

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

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12 ABSTRACT

13 Dinoflagellates and coccolithophores are two of the most important groups of phytoplankton
14 in the modern oceans. These groups originated in the Triassic and radiated through the early
15 Mesozoic, rising to ecological prominence. Within this long-term radiation, important short-
16 term intervals of evolutionary and ecological change can be recognised. The Bajocian
17 (Middle Jurassic, ~170–168 Ma) was characterised by an important ecological transition
18 within the coccolithophores, and the radiation of one of the principal families of cyst-forming
19 dinoflagellates, the Gonyaulacaceae. During the Early Bajocian, the coccolith genus
20 *Watznaueria* diversified and expanded ecologically to dominate coccolith floras, a situation
21 which continued for the remainder of the Mesozoic. This pattern was paralleled within
22 dinoflagellate cyst floras by the ecological dominance of the genus *Dissiliodinium* in the mid-
23 palaeolatitudes. These phenomena appear to be linked to a positive carbon isotope shift, and

24an interval of enhanced productivity driven by a shift to a more humid climate, enhanced
25continental weathering and nutrient flux, or by changes in ocean circulation and upwelling.
26The latest Early Bajocian to earliest Bathonian was then characterised by the rapid increase in
27diversity of dinoflagellate cysts within the family Gonyaulacaceae. Through this interval, the
28Gonyaulacaceae transitioned from being a relatively minor component of dinoflagellate cyst
29floras, to becoming one of the prominent groups of cyst-forming dinoflagellates, which has
30persisted to the Holocene. In Europe, the pattern of this radiation was strongly influenced by
31sea level, with the increase in gonyaulacacean diversity reflecting a major second-order
32transgression. On a finer scale, the main pulses of first appearances correlate with third-order
33transgressive episodes. A rise in sea level, coupled with changes in the tectonic configuration
34of ocean gateways, appears to have controlled the pattern of plankton diversification in
35Europe. These palaeoceanographic changes may have enhanced water-mass transfer between
36Europe, the northwest Tethys Ocean and the Hispanic Corridor, which promoted the floral
37interchange of dinoflagellates. Whilst sea level rise and associated large-scale
38palaeoenvironmental shifts appear to have controlled the pattern of dinoflagellate cyst
39appearances in several regions outside Europe, there is no direct correlation between
40dinoflagellate cyst diversity and sea level rise on a global scale. Although the Bajocian was
41transgressive in several regions, widespread flooded continental area was also present
42throughout the preceding Aalenian, an interval of low gonyaulacacean diversity. Moreover,
43although the Middle Jurassic was an interval of major climatic cooling, there was a ~5 myr
44gap between the onset of cooling and the radiation of gonyaulacaceans during the Bajocian.
45The Bajocian was, however, marked by a major evolutionary radiation in the pelagic realm,
46including ammonites, giant suspension feeding fishes and planktonic foraminifera. These
47phenomena may indicate an underlying ecological driver to the radiation of dinoflagellates

48during the Bajocian evolutionary explosion which could represent an extension of the
49Mesozoic Marine Revolution.

50Keywords: dinoflagellates; coccolithophores; radiation; Mesozoic Marine Revolution

51

521. Introduction

53 Dinoflagellates and coccolithophores are two of the most important groups of primary
54producers in the modern oceans, forming a significant part of the base of ocean food webs.
55Moreover, the downward flux of phytoplankton to the interior of the oceans forms a
56significant component of the biological pump. Dinoflagellates and coccolithophores are part
57of the polyphyletic ‘red lineage’ of phytoplankton, as they utilize chlorophyll *c* as a primary
58accessory pigment (Falkowski et al., 2004a).

59 While it has been argued that on the basis of molecular and biogeochemical evidence,
60the coccolithophores and dinoflagellates have a Neoproterozoic origin, they are essentially a
61product of the post-Palaeozoic world, rising to ecological prominence through the Mesozoic
62(Fensome et al., 1996; Falkowski et al., 2004a, 2004b; Bown, 2005; Janoušek et al.,
632017). The early Mesozoic, defined here as the Middle Triassic to Middle Jurassic (~247–164
64Ma), represents a critical interval in the evolution of the modern phytoplankton, when the
65coccolithophores and dinoflagellates emerged and underwent major evolutionary radiations
66(Fensome et al., 1996; Falkowski et al., 2004b; Bown et al., 2004). While many authors have
67reviewed the broad macroecological and macroevolutionary trajectories of the eukaryotic
68phytoplankton during the Mesozoic–Cenozoic (e.g. Bown et al., 2004, Falkowski et al.,
692004a,b, Bown, 2005, Falkowski and Knoll 2007), many short-term diversifications within
70this broader radiation remain poorly documented.

71 In this contribution, we review the pattern of coccolithophore and dinoflagellate
72 evolution through the early Mesozoic, primarily from the perspective of the fossil record,
73 focussing on the Bajocian (Middle Jurassic, ~170–168 Ma [Ogg et al., 2016]). The driving
74 mechanisms behind ecological and evolutionary change in phytoplankton during the Bajocian
75 remain poorly understood, but it is clearly a critical interval in the evolutionary history of the
76 two groups. During the Bajocian, coccolith floras became ecologically dominated by the
77 genus *Watznaueria*, a condition that prevailed for the remainder of the Mesozoic (Giraud et.
78 al., 2016; Aguado et al., 2017). Among the dinoflagellates, the Bajocian was characterised by
79 the diversification of the family Gonyaulacaceae, which became one of the most prominent
80 groups of encysting dinoflagellates ranging through to the present day (Fensome et al., 1996;
81 Feist-Burkhardt and Götz, 2016; Wiggan et al., 2017). To set the Bajocian radiation in
82 context, we provide an overview of the coccolith and dinoflagellate cyst fossil records,
83 documenting the evolutionary history of the two groups from their emergence in the Triassic
84 to their radiation through the Early–Middle Jurassic.

