscula ammonite zone. For these three species, there

is a slight decrease toward the top of the section but never as low as in the Aalenian. Absolute abundances of *W. britannica* and *W.* aff. *manivitiae* increase until the middle and upper part of the Laeviuscula ammonite zone, respectively, and then remain relatively stable.

W. colacicchii has its highest relative abundance, up to 13%, between the Discites ammonite zone and the beginning of the Laeviuscula ammonite zone; then it gradually decreases to few percent. *W. contracta* and *W.* aff. *contracta* have their maximum percentages in the same interval as *W. colacicchii* then gradually decrease except for two spikes in *W.* aff. *contracta*, to ~15%, in the Propinquans ammonite zone. The relative abundances of *W. contracta* and *W.* aff. *contracta* are in the same range as *W. colacicchii* in the latest Aalenian and Discites ammonite zone and at the end of the Propinquans ammonite zone, but in the rest of the section their percentages are two to three times higher than those of *W. colacicchii*. *W. britannica* has relative abundances of 0–5% in the latest Aalenian and Discites ammonite zone, followed by an increase in the Laeviuscula ammonite zone up to values over 20%. The beginning of the Propinquans ammonite zone is marked by a decrease, with the lowest value down to 8%. The middle part of this ammonite zone is marked by an increase in *W. britannica* relative abundance up to 20%, followed by another decrease down to 10%. Finally, *W.* aff. *manivitiae* remains poorly represented, with percentages under 5% until an increase in the upper part of the Laeviuscula ammonite zone. Then, percentages generally fluctuate between 5% and 20%, with a maximum around 40% in the Humphriesianum ammonite zone.

Figure 6 represents absolute abundances of *W. colacicchii*, *W. contracta*, *W.* aff. *contracta*, *W. britannica*, and *W.* aff. *manivitiae* and their relative abundances with respect to the coccolith assemblage at Chaudon-Norante. Absolute abundances of *W. colacicchii* and *W. contracta* increase in the Aalenian and Discites ammonite zone up to a maximum between the end of the Discites ammonite zone and the beginning of the Laeviuscula ammonite zone. Then, a slight decrease is observed. The same pattern occurs in *W.* aff. *contracta*, except that the maximum is reached mainly in the Laeviuscula
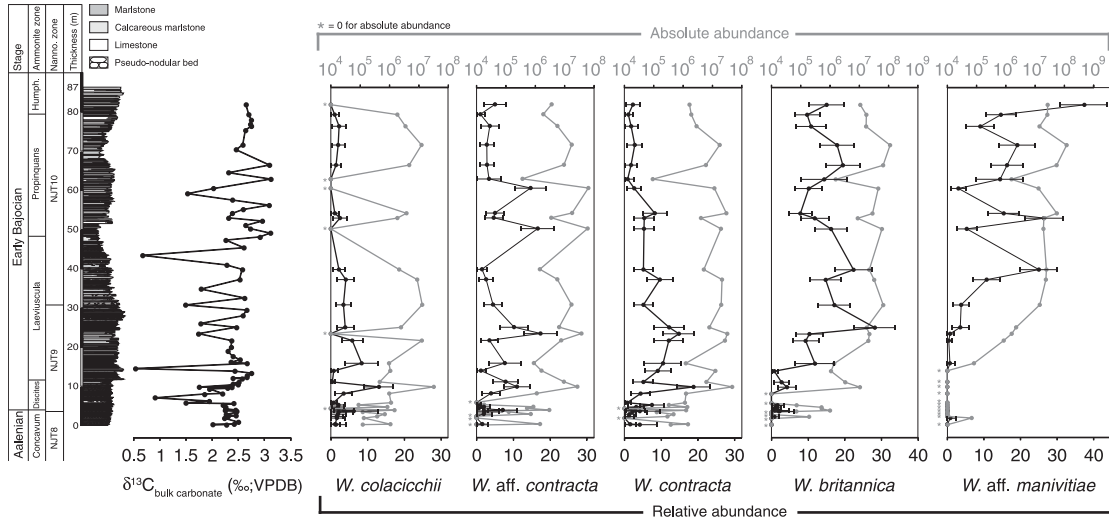
FIGURE 5.   The Cabo Mondego section showing the δ¹³C (Suchéras-Marx et al. 2012) and the *W. colacicchii*, *W. contracta*, *W.* aff. *contracta*, *W. britannica* and *W.* aff. *manivitiae* absolute (gray) and relative (black) abundances in the coccolith assemblage.
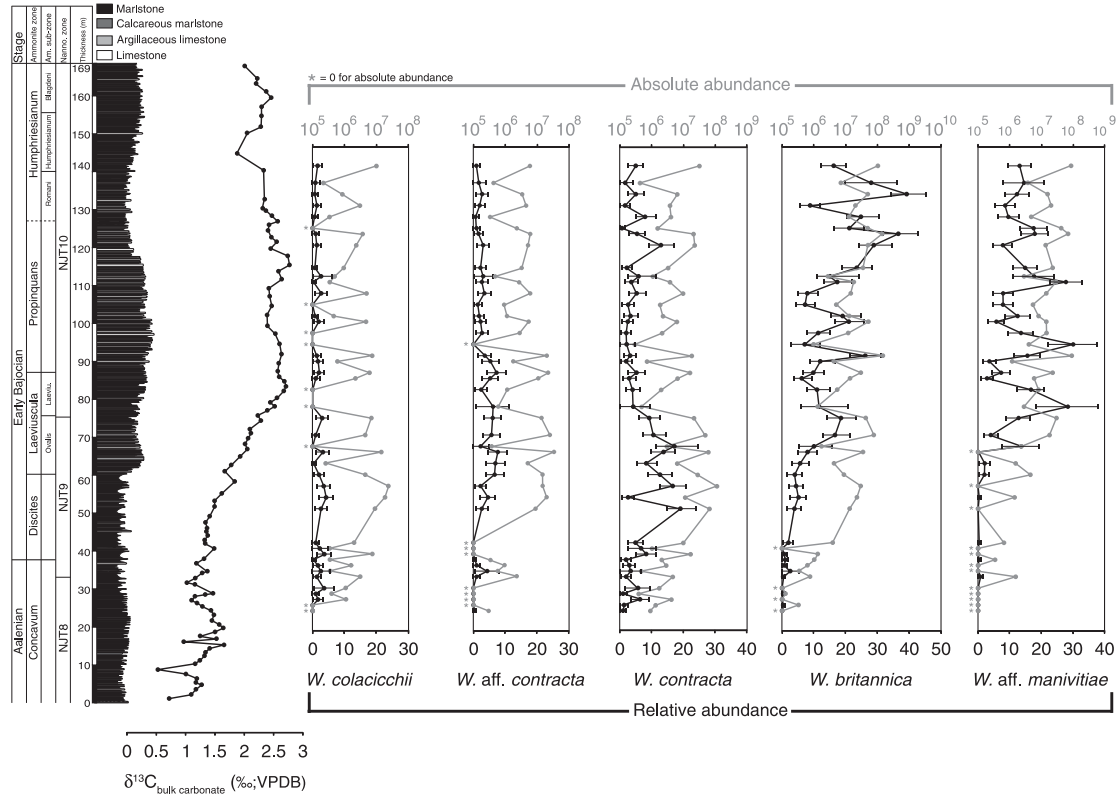
FIGURE 6. The Chaudon-Norante section. Details as in Figure 5.

