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Paleoenvironmental and paleobiological origins of coccolithophorid genus *Watznaueria* emergence during the Late Aalenian-Early Bajocian

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Abstract.—The latest Aalenian-Early Bajocian time interval (*ca.* 171-169 Ma) is marked by a global re-organization 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 $\delta^{13}\text{C}$ 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 impact on the coccolith assemblages through quantification of the absolute and relative abundances of calcareous nannofossils in two Middle Jurassic key-sections: Cabo Modego (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 the calcareous nannoplankton community in two successive evolutionary steps involving: first *W. contracta* and *W. colaccicchii*, and second *W. britannica* and *W. aff. manivittiae*. 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 hegemony of *Watznaueria* over the calcareous nannoplankton community.

Introduction

The Aalenian-Bajocian (Middle Jurassic, \sim 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 towards 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 $\delta^{13}\text{C}$ 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, produced by injection of volcanic ^{12}C in the atmospheric carbon reservoir, is also observed on $\delta^{13}\text{C}$ coal deposits of Yorkshire and may be at the origin of an increase in $p\text{CO}_2$ observed during the negative excursion based on leaf stomatal density (Hesselbo et al. 2003). Following the Aalenian-Bajocian negative excursion, a $\delta^{13}\text{C}$ 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 on terrestrial material. It has been proposed that the $\delta^{13}\text{C}$ positive excursion of the Early Bajocian is linked to increase in oceanic primary productivity due to eutrophication by nutrient input (Bartolini et al. 1996; Bartolini and Cecca 1999).

In the same time interval, different paleontological changes are observed. The most striking change is a major turnover in ammonite fauna, where the latest Aalenian-Early Bajocian ammonites, at the origin 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 towards diversification, related to the increase in primary production during the $\delta^{13}\text{C}$ 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 have dominated the pelagic realm during ~70 Ma, from the Middle Jurassic until the end of the Early Cretaceous, and have 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 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 present absolute and relative abundance quantification of calcareous nannofossils in the latest Aalenian-Early Bajocian time interval in order to estimate the impact of *Watznaueria* diversification on the calcareous nannofossil assemblages and its relation with the $\delta^{13}\text{C}$ 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 (Rugé-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. 2–5) follow Mattioli and Erba (1999), using the *W. britannica* occurrence for NTJ9 and *W. manivittiae* 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 is partly in agreement with Henriques et al. (1994), the mean difference lasting 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) and 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).

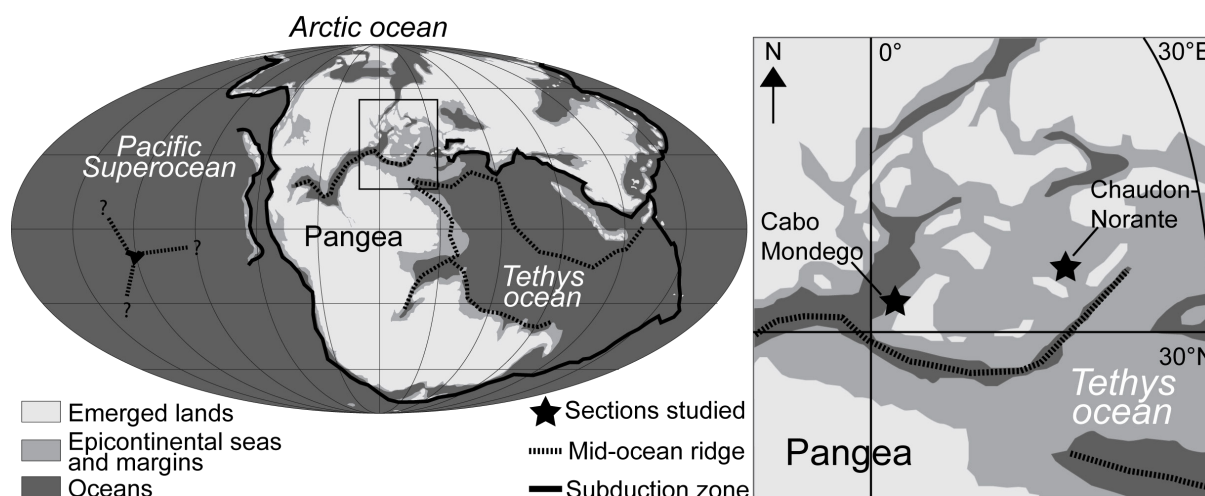


Figure 1: Paleogeographic distribution of oceans and lands during the Middle Jurassic (after Blakey 2008). On the left, a global view with subduction zones and mid-ocean ridges; and on the right, focus on the western Tethys with the localization of the Cabo Mondego, Lusitanian Basin and Chaudon-Norante, French Subalpine Basin.

Chaudon-Norante

The Chaudon-Norante section, located in the Ravin de Coueste (Digne tectonic Nappe, Southern Alps), emplaced during the Mio-Pliocene (Lemoine 1973; Gidon and Pairis 1992), 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; Pavia 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 spans 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, whilst the Humphriesianum ammonite Zone displays regular marlstone-limestone alternations (Suchéras-Marx et al. 2013).

Material and methods

Nannofossils (both coccoliths and the nannolith *Schizosphaerella*) have been quantified in 41 samples from Cabo Mondego (collected on 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 was made using the random-settling method proposed by Beaufort (1991) and calibrated by Geisen et al. (1999), consisting in 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 dried, they have been glued to a microscope slide using eukitt[®]. Usually 300 nannofossils were counted using a Zeiss optical microscope with a $\times 1000$ 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 have been excluded from the relative abundance dataset. The preservation of coccoliths has been 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.