85

86 1.1. *Dinoflagellates*

87 Dinoflagellates are a diverse group of flagellated eukaryotes, represented by around 2,400
88 extant species, of which ~2000 are marine plankton (Fensome et al., 1996; de Vernal and
89 Marret, 2007; Janouškovec et al., 2017). Dinoflagellates are characterised by the possession
90 of a unique nucleus, the dinokaryon; and/or by having a life cycle stage with two dissimilar
91 flagella, one transverse and one longitudinal, which allow the motile cell to propel itself
92 through water (Fensome et al., 1996). The group can be broadly split into naked and thecate
93 forms. Thecate (or armoured) dinoflagellates have a series of cellulosic plates held within
94 vesicles (alveolae) in the cortex (amphiesma) of the cell. The arrangement of the thecal plates

95forms a pattern, known as tabulation, tends to be consistent within taxa and is thus a critical
96feature in dinoflagellate classification (Dale, 1983; Evitt, 1985; Fensome et al., 1993, 1999;
97Janouškovec et al., 2017). It is usually reflected, at least partially, on the cysts that comprise
98the vast majority of fossil dinoflagellates. Thus, tabulation is used to classify both fossil and
99living dinoflagellates (Fensome et al., 1993).

100Around half of all dinoflagellates are autotrophic or mixotrophic and, together with the
101diatoms and coccolithophores, are responsible for a significant proportion of primary
102production in the world's oceans (Delwiche, 2007). Heterotrophic dinoflagellates are an
103important component of the microzooplankton (Calbet, 2008). Around 13% of modern
104dinoflagellate species produce a zygotic resting cyst (Head, 1996). The wall of most
105preservable dinoflagellate cysts is composed of the complex macromolecule dinosporin
106(Head, 1996; Bogus et al., 2014). The fossil record of dinoflagellates is based on their
107(refractory) resting cysts, adding a layer of complexity to the dinoflagellate fossil record with
108respect to other phytoplankton groups, as the dinoflagellate motile stage is virtually never
109preserved, as the theca is extremely labile (Evitt, 1985; Versteegh et al., 2004). With only
110around 13% of living motile species producing preservable cysts, the dinoflagellate cyst
111fossil record is inherently incomplete, and it is not known whether this percentage has
112changed through time (Head, 1996; Fensome et al., 1996; Riding and Lucas-Clark 2016).

113 Some earlier workers cast doubt on the ability of a highly selective fossil record to
114shed light on dinoflagellate evolution (Evitt, 1985). However, some higher taxa are far better
115represented than others in the record, notably the orders Gonyaulacales and Perdiniales
116(Fensome et al., 1999; de Vernal and Marret, 2007). Such groups have a much richer and
117more extensive fossil record than would be suggested by the low overall proportion of
118encysting dinoflagellates in the Recent (Fensome et al., 1999). Utilising patterns of
119dinoflagellate cyst occurrences in the fossil record (Fensome et al. 1996) along with quasi-

120cladistic analyses of all dinoflagellates (i.e. the basis of the phylogenetic classification of
121Fensome et al. [1993]) provide significant evidence for the general evolutionary pattern. For
122example, that the appearance and expansion of dinoflagellates during the early Mesozoic is a
123true evolutionary radiation is compellingly shown by the extent of morphological
124‘experimentation’, particularly in the Early–Middle Jurassic. Moreover, the mixing of
125features in individual taxa that would subsequently characterise separate higher-level taxa
126(e.g. *Nannoceratopsis* is part dinophysialean and part peridiniphycidean) and later
127morphological innovations becoming restricted to lower taxonomic ranks (Piel and Evitt,
1281980; Fensome et al, 1996). The latest molecular data supports this general scenario, as
129tentatively does biogeochemical data (Janouškovec et al. 2016).

130 The radiation of dinoflagellates through the early Mesozoic was characterised by the
131appearance of stem forms with a gonyaulacoid-peridinoid tabulation, and ultimately by crown
132thecate clades, such as the Gonyaulacales and Peridiniales (Fensome et al., 1996;
133Janouškovec et al., 2017). The increase in dinoflagellate cyst diversity through the Mesozoic
134was accompanied by a synchronous increase in the abundance of dinosteranes in Mesozoic
135sedimentary rocks (Moldowan et al., 1996). Triaromatic dinosteranes are types of lipid
136biomarkers derived from dinosterols, and are primarily associated with dinoflagellates
137(Moldowan and Talyzina, 1998). However, recent molecular phylogenetic research has
138revealed that the acquisition of dinosterols within the dinoflagellate lineage occurred during
139the Mesozoic, shedding doubt on the reliability of dinosteranes as an unequivocal biomarker
140for dinoflagellates in pre-Mesozoic rocks (Janouškovec et al., 2017). Despite this, the
141concomitant increase in the abundance of dinosteranes and increase in dinoflagellate cyst
142diversity through the Jurassic strongly suggests that dinoflagellates rose to ecological
143prominence in the early Mesozoic. In summary, the appearance of high-level dinoflagellate
144taxa, which are supported by molecular data as distinct clades, and progressive innovations at

145lower taxonomic ranks, along with transitional forms such as *Nannoceratopsis*, and an
146increase in dinosterane abundance, strongly suggest that dinoflagellates underwent a true
147evolutionary radiation through the early Mesozoic (Fensome et al., 1996).

148

1491.2. *Coccolithophores*

150 Coccolithophores are unicellular phytoplankton belonging to the division Haptophyta.
151They are defined by a cell-bounding series of calcareous plates, known as coccoliths, which
152interlock to form a coccosphere. Coccolithophores form part of a wider clade of
153noncalcifying/potentially calcifying/califying haptophytes termed the Calcihaptophycidae
154(de Vargas et al., 2007). Coccolithophores are the most important calcifying organisms in the
155modern ocean and thus the downward flux of coccolithophores to the sea floor contributes
156significantly to the biological pump, making coccolithophores an important agent of oceanic
157biogeochemical cycles (Brownlee and Taylor, 2004; Rost and Riebesell, 2004).