ammonite zone. Absolute abundances of *W. britannica* and *W.* aff. *manivitiae* increase by steps during the whole interval studied. The first step is reached in the middle part of the Laeviuscula ammonite zone, the second in the lower part of the Propinquans ammonite zone, and the third one around the Propinquans/ Humphriesianum ammonite zones boundary.

W. colacicchii relative abundances are low at Chaudon-Norante, most of the values ranging between 0% and 4% except for a maximum in the Discites ammonite zone up to 8%. *W.* aff. *contracta* is common only in the Laeviuscula ammonite zone where percentages reach 6%. *W. contracta* is abundant mainly in the Discites and the lower part of the Laeviuscula ammonite zones, with relative abundances over 15%. In the rest of the section, values mainly range between 0% and 5%. *W. britannica* is almost absent in the Aalenian and the beginning of the Discites ammonite zone. Then its relative abundance gradually increases to a maximum around 40% in the Humphriesianum ammonite zone. Finally, *W.* aff. *manivitiae* is almost absent until the Laeviuscula ammonite zone; then, its relative abundance is extremely variable from a few percent to 25% but tends to increase until the upper part of the Propinquans ammonite zone, where it gradually decreases to values between 10% and 15%.

Discussion

Given the calcareous nannofossil assemblage turnover described above, we discuss in the following sections the possible oceanographic, environmental, and biological triggers of such changes.

Origin of the Oceanic Eutrophication

The early Bajocian is marked by a positive excursion of $\delta^{13}C_{bulk\ carbonate}$ documented in several localities in Europe, e.g., Italy (Bartolini et al. 1996, 1999), Spain (O'Dogherty et al. 2006), Portugal (Suchéras-Marx et al. 2012) (Fig. 2), and France (Brigaud et al. 2009; Suchéras-Marx et al. 2013) (Fig. 3). This carbon isotope positive excursion, coupled with the radiolarian fossil record, is interpreted as corresponding to a period of eutrophication of the oceans, at least

over the western Tethys (Bartolini et al. 1996, 1999). The origin of this major environmental change event remains unclear and could have been triggered by paleoceanographic or climatic changes discussed in this section.

Oceanic Eutrophication by Paleoceanographic Changes.—The opening of the Ligurian-Piemontese Ocean (Bill et al. 2001) and enhanced rates of opening in the Atlantic Ocean (Labails et al. 2010) are recorded during the latest Aalenian–early Bajocian time interval. Cabo Mondego is located in the Lusitanian Basin adjacent to the Atlantic Ocean, whereas Chaudon-Norante is located in the French Subalpine Basin close to the Liguro-Piemontese Ocean. Hence, the paleoceanographical settings in these sections may have been highly influenced by these tectonically driven changes, leading to a reorganization of the ocean circulation within the Western Tethys, and most particularly to the onset of upwelling zones (O'Dogherty et al. 2006; Leonide et al. 2007). Indeed, the neodymium isotope signal suggests that the tectonic reorganization promoted cold-water upwelling in the tropics during the Aalenian–Bathonian interval (Dera et al. 2015). Nevertheless, this hypothesis does not seem to apply to the early Bajocian interval, the Humphriesianum ammonite zone being marked by an increase in seawater temperature at low latitudes (Dera et al. 2011). The neodymium isotope signal may be linked to an increase in radiogenic fluxes through volcanic activity related to major tectonics changes (Dera et al. 2015). Eutrophication due to paleoceanographic changes during the early Bajocian, though not excluded, is still difficult to demonstrate because the early Bajocian geochemical record is rather scarce, with the few available data not having the same time resolution.

Oceanic Eutrophication by Climate Changes.— The increase in $\delta^{13}C_{bulk\ carbonate}$ resulting from eutrophic conditions may have been triggered by climate changes. On the one hand, during the early Bajocian and more precisely in the Humphriesianum ammonite zone, a climate warming has been inferred from $\delta^{18}O$ records in belemnite and oyster calcite from the Paris Basin (Brigaud et al. 2009; Dera et al. 2011) (Fig. 7). On the other hand, a climate cooling
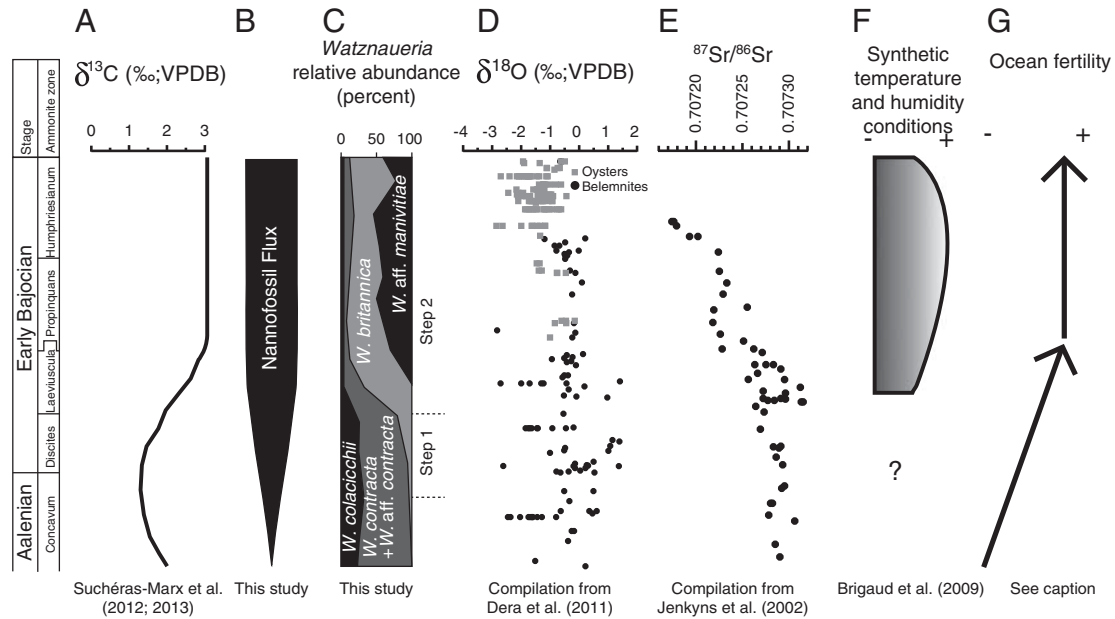
FIGURE 7.   Summary illustration for the latest Aalenian–early Bajocian interval. A, δ^{13}C global trend. B, Nannofossil flux (Suchéras-Marx et al. 2012, 2013). C, *Watznaueria* species relative abundance and integration steps (this study). D, δ^{18}O of belemnites and oysters (Podlaha et al. 1998; Jenkyns et al. 2002; Metodiev and Koleva-Rekalova 2008; Brigaud et al. 2009; Gomez et al. 2009; Price 2010 in Dera et al. 2011). E, ^{87}Sr/^{86}Sr of belemnites from Canada, England, Portugal, and Scotland (Jenkyns et al. 2002). F, Synthetic temperature and humidity conditions (Brigaud et al. 2009). G, Ocean fertility based on δ^{13}C (Bartolini et al. 1996; Brigaud et al. 2009; O'Dogherty et al. 2006; Suchéras-Marx et al. 2012, 2013).