Based on the counting, absolute abundance has been calculated in each sample and represents the number of specimens per gram of rock (Geisen et al. 1999); relative abundance of the nannolith *Schizosphaerella* has been calculated considering the whole nannofossil assemblage, while relative abundances of coccolith species (including *Watznaueria* species) have been calculated considering only the coccolith assemblage. Confidence limits of the sample relative abundances were derived from their underlying binomial distributions using the algorithm used by Beaudoin et al. (2007a, 2007b). Given a type I error rate $\alpha = 0.05$, these limits define the 95% confidence intervals associated to each sample relative abundances, that is, the range of percentage values within which there is $1 - \alpha = 95\%$ of chance to find the unknown true (parametric) percentage. Eventually, nannofossil fluxes in number of nannofossil per m² per year have been calculated using ammonite zones duration based on Suchéras-Marx et al. (2013), or on 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 10 samples (and $> 90\%$ of all identified nannofossils when considered together) are presented in the results.

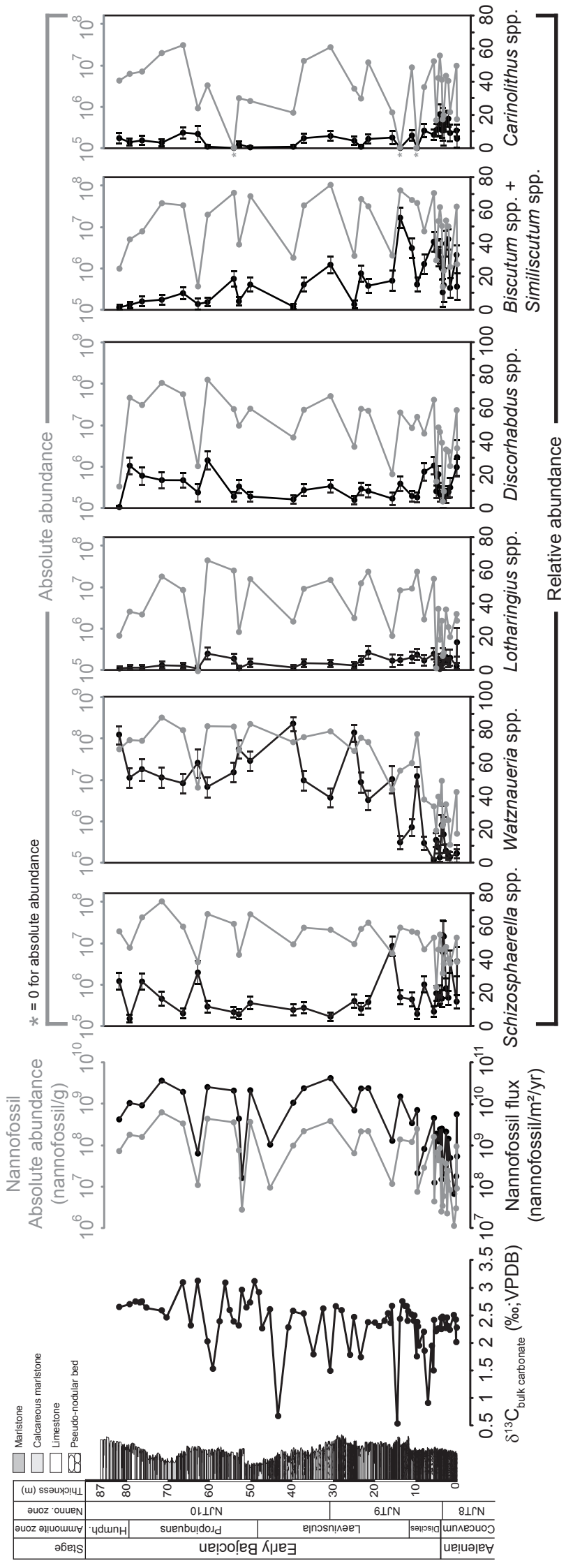


Figure 2: Cabo Mondego section with the $\delta^{13}\text{C}$ (Suchéras-Marx et al. 2012), nannofossil absolute abundance (grey) and nannofossil flux (black) based on time estimation of Early Bajocian ammonite zones (Suchéras-Marx et al. 2013). *Schizosphaerella* spp. absolute (grey) and relative (black) abundances in the nannofossil assemblage; *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp. and *Carinolithus* spp. absolute (grey) 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.

Results

At Cabo Mondego, 50 nannofossil species have been identified (partly presented in Plate 1). 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, 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, with poor as well as moderate preservation samples found all along the section. At Chaudon-Norante, preservation in limestones is poor to moderate (but mostly moderate); in marlstones it is moderate to moderate-good. There is also no stratigraphic pattern in preservation, except marlstone-limestone alternations. Overall, there is a very similar nannofossil preservation state at Cabo Mondego and Chaudon-Norante, thus allowing a direct comparison between the two sections.