158 For many species of coccolithophore, coccolith morphology varies with the haploid-
159diploid lifecycle. During the diploid phase, cells produce heterococcoliths, formed from a
160structurally complex arrangement of radial calcite crystals. In contrast, during the haploid
161phase, cells are naked (such as for the blooming species *Emiliana huxleyi*) or holococcoliths
162are produced, which are characterised by simple calcite rhombohedra.

163 The fossil record of coccolithophores is primarily based on coccoliths, as
164coccospheres are rarely preserved intact. Moreover, the record comprises primarily of
165heterococcoliths (de Vargas et al., 2007). Although fossil holococcoliths are known, the
166nature of the tiny calcite rhombohedra from which they are constructed makes them
167extremely susceptible to dissolution (Crudeli et al., 2006 and references therein). Hence, the
168dearth of fossil holococcoliths reflects a substantial taphonomic bias.

169 Within the early Mesozoic coccolith record, heterococcoliths are represented by two
170 broad morphological groups, the muroliths and the placoliths (Bown, 1987; Bown et al.,
171 2004). Muroliths represent the earliest coccoliths, and are characterised a simple structure
172 with calcite elements extending vertically (Bown, 1987; Gardin et al., 2012). In the Early
173 Jurassic, placolith coccoliths appeared and radiated to become the dominant coccolith group.
174 The placolith structure is defined by two discs which lie on top of one another, and are
175 connected by a central pillar with radial calcite elements (Bown, 1987).

176 Unlike dinoflagellates, there is no appreciable pre-Cenozoic biomarker record of the
177 coccolithophores. Coccolithophores produce alkenones which are widely used in Cenozoic
178 palaeoceanography as temperature and $p\text{CO}_2$ proxies. However, the oldest alkenones are only
179 known from marine sediments of Early Cretaceous age (Knoll et al., 2007). Consequently,
180 there is no alkenone record of coccolithophores through the Early Mesozoic, making the
181 coccolith fossil record the only tool for directly tracking coccolithophore evolution through
182 deep time.

183

184 **2. Middle Triassic to Early Jurassic: emergence and radiation of dinoflagellates and** 185 **coccolithophores**

186 *2.1. Emergence in the Middle to Late Triassic*

187 The onset of the Mesozoic phytoplankton radiation in the fossil record is signalled by
188 the appearance in Australia of the earliest unequivocal dinoflagellate cyst species,
189 *Sahulidinium ottii* in the Middle Triassic (late Ladinian, ~238 Ma) (Riding et al., 2010a).
190 Dinoflagellate cyst diversity increased through the Middle to Late Triassic with the
191 appearances of the families Rhaetogonyaulacaceae and Suessiaceae (Figure 1; Fensome et al.,
192 1996). The former represents the first appearance of the order Gonyaulacales, one of the the

193two main orders represented by fossil dinoflagellate cysts (Fensome et al., 1999; Janoušková
194et al., 2017). This later Triassic expansion of dinoflagellate cysts coincides with an increase
195in the abundance of dinosteranes (Moldowan et al., 1996), suggesting that dinoflagellates
196began their rise to ecological prominence through this interval (Fensome et al., 1996).

197 The earliest coccoliths appeared in the latest Norian (~209 Ma), with the oldest
198identifiable species, *Crucirhabdus minutus*, appearing in the earliest Rhaetian (~207 Ma) of
199the Austrian Alps (Gardin et al., 2012). These early coccoliths are extremely small (2–3 µm),
200and have a murolith structure (Bown, 1987; Bown and Young, 1998; Bown et al., 2004).
201*Crucirhabdus* is also known from the Rhaetian of Australia, thus indicating a global
202distribution for coccoliths during the Late Triassic (Bralower et al., 1992; Gardin et al.,
2032012). However, diversity remained low during this interval, with a maximum of five species
204(Bown et al., 2004). Although there is no biomarker record of coccolithophores through the
205early Mesozoic, molecular divergence times are broadly in agreement with the coccolith
206fossil record. Molecular clocks based on SSU and LSU rDNA give ~270–240 and ~ 200 Ma
207respectively as the earliest possible dates for the origin of the coccolithophores (de Vargas et
208al. 2007; Medlin et al., 2008).

209 Falkowski et al. (2004a, b) argued that the emergence of the ‘red lineage’ of
210phytoplankton during the Triassic was driven by changes in ocean chemistry in the aftermath
211of the Permo-Triassic mass extinction. These authors postulated that prolonged periods of
212oceanic anoxia during the Early Triassic forced heterotrophic cells to acquire and retain
213plastids. In this hypothesis, prolonged euxinic conditions may have induced widespread
214denitrification, generating a paucity of fixed nitrogen, one of the most important
215macronutrients in the Triassic seas. Although photoautotrophs would have been affected by
216the limited availability of fixed nitrogen, a reduction in primary production and decline in
217upward transfer of biomass would have severely affected consumers. Acquisition of plastids

218by heterotrophic cells, via endosymbiosis of a red alga, would have provided a mixotrophic
219‘duel fuel’ strategy. This would have been an advantageous ecological strategy in unstable
220and stressed intervals of environmental change during the Early Triassic (Falkowski et al.,
2212004a).

222

2232.2. *The End-Triassic Mass Extinction*

224 The end-Triassic mass extinction (~201 Ma) significantly affected the diversity of
225phytoplankton. Only four dinoflagellate cyst genera and one coccolith species survived this
226major environmental perturbation (Bown et al., 2004; van de Schootbrugge et al., 2007). The
227temporal coincidence between the diversity collapse at the end of the Triassic and the
228emplacement of the Central Atlantic Magmatic Province (CAMP) has led many workers to
229suggest a causal relationship between these phenomena (e.g. Schoene et al., 2010; Blackburn
230et al., 2013; Percival et al., 2017). Volcanic outgassing may have driven an increase in $p\text{CO}_2$,
231resulting in acidification of epicontinental seas and prolonged euxinia (Ruhl et al., 2011;
232Schaller et al., 2011; Hönisch et al., 2012; Richoz et al., 2012). As such, prolonged
233anaerobic/euxinic conditions, and ocean acidification may have driven the decline in
234dinoflagellate cyst and coccolith diversity (van de Schootbrugge et al., 2007; 2013).

