The Bajocian (Middle Jurassic): a key interval in the early Mesozoic phytoplankton radiation

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ABSTRACT

Dinoflagellates and coccolithophores are two of the most important groups of phytoplankton in the modern oceans. These groups originated in the Triassic and radiated through the early Mesozoic, rising to ecological prominence. Within this long-term radiation, important short-term intervals of evolutionary and ecological change can be recognised. The Bajocian (Middle Jurassic, ~170–168 Ma) was characterised by an important ecological transition within the coccolithophores, and the radiation of one of the principal families of cyst-forming dinoflagellates, the Gonyaulacaceae. During the Early Bajocian, the coccolith genus *Watznaueria* diversified and expanded ecologically to dominate coccolith floras, a situation which continued for the remainder of the Mesozoic. This pattern was paralleled within dinoflagellate cyst floras by the ecological dominance of the genus *Dissiliodinium* in the mid-palaeolatitudes. These phenomena appear to be linked to a positive carbon isotope shift, and an interval of enhanced productivity driven by a shift to a more humid climate, enhanced continental weathering and nutrient flux. The latest Early Bajocian to earliest Bathonian was then characterised by the rapid increase in diversity of dinoflagellate cysts within the family Gonyaulacaceae. Through this interval, the Gonyaulacaceae transitioned from being a relatively minor component of dinoflagellate cyst floras, to becoming one of the prominent groups of cyst-forming dinoflagellates, which has persisted to the Holocene. In Europe, the pattern of this radiation was strongly influenced by sea level, with the increase in gonyaulacacean diversity reflecting a major second-order transgression. On a finer scale, the main pulses of first appearances correlate with third-order transgressive episodes. A rise in sea level, coupled with changes in the tectonic configuration of ocean gateways, appears to have controlled the pattern of plankton diversification in Europe. These palaeoceanographic changes may have enhanced water-mass transfer between Europe, the northwest Tethys Ocean and the Hispanic Corridor, which promoted the floral interchange of dinoflagellates.

Whilst sea level rise and associated large-scale palaeoenvironmental shifts appear to have controlled the pattern of dinoflagellate cyst appearances in several regions outside Europe, there is no direct correlation between dinoflagellate cyst diversity and sea level rise on a global scale. Although the Bajocian was transgressive in several regions, widespread flooded continental area was also present throughout the preceding Aalenian, an interval of low gonyaulacacean diversity. Moreover, although the Middle Jurassic was an interval of major climatic cooling, there was a ~5 myr gap between the onset of cooling and the radiation of gonyaulacaceans during the Bajocian. The Bajocian was, however, marked by a major evolutionary radiation in the pelagic realm, including ammonites, giant suspension feeding fishes and planktonic foraminifera. These phenomena may indicate an underlying ecological driver to the radiation of dinoflagellates during the Bajocian evolutionary explosion which could represent an extension of the Mesozoic Marine Revolution.

Keywords: evolution, geochemistry, Middle Jurassic (Bajocian), palaeogeography, phytoplankton, sea level

1. Introduction

Dinoflagellates and coccolithophores are two of the most important groups of primary producers in the modern oceans, and as such they are a significant part of the base of ocean food webs. Moreover, the downward flux of phytoplankton to the interior of the oceans forms a significant component of the biological pump. Dinoflagellates and coccolithophores are part of the polyphyletic ‘red lineage’ of phytoplankton, as they utilize chlorophyll *c* as a primary accessory pigment (Falkowski et al., 2004a).

While it has been argued that, on the basis of molecular and biogeochemical evidence, the coccolithophores and dinoflagellates have a Neoproterozoic origin, they are essentially a product of the post-Palaeozoic world, rising to ecological prominence throughout the Mesozoic (Fensome et al., 1996; Falkowski et al., 2004a, 2004b; Bown, 2005; Janouškovec et al., 2017). The early Mesozoic, defined here as the Middle Triassic to Middle Jurassic (~247–164 Ma), represents a critical interval in evolution of the modern phytoplankton, when the coccolithophores and dinoflagellates emerged and underwent major evolutionary radiations (Fensome et al., 1996; Falkowski et al., 2004b; Bown et al., 2004). While many authors have reviewed the broad macroecological and macroevolutionary trajectories of the eukaryotic phytoplankton during the Mesozoic–Cenozoic (e.g. Bown et al., 2004, Falkowski et al., 2004a,b, Bown, 2005, Falkowski and Knoll 2007), many short-term diversifications within this broader radiation remain poorly documented.

In this contribution, we review the pattern of coccolithophore and dinoflagellate evolution through the early Mesozoic, primarily from the perspective of the fossil record, focussing on the Bajocian (Middle Jurassic, ~170–168 Ma). The driving mechanisms behind ecological and evolutionary change in phytoplankton during the Bajocian remain poorly understood, but it is clearly a critical interval in the evolutionary history of the two groups. During the Bajocian, coccolith floras became ecologically dominated by the genus *Watznaueria*, a condition that prevailed for the remainder of the Mesozoic. Among the dinoflagellates, the Bajocian was characterised by the diversification of the family Gonyaulacaceae, which became one of the most prominent groups of encysting dinoflagellates ranging through to the present day. To set the Bajocian radiation in context, we provide an overview of the coccolith and dinoflagellate cyst fossil records, documenting the evolutionary history of the two groups from their emergence in the Triassic to their radiation through the Early–Middle Jurassic.

1.1. Dinoflagellates

Dinoflagellates are a diverse group of flagellated eukaryotes, represented by around 2,400 extant species, of which ~2000 are marine plankton (Fensome et al., 1996; de Vernal and Marret, 2007; Janouškovec et al., 2017). The dinoflagellates are characterised by the possession of a unique nucleus, the dinokaryon; and/or by having a life cycle stage with two dissimilar flagella, one transverse and one longitudinal, which allow the motile cell to propel itself through water (Fensome et al., 1996). Dinoflagellates can be broadly split into naked and thecate forms. Thecate (or armoured) dinoflagellates have a series of cellulosic plates held within vesicles (alveolae) in the cortex (amphiesma) of the cell. The arrangement of the thecal plates forms a pattern, known as tabulation, that tends to be consistent within taxa and is thus a critical feature in dinoflagellate classification (Dale, 1983; Evitt, 1985; Fensome et al., 1993, 1999; Janouškovec et al., 2017). It is usually reflected, at least partially, on the cysts that comprise the vast majority of fossil dinoflagellates. Thus, tabulation is used to classify both fossil and living and dinoflagellates (Fensome et al., 1993).

Around half of all dinoflagellates are autotrophic or mixotrophic and, together with the coccolithophores and diatoms, are responsible for a significant proportion of primary production in the oceans of the world (Delwiche, 2007). Heterotrophic dinoflagellates are an important component of the microzooplankton (Calbet, 2008). Around 13% of modern dinoflagellate species produce a zygotic resting cyst (Head, 1996). The wall of most preservable dinoflagellate cysts is composed of the complex macrobiomolecule dinosporin (Head, 1996; Bogus et al., 2014). The fossil record of dinoflagellates is based on their refractory resting cysts, adding a layer of complexity to the dinoflagellate fossil record with respect to other phytoplankton groups, as the dinoflagellate motile stage is virtually never preserved, as the theca is extremely labile (Evitt, 1985; Versteegh et al., 2004). With only around 13% of living motile species producing preservable cysts, the dinoflagellate cyst fossil record is inherently incomplete, and it is not known whether this percentage has changed through time (Head, 1996; Fensome et al., 1996; Riding and Lucas-Clark 2016).

Some earlier workers cast doubt on the ability of a highly selective fossil record to shed light on dinoflagellate evolution (Evitt, 1985). However, some higher taxa are far better represented than others in the record, notably the orders Gonyaulacales and Perdiniales (Fensome et al., 1999; de Vernal and Marret, 2007). Such groups have a much richer and extensive fossil record than the overall selectivity of dinoflagellates as a whole would suggest. Observations of patterns of occurrences in the fossil record (Fensome et al 1996) and quasi-cladistic approaches on all dinoflagellates (i.e. the basis of the phylogenetic classification of Fensome et al. [1993]) provide significant evidence for the general evolutionary pattern. For example, that the appearance and expansion of dinoflagellates during the early Mesozoic is a true evolutionary radiation is compellingly shown by the extent of morphological ‘experimentation’ early in the fossil record. Moreover, the mixing of features in individual taxa that would subsequently characterise separate higher level taxa (e.g. that *Nannoceratopsis* is part dinophysialean and part peridiniphycidean) and later morphological innovations becoming restricted to lower taxonomic ranks (Piel and Evitt, 1980; Fensome et al, 1996). The latest molecular data supports this general scenario, as tentatively does biogeochemical data (Janouškovec et al. 2016).