Nannofossil Absolute Abundances and Fluxes

In Figure 2, 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 nannofossil/g. The nannofossil absolute abundance gradually increases from the Discites ammonite Zone up to a maximum of $\sim 10^9$ nannofossil/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 nannofossil/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 nannofossil/m²/year and the highest values exceeding 10^{11} nannofossil/m²/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 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

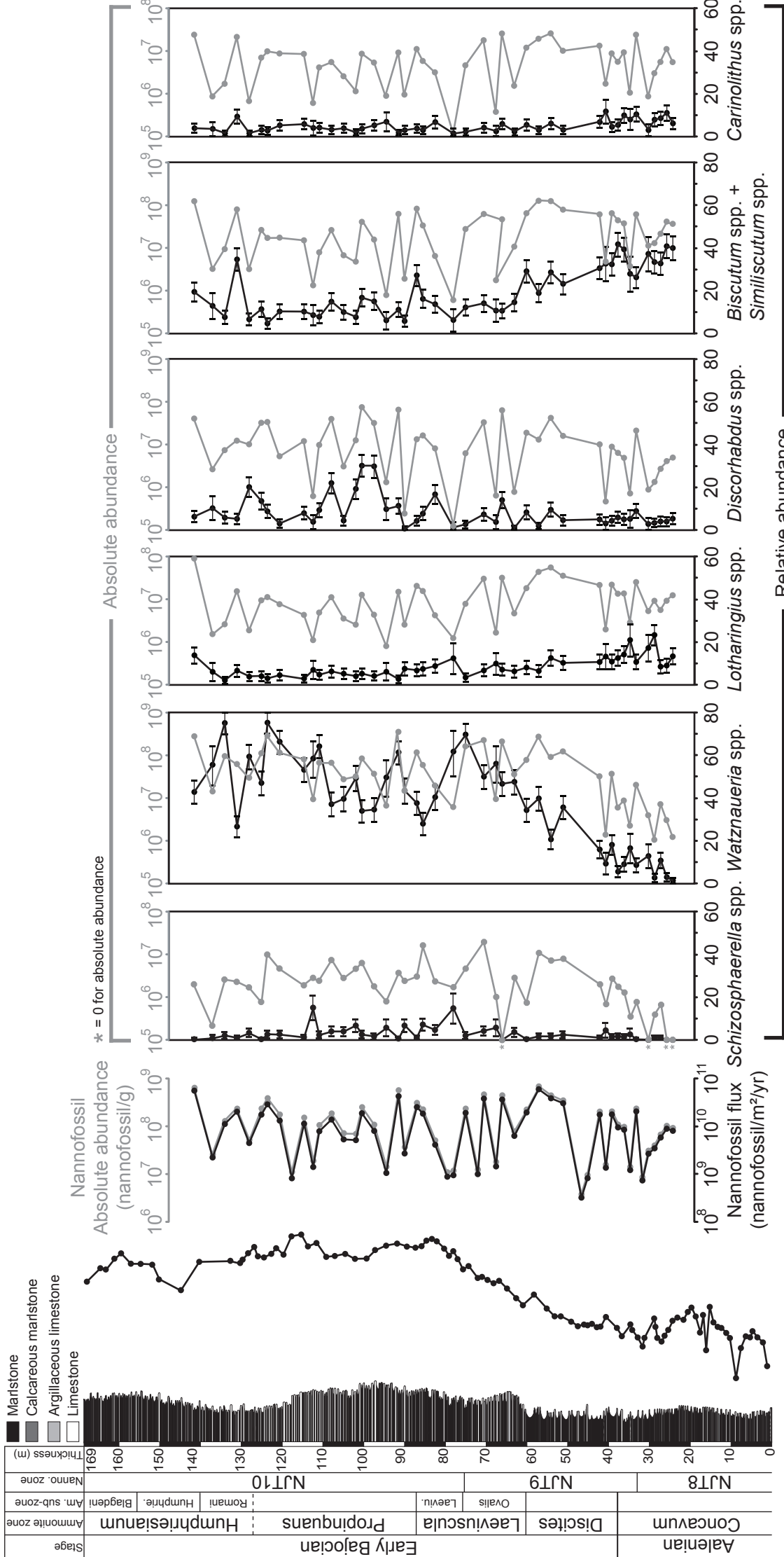


Figure 3: Chaudon-Norante section with the $\delta^{13}\text{C}$ (Suchéras-Marx et al. 2013), Nannofossil absolute abundance (grey) and nannofossil flux (black) based on time estimation of Early Bajocian ammonite zones (Suchéras-Marx et al. 2013). *Schizosphaerella* spp. absolute (grey) and relative (black) abundances in the nannofossil assemblage; *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp. and *Carinolithus* spp. absolute (grey) and relative (black) abundances in the coccolith assemblage. Ammonite biostratigraphy is based on Pavia (1983) and nannofossil biostratigraphy derived from this study.

fluctuate between 8×10^7 and 10^9 nannofossil/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. 3) increased 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 than 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 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

At Cabo Mondego, relative abundance of *Schizosphaerella* spp. over the whole nannofossil assemblage is reported in Figure 2, as well as relative abundances of *Watznaueria* spp., *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. over the coccolith assemblage. *Schizosphaerella* spp. relative abundance decreased from Aalenian to Lower Bajocian except one sample at the base of the Laeviuscula ammonite Zone and three samples at the top of the section. *Watznaueria* spp. relative abundance gradually increased from the base of the section until the upper part of the Laeviuscula ammonite Zone, with maximum values around 80%. Then it decreased and stabilized between 50% and 60%. The percentages of *Lotharingius* spp., *Discorhabdus* spp., *Biscutum* spp. + *Similiscutum* spp., and *Carinolithus* spp. decreased, 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, the relative abundance of *Schizosphaerella* spp. remains relatively low except 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. Contrarily to Cabo Mondego, the relative abundance of *Schizosphaerella* spp. has higher values in the upper part of the Laeviuscula ammonite Zone and 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.