235 In many areas through Europe, the collapse in dinoflagellate cyst and coccolith
236diversity through the Triassic–Jurassic transition is concomitant with an increase in the
237abundance of the phycoma (resting cysts) of prasinophytes (chlorophyte green algae)
238(Kuerschner et al., 2007; van de Schootbrugge et al., 2007; Bonis et al., 2009). Moreover, the
239earliest Hettangian (~200 Ma, earliest Jurassic) is marked by an increase in the abundance of
240diaryl isoprenoid molecules, derived from green sulphur bacteria (Richoz et al., 2012; van de
241Schootbrugge et al., 2013). The turnover in organic-walled phytoplankton communities, and

242presence of green sulphur bacteria, indicates that the photic zone became euxinic (Richoz et
243al., 2012). Green sulphur bacteria require both light and free hydrogen sulphide (H₂S) to
244photosynthesise, whereas prasinophytes appear to have thrived during intervals of
245palaeoenvironmental stress during the Mesozoic (van de Schootbrugge et al., 2013).

246

2472.2. Early to Middle Jurassic: recovery and radiation

248 Both dinoflagellates and coccolithophores recovered during the earliest Jurassic and
249radiated through the late Early and Middle Jurassic, with the appearances of numerous
250families (Figure 1; Fensome et al., 1996; Bown et al., 2004). Dinoflagellate cyst are generally
251sparse in Hettangian strata, with low-diversity assemblages (Wall, 1965; van de
252Schootbrugge et al., 2013). The succeeding Sinemurian was marked by the sudden, and short-
253lived, appearance of *Liasidium variable* (see Brittain et al. 2010). The appearance of
254*Liasidium variable* is significant as it marks the first appearance in the fossil record of the
255order Peridinales, and although its precise taxonomic affinity is unclear due to lack of a fully
256reflected tabulation, *Liasidium variable* may be the earliest representative of the family
257Peridiniaceae (Feist-Burkhardt, 2009). It is also possible that *Liasidium variable* was
258heterotrophic, as it has a pigmented wall structure (Feist-Burkhardt 2009; Riding et al.,
2592013). The sudden appearance of this species in the Late Sinemurian has been related to the
260opening of the Hispanic Corridor, which allowed *Liasidium variable* to invade the Tethys
261Ocean from the Panthalassa Ocean (van de Schootbrugge et al., 2005). Recent work has
262linked the acme of *Liasidium variable* to a negative carbon isotope excursion, and a brief
263interval of global warming (Riding et al., 2013).

264 A significant increase in dinoflagellate cyst diversity occurred during the Late
265Pliensbachian, with the radiation of numerous families of gonyaulacaleans and peridinialeans

266(Figure 1; Morgenroth, 1970; Feist-Burkhardt and Wille, 1992). Another important first
267appearance in the Late Pliensbachian was that of *Nannoceratopsis*, a genus confined to the
268Jurassic and the only representative of the family Nannoceratopsiaceae. *Nannoceratopsis* has
269a tabulation that is a combination of dinophysoid and gonyaulacoid-peridinoid, and as such
270appears to be an evolutionary link between the Peridiniphyceae and the Dinophysiales. The
271latter has virtually no fossil record (Janouškovec et al., 2017).

272 The most significant radiation of the coccolithophores during the Mesozoic occurred
273in the Early Jurassic. During that interval, 10 of the known 16 coccolith families appeared.
274The Hettangian to Sinemurian was characterised by the recovery and radiation of murolith
275forms, which had survived the end-Triassic mass extinction (Bown et al. 2004). The family
276Biscutaceae appeared around the Sinemurian–Pliensbachian boundary and radiated rapidly
277through the Pliensbachian, becoming an important component of coccolith floras (Mattioli et
278al., 2004). The Biscutaceae represent the emergence of the placolith morphology, making the
279Pliensbachian one of the most important intervals in coccolithophore evolution (de Kaenel
280and Bergen, 1993; Bown and Cooper, 1998; Mattioli and Erba, 1999; Mattioli et al., 2013).
281The emergence of the placolith morphology was extremely important because it allowed
282coccoliths to physically lock together to form a coccosphere for the first time. Prior to the
283development of placoliths, elements in the muroliths were presumed to have been bound
284together by organic material (Bown, 1987). The initial development of placoliths occurred in
285two steps. In the Early Pliensbachian, radiating placoliths first appeared; these have a simple
286structure comprising proximal and distal shields (Bown, 1987). In the Late Pliensbachian,
287more complex imbricating coccoliths with a bicyclic distal shield appeared, and this
288morphology dominated coccolith floras for the remainder of the Jurassic (Bown, 1987;
289Mattioli and Erba, 1999; Mattioli et al., 2013).

290 The Pliensbachian was clearly an important interval in the evolution of the
291dinoflagellates and coccolithophores. It was also an interval of major palaeoclimatic and
292palaeoceanographic change. The Late Pliensbachian was marked by cooling
293palaeotemperatures, with a pronounced fall in seawater temperature of $\sim 5^{\circ}\text{C}$ (Dera et al.,
2942011). This cooling may have allowed continental ice sheets to develop, and the Late
295Pliensbachian regression may have reflected glacioeustasy (Suan et al., 2010; Bougeault et
296al., 2017). van de Schootbrugge et al. (2005) argued that cooling temperatures drove the
297radiation of dinoflagellates during the Late Pliensbachian. These authors argued that cooling
298increased ocean turbulence and enhanced vertical mixing, which resulted in well-ventilated
299bottom waters, creating conditions ideal for cyst-forming dinoflagellates. Moreover, an
300increase in upper ocean turbulence may have driven, larger, more frequent pulses of nutrients
301to the photic zone, which in turn may have favoured bloom-forming dinoflagellates
302(Falkowski et al., 2004b). In contrast to the dinoflagellates, the drivers behind the emergence
303of placolith coccoliths are unclear. The Sinemurian–Pliensbachian transition was marked by a
304negative carbon isotope shift, and the burial of organic-rich marine sediments (Boussaha et
305al., 2014; Price et al., 2016; Ruhl et al., 2016; Bougeault et al., 2017). The negative shift in
306carbon isotopes has been linked to volcanic outgassing from an interval of CAMP volcanism
307(Ruhl et al., 2016). Moreover, volcanic outgassing may driven a switch to more humid
308climatic conditions in Europe, with enhanced weathering and run-off (Cohen et al., 2004;
309Brazier et al., 2015; Ruhl et al., 2016; Bougeault et al., 2017). As such, it is likely that
310nutrient flux was elevated at this time. The temporal coincidence between these phenomena
311and the appearance of placolith coccoliths may indicate that elevated nutrient levels were a
312driver of coccolith evolution during the Early Jurassic. Indeed, elevated nutrient levels have
313been linked to evolutionary changes in coccolithophores during the Middle Jurassic (section
3143; Suchéras-Marx et al., 2015). Moreover, the Early Pliensbachian was marked by sea level