The radiation of dinoflagellates through the early Mesozoic was characterised by the appearance of the rising prominence of stem forms with a gonyaulacoid-peridinoid tabulation, and ultimately by crown thecate clades, such as the Gonyaulacales and Peridiniales (Fensome et al., 1996; Janouškovec et al., 2017). The increase in dinoflagellate cyst diversity through the Mesozoic was accompanied by a synchronous increase in the abundance of dinosteranes in Mesozoic sedimentary rocks (Moldowan et al., 1996). Triaromatic dinosteranes are types of lipid biomarkers derived from dinosterols, and are primarily associated with dinoflagellates (Moldowan and Talyzina, 1998). However, recent molecular phylogenetic research has revealed that the acquisition of dinosterols within the dinoflagellate lineage occurred during the Mesozoic, shedding doubt on the reliability of dinosteranes as an unequivocal biomarker for dinoflagellates in pre-Mesozoic rocks (Janouškovec et al., 2017). Despite this, the concomitant increase in the abundance of dinosteranes and increase in dinoflagellate cyst diversity through the Jurassic strongly suggests that dinoflagellates rose to ecological prominence in the early Mesozoic. In summary, the appearance of high-level taxa dinoflagellate taxa, which are supported by molecular data as distinct clades, and progressive innovations at lower taxonomic ranks, along with transitionary forms such as *Nannoceratopsis* and an increase in dinosterane abundance, strongly suggest that dinoflagellates underwent a true evolutionary radiation through the early Mesozoic (Fensome et al., 1996).

1.2. Coccolithophores

Coccolithophores are unicellular phytoplankton belonging to the division Haptophyta. They are defined by a cell-bounding series of calcareous plates, known as coccoliths, which interlock to form a coccosphere. Coccolithophores form part of a wider clade of noncalcifying/potentially calcifying/calficying haptophytes termed the Calcihaptophycidae (de Vargas et al., 2007). Coccolithophores are the most important calcifying organisms in the modern ocean and thus the downward flux of coccolithophores to the sea floor contributes significantly to the biological pump, making coccolithophores and important agent of oceanic biogeochemical cycles (Brownlee and Taylor, 2004; Rost and Riebesell, 2004).

In many species, coccolith morphology varies with the diploid-haploid life cycle. During the diploid phase, cells produce heterococcoliths, formed from a structurally complex arrangement of radial calcite crystals. In contrast, during the haploid phase, holococcoliths are produced, which are characterised by simple calcite rhombohedra. The fossil record of coccolithophores is primarily based on coccoliths, as coccospheres are rarely preserved intact. Moreover, the record comprises primarily of heterococcoliths (de Vargas et al., 2007). Although fossil holococcoliths are known, the nature of the tiny calcite rhombohedra from which they are constructed makes them extremely susceptible to dissolution. Hence, the dearth of fossil holococcoliths reflects a substantial taphonomic bias.

Within the early Mesozoic coccolith record, heterococcoliths are represented by two broad morphological groups, the muroliths and the placoliths (Bown, 1987; Bown et al., 2004). Muroliths represent the earliest coccoliths, and are characterised a simple structure with calcite elements extending vertically (Bown, 1987; Gardin et al., 2012). In the Early Jurassic, placolith coccoliths appeared and radiated to become the dominant coccolith group. The placolith structure is defined by two discs which lie on top of one another, and are connected by a central pillar with radial calcite elements (Bown, 1987).

Unlike the dinoflagellates, coccolithophores have left no appreciable pre-Cenozoic biogeochemical marker record. Coccolithophores produce alkenones, which are widely used in Quaternary palaeoceanography as temperature proxies. However, these substances are inherently unstable and highly susceptible to diagenetic alteration, and consequently alkenones are unknown from marine sediments older than Cretaceous (Knoll et al., 2007). Thus, the coccolith fossil record is the only tool for directly tracking coccolithophore evolution intervals of deeper time.

2. Middle Triassic to Early Jurassic: emergence and radiation of dinoflagellates and coccolithophores

2.1. Emergence in the Middle–Late Triassic

The onset of the Mesozoic phytoplankton radiation in the fossil record is signalled by the appearance in Australasia of the earliest unequivocal dinoflagellate cyst species, *Sahulidinium ottii* in the Middle Triassic (Late Ladinian, ~235 Ma) (Riding et al., 2010a). Dinoflagellate cyst diversity increased through the Middle to Late Triassic with the appearances of the families Rhaetogonyaulacaceae and Suessiaceae (Figure 1; Fensome et al., 1996). The former represents the first appearance of the order Gonyaulacales, one the two main orders represented by fossil dinoflagellate cysts (Fensome et al., 1999; Janouškovec et al., 2017). This later Triassic expansion of dinoflagellate cysts coincides with an increase in the abundance of dinosteranes (Moldowan et al., 1996), suggesting that dinoflagellates began their rise to ecological prominence through this interval (Fensome et al., 1996).

The earliest coccoliths appeared in the latest Norian (~209 Ma), with the oldest identifiable species, *Crucirhabdus minutus*, appearing in the earliest Rhaetian (~207 Ma) of the Austrian Alps (Gardin et al., 2012). These early coccoliths are extremely small (2–3 µm), and have a murolith structure (Bown, 1987; Bown and Young, 1998; Bown et al., 2004). *Crucirhabdus* is known from the Rhaetian of Australia, indicating a global distribution for coccoliths during the Late Triassic (Bralower et al., 1992; Gardin et al., 2012). However, diversity remained low during this interval, with a maximum of five species (Bown et al., 2004). Although there is no biomarker record of coccolithophores through the Early Mesozoic, molecular divergence times are broadly in agreement with the coccolith fossil record. Molecular clocks based on SSU and LSU rDNA give ~270–240 and ~ 200 Ma respectively as the earliest possible dates for the origin of the coccolithophores (de Vargas et al. 2007; Medlin et al., 2008).

Falkowski et al. (2004a, b) argued that the emergence of the ‘red lineage’ of phytoplankton during the Triassic was driven by changes in ocean chemistry in the aftermath of the Permo-Triassic mass extinction. These authors postulated that prolonged periods of oceanic anoxia during the Early Triassic forced heterotrophic cells to acquire and retain plastids. In this hypothesis, prolonged euxinic conditions may have induced widespread denitrification, generating a paucity of fixed nitrogen, one of the most important macronutrients in the Triassic seas. Although photoautotrophs would have been affected by the limited availability of fixed nitrogen, a reduction in primary production and decline in upward transfer of biomass would have severely affected consumers. Acquisition of plastids by heterotrophic cells, via endosymbiosis of a red alga, would have provided a mixotrophic ‘duel fuel’ strategy. This would have been an advantageous ecological strategy in unstable and stressed intervals of environmental change during the Early Triassic (Falkowski et al., 2004a).

2.2. The End-Triassic Mass Extinction

The end-Triassic mass extinction (~201 Ma) significantly affected the diversity of phytoplankton. Only four dinoflagellate cyst genera and one coccolith species survived this major environmental perturbation (Bown et al., 2004; van de Schootbrugge et al., 2007). The temporal coincidence between the diversity collapse at the end of the Triassic and the emplacement of the Central Atlantic Magmatic Province (CAMP) has led many workers to suggest a causal relationship between these phenomena (e.g. Schoene et al., 2010; Blackburn et al., 2013; Percival et al., 2017). Volcanic outgassing may have driven an increase in *p*CO2, resulting in acidification of epicontinental seas and prolonged euxinia (Ruhl et al., 2011; Schaller et al., 2011; Hönisch et al., 2012; Richoz et al., 2012). As such, prolonged anaerobic/euxinic conditions, and ocean acidification may have driven the decline in dinoflagellate cyst and coccolith diversity (van de Schootbrugge et al., 2007; 2013).

In many areas through Europe, the collapse in dinoflagellate cyst and coccolith diversity through the Triassic–Jurassic transition is concomitant with an increase in the abundance of the phycoma (resting cysts) of prasinophytes (chlorophyte green algae) (Kuerschner et al., 2007; van de Schootbrugge et al., 2007; Bonis et al., 2009). Moreover, the earliest Hettangian (~200 Ma, earliest Jurassic) is marked by an increase in the abundance diaryl isoprenoid molecules, derived from green sulphur bacteria (Richoz et al., 2012; van de Schootbrugge et al., 2013). The turnover in organic-walled phytoplankton communites, and presence of green sulphur bacteria, indicates that the photic zone became euxinic (Richoz et al., 2012). Green sulphur bacteria require both light and free hydrogen sulphide (H_2S) to photosynthesise, whereas prasinophytes appear to have thrived during intervals of palaeoenvironmental stress during the Mesozoic (van de Schootbrugge et al., 2013).

2.2. Early to Middle Jurassic: recovery and radiation

Both dinoflagellates and coccolithophores recovered during the earliest Jurassic and radiated through the Early and Middle Jurassic, with the appearances of numerous families (Figure 1; Fensome et al., 1996; Bown et al., 2004). Dinoflagellate cyst diversity was low during the Hettangian, and dinoflagellate cysts are generally sparse in Hettangian strata (Wall, 1965; van de Schootbrugge et al., 2013). The succeeding Sinemurian was marked by the sudden, and short-lived, appearance of *Liasidium variabile* (see Brittain et al. 2010). The appearance of *Liasidium variable* is significant as it marks the first appearance in the fossil record of the order Peridiniales, and although its precise taxonomic affinity is unclear due to lack of a fully reflected tabulation, *Liasidium variable* may be the earliest representative of the family Peridiniaceae (Feist-Burkhardt, 2009). It is also possible that *Liasidium variabile* was heterotrophic, as it has a pigmented wall structure (Feist-Burkhardt 2009; Riding et al., 2013). The sudden appearance of this species in the Late Sinemurian has been related to the opening of the Hispanic corridor, which allowed *Liasidium variabile* to invade the Tethys

Ocean from the Panthalassa Ocean (van de Schootbrugge et al., 2005). Recent work has linked the acme *Liasidium variabile* to a negative carbon isotope excursion, and a brief interval of global warming (Riding et al., 2013).