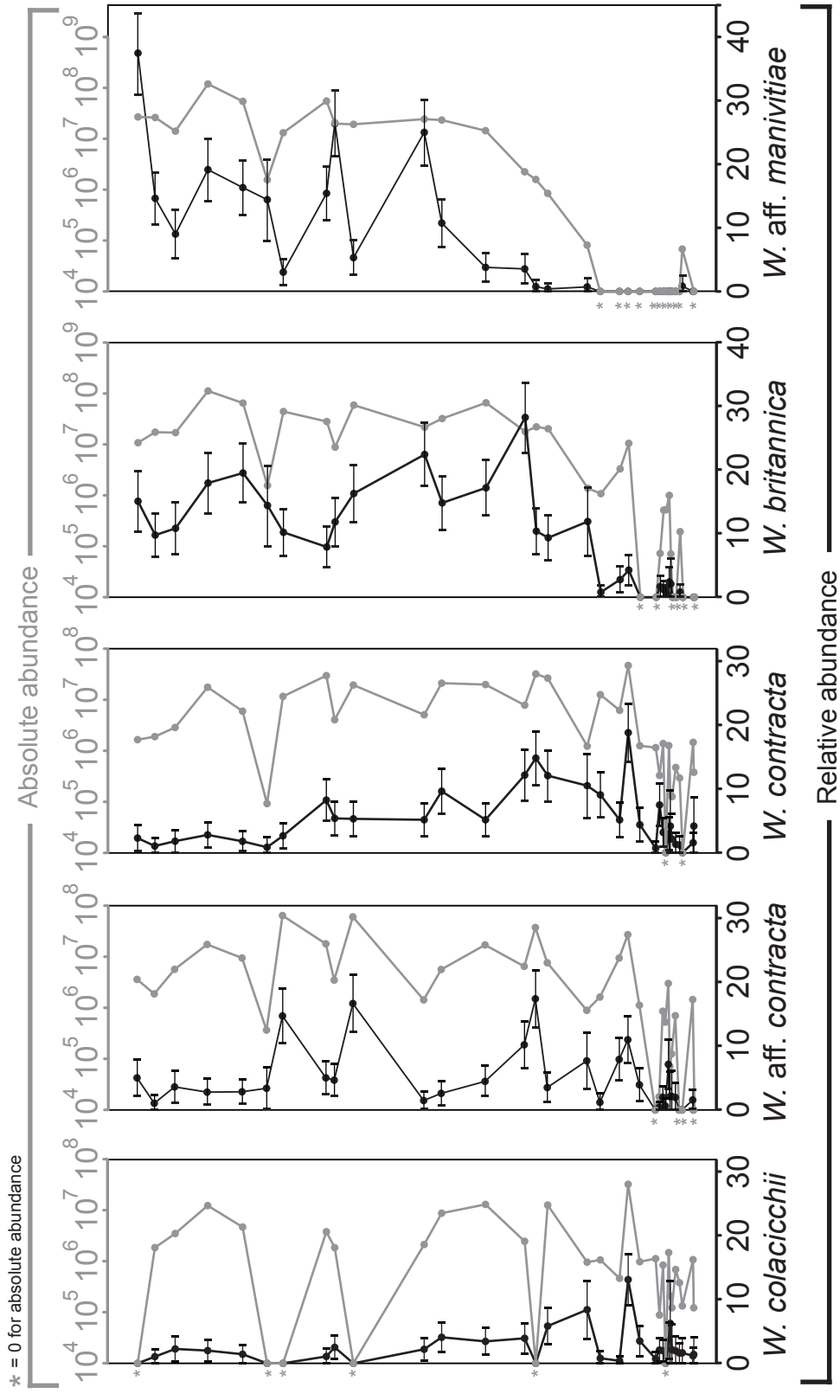
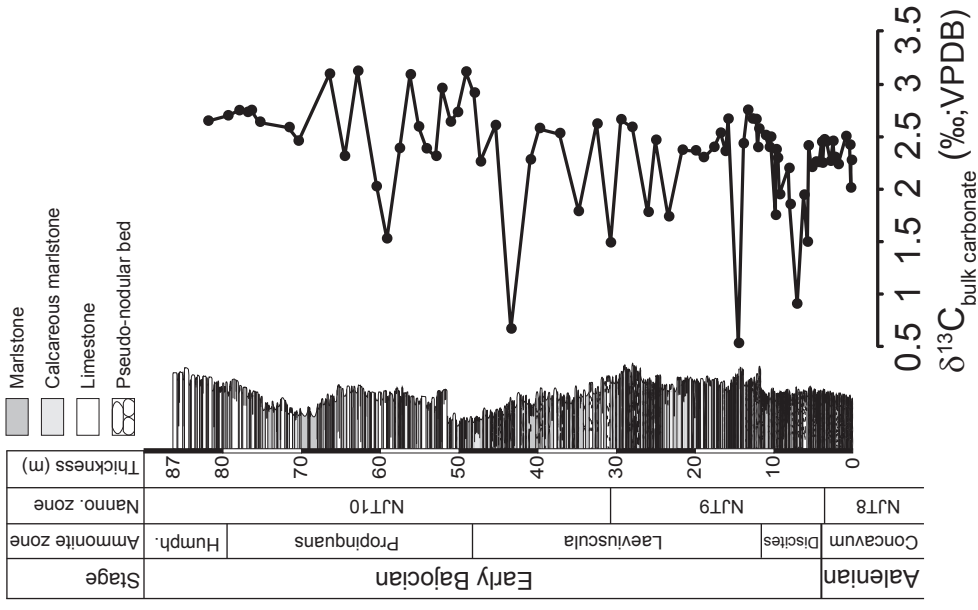


Figure 4: Cabo Mondego section with the $\delta^{13}\text{C}$ (Suchéras-Marx et al. 2012), *W. colacicchii*, *W. contracta*, *W. aff. contracta*, *W. britannica* and *W. aff. manivittiae* absolute (grey) and relative (black) abundances in the coccolith assemblage.