315rise (Hallam, 2001), which would have increased shallow-sea ecospace for neritic
316phytoplankton. An alternative scenario for the sudden onset of placolith coccoliths within the
317western Tethys may be related to the opening of the Hispanic Corridor during the Late
318Sinemurian–Early Pliensbachian (Aberhan, 2001; van de Schootbrugge et al., 2005). The
319circulation pattern through the Hispanic Corridor was most likely eastward, from the
320Panthalassic Ocean, which may have allowed placoliths to colonize the Tethys Ocean from
321the Panthalassic Ocean (Plancq et al., 2016). Alternatively, changes in ocean circulation
322related to the opening of the Hispanic Corridor could have stimulated the emergence of
323placolith coccoliths in the Tethys Ocean (Plancq et al., 2016)

324 The Early Toarcian was marked by the Toarcian Oceanic Anoxic Event (T-OAE)
325(~180 Ma), a relatively brief (~900 kyr) phase of widespread oceanic anoxia/euxinia and
326climate change. It was characterised by extensive, coeval organic-rich shales and a negative
327carbon isotope excursion, which affected the entire carbon cycle (Hesselbo et al., 2000;
328Kemp et al., 2005; van de Schootbrugge et al., 2005; Suan et al., 2008, 2011; Xu et al., 2017).

329 Dinoflagellate cyst diversity was temporarily affected by the T-OAE, as diversity
330declined sharply (Bucefalo Palliani et al., 2002; van de Schootbrugge et al., 2005; Correia et
331al., 2017a, b). Both the diversity and abundance of coccoliths declined through the T-OAE,
332and this was accompanied by a trend to decreasing coccolith size through the T-OAE, which
333has been linked to enhanced $p\text{CO}_2$ driving a biocalcification crisis (Mattioli et al., 2004;
334Tremolada et al., 2005; Suan et al., 2010) or, alternatively, the effects of $p\text{CO}_2$ increase were
335indirect, acting on sea-surface temperatures and marine stratification, giving rise to stressed
336conditions in surface waters (Mattioli et al., 2009; Fraguas et al., 2012). Therefore, as in the
337latest Triassic, organic-walled phytoplankton communities became dominated by
338prasinophytes during the T-OAE (van de Schootbrugge et al., 2005). Similarly, green sulphur

339bacteria appear to have thrived at this time, indicating photic zone euxinia (van de
340Schootbrugge et al., 2013).

341 After the T-OAE, normal oceanographic conditions, with fully aerobic water
342columns, were re-established during the *Hildoceras bifrons* ammonite biozone. The majority
343of the dinoflagellate cyst taxa that had characterised the Late Pliensbachian reappeared. The
344Late Toarcian was characterised by an important evolutionary event. This was the appearance
345of the first Gonyaulacaceae, heralded by the emergence of *Sentusidinium* in the Late Toarcian
346of Yorkshire, northern England and northern Germany (Riding, 1984; Prauss, 1989).
347Dinoflagellate cysts belonging to the family Gonyaulaceae are defined by several characters,
348including the presence a particular configuration of plates on the hypocyst, termed a sexiform
349tabulation (Evitt, 1985). Other key characters include a mid-ventral sulcus, and a symmetrical
350posterior outline. Although *Sentusidinium* lacks a fully reflected tabulation, its overall
351morphology is strongly gonyaulacacean (Wood et al., 2016). The Gonyaulacaceae would go
352on to become the most important and diverse family of encysting dinoflagellates in the fossil
353record (section 3).

354 The coccolithophores recovered gradually from the T-OAE; the re-appearance of
355deep-dwelling coccoliths such as *Crepidolithus crassus* indicated the end of anoxic/dysoxic
356conditions within the deep photic zone. Subsequently, the entire calcareous nannoplankton
357flora recovered (Mattioli et al., 2008). The post-T-OAE recovery interval was characterised
358by the appearance of the genus *Watznaueria* (see Mattioli and Erba, 1999), which is
359significant because *Watznaueria* became ecologically and numerically the dominant Middle
360Jurassic to Cretaceous coccolith genus (Suchéras-Marx et al., 2015; Giraud et al., 2016). The
361*H. bifrons* zone was also marked by a significant increase in size of all the dominant
362*Lotharingius* morphospecies (Ferreira et al., 2017). This size change is partly related to a
363species-specific replacement within the *Lotharingius*, with small-sized morphospecies being

364abundant in the Early Toarcian and large-sized morphospecies in the Middle–Late Toarcian.

365However, this pattern was also accompanied by a size increase of all the *Lotharingius*

366morphospecies across the middle Toarcian.