has also been proposed, based on glendonite deposits in Siberia (Price 1999; Rogov and Zakharov 2010) and fossil wood occurrence during the Bajocian. *Xenoxylon* wood is supposed to have developed under mean annual temperatures between 5° and 15°C. Its occurrence at low latitudes and absence at high latitudes may reflect temperatures <5°C at high latitudes (Philippe and Thevenard 1996). Given the concurrence of the low-latitude temperature increase supported by oyster $\delta^{18}O$ and the high-latitude temperature decrease supported by glendonites and *Xenoxylon* wood, these climatic records point to an increased latitudinal temperature gradient during the early Bajocian. Studies on clay minerals show an assemblage of illite-smectite mixed-layer with moderate illite concentrations, reflecting warm and humid conditions in the Mecsek Mountains in Hungary during the early Bajocian (Raucsik et al. 2001; Raucsik and Varga 2008). In the Humphriesianum ammonite zone of the eastern part of the Paris Basin, the association of illite (50%), illite-smectite mixed layers (30%), and kaolinite (20%) reflects humid conditions (Brigaud et al. 2009). The abundance of coal over charcoal in Yorkshire (England) in the lower Bajocian also arguably reflects more humid conditions and less fire-prone (presumably seasonal arid) environments (Hesselbo et al. 2003). The increase of a latitudinal temperature gradient may have enhanced atmospheric circulation and increased humidity at low to middle latitudes (Price et al. 1998), which in turn may have enhanced the oceanic primary production through continental weathering and bio-limiting nutrient transfer (e.g. phosphorus, iron) during the early Bajocian. This hypothesis of climatically driven fertilization of the oceans remains to be confirmed by further isotopic and mineralogical data with better time calibration.

Integration of *Watznaueria* in the Nannoplankton Community

The increase in nannofossil absolute abundances and fluxes during the early Bajocian observed in this study is coeval with the oceanic fertilization and eutrophication event, and marks the onset of the *Watznaueria* dominance in the calcareous nannoplankton community throughout the Mesozoic. Indeed, calcareous nannofossil production and sedimentation are dependent on nutrient concentration (Broerse et al. 2000; Kinkel et al. 2000; Andruleit et al. 2003); with the increase in continental flux of bio-limiting nutrients, calcareous nannoplankton flourished during the early Bajocian. While increasing the nannoplankton productivity, such high-fertility environments triggered changes within the calcareous nannoplankton community organization and interactions. At the Aalenian–Bajocian transition, the *Watznaueria* spp. represented less than 20% of the coccolith assemblage. Then *Watznaueria* spp. seemingly replaced the other species, which all decreased in relative abundances. By the Laeviuscula ammonite zone, *Watznaueria* spp. reached >50% of the coccolith assemblage (Figs. 3, 4). Given the relative abundances in both sections, *Watznaueria* spp. increase is synchronous with a decrease in *Biscutum* spp. + *Similiscutum* spp. and, to a lesser extent, all the other coccolith genera, suggesting that *Watznaueria* spp. replaced these taxa.

At the same time, however, there is also an increase in nannofossil absolute abundance and flux observed during the earliest Bajocian in the two studied sections. This increase in nannofossil absolute abundance is mostly related to the increase in the absolute abundance of *Watznaueria* spp.; it is not accompanied by any decrease in absolute abundance of other nannofossil species. In fact, there is also in the Discites ammonite zone a slight increase in absolute abundance of *Lotharingius* spp., *Discorhabdus* spp., and *Biscutum* spp. + *Similiscutum* spp. (observed only at Cabo Mondego).

Therefore, the combined relative and absolute abundance signals indicate that *Watznaueria* spp. actually integrated into (without ecological displacement/replacement of previous species) rather than invaded (with displacement/replacement of previous species) the early Bajocian nannoplankton community. With this integration, *Watznaueria* spp. started to dominate the coccolith assemblage without replacing any species, and thus possibly without significantly affecting the ecological

organization and functioning of the already present nannoplankton community. At that time, carrying capacity of the nannoplankton community increased with the influx of nutrients, favoring the *Watznaueria* spp. as new actors playing a new ecological role in the community, and ultimately leading to changes of the relative, but *not* absolute, abundances of the already existing species.

The *Watznaueria* integration was achieved through two successive evolutionary steps: first during the late Aalenian up to the end of the Discites ammonite zone, and then during the Laeviuscula ammonite zone up to the Propinquans ammonite zone. During the first step, the striking rise in *Watznaueria* spp. absolute abundance in the Discites ammonite zone is mainly supported by *W. contracta* and *W. colacicchii* (Figs. 5, 6). The increases in absolute abundance of these two species are synchronous and associated with a slight increase in the absolute abundance of other genera, e.g., *Discorhabdus* spp. and *Biscutum* spp. + *Similiscutum* spp. (all belonging to the family Biscutaceae). The second step, corresponding to the end of the increase and the stabilization of *Watznaueria* spp. absolute abundances, is supported mainly by *W. britannica* and *W.* aff. *manivitiae* (Figs. 5, 6).