A significant increase in dinoflagellate cyst diversity occurred during the Late Pliensbachian, with the radiation of numerous families of gonyaulacaleans and peridinialeans (Figure 1; Morgenroth, 1970; Feist-Burkhardt and Wille, 1992). Another important first appearance in the Late Pliensbachian was that of *Nannoceratopsis*, a genus confined to the Jurassic and the only representative of the family Nannoceratopsiaceae. *Nannoceratopsis* has a tabulation that is a combination of dinophysioid and gonyaulacoid-peridinoid, and as such appears to be an evolutionary link between the Peridiniphycidae and the Dinophysiales. The latter has virtually no fossil record (Janouškovec et al., 2017).

The most significant radiation of the coccolithophorids during the Mesozoic occurred in the Early Jurassic. During that interval, 10 of the known 16 coccolith families appeared. The Hettangian to Sinemurian was characterised by the recovery and radiation of murolith forms, which had survived the end-Triassic mass extinction (Bown et al. 2004). The family Biscutaceae appeared around the Sinemurian–Pliensbachian boundary and radiated rapidly through the Pliensbachian, becoming an important component of coccolith floras (Mattioli et al., 2004). The Biscutaceae represent the emergence of the placolith morphology, making the Pliensbachian one of the most important intervals in coccolithophore evolution (de Kaenel and Bergen, 1993; Bown and Cooper, 1998; Mattioli and Erba, 1999; Mattioli et al., 2013). The evolution of the placolith morphology was extremely important because it allowed coccoliths to physically lock together to form a coccosphere for the first time. Prior to the development of placoliths, elements in the muroliths were presumed to have been bound together by organic material (Bown, 1987). The initial development of placoliths occurred in two steps. In the Early Pliensbachian, radiating placoliths first appeared; these have a simple structure comprising proximal and distal shields (Bown, 1987). In the Late Pliensbachian, more complex imbricating coccoliths appeared, and this morphology dominated coccolith floras for the remainder of the Jurassic (Bown, 1987; Mattioli and Erba, 1999; Mattioli et al., 2013).

The Pliensbachian was clearly an important interval in the evolution of the dinoflagellates and coccolithophores. It was also an interval of major palaeoclimatic and palaeoceanographic change. The Late Pliensbachian was marked by cooling palaeotemperatures, with a pronounced fall in seawater temperature of ~5℃ (Dera et al., 2011). This cooling may have allowed continental ice sheets to develop, and the Late Pliensbachian regression may have reflected glacioeustasty (Bougeault et al., 2017). Van de Schootbrugge et al. (2005) argued that cooling temperatures drove the radiation of dinoflagellates during the Late Pliensbachian. These authors argued that cooling increased ocean turbulence and enhanced vertical mixing, which resulted in well-ventilated bottom waters, creating conditions ideal for cyst-forming dinoflagellates. Moreover, an increase in upper ocean turbulence may have driven, larger, more frequent pulses of nutrients to the photic zone, which in turn may have favoured bloom-forming dinoflagellates (Falkowski et al., 2004b). In contrast to the dinoflagellates, the drivers behind the emergence of placolith coccoliths are unclear. The Sinemurian–Pliensbachian transition was marked by a negative carbon isotope shift, and the burial of organic-rich marine sediments (Price et al., 2016; Ruhl et al., 2016; Bougeault et al., 2017). This has been linked to an interval of CAMP volcanism, and a switch to more humid conditions in Europe, with enhanced weathering and run-off (Bougeault et al., 2017). As such, it is likely that nutrient flux was elevated at this time. The temporal coincidence between these phenomena and the appearance of placolith coccoliths may indicate that elevated nutrient levels were a driver of coccolith evolution during the Early Jurassic. Indeed, elevated nutrient levels have been linked to evolutionary changes in coccolithophores during the Middle Jurassic (section 3; Suchéras-Marx et al., 2015). Moreover, the Early Pliensbachian was marked by sea level rise (Hallam, 2001), which would have increased shallow-sea ecospace for neritic phytoplankton.

The Early Toarcian was marked by the Toarcian Oceanic Anoxic Event (T-OAE) (~180 Ma), a relatively brief (~200–900 kyr) phase of widespread oceanic anoxia/euxinia and climate change. It was characterised by extensive, coeval organic-rich shales and a negative carbon isotope excursion, which affected the entire carbon cycle (Hesselbo et al., 2000; Kemp et al., 2005; van de Schootbrugge et al., 2005; Suan et al., 2008; Xu et al., 2017). Dinoflagellate cyst diversity was temporarily affected by the T-OAE, as diversity declined sharply (Bucefalo Palliani et al., 2002; van de Schootbrugge et al., 2005; Correia et al., 2017a,b). Both the diversity and abundance of coccoliths declined through the T-OAE, accompanied by a trend of decreasing coccolith size, which has been linked to enhanced $p\mathrm{CO}_2$ driving a biocalcification crisis (Mattioli et al., 2004; Suan et al., 2010; Fraguas and Young, 2011). Therefore, as in the latest Triassic, organic-walled phytoplankton communities became dominated by prasinophytes during the T-OAE (van de Schootbrugge et al., 2005).

Similarly, green sulphur bacteria appear to have thrived at this time, indicating photic zone euxinia (van de Schootbrugge et al., 2013).

After the T-OAE, normal oceanographic conditions, with fully aerobic water columns, were re-established during the *Hildoceras bifrons* ammonite biozone. The majority of the dinoflagellate cyst taxa that had characterised the Late Pliensbachian reappeared. The Late Toarcian was characterised by an important evolutionary event. This was the appearance of the first Gonyaulacaceae, heralded by the emergence of *Sentusidinium* in the Upper Toarcian of Yorkshire, northern England and northern Germany (Riding, 1984; Prauss, 1989). Dinoflagellate cysts belonging to the family Gonyaulaceae are defined by several characters, including the presence a particular configuration of plates on the hypocyst, termed a sexiform tabulation (Evitt, 1985). Other key characters include a mid-ventral sulcus, and a symmetrical posterior outline. Although *Sentusidinium* lacks a fully reflected tabulation, its overall morphology is strongly gonyaulacacean (Wood et al., 2016). The Gonyaulacaceae would go on to become the most important and diverse family of encysting dinoflagellates in the fossil record (section 3).

The coccolithophores recovered gradually from the T-OAE; the re-appearance of deep-dwelling coccoliths such as *Crepidolithus crassus* indicate the end of anoxic/dysoxic conditions within the deep photic zone. Subsequently, the entire calcareous nannoplankton flora recovered (Mattioli et al., 2008). The post-T-OAE recovery interval was characterised by the appearance of the genus *Watznaueria* (see Mattioli and Erba, 1999), which is significant because *Watznaueria* became ecologically and numerically the dominant Middle Jurassic to Cretaceous coccolith genus (Suchéras-Marx et al., 2015; Giraud et al., 2016).

3. The Bajocian: a critical interval of dinoflagellate and coccolithophore evolution and ecology

The Bajocian was an important interval of dinoflagellate and coccolithophore ecological development and evolution. During the latest Aalenian to Early Bajocian, the coccolith genus *Watznaueria* diversified and expanded to become the most abundant, and thus ecologically dominant coccolith genus. The ecological transition with coccolithophores was paralleled by the diversification, and rise to ecological dominance, of the genus *Dissiliodinium* within dinoflagellate cyst floras. This was followed by the rapid diversification of gonyaulacacean cysts from latest Early Bajocian to Early Bathonian.

Through this interval, the Gonyaulacaceae went from a relatively minor component of dinoflagellate cyst floras (represented by four genera in the Aalenian) to the dominant group of encysting dinoflagellates over 2–4 myr (Figure 1; Feist-Burkhardt and Wille, 1992; Riding and Thomas, 1992; Mantle and Riding, 2012; Feist-Burkhardt and Götz, 2016; Wiggan et al., 2017). However, the patterns and underlying driving mechanisms behind this diversification remain poorly understood. We relate the diversification and expansion of *Watznaueria* to the dinoflagellate cyst record, and assess the patterns and possible drivers of ecological and evolutionary changes in gonyaulacacean dinoflagellates.