367

3683. The Bajocian: a critical interval of dinoflagellate and coccolithophore evolution and

369ecology

3703.1. Late Aalenian to Early Bajocian: expansion of Watznaueria and the ecological

371dominance of Dissiliodinium

372 The Bajocian was an important interval of dinoflagellate and coccolithophore
373ecological development and evolution. The latest Aalenian to Early Bajocian was marked by
374the diversification and ecological expansion of the coccolith genus *Watznaueria*, marking the
375beginning of 100 myr of ecological dominance by this genus within coccolithophore
376communities (Giraud et al., 2016). Through the Aalenian–Bajocian transition, *Watznaueria*
377replaced *Lotharingus* as the dominant coccolith genus (Suchéras-Marx et al., 2012, 2015;
378Giraud et al., 2016; Aguado et al., 2017; Ferreira et al., 2017). Suchéras-Marx et al. (2015)
379examined the diversification and expansion of *Watznaueria* from two areas within the
380European Epicontinental Seaway, namely the French Subalpine Basin and the Lusitanian
381Basin of Portugal. These authors recorded an increase in both the absolute and relative
382abundance of *Watznaueria* through the Early Bajocian, and noted that the absolute abundance
383of coccoliths as a whole increased through that interval, driven by the increase in the
384abundance of *Watznaueria* (Figure 2). The majority of other coccolith taxa did not decrease
385in absolute abundance, but decreased in relative abundance during the same interval,
386implying that *Watznaueria* did not outcompete other genera but integrated into the coccolith
387community. Further, the expansion of *Watznaueria* appears to have had two critical steps.

388First, in the earliest Bajocian (*Hyperlioceras discites* ammonite biozone), coccolith floras
389were dominated by the species *Watznaueria contracta* and *Watznaueria colacicchii*. Second,
390towards the end of the Early Bajocian, coccolith abundances stabilised as communities
391became dominated by *Watznaueria britannica* and *Watznaueria* aff. *manivittiae*. Giraud et al.
392(2016) compiled data on coccolith records from the Late Aalenian to Early Bajocian of
393northwest Europe. These authors noted a similar pattern, with the increase in abundance of
394*Watznaueria*, beginning around the Aalenian–Bajocian transition. This initial increase in the
395abundance of *Watznaueria* was produced by the rise to dominance of a group of *Watznaueria*
396species characterised by a central cross area (Figure 3). This group comprises *Watznaueria*
397*colacicchii*, *Watznaueria contracta* and *Watznaueria* aff. *Watznaueria contracta*. The next
398step in this transition, in the Early Bajocian, was characterised by the increase in the
399abundance of species lacking a central cross, and those with a central bar, including
400*Watznaueria britannica* and *Watznaueria* aff. *Watznaueria manivittiae* (Figure 3).
401Furthermore, Aguado et al. (2017) documented the coccolith record through the Late
402Aalenian to Early Bajocian of the southern Iberian palaeomargin. These authors reported a
403similar pattern, with an increase in the relative and absolute abundance of *Watznaueria*
404through the latest Aalenian–earliest Bajocian, particularly that of *Watznaueria contracta*.
405Coccolith assemblages around the middle of the Lower Bajocian (*Witchellia laeviuscula*
406ammonite biozone) are marked by an increase in *Watznaueria britannica* and *Watznaueria*
407*manivittiae*, an increase that persisted throughout the remainder of the Early Bajocian.
408Significantly, Aguado et al. (2017) noted that the Early Bajocian was marked by a decline in
409*Crepidolithus crassus*, a coccolith interpreted as deep-photic zone dwelling (Figure 4).

410 Within the dinoflagellate cysts, the Early Bajocian was characterised by the ecological
411dominance of the gonyaulacacean genus *Dissiliodinium* (Wiggan et al., 2017). *Dissiliodinium*
412first appeared in the Middle Aalenian as the species *Dissiliodinium lichenoides* (see Feist-

413Burkhardt and Pross, 2010). During the latest Aalenian and Early Bajocian, *Dissiliodinium*
414diversified with the appearances of *Dissiliodinium caddaense*, *Dissiliodinium giganteum* and
415*Dissiliodinium psilatum* (see Helby et al., 1987; Prauss, 1989; Feist-Burkhardt, 1990; Wiggan
416et al., 2017). During this interval, *Dissiliodinium* was also ecologically dominant in several
417mid-palaeolatitude regions. *Dissiliodinium giganteum* dominated dinoflagellate cyst floras in
418the southern German Basin, Poland/northern Slovakia, and Switzerland (Figures 5, 6; Gedl,
4192008; Hostettler et al., 2017; Wiggan et al., 2017). Outside Europe, dinoflagellate cyst floras
420from the Early Bajocian of offshore Western Australia were dominated by *Dissiliodinium*
421*caddaense* (Figure 6; Riding et al., 2010b). The *Dissiliodinium caddaense* dinoflagellate cyst
422biozone has been correlated by ammonites and strontium isotopes to the Early Bajocian
423*Witchellia laeviuscula* ammonite biozone of Europe (Riding et al., 2010b). Consequently, the
424acme of *Dissiliodinium caddaense* is synchronous with the acme of *Dissiliodinium*
425*giganteum* in Europe (Figure 6). Furthermore, *Dissiliodinium* was also abundant in the Early
426Bajocian of the Neuquén Basin in Argentina (Stukins et al., 2013). In this region,
427dinoflagellate cyst assemblages were dominated by *Dissiliodinium psilatum* (Figure 6).

428

4293.2. *Latest Early Bajocian to Early Bathonian: stabilisation of coccolithophore communities*
430*and the rapid diversification of gonyaulacacean dinoflagellates*

431Through the latest Early Bajocian to Early Bathonian, coccolith floras were dominated by
432morphotypes of *Watznaueria* defined by a central bridge, or lacking a central area (Figure 3;
433Giraud et al., 2016). The Early Bathonian was marked by the appearance of *Watznaeuria*
434*barnesiae*, a form belonging to the morphological group of taxa defined by lacking a central
435area. This group steadily increased in abundance through the Bathonian as taxa defined by a
436central bridge declined (Figure 3; Giraud et al., 2016). *Watznaueria barnesiae* became a

437 prominent component of coccolith communities from its appearance in the Early Bathonian,
438 to the end of Cretaceous, and underwent little change in morphology over this 100 myr
439 interval (Lees et al., 2005; Bornemann and Mutterlose, 2006; Tiraboschi and Erba, 2010).