No increase in the absolute abundance of other nannofossil genera is observed during this step. The integration of *W. contracta* and *W. colacicchii* thus appears as a slightly different event than the integration of *W. britannica* and *W.* aff. *manivitiae*. The former were rare species before the end of the Aalenian, having been present in the nannoplankton community since the Toarcian (Mattioli and Erba 1999; Aguado et al. 2008), whereas the latter are new species that appeared between the end of the Aalenian and the beginning of the Bajocian (Mattioli and Erba 1999). The two-step integration of *Watznaueria* spp. thus possibly resulted from different species adaptations leading to different paleoecological preferences during each step.

Origin of the *Watznaueria* Integration: Changes in Exploitation of Environmental and Ecological Resources

The two-step scenario discussed above calls for at least two possible hypotheses explaining the ecological integration of *Watznaueria* into the early Bajocian nannoplankton community: (1) integration achieved through environmental (physico-chemical parameters) changes, namely increasing ecosystem's carrying capacity (i.e., opening new, previously unfilled ecological spaces), or (2) integration facilitated by ecological change (interaction between organisms and their environment), namely species' niche shifting. These two hypotheses are not mutually exclusive and may have co-occurred. Linking them to the two integration steps defined earlier suggests that step 1 was related to the environmental change hypothesis, whereas step 2 was related to the interplay between environmental and ecological changes hypotheses.

Step 1: Integration via Carrying Capacity Increase.—The hypothesis of integration rather than invasion of *Watznaueria* spp. is related to an increase in the carrying capacity of the ecological niche occupied by the calcareous nannoplankton: the oceanic photic zone. The vertical and lateral organization of the nannoplankton community actually involves a complex fragmentation of this niche (e.g., upper and lower photic zone, from coastal to oceanic domains, from upwelling zones to oceanic gyres, in equatorial to polar latitudes [Winter and Siesser 1994]). Therefore, any modification (by collapse, development, or origination) of the carrying capacity of the calcareous nannoplankton ecological niche is at least potentially related to several more or less independent factors, such as changes in surface-water parameters (e.g., water transparency, temperature or salinity stratification [Ahagon et al. 1993; Solignac et al. 2008]), sea-level change (Roth 1987), biological competition, or nutrient availability.

Some of those factors are very difficult to detect in the geological record (e.g., water transparency); others are still unknown for the early Bajocian (e.g., water-mass stratification), but for the studied time interval, sea-level and nutrient availability changes are documented. Sea-level rise may have participated in the formation of new niches or an increase in niches' carrying capacities (Roth 1987). Indeed, the early Bajocian is marked by a transgression in the southeastern part of the Paris Basin

(Durlet and Thierry 2000), the northern French Subalpine Basin (Ferry and Mangold 1995), and the Betic cordillera (Vera 1988). Also, transgressive deposits are documented in the time interval corresponding to the first two ammonite zones of the Bajocian in Greenland (Surlyk 2003) as well as in England (Hesselbo 2008). Conversely, a regressive pattern is observed in Germany (Deutsche Stratigraphische Kommission 2002). The difference in relative sea-level variation in Western Tethys is related to the regional control exerted by major tectonic changes, which is highlighted by the shift of strontium isotope toward unradiogenic values (Fig. 7) (data compiled by Jenkyns et al. 2002) and was induced by the opening of the Liguro-Piemontese Ocean and Atlantic Ocean, as well as the North Sea bulging. Sea-level rise can increase the size of the photic zone in a shallow proximal environment. A marked deepening of proximal environment could also remove the continental source of limiting nutrients, thus reducing the nannoplankton productivity, which is more important in proximal environment than in pelagic environment (Baumann et al. 2004).

Nevertheless, even if the contribution of sea-level changes to ecological niche modification cannot be ruled out, the most significant environmental change recorded during the early Bajocian may have been the eutrophication event discussed earlier. Indeed, nannofossil assemblages are classically more affected by nutrient availability (e.g., Erba 2004; Lees et al. 2005; Aguado et al. 2008; Giraud et al. 2009), than by sea-level variations. Actually, the receptivity of calcareous nannoplankton to sea-level changes seems to be indirectly related to nutrient availability, given that offshore environments are relatively more oligotrophic and nearshore environments more meso- to eutrophic due to the proximity of bio-limiting elements supplied by continental weathering. For instance, the higher absolute and higher relative abundances of *Schizosphaerella* spp. in the distal ramp setting of Cabo Mondego section, as compared with the hemipelagic setting of Chaudon-Norante, are in agreement with this taxon's affinities for nearshore carbonate environments (Pittet and Mattioli 2002; Mattioli and Pittet 2004).

Hence, we hypothesize that step 1, the integration of *W. contracta* and *W. colacicchii* in the community, was chiefly related to an environmental change, namely the increase in nutrient availability. With such increase, the carrying capacity of the photic zone increased, opening a new ecological space first filled by these two species. Prior to the latest Aalenian, these two species (already present since the Toarcian) were scarce in the nannoplankton assemblages, possibly because they were unable to develop in nutrient-limited environments. Remarkably, these two species show similar morphological characters, being characterized by the presence of a cross spanning the central area of the coccolith. Nevertheless, the biological mechanisms linking a coccolith's morphology to its ecological preferences remain difficult to assess. Incidentally, this hypothesis is compatible with the slight increase in Biscutaceae coccoliths; these are species often associated with eutrophic environments (e.g., Erba 2004; Lees et al. 2005) and their increase testifies to global oceanic eutrophication that mainly favored *Watznaueria* spp. but also other species production.