Absolute and Relative Abundance of Most Abundant *Watznaueria* Species

In Figure 4, absolute and relative abundances of *W. colacicchii*, *W. contracta*, *W. aff. contracta*, *W. britannica*, and *W. aff. manivittiae* over the coccolith assemblage are presented for 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 the highest values reached in the Laeviuscula ammonite Zone. For this three species, there is a slight decrease towards the top of the section but never as low as in the Aalenian. Absolute abundances of *W. britannica* and *W. aff. manivittiae* 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 percents. *W. contracta* and *W. aff. contracta* have their maximum percentages in the same interval as *W. colacicchii* then gradually decrease except two spikes for *W. aff. contracta* around 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 comprised between 0% and 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%. Eventually, *W. aff. manivittiae* remains poorly represented, with percentages under 5% until an increase in the upper part of the Laeviuscula ammonite Zone. Then, percentages fluctuate between 5% and 20% with a maximum around 40% in the Humphriesianum ammonite Zone.

Figure 5 represents absolute and relative abundances of *W. colacicchii*, *W. contracta*, *W. aff. contracta*, *W. britannica*, and *W. aff. manivittiae* over 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 is observed for *W. aff. contracta* except the maximum, reached mostly in the Laeviuscula ammonite Zone. Absolute abundances of *W. britannica* and *W. aff. manivittiae* 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 a maximum in the Discites ammonite Zone up to 8%. *W. aff. contracta* is only common in the Laeviuscula ammonite Zone with percentages up to 6%. *W. contracta* is mainly abundant 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. manivittiae* is

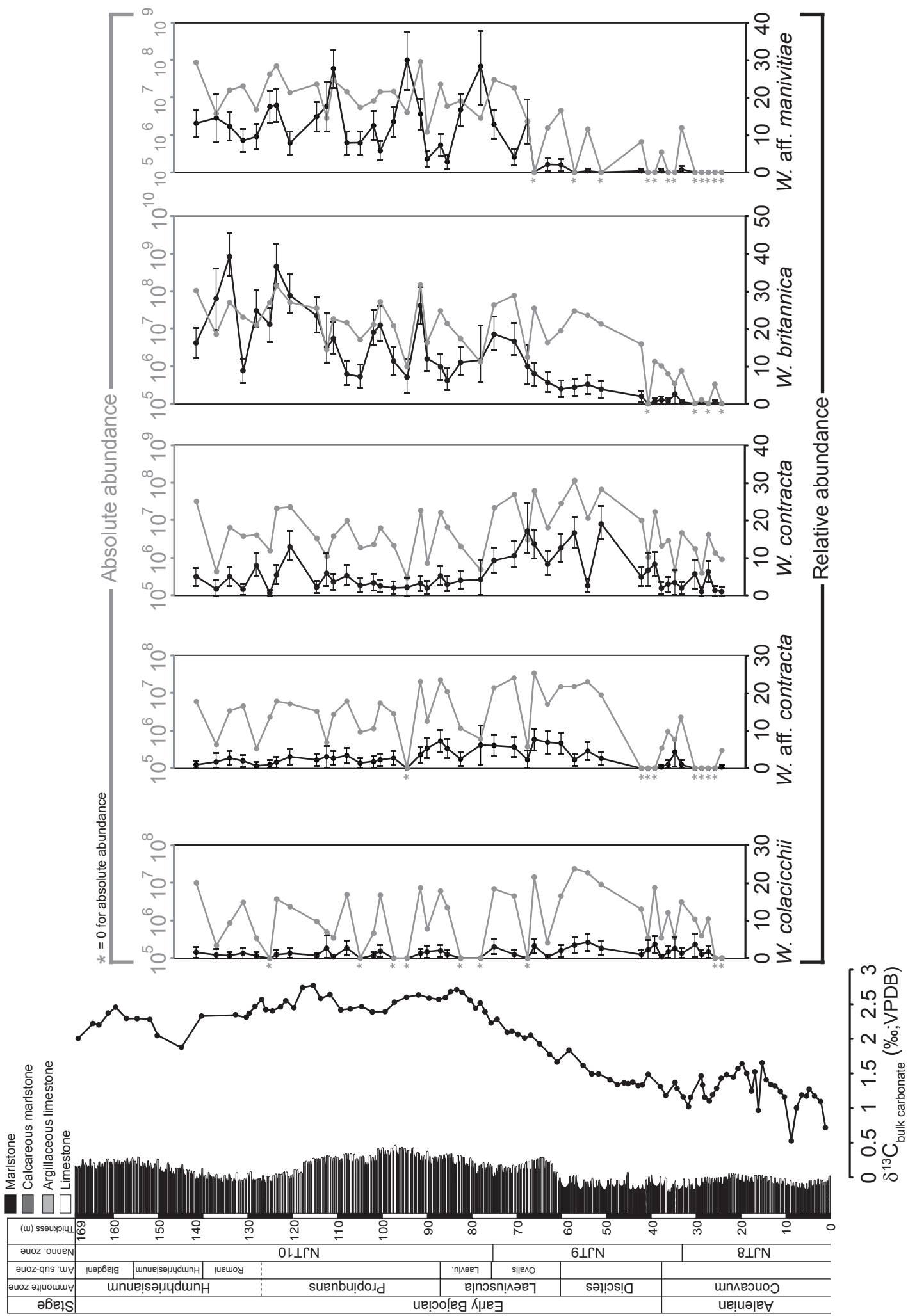


Figure 5: Chaudon-Norante section with the $\delta^{13}\text{C}$ (Suchéras-Marx et al. 2013), *W. colacicchii*, *W. contracta*, *W. aff. contracta*, *W. britannica* and *W. aff. manivittiae* absolute (grey) and relative (black) abundances in the coccolith assemblage.