3.1. Late Aalenian to Early Bajocian: expansion of Watznaueria *and the ecological dominance of* Dissiliodinium

The latest Aalenian to Early Bajocian was marked by the diversification and ecological expansion of the coccolith genus *Watznaueria*, marking the beginning of 100 myr of ecological dominance by this genus within coccolithophore communities (Giraud et al., 2016). Through the Aalenian–Bajocian transition, *Watznaueria* replaced *Lotharingus* as the dominant coccolith genus (Suchéras-Marx et al., 2012, 2015; Giraud et al., 2016; Aguado et al., 2017). Suchéras-Marx et al. (2015) examined the diversification and expansion of *Watznaueria* from two areas within the European Epicontinental Seaway, namely the French Subalpine Basin and the Lusitanian Basin of Portugal. These authors recorded an increase in both the absolute and relative abundance of *Watznaueria* through the Lower Bajocian, and noted that the absolute abundance of coccoliths as a whole increased through that interval, driven by the increase in the abundance of *Watznaueria* (Figure 2). Other coccolith taxa did not decrease in abundance during the same interval, implying that *Watznaueria* did not outcompete other genera but integrated into the coccolith community. Further, the expansion of *Watznaueria* appears to have had two critical steps. First, in the earliest Bajocian (*Hyperlioceras discites* ammonite biozone), coccolith floras were dominated by the species *Watznaueria contracta* and *Watznaueria colacicchii*. Second, towards the end of the Early Bajocian, coccolith abundances stabilised as communities became dominated by *Watznaueria britannica* and *Watznaueria* aff. *manivitiae*. Giraud et al. (2016) compiled data on coccolith records from the Upper Aalenian to Lower Bajocian of northwest Europe. These authors noted a similar pattern, with the increase in abundance of *Watznaueria*, beginning around the Aalenian–Bajocian transition. This initial increase in the abundance of *Watznaueria* was produced by the rise to dominance of a group of *Watznaueria* species characterised by a central cross area (Figure 3). This group comprises *Watznaueria colacichii*, *Watznaueria contracta* and *Watznaueria* aff. *Watznaueria contracta*. The next step in this transition, in the Early Bajocian, was characterised by the increase in the abundance of species lacking a central cross, and those with a central bar, including *Watznaueria britannica* and *Watznaueria* aff. *Watznaueria manivitiae* (Figure 3). Furthermore, Aguado et al. (2017) documented the coccolith record through the Upper Aalenian to Lower Bajocian of the southern Iberian palaeomargin. These authors reported a similar pattern, with an increase in the relative and absolute abundance of *Watznaueria* through the uppermost Aalenian–lowermost Bajocian, particularly that of *Watznaueria contracta*. Coccolith assemblages around the middle of the Lower Bajocian (*Witchellia laeviuscula* ammonite biozone) are marked by an increase in *Watznaueria britannica* and *Watznaueria manivitiae*, an increase that persisted throughout the remainder of the Lower Bajocian. Significantly, Aguado et al. (2017) noted that the Lower Bajocian is marked by a decline in *Crepidolithus crassus,* a coccolith interpreted as deep-photic zone dwelling (Figure 4).

Within the dinoflagellate cycts, the Early Bajocian was characterised by the ecological dominance of the gonyaulacacean genus *Dissiliodinium* (Wiggan et al., 2017). *Dissiliodinium* first appeared in the Middle Aalenian as the species *Dissiliodinium lichenoides* (see Feist-Burkhardt and Pross, 2010). During the latest Aalenian and Early Bajocian, *Dissiliodinium* diversified with the appearances of *Dissiliodinium caddaense, Dissiliodinium giganteum* and *Dissiliodinium psilatum* (see Helby et al., 1987; Prauss, 1989; Feist-Burkhardt, 1990; Wiggan et al., 2017). During this interval, *Dissiliodinium* was also ecologically dominant in several mid-palaeolatitude regions. *Dissiliodinium giganteum* dominated dinoflagellate cyst floras in the southern German Basin, Poland/northern Slovakia, and Switzerland Figures 5, 6; Gedl, 2008; Hostettler et al., 2017; Wiggan et al., 2017). Outside Europe, dinoflagellate cyst assemblages from the Lower Bajocian of offshore Western Australia were dominated by *Dissiliodinium caddaense* (Figure 6; Riding et al, 2010b). The *Dissiliodinium caddaense* dinoflagellate cyst biozone has been correlated by ammonites and strontium isotopes to the Early Bajocian *Witchellia laeviuscula* ammonite biozone of Europe (Riding et al., 2010b). Consequently, the acme of *Dissiliodinium caddaense* is synchronous with the acme of *Dissiliodinium giganteum* in Europe (Figure 6). Furthermore, *Dissiliodinium* is also abundant in the Lower Bajocian of the Neuquén Basin in

Argentina (Stukins et al., 2013). In this region, dinoflagellate cyst assemblages are dominated by *Dissiliodinium psilatum* (Figure 6).

3.2. Latest Early Bajocian to Early Bathonian: rapid diversification of gonyaulacacean dinoflagellates

Whereas the Late Aalenian to Early Bajocian interval marks the transition to long-term ecological dominance of *Watznueria* within coccolithophore communities, the acme of *Dissiliodinium* within the dinoflagellate cysts was comparatively short-lived. *Dissiliodinium* declined in abundance towards the end of the Early Bajocian in Europe, and formed a relatively minor component of dinoflagellate cyst floras through the Late Bajocian (Figure 5, Wiggan et al. 2017). Similarly, in Australia, *Dissiliodinium caddaense* became extinct around the Early–Late Bajocian transition, and the genus formed a comparatively minor component of dinoflagellate cyst floras in the Late Bajocian to Early Bathonian (Riding et al., 2010a; Mantle and Riding, 2012). As such, the acme of *Dissiliodinium* represents a small component of the wider diversification and ecological expansion of gonyaulacacean dinoflagellates, and this genus may have been out-competed by newly emerging taxa. In particular, ~50 species appeared between the latest Early Bajocian and the Early Bathonian (Feist-Burkhardt and Monteil, 1997; Wiggan et al., 2017). Wiggan et al. (2017) demonstrated that, in Europe, there was a continuous pattern of appearances through the Late Aalenian to Early Bathonian, but the highest number of first appearances were in the *Stephanoceras humphriesianum* (latest Early Bajocian) and *Parkinsonia parkinsoni* ammonite biozones (latest Bajocian) (Figures 7a, b). Moreover, from the *Stephanoceras humphriesianum* ammonite biozone onwards, appearances were dominated by gonyaulacacean taxa. The stratigraphical data presented by Wiggan et al. (2017) have been used to construct a species richness curve per ammonite zone from the Late Aalenian *Graphoceras concavum* ammonite biozone to the earliest Bathonian *Zigzagiceras zigzag* ammonite biozone (Figure 8). It is clear that richness steadily increased through the Late Aalenian to Early Bajocian, but there was a particularly pronounced increase in richness in the *Stephanoceras humphriesianum* and *Parkinsonia parkinsoni* ammonite biozones (Figure 8). During the Late Aalenian, gonyaulacacean taxa comprised around 25% of dinoflagellate cyst taxa, but by the earliest Bathonian, *Zigzagiceras zigzag* ammonite biozone, this family represented over 60% of all dinoflagellate cyst taxa. Thus, the Bajocian represents a critical interval in the evolutionary history of the Gonyaulacaceae.

The diversification of gonyaulacaceans during the Bajocian–Bathonian is observed from the low to mid palaeolatitudes of the northern and southern hemispheres, indicating a global increase in diversity. There was an increase in the diversity of gonyaulacacean dinoflagellate cysts through the Middle Jurassic in offshore eastern Canada, but in this region the majority of appearances are recorded from the Bathonian, rather than the Bajocian (Bujak and Williams, 1977). Outside of the mid-northerly palaeolatitudes, the radiation of gonyaulacaceans is observed in the Middle Jurassic of Australia, which was then located on the southern edge of the Tethys Ocean, around 30°S. The pattern of dinoflagellate cyst appearances in the Northwest Shelf of Australia is comparable to that of Europe, with a significant increase in the diversity of gonyaulacaceans from the latest Early Bajocian to Early Bathonian (Mantle and Riding, 2012). Gonyaulacaceans also diversified through the low palaeolatitude regions; there is a significant increase in the appearances and diversity of gonyaulacacean dinoflagellate cysts through the Bajocian–Bathonian of Egypt, Israel and Qatar (Conway, 1990; Ibrahim et al., 2002, 2003). Gonyaulacaceans do not appear to have radiated through the Bajocian–Bathonian in the high palaeolatitudes, as this group comprises only a minor component of dinoflagellate cyst floras from the Middle Jurassic of Arctic Canada (Figure 9; Davies, 1983). As such, the Gonyaulacaceae appear to have been taxonomically and ecologically dominant in the low to mid-palaeolatitudes.

The radiation of gonyaulacaceans was accompanied by a significant increase in the diversity of form, or disparity of dinoflagellate cysts, and innovations in the archaeopyle (the excystment aperture). Prior to the Bajocian, gonyaulacaceans were represented by *Batiacasphaera*, *Dissiliodinium, Kallosphaeridum* and *Sentusidinium* (see Feist-Burkhardt and Pross, 2010; Feist-Burkhardt and Wille, 1992). These genera are characterised by simple, mostly non-tabulate cysts (Figure 10). *Batiacasphaera*, *Kallosphaeridium* and *Sentusidinium* have apical archaeopyles, whereas *Dissiliodinium* has a multi-plate precingular archaeopyle (Figure 10). Through the Bajocian 19 gonyaulacacean genera appeared, which exhibit a wide array of morphologies (Figure 10). The Early Bajocian was marked by the diversifications of genera with multiplate precingular archaeopyles such as *Dissiliodinium* and *Durotrigia*, and included the first gonyaulacaceans with more-or-less fully reflected tabulation, such as *Durotrigia daveyi* (Figure 10). Morphological features such as cavation (the separation of wall layers) appeared within the Gonyaulacacae, as represented by the appearances of the genera *Cavatodissiliodinium* and *Endoscrinium* (Feist-Burkhardt and Götz, 2016). Moreover, gonyaulacaceans developed ornamental features such as distally-complex processes and prominent sutural crests (Figure 10). These morphological features were accompanied by an increase in the number of archaeopyle types. Over the course of the Bajocian, genera with epicystal, one-plate precingular and two-plate precingular archaeopyles appeared. While both fossil and recent dinoflagellate cyst taxa can exhibit intraspecific variability within archaeopyle formation (e.g. Evitt, 1985; Harding, 1986; Ellegaard et al., 2002), the one-plate precingular archaeopyle appears to have been developed with the Gonyaulacacae during the Bajocian, which has remained a common gonyaualacean excystment strategy to the present day. Therefore, the increase in taxonomic diversity of gonyaulacacean dinoflagellate cysts through the Bajocian was accompanied by morphological innovations in archaeopyle formation, and a rapid increase in morphological disparity.