440 Whereas the Late Aalenian to Early Bajocian interval marks the transition to long-
441 term ecological dominance of *Watznaueria* within coccolithophore communities, the acme of
442 *Dissiliodinium* within the dinoflagellate cysts was comparatively short-lived. *Dissiliodinium*
443 declined in abundance towards the end of the Early Bajocian in Europe, and formed a
444 relatively minor component of dinoflagellate cyst floras through the Late Bajocian (Figure 5,
445 Wiggan et al. 2017). In Australia, *Dissiliodinium caddaense* became extinct around the
446 Early–Late Bajocian transition, and the genus formed a more moderate component of
447 dinoflagellate cyst floras in the Late Bajocian to Early Bathonian (Riding et al., 2010a;
448 Mantle and Riding, 2012). As such, the acme of *Dissiliodinium* represents a small component
449 of the wider diversification and ecological expansion of gonyaulacacean dinoflagellates, and
450 this genus may have been out-competed by newly emerging taxa. In particular, ~50 species
451 appeared between the latest Early Bajocian and the Early Bathonian (Feist-Burkhardt and
452 Monteil, 1997; Wiggan et al., 2017). Wiggan et al. (2017) demonstrated that, in Europe, there
453 was a continuous pattern of appearances through the Late Aalenian to Early Bathonian, but
454 the highest number of first appearances were in the *Stephanoceras humphriesianum* (latest
455 Early Bajocian) and *Parkinsonia parkinsoni* ammonite biozones (latest Bajocian) (Figures 7,
456 8). Moreover, from the *Stephanoceras humphriesianum* ammonite biozone onwards,
457 appearances were dominated by gonyaulacacean taxa. Similarly, in terms of diversity,
458 species richness steadily increased through the Late Aalenian to Early Bajocian, and there
459 was a particularly pronounced increase in richness in the *Stephanoceras humphriesianum* and
460 *Parkinsonia parkinsoni* ammonite biozones, as result of the large number of first appearances
461 in these zones (Figure 9). During the Late Aalenian, gonyaulacacean taxa comprised around

46225% of dinoflagellate cyst taxa, but by the earliest Bathonian, *Zigzagiceras zigzag* ammonite
463biozone, this family represented over 60% of all dinoflagellate cyst taxa (Figure 9). Thus, the
464Bajocian represents a critical interval in the evolutionary history of the Gonyaulacaceae.

465 The diversification of gonyaulacaceans during the Bajocian–Bathonian is observed
466from the low to mid palaeolatitudes of the northern and southern hemispheres, indicating a
467global increase in diversity. There was an increase in the diversity of gonyaulacacean
468dinoflagellate cysts through the Middle Jurassic in offshore eastern Canada, but in this region
469the majority of appearances are recorded from the Bathonian, rather than the Bajocian (Bujak
470and Williams, 1977). Outside of the mid-northerly palaeolatitudes, the radiation of
471gonyaulacaceans is observed in the Middle Jurassic of Australia, which was then located on
472the southern edge of the Tethys Ocean, around 30°S. The pattern of dinoflagellate cyst
473appearances in the Northwest Shelf of Australia is comparable to that of Europe, with a
474significant increase in the diversity of gonyaulacaceans from the latest Early Bajocian to
475Early Bathonian (Mantle and Riding, 2012). Gonyaulacaceans also diversified through the
476low palaeolatitude regions; there is a significant increase in the appearances and diversity of
477gonyaulacacean dinoflagellate cysts through the Bajocian–Bathonian of Egypt, Israel and
478Qatar (Conway, 1990; Ibrahim et al., 2002, 2003). Gonyaulacaceans do not appear to have
479radiated through the Bajocian–Bathonian in the high palaeolatitudes, as this group comprises
480only a minor component of dinoflagellate cyst floras from the Middle Jurassic of Arctic
481Canada (Figure 10; Davies, 1983). As such, the Gonyaulacaceae appear to have been
482taxonomically and ecologically dominant in the low to mid-palaeolatitudes.

483 The radiation of gonyaulacaceans was accompanied by a significant increase in the
484diversity of form, or disparity of dinoflagellate cysts, and innovations in the archaeopyle (the
485excystment aperture). Prior to the Bajocian, gonyaulacaceans were represented by
486*Batiacasphaera*, *Dissiliodinium*, *Kallosphaeridium* and *Sentusidinium* (see Feist-Burkhardt

487and Wille 1992; Feist-Burkhardt and Pross, 2010). These genera are characterised by simple,
488mostly non-tabulate cysts (Figure 11). *Batiacasphaera*, *Kallosphaeridium* and *Sentusidinium*
489have apical archaeopyles, whereas *Dissiliodinium* has a multi-plate precingular archaeopyle
490(Figure 11). Through the Bajocian 19 gonyaulacacean genera appeared, which exhibit a wide
491array of morphologies (Figure 11). The Early Bajocian was marked by the diversifications of
492genera with multi-plate precingular archaeopyles such as *Dissiliodinium* and *Durotrigia*, and
493included the first gonyaulacaceans with more-or-less fully reflected tabulation, such as
494*Durotrigia daveyi* (Figure 11). Morphological features such as cavation (the separation of
495wall layers) appeared within the Gonyaulacaceae, as represented by the appearances of the
496genera *Cavatodissiliodinium* and *Endoscrinium* (Feist-Burkhardt and Götz, 2016). Moreover,
497gonyaulacaceans developed ornamental features such as distally complex processes and
498prominent sutural crests (Figure 11). These morphological features were accompanied by an
499increase in the number of archaeopyle types. Over the course of the Bajocian, genera with
500epicystal, one-plate precingular and two-plate precingular archaeopyles appeared. While both
501fossil and recent dinoflagellate cyst taxa can exhibit intraspecific variability within
502archaeopyle formation (e.g. Evitt, 1985; Harding, 1986; Ellegaard et al., 2002), the one-plate
503precingular archaeopyle appears to have been developed with the Gonyaulacaceae during the
504Bajocian, and has remained a common gonyaulacacean excystment strategy to the present day.
505Therefore, the increase in taxonomic diversity of gonyaulacacean dinoflagellate cysts through
506the Bajocian was accompanied by morphological innovations in archaeopyle formation, and a
507rapid increase in morphological disparity.