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 $\delta^{13}\text{C}_{\text{bulk carbonate}}$ documented in several localities in Europe (Italy, Bartolini et al. 1996, 1999; Spain, O'Dogherty et al. 2006; Portugal, Suchéras-Marx et al. 2012, Fig. 2; 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, while 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 re-organization 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, based on the neodymium isotope signal, there is a possibility that the tectonic re-organization promoted cold-water upwelling in the tropics during the Aalenian-Bathonian interval (Dera et al. 2014). 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. 2014). An eutrophication by paleoceanographic changes during the Early Bajocian, 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 $\delta^{13}\text{C}_{\text{bulk carbonate}}$, 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 based on $\delta^{18}\text{O}$ records in belemnite and oyster calcite from the Paris Basin (Brigaud et al. 2009; Dera et al. 2011; Fig. 6). On the other hand, a climate cooling 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 comprised 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). Provided the low latitude temperature increase supported by oyster $\delta^{18}\text{O}$ and the high latitudes temperature decrease supported by glendonites and *Xenoxylon* wood are synchronous, 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 Lower Bajocian (Raucsik et al. 2001; Raucsik and Varga 2008). In the Humphriesianum ammonite Zone of the eastern part of the Paris Basin, association of illite (50%), illite-smectite mixed layers (30%), and kaolinite (20%) reflect humid conditions (Brigaud et al. 2009). The abundance of coal over charcoal in Yorkshire (England) during the Lower Bajocian also arguably reflects more humid conditions with shorter 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-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 of the studied deposits.

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* hegemony over the calcareous nannoplankton community throughout the Mesozoic. Indeed, calcareous nannofossil production and sedimentation is 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 has flourished during the Early Bajocian. While increasing the nannoplankton productivity, such high-fertility environments have 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 (Fig. 2 and 3). Given the relative abundances in both sections, *Watznaueria* spp. increase is synchronous with *Biscutum* spp. + *Similiscutum* spp. decrease and, to a lesser extent, all the other coccolith genus, suggesting that *Watznaueria* spp. replaced the latter. Meanwhile, 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 *Watznaueria* spp. absolute abundance; it is not accompanied by any decrease in absolute abundance of other nannofossil species. Actually, there is also in the Discites ammonite Zone a slight increase in absolute abundance of *Lotharingius* spp., *Discorhabdus* spp., and *Biscutum* spp. + *Similiscutum* spp. (only observed at Cabo Mondego).

Therefore, based on the combined relative and absolute abundance signals, it seems that *Watznaueria* spp. actually integrated (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 previous species, and thus possibly without significantly impacting the ecological organization and functioning of the already present nannoplankton species. At that time, the nannoplankton community carrying

capacity increased with the influx of nutrients, favoring the *Watznaueria* spp. as new actors playing a new ecological role in the nannoplankton 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. 4 and 5). The increase in absolute abundance of these two species is 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 stabilization of *Watznaueria* spp. absolute abundances, is mainly supported by *W. britannica* and *W. aff. manivittiae* (Figs. 4 and 5).

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. manivittiae*. The formers were rare species before the end of the Aalenian, being present in the nannoplankton community since the Toarcian (Mattioli and Erba 1999; Aguado et al. 2008), while the latter are species newly-occurred 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* within the Early Bajocian nannoplankton community: (i) integration by environmental (physico-chemical parameters) changes, namely increasing ecosystem's carrying capacity (i.e., opening new, previously unfilled ecological spaces), or (ii) integration 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 by Carrying Capacity Increase. — The hypothesis taking into account the 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, etc.; Winter and Siesser 1994). Therefore, any modification (by collapse, development or origination) of the calcareous nannoplankton ecological niche carrying capacity 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 to the

formation of new niches or increase in niches carrying capacities (Roth 1987). Indeed, the Early Bajocian is marked by a transgression in the southeastern part of the Paris Basin (Durllet 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 (Stratigraphische Tabelle von Deutschland 2002). The difference in relative sea-level variation in Western Tethys is related to the occurrence of a regional control by major tectonic changes highlighted by the shift of strontium isotope towards unradiogenic values (Fig. 6; data compiled by Jenkyns et al. 2002) and 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 some shallow proximal environment. But conversely to Roth's (1987) statement, marked deepening of proximal environment could also move away the continental source of limiting nutrients, thus reducing the nannoplankton productivity, more important in proximal environment than in pelagic environment (Baumann et al. 2004). Nevertheless, even if the contribution of sea level changes to ecological niches 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, distal environment being relatively more oligotrophic and proximal environments more meso- to eutrophic due to the proximity of bio-limiting elements source by continental weathering. For instance, both higher absolute and relative abundances of *Schizosphaerella* spp. encountered in the distal ramp setting of Cabo Mondego section with respect to the hemipelagic setting of Chaudon-Norante, is in agreement with affinities of this taxon for proximal carbonate environments (Pittet and Mattioli 2002; Mattioli and Pittet 2004).

Hence, we hypothesize that during step 1, the integration of *W. contracta* and *W. colacicchii* 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 due to their disability 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 coccolith's morphology to ecological preferences remain difficult to assess. Incidentally, this hypothesis is compatible with the slight increase in Biscutaceae coccoliths, species often associated with eutrophic environments (e.g., Erba 2004; Lees et al. 2005), and testifying for a global oceanic eutrophication that mainly favored *Watznaueria* spp. but also other species production.