3.3. Drivers behind the ecological and evolutionary change in dinoflagellates and coccolithophores during the Bajocian

The Middle Jurassic, and the Bajocian in particular, was marked by changes in climate, ocean gateway configuration and sea level. The Aalenian–Bathonian was characterised by significant changes in the tectonic configuration of ocean gateways, particularly the gateways which connected the European Epicontinental Seaway (EES) to the Tethys and Panthalassa oceans, and the Boreal Sea. In the north, the Viking Corridor, which at times provided a marine connection from the EES to the Boreal Sea (Figure 11), was largely blocked during the Aalenian due to magmatic doming in the North Sea area (Korte et al., 2015). The Hispanic Corridor to the west, which opened as a marine connection between Gondwana and Laurentia during the Early Jurassic (Figure 11), was affected by changes in plate relative motion and spreading rate between Africa and North America. These changes drove a widening and deepening of the Hispanic Corridor during the Bajocian (Aberhan, 2001; Labails et al., 2010; Dera et al., 2014). As well as changes in the configuration of ocean gateways, the Bajocian was a time of major sea-level rise. In Europe, this took the form of the T7 second-order transgression, which lasted from the Late Aalenian to the Early Bathonian (Jacquin et al., 1998). In turn, this second-order transgression comprised a series of third-order cycles. In the Boreal realm, this transgression had two pulses, the first lasting from the Late Aalenian to Early Bajocian and the second from the latest Early Bajocian to Early Bathonian (Figure 12). In the Tethyan realm, this transgression comprised one pulse, which lasted from the Late Aalenian to Early Bathonian (Figure 12). Maximum transgression of the

T7 cycle as a whole corresponds to the maximum flooding surface above Bj5 of the Lower Bathonian (*Zigzagiceras zigzag* ammonite biozone) (Jacquin et al., 1998). Hallam (2001) argued that this transgression was eustatic, as there is evidence of sea level rise in Europe, South America and the Himalayas.

In terms of palaeoclimate, the Middle Jurassic in particular is increasingly being recognised as a 'cool mode' of the Jurassic (Korte et al., 2015). In Europe, oxygen isotope data from belemnites, bivalves and brachiopods, indicate that there was a cooling of seawater temperature of ~10°C across the Early–Middle Jurassic transition (Figure 13; Korte et al., 2015). Relatively cool temperatures persisted until the Bathonian, with possible short-term warm intervals in the latest Early Bajocian (Dera et al., 2011; Korte et al., 2015). The initiation of cooling through the Early–Middle Jurassic transition is thought to have been driven by the magmatic doming in the North Sea, which blocked water-mass exchange through the Viking Corridor, and resulted in the thermal isolation of the Boreal Sea (Korte et al., 2015).

The Middle Jurassic was also marked by perturbations in the carbon cycle. In particular, the Early Bajocian was marked by a positive $\delta^{13}C$ shift, which has been reported from central Italy (Bartolini et al., 1996, 1999; Bartolini and Cecca, 1999), the Isle of Skye, Scotland, (Jenkyns et al., 2002; Korte et al., 2015), Yorkshire, northern England (Hesselbo et al., 2003), southern Spain (O'Dogherty et al., 2006), northern France (Brigaud et al., 2009), Portugal (Suchéras-Marx et al., 2012; Giraud et al., 2016), south-eastern France (Suchéras-Marx et al., 2013), and most recently, Morocco (Bodin et al., 2017). A composite δ^{13}-carbonate curve for the Upper Aalenian–Lower Bathonian is shown in Figure 14.

3.3.1. The diversification and expansion of Watznaueria*, and the ecological dominance of* Dissiliodinium

The drivers behind the ecological and evolutionary patterns seen in phytoplankton during the Bajocian have been relatively well researched for the coccolithophores, but little attention has been paid to the dinoflagellate cysts. Existing work has linked the diversification and expansion of *Watznaueria* during the Late Aalenian to Early Bajocian to palaeoenvironmental changes. In particular, it has been demonstrated that the diversification and expansion of *Watznaueria* was coincident with the Europe-wide positive carbon isotope excursion (CIE), and an increase in biosiliceous sedimentation through the western Tethys (Figures 3, 4; Suchéras-Marx et al., 2015; Giraud et al., 2016; Aguado et al., 2017). The temporal coincidence between the positive $\delta^{13}C$ shift and increase in biosiliceous sedimentation in Europe may reflect a eutrophication of surface waters through the western Tethys during the Early Bajocian (Bartolini and Cecca, 1999; Bartolini et al., 1999; O'Dogherty et al., 2006).

This Early Bajocian phase of elevated nutrient levels has been invoked as the causal mechanism behind the diversification and expansion of *Watznaueria* (see Suchéras-Marx et al., 2015; Giraud et al., 2016; Aguado et al., 2017). Suchéras-Marx et al. (2015) suggested that the increase in the abundance of *Watznaueria,* and coccoliths as a whole (and the fact that *Watznaueria* did not directly replace other coccolith taxa), may reflect an increase in ecosystem-carrying capacity driven by enhanced nutrient levels. Moreover, the two-step pattern of the diversification of *Watznaueria* may represent an increase in nutrient levels, with the initiation of the expansion of *Watznaueria* triggered by the increase in nutrient levels. The second step reflects the acquisition of a bloom-forming ecological strategy by *Watznaueria brittanica* and *Watznaueria aff. Watznaueria manivitiae* (see Suchéras-Marx et al., 2015; Giraud et al., 2016).

Two possible scenarios have been invoked as the drivers behind an increase in nutrient levels through the Late Aalenian to Early Bajocian (Suchéras-Marx et al., 2015; Aguado et al., 2017). The first hypothesis is a switch to a more humid climate in the mid-palaeolatitudes during the Early Bajocian from an enhanced latitudinal temperature gradient, which led to increased continental weathering and nutrient flux. Although the Aalenian to Bathonian was a largely cool interval, oxygen isotopes record a shift to warmer temperatures in the *Stephanoceras humphriesianum* ammonite biozone of the latest Early Bajocian in Europe, indicating an increase in latitudinal temperature gradient between the mid and high palaeolatitudes (Figure 13; Korte et al., 2015). A humid climate mode in Europe during the Early Bajocian is evidenced by the switch from charcoal to coal as the dominant preservational mode of fossil wood through the Upper Aalenian to Lower Bajocian of the Cleveland Basin of Yorkshire (Hesselbo et al., 2003). Changes in clay mineral assemblages may also be indicative of a warm, humid climate. Brigaud et al. (2009) noted that clay mineral assemblages from the *Stephanoceras humphrieisianum* ammonite biozone of the Paris Basin contain around 20% kaolinite. In modern environments, kaolinite forms in humid tropical climates from intense chemical weathering, which led Brigaud et al. (2009) to argue that there was a change to a warmer, more humid, climate during the Early Bajocian. Rausik et al. (2001) and Raucsik and Varga (2008) documented clay mineral assemblages dominated by mixed-layer illite/smectite from the Lower Bajocian of the Mecsek Mountains of Hungary. Mixed-layer illite/smectite clays form in modern environments of warm, arid conditions punctuated by short, intense wet seasons; therefore, Raucsik and Varga (2008) argued the climate of the Early Bajocian in Europe was monsoon-like. Taken together, Sucheras-Marx et al. (2015) and Aguado et al. (2017) argued that these lines of geochemical, mineralogical and palaeontological evidence are indicative of a warm, humid climate during the Early Bajocian, which enhanced chemical weathering and increased the flux of biolimiting nutrients into the European Epicontinental Seaway. Moreover, Philippe et al. (2017) reported the northward spread of the low-latitude fossil-wood genus *Brachyoxylon* during the Early Bajocian, which may be indicative of a warming and/or an increase in humidity in the mid-latitudes.

The alternative scenario is an increase in surface water productivity driven by changes in enhanced upwelling and ocean circulation during the Early Bajocian. Dera et al. (2014) reported a marked positive shift in neodymium isotopes during the Aalenian–Bathonian, which these authors suggested may have been forced by a stronger influence of radiogenic Tethyan waters in the European epicontinental seaway. These authors argued that the widening of the Hispanic Corridor, combined with the restriction of the Viking Corridor may have promoted enhanced upwelling along the Tethyan margin, as evidenced by the positive neodymium isotope shift. Consequently, enhanced upwelling may have brought nutrient-rich waters into the photic zone and driven an increase in productivity.