Step 2: Integration via Innovation in Ecological Niche Exploitation.—The second step, *Watznaueria* spp.'s stabilization in early Bajocian nannoplankton assemblages, is based on a biological innovation leading to an improvement in ecological niche exploitation. This phase is marked by the increase and then stabilization of the nutrient-rich environment based on the $\delta^{13}C$ record. In that context, two new species (*W. britannica* and *W.* aff. *manivitiae*) increased in absolute and relative abundances while *W. contracta* and *W. colacicchii*, at first predominant in these nutrient-rich environments, remained stable in absolute abundance. Given the likely absence of competition between *W. contracta/ W. colacicchii* and *W. britannica/W.* aff. *manivitiae* (the increase in absolute abundance of the latter is not associated with a decrease in absolute abundance of the former), *W. britannica/W.* aff. *manivitiae* likely developed new biological traits allowing exploitation of a still-unoccupied, potentially newly formed ecological niche. This hypothesis is supported by studies that identify *W. britannica* and

W. aff. *manivitiae* as species newly occurring in the early Bajocian (Mattioli and Erba 1999) and developing new ecological capabilities in a nutrient-rich environment. *W. britannica* across the Middle-Late Jurassic in France has already been identified as an opportunistic species highly competitive in nutrient-rich environment (Giraud 2009).

The available temporal resolution is obviously too low to directly observe the seasonal to yearly nannoplankton community dynamics, but the biological innovation characterizing *W. britannica* and *W.* aff. *manivitiae* very likely resides in their blooming ability. Monospecific laminae of coccolith are described in the fossil record as old as the lower Toarcian (Early Jurassic, ca. 183 Ma) in the Paris Basin *Schistes Carton* (Goy 1981). This is the oldest evidence of coccolithophore bloom in the fossil record—although this phenomenon is well known in living assemblages—but the species observed in those layers are murolith and *Calyculus* species with no evolutionary relation to Watznaueriaceae (Bown 1987). In Upper Jurassic sediments, monospecific laminae containing coccospheres of *Watznaueria barnesiae* and *W. britannica* (Gallois and Medd 1979; Medd 1979; Lees et al. 2004) are interpreted as the evidence for blooms occurring under eutrophic conditions (Lees et al. 2004, 2006). This is the earliest unequivocal record for blooms of *Watznaueria* coccolithophores. Similarly, *W. barnesiae* in the Early Cretaceous is interpreted as a blooming species, because seasonal changes led to the proliferation of these opportunistic taxa first, followed by the development of other calcareous nannofossils (Thomsen 1989). *W. britannica* has been interpreted as an opportunistic "r-strategist" blooming in eutrophic conditions, but not *W.* aff. *manivitiae* (Lees et al. 2004, 2006). The latter is actually poorly documented in Jurassic calcareous nannofossil studies. Nevertheless, this species has a morphology very similar to another *Watznaueria* r-strategist blooming in eutrophic conditions during the Early Cretaceous: *W. barnesiae* (Lees et al. 2004, 2006). Likewise, *W. manivitiae/britannica*, a *Watznaueria* morphotype with still unclear taxonomical affinities and sharing morphological features from *W. britannica* and *W.* aff.

manivitiae, is also described as a morphotype inhabiting instable meso-eutrophic environments (Giraud 2009; Giraud et al. 2009), environments often dominated by opportunistic species. Even if a direct relationship between a coccolith's general morphology and its ecological preferences is questionable, we hypothesize that during the early Bajocian, *W.* aff. *manivitiae* may have had an ecology close to *W. barnesiae*. Eventually, *W. britannica* and *W.* aff. *manivitiae* integrated into the nannoplankton community thanks to their adaptation to seasonal blooms in nutrient-rich niches previously unexploited by other species.

Because at this time only *W. britannica* and *W.* aff. *manivitiae* increased in both absolute and relative abundances, other environmental conditions may have favored their growth (or limited growth of other species). The fact that certain species bloomed, but not the others, results from (1) their presence before the blooming conditions became settled, and (2) the coincidence in time between nutrient enrichment and ecological preferences of the blooming species (e.g., temperature, water turbulence, day length; Balch 2004). The general increase in nutrient availability during the early Bajocian resulted in seasonal increase in nutrients, which either allowed calcareous nannoplankton blooms to occur or increased the blooming period. Already existing species, with more restrictive ecological preferences (e.g., temperature, water turbulence, day length; Balch 2004) were not adapted to such conditions, but the opportunistic taxa *W. britannica* and *W.* aff. *manivitiae* were adapted to those conditions and could efficiently develop. If both species show common trends in the early Bajocian, however, only *W. britannica* continued to be abundant afterward. The scarcity of *W.* aff. *manivitiae* in the rest of the Mesozoic suggests that both species did not share exactly the same ecological preferences. *W.* aff. *manivitiae* may have disappeared because by the Bathonian a new species, namely *W. barnesiae*, invaded the oceans, replacing *W.* aff. *manivitiae*. In order to clarify these points, further quantitative studies on the late Bajocian and Bathonian calcareous nannofossils are needed (e.g., Tiraboschi and Erba 2010).

Conclusion

The early Bajocian is characterized by major changes in geology, paleoceanography, climate, and biodiversity. This time interval is notably marked by the diversification of the coccolith genus *Watznaueria*, the most successful Mesozoic coccoliths (Lees et al. 2005; Erba 2006). We evaluated the conditions in which this diversification occurred and its effect on the nannofossil assemblages. Our conclusions are as follows:

- During the latest Aalenian–early Bajocian (171-169 Ma), relative abundance of *Watznaueria* increased over other coccoliths; meanwhile, their absolute abundance also increased without significant concomitant decrease in absolute abundances of other coccoliths. Although estimation of calcareous nannofossil absolute abundance has been possible for more than 20 years (e.g., Beaufort 1991; Geisen et al. 1999), such quantification remains much less common than relative abundance studies. Nevertheless, as our results suggest, it offers interesting outcomes, complementary to relative abundance data, for studying nannoplankton community dynamics;
- The increase in nannofossil absolute abundance and flux is mostly due to the emergence of *Watznaueria* spp.
- The diversification and emergence of *Watznaueria* spp. during the early Bajocian was likely related to a climatically driven eutrophication event.
- *Watznaueria* spp. integrated into rather than invaded the nannoplankton community.
- This integration was achieved in two subsequent steps: step 1, involving *W. contracta* and *W. colacicchii*, likely relates to an increase in the carrying capacity of the ecological niche due to increased nutrient supply; and step 2, involving *W. britannica* and *W.* aff. *manivitiae*, likely relates to a newly acquired blooming capacity in a previously unoccupied ecological niche.

Our results suggest that *Watznaueria* started to dominate the calcareous nannofossil assemblages thanks to peculiar ecological preferences during the early Bajocian critical environmental perturbation. Later on, this genus remained dominant in nannoplankton assemblages until the Upper Cretaceous thanks to an opportunistic mode of life. It finally lost the throne with the K/Pg mass extinction, which completely changed the calcareous nannoplankton community structure (Bown 2005), giving the way to a new calcareous nannofossil dynasty.