Step 2: Integration by Innovation in Ecological Niche Exploitation. — The second-step hypothesis explaining the integration of *Watznaueria* spp. in Early Bajocian nannoplankton assemblages is based on a biological innovation leading to an improvement in ecological niche exploitation. This second step is marked by the increase and then stabilization of the nutrient-rich environment based on the $\delta^{13}\text{C}$ 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*, who first dominated these nutrient-rich environments, remained stable in absolute abundance. Given the likely absence of

Stage	Early Bajocian					Amenite zone
	Concavum	Discites	Laeviuscula	Propinquans	Humphriesianum	

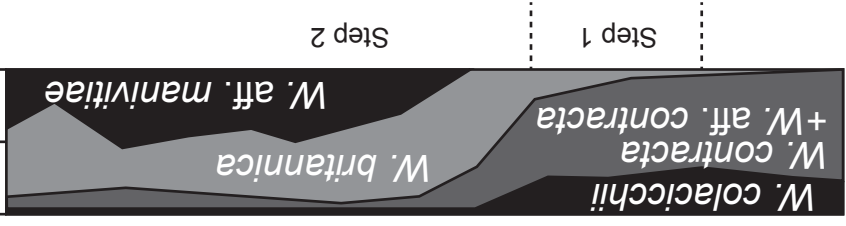
$\delta^{13}\text{C}$ (‰; VPDB)



Suchéras-Marx et al. (2012; 2013)

A

Watznaueria relative abundance (percent)



This study

C

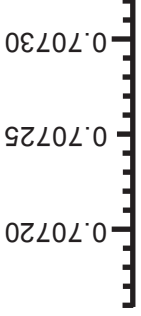
$\delta^{18}\text{O}$ (‰; VPDB)



Compilation from Dera et al. (2011)

D

$^{87}\text{Sr}/^{86}\text{Sr}$



Compilation from Jenkyns et al. (2002)

E

Synthetic temperature and humidity conditions



Brigaud et al. (2009)

F

Ocean fertility



See caption

G

Figure 6: Summary illustration for the latest Aalenian-Early Bajocian interval of: A) $\delta^{13}\text{C}$ global trend; B) Nannofossil flux (Suchéras-Marx et al. 2012; 2013); C) *Watznaueria* species relative abundance and integration steps (this study); D) $\delta^{18}\text{O}$ 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) $^{87}\text{Sr}/^{86}\text{Sr}$ 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 $\delta^{13}\text{C}$ (Bartolini et al. 1996; Brigaud et al. 2009; O'Dogherty et al. 2006; Suchéras-Marx et al. 2012; 2013).

competition between *W. contracta*/*W. colacicchii* and *W. britannica*/*W. aff. manivittiae* (as the absolute abundance increase of the latter is not associated with an absolute abundance decrease of the former), the *W. britannica*/*W. aff. manivittiae* should have developed new biological traits opening a still-unoccupied, potentially newly-formed ecological niche. This hypothesis fits well to *W. britannica* and *W. aff. manivittiae* which are new species 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). Even if the available temporal resolution is obviously too low to directly observe the seasonal to yearly nannoplankton community dynamics, the biological innovation characterizing *W. britannica* and *W. aff. manivittiae* 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, ~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 with 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 bloom occurrence under eutrophic conditions (Lees et al. 2004, 2006). This is the earliest unequivocal record for blooms of *Watznaueria* coccolithophores. In a similar way, *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. manivittiae* (Lees et al. 2004, 2006). The latter is actually poorly documented in Jurassic calcareous nannofossil studies. Nevertheless, this species has a morphology closely similar to another *Watznaueria* r-strategist blooming in eutrophic conditions during the Early Cretaceous: *W. barnesiae* (Lees et al. 2004, 2006). Similarly, *W. manivittiae*/*britannica*, a *Watznaueria* morphotype with still unclear taxonomical affinities and sharing morphological features from *W. britannica* and *W. aff. manivittiae*, is also described as a morphotype inhabiting instable meso-eutrophic environments (Giraud 2009; Giraud et al. 2009), environment often dominated by opportunistic species. Even if a direct relationship between coccolith general morphology and their ecological preferences is questionable, we hypothesize that during the Early Bajocian, *W. aff. manivittiae* may have had an ecology close to *W. barnesiae*. Eventually, *W. britannica* and *W. aff. manivittiae* have integrated the nannoplankton community thanks to their adaptation to seasonal blooms in nutrient-rich niches previously not exploited by other species.

Because only *W. britannica* and *W. aff. manivittiae* absolute and relative abundances increased, other environmental conditions may have favored their growth (or limited growth of other species). The fact that a species bloomed but not the others result from (1) the presence of the species prior the blooming conditions are 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 has resulted in seasonal increase in nutrients allowing calcareous nannoplankton blooms or increase in the blooming time period of the year. Formerly existing species were not adapted to such conditions due to more restrictive ecological preferences (e.g., temperature, water turbulence, day length; Balch 2004) but 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, only *W. britannica* will continue to be abundant after the Early Bajocian. The scarcity of *W. aff. manivitiae* in the rest of the Mesozoic suggests that both species did not have exactly the same ecological preferences. *W. aff. manivitiae* may have disappeared because a new species, namely *W. barnesiae*, invaded the oceans by the Bathonian, 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 geological, paleoceanographical, climatic and biodiversity changes. 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). The conditions in which this diversification occurred and its impact on the nannofossil assemblages are evaluated in the present study. The main results we achieved are:

- During the latest Aalenian–Early Bajocian (171-169 Ma), *Watznaueria* relative abundance increased over other coccoliths meanwhile their absolute abundance increased without significant decrease in absolute abundances of other coccoliths. Indeed, calcareous nannofossil absolute abundance estimation methods are used for more than 20 years (e.g., Beaufort 1991; Geisen et al. 1999), but such quantification remains uncommon in comparison to 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 *Watznaueria* spp. emergence;
- The diversification and emergence of *Watznaueria* spp. during the Early Bajocian was likely related to a climatically-driven eutrophication event;
- *Watznaueria* spp. have integrated rather than invaded the nannoplankton community;
- This integration has been done in two subsequent steps: step 1, involving *W. contracta* and *W. colacicchii*, likely relates to an increase of the ecological niche carrying capacity due to increase in 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* has 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 thrown 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.