Although these mechanisms are not mutually exclusive, recent work argues against the upwelling and ocean circulation hypothesis. Aguado et al. (2017) noted that the expansion of *Watznaueria* through the Early Bajocian was concomitant with a decline in the coccolith *Crepidolithus crassus* (Figure 4). This species is characterised by thick, robust coccoliths, which has been interpreted as reflecting a deep-dwelling ecological strategy, as the thick coccoliths act to ballast the coccosphere, while increase the refractive index with water, and thus allowing a greater amount of light to pass into the cell (Aguado et al. 2017). As such, the decline in the abundance of this deep-dwelling species is more consistent with a shallowing of the nutricline from increase continental runoff, rather than an increase in nutrients supplied from upwelling deep waters (Aguado et al. 2017).

The Early Bajocian eutrophication event has not previously been considered in the context of dinoflagellate ecology and evolution. However, given the diversification and ecological dominance of *Dissiliodinium* in several regions, it is possible that this pattern also reflects a response to elevated nutrient levels, particularly as the acme of this genus in the Early Bajocian is synchronous with the positive carbon isotope excursion (Figure 15). Moreover, the palaeoenvironmental distribution and palaeoecological preferences of *Dissiliodinium* may indicate an increase in nutrient levels from enhanced runoff in the mid-palaeolatitudes during the Early Bajocian. In Europe, *Dissiliodinium giganteum* appears to have thrived in palaeoenvironments which were in close proximity to terrestrial discharge (Wiggan et al., 2017). Moreover, this species is typified by a large size (~100 µm). As such, *Dissiliodinium giganteum* may have proliferated under high-nutrient conditions (Wiggan et al. 2017), as large phytoplankton cells require high nutrient levels due to the diffusion limitation of nutrient uptake (Marañón, 2015). Moreover, *Dissiliodinium caddaense* is also typified by a large size (~150 µm; Helby et al., 1987) and is recorded in abundance from the Athol Formation of Australia, which was deposited in a nearshore depositional setting (Riding et al., 2010b). These data suggest that, like *Dissiliodinium giganteum*, *Dissiliodinium caddaense* was adapted to high nutrient levels, and could tolerate lowered salinities. Similarly, *Dissiliodinium psilatum* appears to show similar morphological and ecological adaptations. In the Lower Bajocian of Argentina, *Dissiliodinium psilatum* dominates assemblages in the marginal/deltaic palaeoenvironments of the Neuquén Basin (Stukins et al., 2013). *Dissiliodinium psilatum* is of comparable morphology to *Dissiliodinium giganteum* and, although slightly smaller, is still relatively large with an average width of 80 µm (Prauss, 1989). The abundance of this species in nearshore and deltaic deposits indicates it could have tolerated reduced salinities, and the proximity to terrigenous discharge and its relatively large size indicate an adaption to high nutrient levels. The proliferation of *Dissiliodinium* in palaeoenvironments close to sources of terrestrial discharge through the Early Bajocian could have been driven by enhanced runoff, and as such palynological data suggest that a shallowing of the nutricline from enhanced weathering may have driven by the Early Bajocian positive CIE.

3.3.2. The Bajocian radiation of dinoflagellate cysts

To date, few works have attempted to link the Bajocian dinoflagellate radiation to wider Middle Jurassic climatic or oceanographic changes. Feist-Burkhardt and Götz, (2016) suggested that the Bajocian radiation may have been related to opening of the Atlantic Ocean, and changes in ocean circulation. Recently, Wiggan et al. (2017) argued that the pattern of dinoflagellate cyst first appearances in northwest Europe was controlled by transgression. These authors noted that, in the Swabian Basin of southern Germany, the main influx of first appearances was associated with a palaeoenvironmental trend to more distal, offshore conditions. In turn, this palaeoenvironmental trend reflects the T7 second-order transgression.

We have compared the dinoflagellate cyst stratigraphical data from Europe to sequence stratigraphical records. These data demonstrate a correlation between the increase in dinoflagellate cyst diversity and sea level rise through the Bajocian (Figure 16). Moreover, at a zonal level, the large number of appearances recorded from the *Stephanoceras humphriesianum* and *Parkinsonia parkinsoni* ammonite biozones correspond to pronounced third-order transgressive pulses, the latter of which (cycle Bj5) represents the maximum transgression of the T7 cycle (Figure 17). Appearances of taxa through the Late Aalenian to Early Bathonian could therefore have been brought into the European Epicontinental Seaway by transgressive waters, as indicated by the correlation between large numbers of appearances and transgressive pulses around the *Stephanoceras humphriesianum* and *Parkinsonia parkinsoni* ammonite biozones. Further, in addition to sea-level rise, changes in ocean circulation related to the widening of the Hispanic Corridor and thermal doming in the Viking Corridor may have influenced the pattern of dinoflagellate cyst appearances. Due to the restriction of the Viking Corridor, the main path for the passive dispersal of dinoflagellates would have been to the south, from the northwest Tethys Ocean, and the Hispanic Corridor. The widening of the Hispanic Corridor, and rise in sea level may have driven a rapid influx of gonyaulacacean taxa into Europe during the Bajocian, as intervals of higher sea level can promote the interconnectivity and floral interchange between ocean basins (van de Schootbrugge et al., 2005). As such, enhanced water-mass transfer may have increased floral interchange between the European Epicontinental Seaway, the northwestern Tethys and the Panthalassa Ocean via the Hispanic Corridor. This idea is supported by the occurrence of typically European dinoflagellate cyst taxa, such as *Dissiliodinium psilatum* in Argentina (Stukins et al., 2013). Additionally, climatic factors may have also influenced the pattern of appearances in Europe. A brief interval of warming occurred in the *Stephanoceras humphriesianum* ammonite biozone in Europe. As this zone also corresponds to a major influx of gonyaulacacean taxa, warmer seawater temperatures, coupled with sea-level rise, could have promoted the spread of taxa from lower palaeolatitude Tethyan regions into the European Epicontinental Seaway. Further, the temporal coincidence between climatic warming and transgression in the *Stephanoceras humphriesianum* ammonite biozone may indicate a common cause via a glacioeustatic control on third-order sea level oscillations.

The correlation between the increase in dinoflagellate cyst diversity and sea level rise suggests that an increase in the area of epicontinental seas may have directly driven the radiation of dinoflagellates, via an increase in available ecospace. Indeed, cyst-forming dinoflagellates predominantly inhabit shallow seas as cyst formation is most viable in water depth of <200 m (Fensome et al., 1996). However, while the preceding Aalenian was a largely regressive interval in Europe, sea level was relatively high globally (Hallam, 2001), yet gonyaulacaceans were low in diversity through the Aalenian (Feist-Burkhardt and Pross, 2010). As such, it does not appear that sea level directly drove the diversification of gonyaulacacean dinoflagellates. Furthermore, the Late Pliensbachian was a critical interval of dinoflagellate evolution even though it was a time of widespread regression (van de Schootbrugge et al., 2005). Similarly, the earliest Jurassic was marked by a widespread marine transgression during the Hettangian, yet dinoflagellate cysts were extremely low in diversity through this interval (Figure 1; Hallam, 2001; van de Schootbrugge et al., 2013).

Dinoflagellates appear to have diversified markedly during cool intervals of the Jurassic (Riding and Michoux 2013). The major pulse of dinoflagellate diversification during the Late Pliensbachian was linked to a phase of climatic cooling, which may have increased upper-ocean turbulence and enhanced vertical mixing, with an increase in bottom-water ventilation, creating conditions ideal for cyst-forming dinoflagellates (van de Schootbrugge et al., 2005). Given that the Aalenian–Bathonian was a time of predominantly cool temperatures in Europe (with the possible exception of the *Stephanoceras humphriesianum* ammonite biozone), a similar situation may have prevailed during the Bajocian. However, the Late Pliensbachian was marked by the incursion of high palaeolatitude Boreal taxa into Europe (Bucefalo Palliani and Riding, 1997). In contrast, in the Bajocian, gonyaulacaceans appear to have formed a comparatively minor component of dinoflagellate cyst floras in the high palaeolatitudes (Figure 9; Davies, 1983). Furthermore, there is a ~5 myr gap between the cooling across the Early–Middle Jurassic transition and the diversification of gonyaulacaceans in the Bajocian (Figure 13). Thus, there is no obvious temporal link between cooling climate and the diversification of gonyaulacaceans which suggests that climate did not drive the diversification of gonyaulacacean dinoflagellates during the Middle Jurassic.