Literature Cited

Aguado, R., L. O'Dogherty, and J. Sandoval. 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the Western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Marine Micropaleontology 68: 268–285.

Ahagon, N., Y. Tanaka, and H. Ujiié. 1993. *Florisphaera profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. Marine Micropaleontology 22:255–274.

Andruleit, H., S. Stäger, U. Rogalla, and P. Cepek. 2003. Living coccolithophores in the northern Arabian Sea: ecological tolerances and environmental control. Marine Micropaleontology 49:157–181.

Balch, W. M. 2004. Re-evaluation of the physiological ecology of coccolithophores. Pp. 165–190 *in* H. R. Thierstein and J. R. Young, eds. Coccolithophores: from molecular processes to global impact. Springer, Berlin.

Bartolini, A., and F. Cecca. 1999. 20 My hiatus in the Jurassic of Umbria-Marche Apennines (Italy): carbonate crisis due to eutrophication. Comptes Rendus Académies des Sciences 329:587–595.

Bartolini, A., and R. L. Larson. 2001. Pacific microplate and the Pangea supercontinent in the Early to Middle Jurassic. Geology 29:735–738.

Bartolini, A., P. O. Baumgartner, and J. C. Hunziker. 1996. Middle and Late Jurassic carbon stable-isotope stratigraphy and radiolarite sedimentation of the Umbria-Marche Basin (Central Italy). Eclogae Geologicae Helvetiae 89:811–844.

Bartolini, A., P. O. Baumgartner, and J. Guex. 1999. Middle and Late Jurassic radiolarian palaeoecology versus carbon-isotope stratigraphy. Palaeogeography, Palaeoclimatology, Palaeoecology 145:43–60.

Baumann, K.-H., B. Böckel, and M. Frenz. 2004. Coccolith contribution to South Atlantic carbonate sedimentation. Pp. 367–402 *in* H. R. Thierstein and J. R. Young, eds. Coccolithophores: From molecular processes to global impact. Springer, Berlin.

Beaudouin, C., G. Jouet, J.-P. Suc, S. Berné, and G. Escarguel. 2007a. Vegetation dynamics in southern France during the last 30 ky BP in the light of marine palynology. Quaternary Science Reviews 26:1037–1054.

Beaudouin, C., J.-P. Suc, G. Escarguel, M. Arnaud, and S. Charmasson. 2007b. The significance of pollen signal in present-day marine terrigenous sediments: the example of the Gulf of Lions (western Mediterranean Sea). Geobios 40:159–172.

Beaufort, L. 1991. Adaptation of the random settling method for quantitative studies of calcareous nannofossils. Micropaleontology 37:415–418.

Bernaola, G., and S. Monechi. 2007. Calcareous nannofossil extinction and survivorship across the Cretaceous-Paleogene boundary at Walvis Ridge (ODP Hole 1262C, South Atlantic Ocean). Palaeogeography, Palaeoclimatology, Palaeoecology 255:132–156.

Bill, M., L. O'Dogherty, J. Guex, P. O. Baumgartner, and H. Masson. 2001. Radiolarite ages in Alpine-Mediterranean ophiolites: constraints on the oceanic spreading and the Tethys-Atlantic connection. Geological Society of America Bulletin 113:129–143.

Blakey, R. C. 2008. Gondwana paleogeography from assembly to breakup: a 500 m.y. odyssey. Geological Society of America Special Papers 441:1–28. http://www. http://cpgeosystems.com/170moll.jpg.

Bown, P. R. 1987. Taxonomy, evolution, and biostratigraphy of the late Triassic-early Jurassic calcareous nannofossils (Special Papers in Palaeontology 38 Palaeontological Association, London.

——. 2005. Calcareous nannoplankton evolution: a tale of two oceans. Micropaleontology 51:299–308.

Bown, P. R., and J. R. Young. 1998. Techniques *in* P. R. Bown, ed. Calcareous nannofossil biostratigraphy. Chapman and Hall/Kluwer Academic, Dordrecht.

Brigaud, B., C. Durlet, J.-F. Deconinck, B. Vincent, E. Pucéat, J. Thierry, and A. Trouiller. 2009. Facies and climate/environmental changes recorded on a carbonate ramp: a sedimentological and geochemical approach on Middle Jurassic carbonates (Paris Basin, France). Sedimentary Geology 222:181–206.

Broerse, A. T. C., P. Ziveri, J. E. van Hinte, and S. Honjo. 2000. Coccolithophore export production, species composition, and coccolith-CaCO3 fluxes in the NE Atlantic (34°N 21°W and 48°N 21°W). Deep-Sea Research Part II: Topical Studies in Oceanography 47:1877–1905.

Canales, M. L., and M. H. Henriques. 2008. Foraminifera from the Aalenian and the Bajocian GSSP (Middle Jurassic) of Murtinheira section (Cabo Mondego, West Portugal): biostratigraphy and paleoenvironmental implications. Marine Micropaleontology 67:155–179.

——. 2013. Foraminiferal assemblages from the Bajocian Global Stratotype Section and Point (GSSP) at Cape Mondego (Portugal). Journal of foraminiferal Research 43:182–206.

Cobianchi, M., E. Erba, and C. Pirini-Radrizzani. 1992. Evolutionary trends of calcareous nannofossil genera *Lotharingius* and *Watznaueria* during the Early and Middle Jurassic. Memorie di Scienze Geologiche, Padova 43:19–25.

Dera, G., B. Brigaud, F. Monna, R. Laffont, E. Puceat, J.-F. Deconinck, P. Pellenard, M. M. Joachimski, and C. Durlet. 2011. Climatic ups and downs in a disturbed Jurassic world. Geology 39:215–218.

Dera, G., J. Priunier, P. L. Smith, J. W. Haggart, E. Popov, A. Guzhov, M. A. Rogov, D. Delsate, D. Thies, G. Cuny, E. Pucéat, G. Charbonnier, and G. Bayon. 2015. Nd isotope constraints on ocean circulation, paleoclimate, and continental drainage during the Jurassic breakup of Pangea. Gondwana Research. http://dx.doi.org/10.1016/j.gr.2014.02.006.

Deutsche Stratigraphische Kommission. 2002. Stratigraphische Tabelle von Deutschland.

Durlet, C., and J. Thierry. 2000. Modalités séquentielles de la transgression aaléno-bajocienne sur le sud-est du Bassin parisien. Bulletin de la Société Géologique de France 171:327–339.