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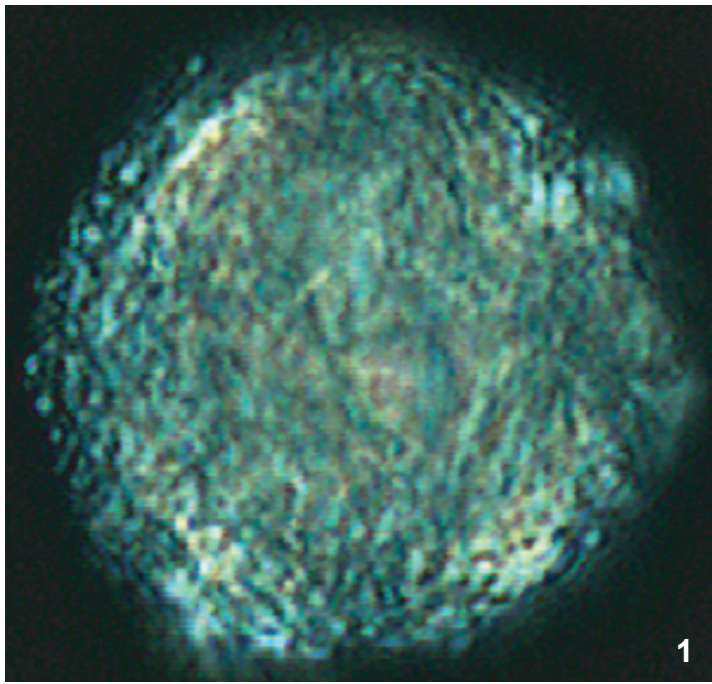
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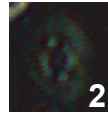
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Supplementary Materials

Nannofossil count charts for Cabo Mondego and Chaudon-Norante



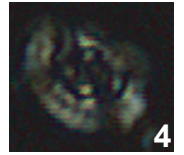
Schizosphaerella sp.



B. dubium



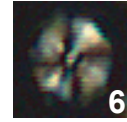
S. precarious



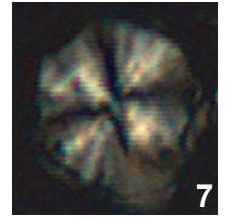
B. depravatum



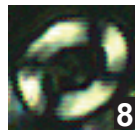
D. criotus



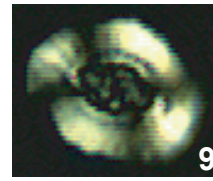
D. ignotus



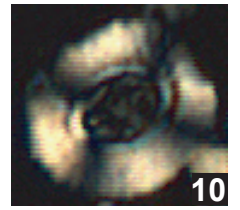
D. striatus



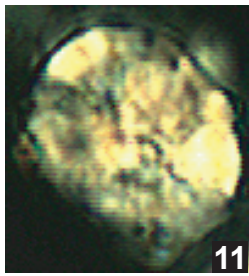
L. barozii



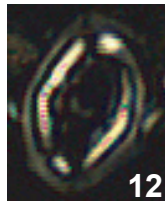
L. crucicentralis



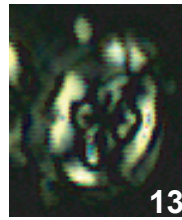
L. velatus



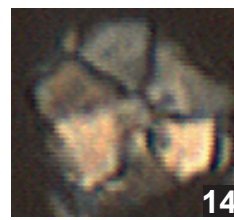
C. crassus



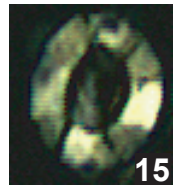
T. patulus



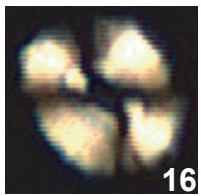
R. incompta



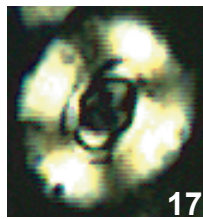
C. magharensis



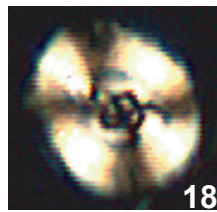
Calyculus sp.



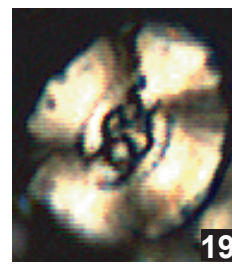
W. fossacincta



W. colacicchii



W. contracta



W. aff. contracta



W. aff. contracta



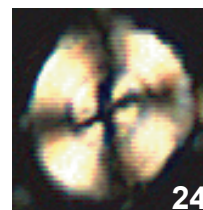
W. britannica E



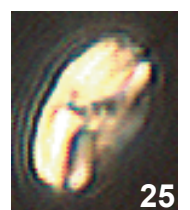
W. britannica F



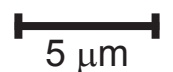
W. communis



W. aff. manivitiae



Watznaueria sp.



5 μ m

Plate 1: Calcareous nannofossils photographs from Cabo-Mondego (CM) and Chaudon-Norante (CN) under cross-polarized light. Full-page portrait.

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. *manivittiae* CM60;
25. *Watznaueria* sp. lateral view CM26.