Palaeoclimatic and palaeoceanographic changes appear to have controlled the stratigraphical pattern of the Bajocian radiation, as well as influencing palaeoecological patterns seen within dinoflagellate cyst floras. However, these factors do not appear to form the underlying driver of diversification. It is notable, however, that the diversity of dinoflagellates and coccolithophores through the Early–earliest Middle Jurassic broadly mirrors that of benthic and pelagic metazoans, suggesting a coupling between phytoplankton and metazoan evolution (Figure 18). The Mesozoic oceans were characterised by the escalatory evolution of predators and their prey, encapsulated in the concept of the Mesozoic Marine Revolution (Vermeij, 1977; 1987; 2008). Although the concept of the Mesozoic Marine Revolution was originally applied to the Cretaceous, it has since been realised that many of the escalation-related adaptions appeared through the Late Triassic to Early Jurassic (Harper et al., 1998; Vermeij, 2008). Notably, during the Middle Jurassic, important ecological and evolutionary changes occurred in planktivorous metazoans. The trophic guild of giant suspension feeding fishes first appeared in the Middle Jurassic, and the earliest fossil evidence of this group comes from the Bajocian (Friedman et al., 2010). Within other nekton, the Late Aalenian to Early Bajocian was characterised by the extinction of ammonite families that dominated Early Jurassic ammonite faunas, and their replacement by families that dominated through the Middle Jurassic (Figure 18; Sandoval et al., 2001). Moreover, the Bajocian was marked by the first appearance of heteromorph ammonites (O’Dogherty et al., 2006). Evidence from buccal morphology and fossilised food remains indicates that diet of both heteromorph and planispiral ammonites included mesozooplankton (Jäger and Fraaye, 1997; Kruta et al., 2011). Given the turnover within ammonites, and the appearance of giant suspension feeding fishes, these patterns may indicate that important evolutionary and ecological changes occurred within mesozooplankton communities. Although the fossil record of mesozooplankton is extremely sparse (Selden et al., 2010), it is notable that many of the gonyaulacacean dinoflagellate cyst taxa that appeared through the Bajocian were characterised by thick walls and/or an ornament of sutural crests/spines e.g. *Acanthaulax*, *Aldorfia*, *Ctenidodinium, Gonyaulacysta* and *Meiourogonyaulax* (Figure 10); perhaps such morphological developments served as defensive adaptations (Sarjeant et al., 1987). Additionally, the presence of dinoflagellate cysts in zooplankton fecal pellets suggests that their predation, although, little-considered, may be an important factor in dinoflagellate ecology (Persson, 2000; Montresor et al., 2003). Given the temporal coincidence between phytoplankton diversification and groups of planktivorous cephalopods and fishes, these phenomena may reflect an underlying ecological driver to the Bajocian radiation, with connecting links provided by the mesozooplankton. Viewed in this light, the Middle Jurassic dinoflagellate radiation might represent a largely-overlooked component of the Mesozoic Marine Revolution.

4. Conclusions

Both dinoflagellates and coccolithophores underwent a major radiation through the Middle Triassic to Middle Jurassic. Within this longer-term radiation, important short-term intervals of ecological and evolutionary change can be recognised. The Bajocian of the Middle Jurassic was characterised by a major ecological transition in coccoliths and the rapid diversification of gonyaulacacean dinoflagellate cysts. The rise to ecological dominance of the coccolith genus *Watznaueria* during the Early Bajocian appears to have been driven by an increase in nutrient levels from enhanced continental weathering. These changes in coccolith floras were paralleled among dinoflagellate cysts by the ecological dominance of the genus *Dissiliodinium* in several mid-palaeolatitude epicratonic basins. The interval of Early Bajocian palaeoenvironmental changes has so far only been documented from Europe and North Africa, which during the Jurassic were located on the northwestern border of the Tethys Ocean. Thus, the global extent of these phenomena remain unclear. However, the Early Bajocian acme of *Dissiliodinium* in Australia and Argentina may suggest that an increase in weathering flux also occurred in the mid-palaeolatitudes of the Southern Hemisphere. Future work could focus on documenting the Bajocian carbon isotope record from areas that lay outside of the northwestern Tethys region to accurately assess whether there was a global shift in the carbon cycle during the Early Bajocian. Moreover, the generation of high resolution osmium and strontium isotope records for the Early Bajocian would provide insight into the extent of weathering increase through this interval, in much the same way that these tracers have been employed for examining hydrological cycling during the Toarcian OAE.

The Bajocian was marked by a significant increase in the diversity of gonyaulacacean dinoflagellate cysts, marking the transition to ecological dominance of the Gonyaulacaceae within cyst-forming dinoflagellates. Thus, the Bajocian represents an important ecological transition for dinoflagellates as well as for coccolithophores. However, this radiation remains poorly documented outside of Europe and Australia. Within Europe, the stratigraphical pattern of the radiation of dinoflagellate cysts appears to have been controlled by sea level, with rising sea level and changes in ocean circulation bringing newly emerging taxa into the European Epicontinetal Seaway, by a combination of enhanced water-mass transfer and the spread of marine palaeoenvironments. However, whereas oceanographic changes may have controlled the pattern of dinoflagellate cyst appearances in Europe, they may not have been the underlying driver of diversification. The preceding Aalenian was marked by large volumes of flooded continental area, yet gonyaulacacean diversity was low. Moreover, while gonyaulacaceans appear to have diversified during a 'cool mode' of Jurassic climate, there is a ~5 my gap between rapid cooling through the Early–Middle Jurassic transition and the radiation of gonyaulacaceans during the Bajocian. Furthermore, the Gonyaulacaceae do not appear to have formed a large component of dinoflagellate cyst floras at high palaeolatitudes during the Bajocian. While climatic and oceanographic factors do not appear to have driven the diversification of gonyaulacaceans, the temporal coincidence between the radiation of dinoflagellates, coccolithophores and multiple trophic levels of benthic and pelagic metazoans may point towards an underlying ecological driver. Knoll and Follows (2016) suggested that the radiation of mixotrophic dinoflagellates through the Mesozoic may have provided a bottom-up mechanism to the Mesozoic Marine Revolution, by enhancing primary production. However, many of the morphological features to appear in dinoflagellate cysts through the Bajocian could be interpreted as defensive mechanisms, which might reflect a co-evolutionary escalation between the primary producers and their immediate consumers, the micro- and mesozooplankton. As such, the radiation of dinoflagellates during the Bajocian might represent an important, but largely overlooked component of the Mesozoic Marine Revolution. Although mesozooplankton represent the most important trophic link between the phytoplankton and higher trophic levels, they have an extremely sparse fossil record. However, 'zooclasts', fragments of metazoans, particularly arthropods, are relatively common in Phanerozoic palynomorph assemblages (e.g. Tyson, 1995). Whereas these small carbonaceous fossils have provided a wealth of palaeobiological insight into the Proterozoic–Phanerozoic transition (e.g. Butterfield and Harvey, 2012), including the first record of the copepods (Harvey et al., 2012; Harvey and Pedder, 2013), they are a relatively unexplored source of micropaleontological data for the Mesozoic and Cenozoic. In part, this is because traditional palynological processing methods may destroy these comparatively delicate organic microfossils (Butterfield and Harvey, 2012). Future work may more closely compare the fossil record of phytoplankton with that of pelagic metazoans such as ammonites and fish, and examine Mesozoic rocks for small carbonaceous fossils in order to link the phytoplankton record to that of the zooplankton, which in turn could be linked to higher trophic levels.

Regardless of driving mechanisms, the Bajocian was a critical interval of ecological and evolutionary changes within the dinoflagellates and coccolithophores, and represents an important step within the wider early Mesozoic phytoplankton radiation, which may in turn form part of the wider Mesozoic Marine Revolution.

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References

Display material captions:

Figure 1. Dinoflagellate cyst and coccolith species richness throughout the Middle Triassic to Jurassic modified from Wiggan et al. (2017, fig. 1). The family-level spindle plot for dinoflagellate cysts clearly shows the significant increase in diversity of the family Gonyaulaceae during the Bajocian. Key bioevents for coccolithophores are indicated, notably the evolution of placolith coccoliths in the Pliensbachian, and the ecological transition to the dominance of *Watnzaueria* in the Bajocian. The dinoflagellate cyst species richness is taken from MacRae et al. (1996), the spindle plot data is after Fensome et al. (1996) and the coccolith species richness is after Bown et al. (2004).

Figure 2. Coccolith abundances and $\delta^{13}C$ for the Upper Aalenian to Lower Bajocian marls of the Subalpine Basin, France. Note that the increase in the absolute and relative abundances of *Watznaueria* through the Lower Bajocian parallels the increase in $\delta^{13}C$. There is also a shift

in the absolute abundance of coccoliths as a whole from 107–108 coccoliths per g in the uppermost Aalenian to lowermost Bajocian, to 108–109 coccoliths per g in the uppermost Lower Bajocian. Modified from Suchéras-Marx et al. (2015, fig. 4).

Figure 3. Synthetic relative abundances of three important morphogroups of the coccolithophore genus *Watznaueria* through the Upper Aalenian to Lower Bathonian from Giraud et al. (2016). Note that at the Aalenian–Bajocian transition, there is an increase in taxa defined by a central cross area. This is then followed by an increase in the abundances of taxa without a central area, and those with a central bar. This increase in the abundance of *Watznaueria* is concomitant with a long-term decline in the abundance of *Lotharingus*. Abundances after Giraud et al. (2016, fig. 8) and coccolith morphologies after Giraud et al. (2016, fig. 2). Ammonite biozone abbrevations: L.m. = *Ludwigia murchisonae*; G.c = *Graphoceras concavum*; H.d. = *Hyperlioceras discites*; W.l. = *Witchellia laeviuscula*; S.p. = *Sonninia propinquans*; S.h. = *Stephanoceras humphriesianum*; S.n. = *Strenoceras niortense*; G.g. = *Garantiana garantiana*; P.p. = *Parkinsonia parkinsoni*; Z.z. = *Zigzagiceras zigzag*; P.a. = *Procerites aurigerus*; P.p. = *Procerites progracilis*, T.s. = *Tulites subcontractus*; M.m. = *Morrisiceras morrisi*; H.r. = *Hecticoceras retrocostatum*; C.d. = *Clydoniceras discus*.

Figure 4. Coccolith abundances and $\delta^{13}C$ for the Upper Aalenian to Lower Bajocian of the southern Iberian palaeomargin, Spain modified after Aguado et al. (2017, fig. 2). Note the increase in the absolute abundance of *Watznaueria* which parallels an increase in $\delta^{13}C$. The increase in the abundance of *Watznaueria* is concomitant with the decline in the abundance of *Crepidolithus crassus*, a coccolith which has been interpreted as inhabiting the deep photic zone.