Erba, E. 1990. Calcareous nannofossil biostratigraphy of some Bajocian sections from the Digne area (SE France). Memorie Descrittive Della Carta Geologica d'Italia XL: 237–256.

——. 2004. Calcareous nannofossils and Mesozoic oceanic anoxic events. Marine Micropaleontology 52:85–106.

——. 2006. The first 150 million years history of calcareous nannoplankton: biosphere-geosphere interactions. Palaeogeography, Palaeoclimatology, Palaeoecology 232:237–250.

Fernandez-Lopez, S., M. H. Henriques, R. Mouterde, R. B. Rocha, and D. Sadki. 1988. Le Bajocien inférieur du Cap Mondego (Portugal) - Essai de biozonation. Pp. 301–313 *in* R. B. Rocha and A. F. Soares, eds. Second international symposium on Jurassic stratigraphy. Instituto Nacional de Investigação Cientifica, Lisbon.

Fernandez-Lopez, S., G. Pavia, E. Erba, M. Guiomar, M. H. Henriques, R. Lanza, C. Mangold, N. Morton, D. Olivero, and D. Tiraboschi. 2009. The Global Boundary Stratotype Section and Point (GSSP) for base of the Bathonian Stage (Middle Jurassic), Ravin du Bès Section, SE France. Episodes 32:222–248.

Ferry, S., and C. Mangold. 1995. Faciès de dépôt et stratigraphie séquentielle des calcaires bajociens du Jura méridional. Documents des Laboratoires de Géologie de Lyon 133:1–96.

Gallois, R. W., and A. W. Medd. 1979. Coccolith-rich marker bands in the English Kimmeridge Clay. Geological Magazine 116: 247–260.

Geisen, M., J. Bollmann, J. O. Herrle, J. Mutterlose, and J. R. Young. 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45:437–442.

Gidon, M., and J. L. Pairis. 1992. The influence of the Digne thrust emplacement upon the autochthonous structures of Bes Valley, Alpes-de-Haute-Provence, France. Eclogae Geologicae Helvetiae 85:327–359.

Giraud, F. 2009. Calcareous nannofossil productivity and carbonate production across the Middle-Late Jurassic transition in the French Subalpine Basin. Geobios 42:699–714.

Giraud, F., B. Courtinat, and F. Atrops. 2009. Spatial distribution patterns of calcareous nannofossils across the Callovian-Oxfordian transition in the French Subalpine Basin. Marine Micropaleontology 72:129–145.

Gomez, J. J., M. L. Canales, S. Ureta, and A. Goy. 2009. Palaeoclimatic and biotic changes during the Aalenian (Middle Jurassic) at the southern Laurasian Seaway (Basque–Cantabrian Basin, northern Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 275:14–27.

Goy, G. 1981. Nannofossiles calcaires des Schistes Carton (Toarcien inférieur) du Bassin de Paris ((Documents de la RCP 459, No. 1: Nature et génèse des faciès confinés). CNRS, Paris.

Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg. 2012. The geologic time scale 2012. Elsevier, Amsterdam.

Henriques, M. H., S. Gardin, C. R. Gomes, A. F. Soares, R. B. Rocha, J. F. Marques, M. R. Lapa, and J. D. Montenegro. 1994. The Aalenian-Bajocian boundary at Cabo Mondego (Portugal). Pp. 63–77 in S. Cresta and G. Pavia, eds. Third international meeting on Aalenian and Bajocian stratigraphy. Miscellanea Servizio Geologico Nazionale, Marrakesh.

Hesselbo, S. P. 2008. Sequence stratigraphy and inferred relative sea-level change from the onshore British Jurassic. Proceedings of the Geologists' Association 119:19–34.

Hesselbo, S. P., H. S. Morgans-Bell, J. C. McElwain, P. M. Rees, S. A. Robinson, and C. E. Ross. 2003. Carbon-cycle perturbation in the middle Jurassic and accompanying changes in the terrestrial paleoenvironment. Journal of Geology 111:259–276.

Jenkyns, H. C., C. E. Jones, D. R. Gröcke, S. P. Hesselbo, and P. N. Parkinson. 2002. Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. Journal of the Geological Society, London 159:351–378.

Kinkel, H., K.-H. Baumann, and M. Cepek. 2000. Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability. Marine Micropaleontology 39:87–112.

Labails, C., J.-L. Olivet, D. Aslanian, and W. R. Roest. 2010. An alternative early opening scenario for the Central Atlantic Ocean. Earth and Planetary Science Letters 297:355–368.

Lees, J. A., P. R. Bown, and E. Mattioli. 2005. Problems with proxies? Cautionary tales of calcareous nannofossil paleoenvironmental indicators. Micropaleontology 51:333–343.

Lees, J. A., P. R. Bown, J. R. Young, and J. B. Riding. 2004. Evidence for annual records of phytoplankton productivity in the Kimmeridge Clay Formation coccolith stone bands (Upper Jurassic, Dorset, UK). Marine Micropaleontology 52:29–49.

Lees, J. A., P. R. Bown, and J. R. Young. 2006. Photic zone palaeoenvironments of the Kimmeridge Clay Formation (Upper Jurassic, UK) suggested by calcareous nannoplankton palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 235:110–134.

Lemoine, M. 1973. About gravity gliding tectonics in the western Alps. Pp. 201–216 in K. A. De Jong and R. Scholten, eds. Gravity and tectonics. Wiley, New York.

Léonide, P., M. Floquet, and L. Villier. 2007. Interaction of tectonics, eustasy, climate and carbonate production on the sedimentary evolution of an early/middle Jurassic extensional basin (Southern Provence Sub-basin, SE France). Basin Research 19:125–152.

Mattioli, E. 1996. New calcareous nannofossil species from the Early Jurassic of Tethys. Rivista Italiana di Paleontologia e Stratigrafia 102:397–412.

Mattioli, E., and E. Erba. 1999. Synthesis of calcareous nannofossil events in Tethyan Lower and Middle Jurassic successions. Rivista Italiana di Paleontologia e Stratigrafia 105:343–376.

Mattioli, E., and B. Pittet. 2004. Spatial and temporal distribution of calcareous nannofossils along a proximal-distal transect in the Umbria-Marche Basin (Lower Jurassic; Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 205:295–316.

Medd, A.W. 1979. The Upper Jurassic coccoliths from the Haddenham and Gamlingay boreholes (Cambridgeshire, England). Eclogae Geologica Helvetica 72:19–109.