Figure 5. Absolute abundances of *Dissiliodinium giganteum* through the Lower Bajocian of borehole B404-2 in southern Germany based on raw data from Wiggan et al. (2017). *Dissiliodinium giganteum* forms a significant proportion (>80%) of the dinoflagellate cyst assemblages throughout the *Witchellia laeviuscula* ammonite biozone, but declined in abundance towards the uppermost Lower Bajocian (*Stephanoceras humphriesianum* ammonite biozone). Two specimens of *Dissiliodinium giganteum* are shown to the left. The

upper specimen is in apical view; the loss of multiple precingular plates during archaeopyle formation can be observed. The lower image is in dorsoventral view. The scale bar represents 10 µm.

Figure 6. The location and relative abundances of *Dissiliodinium* through the mid palaeolatitudes during the Early Bajocian. *Dissiliodinium giganteum* is abundant in basins which bordered the northwest Tethys Ocean on the edge of the European Epicontinental Seaway (i.e. southern Germany, Poland/northern Slovakia and Switzerland). *Dissiliodinium caddaense* is abundant in the Lower Bajocian of Australia, and *Dissiliodinium psilatum* is abundant in the Lower Bajocian of the Neuquén Basin, Argentina. The abundances of *Dissiliodinium giganteum* are based on raw data in Wiggan et al. (2017) and unpublished information. The abundances of *Dissiliodinium caddaense* are based on raw data from Riding et al. (2010b). The abundances of *Dissiliodinium psilatum* are based on raw data from Stukins et al. (2013). The palaeogeography is modified after Scotese (2014).

Figure 7. The stratigraphical ranges of dinoflagellate cysts from the uppermost Aalenian to the lowermost Bathonian of northwest Europe based on data from Wiggan et al. (2017). Note that there is a relatively continuous pattern of first appearances, but there are numerous first appearances in the *Stephanoceras humphriesianum* ammonite biozone (S.h.). The grey fill denotes dinoflagellate cyst taxa which belong to the family Gonyaulacaceae. The ammonite biozone abbreviations are as per Figure 3.

Figure 8. The stratigraphical ranges of dinoflagellate cysts from the uppermost Lower Bajocian to the lowermost Bathonian of northwest Europe based on data from Wiggan et al. (2017). Note the large number of first appearances in the *Stephanoceras humphriesianum* (S.h.) and *Parkinsonia parkinsoni* (P.p.) ammonite biozones. First appearances from the *Stephanoceras humphriesianum* zone upwards are dominated by gonyaulacacean taxa (grey fill). The ammonite biozone abbreviations are as per Figure 3. F-B & M (1997) = Feist-Burkhardt and Monteil (1997).

Figure 9. A dinoflagellate cyst species richness curve from the latest Aalenian to the earliest Bathonian based on stratigraphical data from Wiggan et al. (2017). Note how the increase in diversity is primarily driven by a rise in the number of gonyaulacacean taxa (grey). There are also pronounced increases in species richness in the *Stephanoceras humphriesianum* and *Parkinsonia parkinsoni* ammonite biozones.

Figure 10. Percentage of gonyaulacacean dinoflagellate cyst taxa for the Bajocian and Bathonian low-, mid-, and high-palaeolatitude regions. It is clear that gonyaulacaceans formed a larger proportion of the dinoflagellate cyst floras in the low- to mid-palaeolatitudes than the high-palaeolatitudes during the Middle Jurassic. The graph is based on raw data from: Bujak and Williams (1977) (eastern Canada); Davies (1983) (Arctic Canada); Conway (1990) (Israel); Ibrahim et al. (2003) (Egypt); Mantle and Riding (2012) (Australia); Stukins et al. (2013) (Argentina); and Wiggan et al. (2017) (northwest Europe).

Figure 11. The diversity and disparity of gonyaulacacean dinoflagellate cyst taxa from the Aalenian and Bajocian. Note how, in the Aalenian, the Gonyaulaceae were represented by four genera, all of relatively simple morphology and largely nontabulate (i.e. not exhibiting tabulation). *Batiacasphaera, Kallosphaeridium* and *Sentusidinium* all have apical archaeopyles, whilst *Dissiliodinium* has a multiplate precingular archaeopyle. In the Bajocian, the earliest fully tabulate sexiform gonyaulacaceans appeared, represented by *Durotrigia daveyi*. The taxa also typically developed thick, ornamented cyst walls (e.g. *Acanthaulax, Aldorfia*), and prominent sutural crests (e.g. *Ctendidodinium, Meiourogonyaulax*). Moreover, the single-plate precingular archaeopyle appeared in genera such as *Acanthaulax, Aldorfia* and *Gonyaulacysta*, which has remained a prominent excystment strategy in gonyaulacaceans to the present day. Similarly, the epicystal archaeopyle type appeared in genera such *Ctendodinium, Korystocysta* and *Wanaea*.

Figure 12. Global palaeogeography for the Bajocian and Bathonian, modified from Scotese (2014). The Middle Jurassic was marked by changes in the configuration of important ocean gateways. Through the Early–Middle Jurassic transition, magmatic doming in the North Sea restricted the marine connection through the Viking Corridor, which linked the European

Epicontinental Seaway (EES) to the Boreal Sea (Korte et al., 2015). During the Bajocian, enhanced seafloor spreading and a change in plate relative motions drove a widening and deepening of the Hispanic Corridor, which linked the Tethys to the Panthalassa (Labails et al., 2010).

Figure 13. Bajocian second-order and third-order sea level cycles, after Jacquin et al. (1998). The Bajocian was characterised by the T7 second-order transgression, which lasted from the latest Aalenian *Graphoceras concavum* ammonite biozone to the earliest Bathonian *Zigzagiceras zigzag* ammonite biozone. Maximum transgression is represented by the maximum flooding surface above third-order boundary Bj5 (the dotted line). In the Tethyan Realm, the T7 transgression was represented by a single pulse, whereas in the Boreal Realm, this transgression comprised two distinct pulses.

Figure 14. Seawater palaeotemperatures based on the δ^{18}O of brachiopod and mollusc carbonate for the Lower and Middle Jurassic (Pliensbachian–Bajocian) of Europe redrawn after Korte et al. (2015, fig. 2). It is clear that a shift to cooler palaeotemperatures of ~10°C occurred through the Early–Middle Jurassic transition. The pronounced warming pulse in the latest Early Bajocian corresponds to the *Stephanoceras humphriesianum* ammonite biozone.

Figure 15/16 (obviously this will be #15 if you accept amalgamation). The central column depicts a composite δ^{13}C curve for bulk carbonate from the Upper Aalenian to Lower Bathonian of Europe based on raw data from O'Dogherty et al. (2006) and Suchéras-Marx et al. (2013). Note the shift to more positive values of ~1.5 ‰ δ^{13}C in the Lower Bajocian. The right hand panel illustrates the abundance of the dinoflagellate cyst *Dissiliodinium giganteum* in the Swabian Basin of southern Germany taken from Wiggan et al. (2017) and supplemented by unpublished data. Note that the acme of *Dissiliodinium giganteum* is coeval with the positive shift in δ^{13}C.

THIS MAY NOW BE REDUNDANT. Figure 16. Comparison of composite δ^{13}C records from Europe to *Dissiliodinium giganteum* abundances from the Swabian Basin. Note that the acme of *D. giganteum* is synchronous with the positive shift in carbon isotopes. Carbon isotope data as per Figure 14, *D. giganteum* abundances from Wiggan et al. (2017) and unpublished data.

Figure ?17?. A comparison of sequence stratigraphy, sea level and dinoflagellate cyst species richness throughout the Bajocian. Note how the increase in species richness roughly parallels the rise in sea level. The ammonite biozone abbreviations are as per Figure 3. The sea level cycles are as per Figure 12. The stratigraphy and sea level were generated using Timescale Creator v.6.4.2 (?INCLUDE REFERENCE/WEB ADDRESS ETC.?).

Figure ?18?. The stratigraphical ranges of dinoflagellate cysts and sea level cycles for northwest Europe. The data are taken from Figs. 7, 8, 12. It is clear that the large number of first appearances from the *Stephanoceras humphriesianum* (S.h.) and *Parkinsonia parkinsoni* (P.p.) ammonite biozones correspond to the pronounced third-order transgressive pulses Bj2 and Bj5. The ammonite biozone abbreviations are as per Figure 3.

Figure 19. Species richness curves and the appearances of key marine fossil groups for the Early and Middle Jurassic. It is clear that the species richness curves of coccoliths and dinoflagellate cysts closely parallel those from higher trophic levels. All groups are plotted per stage/substage, except for the ammonites which are plotted per ammonite biozone. Coccolith and dinoflagellate cyst species richness data were taken from Figure 1. The planktonic foraminifera data are from Simmons et al. (1997). The bivalve data are those of Hallam (1976). Data from bryozoans are from Taylor and Ernst (2008). The elasmobranch diversity is after Guinot and Cavin (2015). The belemnite information is after Dera et al. (2016), and the ammonite data are from Sandoval et al. (2001) and O’Dogherty et al. (2006). The range of giant suspension feeders is after Friedman et al. (2010).