Metodiev, L., and E. Koleva-Rekalova. 2008. Stable isotope records ($\delta^{18}O$ and $\delta^{13}C$) of Lower-Middle Jurassic belemnites from the Western Balkan mountains (Bulgaria): palaeoenvironmental application. Applied Geochemistry 23:2845–2856.

Nakanishi, M., K. Tamaki, and K. Kobayashi. 1992. A new Mesozoic isochron chart of the northwestern Pacific Ocean: paleomagnetic and tectonic implications. Geophysical Research Letters 19:693–696.

O'Dogherty, L., J. Sandoval, A. Bartolini, S. Bruchez, M. Bill, and J. Guex. 2006. Carbon-isotope stratigraphy and ammonite faunal turnover for the Middle Jurassic in the Southern Iberian palaeomargin. Palaeogeography, Palaeoclimatology, Palaeoecology 239:311–333.

Pankhurst, R. J., T. R. Riley, C. M. Fanning, and S. P. Kelley. 2000. Episodic silicic volcanism in Patagonia and the Antarctic Peninsula: chronology of magmatism associated with the break-up of Gondwana. Journal of Petrology 41:605–625.

Pavia, G. 1973. Ammoniti del Baiociano superiore di Digne (Francia SE, Dip. Basses-Alpes). Bollettino della Societa Paleontologica Italiana 19:75–142.

——. 1983. Ammoniti e biostratigrafia del Baiociano inferiore di Digne (Francia SE, Dip. Alpes-Haute-Provence). Monografie Museo Regionale di Scienze Naturali, Torino.

Pavia, G., and R. Enay. 1997. Definition of the Aalenian-Bajocian Stage boundary. Episodes 20(1): 16–22.

Philippe, M., and F. Thevenard. 1996. Distribution and palaeoecology of the Mesozoic wood genus Xenoxylon: palaeoclimatological implications for the Jurassic of Western Europe. Review of Palaeobotany and Palynology 91:353–370.

Pittet, B., and E. Mattioli. 2002. The carbonate signal and calcareous nannofossil distribution (Balingen-Tieringen section, Late Oxfordian, south Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 179:73–98.

Podlaha, O. G., J. Mutterlose, and J. Veizer. 1998. Preservation of $\delta^{18}O$ and $\delta^{13}C$ in belemnite rostra from the Jurassic/Early Cretaceous successions. American Journal of Science 298:324–347.

Price, G. D. 1999. The evidence and implications of polar ice during the Mesozoic. Earth-Science Reviews 48:183–210.

——. 2010. Carbon-isotope stratigraphy and temperature change during the Early Middle Jurassic (Toarcian-Aalenian), Raasay, Scotland, UK. Palaeogeography, Palaeoclimatology, Palaeoecology 285:255–263.

Price, G. D., P. J. Valdes, and B. W. Sellwood. 1998. A comparison of GCM simulated Cretaceous 'greenhouse' and 'icehouse' climates: implications for the sedimentary record. Palaeogeography, Palaeoclimatology, Palaeoecology 142:123–138.

Raucsik, B., and A. Varga. 2008. Climato-environmental controls on clay mineralogy of the Hettangian-Bajocian successions of the Mecsek Mountains, Hungary: an evidence for extreme continental weathering during the early Toarcian oceanic anoxic event. Palaeogeography, Palaeoclimatology, Palaeoecology 265:1–13.

Raucsik, B., A. Demény, I. Borbély Kiss, and G. Szabó. 2001. Monsoon-like climate during the Bajocian. Clay mineralogical and geochemical study on a limestone/marl alternation (Komló Calcareous Marl Formation, Mecsek Mountains, Southern Hungary). Hantkeniana 3:149–176.

Rogov, M. A., and V. A. Zakharov. 2010. Jurassic and Lower Cretaceous glendonites occurrences and their implication for Arctic paleoclimatic reconstructions and stratigraphy. Earth Science Frontiers 17(Special Issue): 345–347.

Roth, P. H. 1987. Mesozoic calcareous nannofossil evolution: relation to paleoceanographic events. Paleoceanography 2:601–611.

Ruget-Perrot, C. 1961. Etudes stratigraphiques sur le Dogger et le Malm inférieur du Portugal au Nord du Tage. Memoria Serviços Geologicos de Portugal 7:1–197.

Solignac, S., A. de Vernal, and J. Giraudeau. 2008. Comparison of coccolith and dinocyst assemblages in the northern North Atlantic: how well do they relate with surface hydrography? Marine Micropaleontology 68:115–135.

Suchéras-Marx, B., A. Guihou, F. Giraud, C. Lécuyer, P. Allemand, B. Pittet, and E. Mattioli. 2012. Impact of the Middle Jurassic diversification of Watznaueria (coccolith-bearing algae) on the carbon cycle and $\delta^{13}C$ of bulk marine carbonates. Global and Planetary Change 86-87:92–100.

Suchéras-Marx, B., F. Giraud, V. Fernandez, B. Pittet, C. Lécuyer, D. Olivero, and E. Mattioli. 2013. Duration of the early Bajocian and the associated $\delta^{13}C$ positive excursion based on cyclostratigraphy. Journal of the Geological Society, London 170:107–118.

Surlyk, F. 2003. The Jurassic of East Greenland: a sedimentary record of thermal subsidence, onset and culmination of rifting. Geological Survey of Denmark and Greenland Bulletin 1: 659–722.

Thomsen, E. 1989. Seasonal variation in boreal Early Cretaceous calcareous nannofossils. Marine Micropaleontology 15:123–152.

Tiraboschi, D., and E. Erba. 2010. Calcareous nannofossil biostratigraphy (Upper Bajocian-Lower Bathonian) of the Ravin du Bès section (Bas Auran, Subalpine Basin, SE France): Evolutionary trends of *Watznaueria barnesiae* and new findings of "*Rucinolithus*" morphotypes. Geobios 43:59–76.

Vera, J. A. 1988. Evolución de los sistemas de déposito en el margen ibérico de la cordillera Betica. Revista de la Sociedad Geológica de España 1:373–391.

Winter, A., and W. G. Siesser. 1994. Coccolithophores. Cambridge University Press, Cambridge.

Yin, J., S. Pei, J. Gou, and G. Jiang. 1998. The Middle Jurassic bivalve fauna in the volcanic rock series (Yaiba Formation) of the Lhasa Massif and its paleogeographic significance. Regional Geology of China 17:132–136.