508

5093.3. *Drivers behind the ecological and evolutionary change in dinoflagellates and*
510*coccolithophores during the Bajocian*

5123.3.1. *The diversification and expansion of Watznaueria, and the ecological dominance of*513Dissiliodinium

514 The diversification and expansion of *Watznaueria* during the Early Bajocian was
515coincident with a Europe-wide positive carbon isotope excursion (CIE). This excursion has
516been reported from central Italy (Bartolini et al., 1996, 1999; Bartolini and Cecca, 1999), the
517Isle of Skye, Scotland, (Jenkyns et al., 2002; Korte et al., 2015), Yorkshire, northern England
518(Hesselbo et al., 2003), southern Spain (O'Dogherty et al., 2006), northern France (Brigaud et
519al., 2009), Portugal (Suchéras-Marx et al., 2012), south-eastern France (Suchéras-Marx et al.,
5202013; Giraud et al., 2016), and most recently, Morocco (Bodin et al., 2017). The positive shift
521in $\delta^{13}\text{C}$ was coincident with an increase in biosiliceous sedimentation through the western
522Tethys; which may reflect a eutrophication of surface waters throughout the Western Tethys
523during the Early Bajocian (Figures 3, 4; Bartolini and Cecca, 1999; Bartolini et al., 1999;
524O'Dogherty et al., 2006; Suchéras-Marx et al., 2015; Giraud et al., 2016; Aguado et al.,
5252017).

526 This Early Bajocian phase of elevated nutrient levels has been invoked as the causal
527mechanism behind the ecological expansion of *Watznaueria* (see Suchéras-Marx et al., 2015;
528Giraud et al., 2016; Aguado et al., 2017). Suchéras-Marx et al. (2015) suggested that the
529increase in the abundance of *Watznaueria*, and coccoliths as a whole may reflect an increase
530in ecosystem carrying capacity driven by enhanced nutrient levels. Moreover, the two-step
531pattern of the diversification of *Watznaueria* may represent an increase in nutrient levels,
532with the initiation of the expansion of *Watznaueria* triggered by the increase in nutrient
533levels. The second step reflects the acquisition of a bloom-forming ecological strategy by

534 *Watznaueria britanica* and *Watznaueria* aff. *Watznaueria manivittiae* (see Suchéras-Marx et
535 al., 2015; Giraud et al., 2016).

536 Two possible scenarios have been invoked as the drivers behind an increase in
537 nutrient levels through the Late Aalenian to Early Bajocian (Suchéras-Marx et al.,
538 2015; Giraud et al., 2016; Aguado et al., 2017). The first hypothesis is a climatically driven
539 increase in continental weathering and nutrient flux during the Early Bajocian. The Middle
540 Jurassic is increasingly being recognised as a ‘cool mode’ of the Jurassic climate (Korte et
541 al., 2015). In Europe, oxygen isotope data from belemnites, bivalves and brachiopods,
542 indicate that there was a cooling of seawater temperature of ~10°C across the Early–Middle
543 Jurassic transition, and relatively cool temperatures persisted until the Bathonian (Figure 12;
544 Korte et al., 2015). The initiation of cooling through the Early–Middle Jurassic transition is
545 thought to have been driven by the magmatic doming in the North Sea, which blocked water-
546 mass exchange through the Viking Corridor, and resulted in the thermal isolation of the
547 Boreal Sea (Korte et al., 2015). However, a possible short-term interval of warming may have
548 occurred during the latest Early Bajocian (*S. humphriesianum* ammonite biozone) in Europe
549 (Dera et al., 2011; Korte et al., 2015; Giraud et al., 2016). This has been argued to reflect an
550 increase in latitudinal temperature gradient between the mid and high palaeolatitudes
551 (Suchéras-Marx et al., 2015). A more humid climate in Europe during the Early Bajocian is
552 evidenced by the switch from charcoal to coal as the dominant preservational mode of fossil
553 wood through the Upper Aalenian to Lower Bajocian of the Cleveland Basin of Yorkshire
554 (Hesselbo et al., 2003). Changes in clay mineral assemblages may also be indicative of a
555 warm, humid climate. Brigaud et al. (2009) noted that clay mineral assemblages from the
556 *Stephanoceras humphrieisianum* ammonite biozone of the Paris Basin contain around 20%
557 kaolinite. In modern environments, kaolinite forms in humid tropical climates from intense
558 chemical weathering, which led Brigaud et al. (2009) to argue that there was a change to a

559warmer, more humid, climate during the Early Bajocian. Rausik et al. (2001) and Raucsik
560and Varga (2008) documented clay mineral assemblages dominated by mixed-layer
561illite/smectite from the Lower Bajocian of the Mecsek Mountains of Hungary. Mixed-layer
562illite/smectite clays form in modern environments of warm, arid conditions punctuated by
563short, intense wet seasons; therefore, Raucsik and Varga (2008) argued the climate of the
564Early Bajocian in Europe was monsoon-like. Taken together, Sucheras-Marx et al. (2015)
565and Aguado et al. (2017) argued that these lines of geochemical, mineralogical and
566palaeontological evidence are indicative of a warm, humid climate during the Early Bajocian,
567which enhanced chemical weathering and increased the flux of biolimiting nutrients into the
568European Epicontinental Seaway. Moreover, Philippe et al. (2017) reported the northward
569spread of the low-latitude fossil-wood genus *Brachyoxylon* during the Early Bajocian, which
570may be indicative of a warming and/or an increase in humidity in the mid-latitudes.

571 The alternative scenario is an increase in surface water productivity driven by changes
572in enhanced upwelling and ocean circulation during the Early Bajocian. The Aalenian–
573Bathonian was characterised by significant changes in the tectonic configuration of ocean
574gateways, particularly the gateways which connected the European Epicontinental Seaway
575(EES) to the Tethyan and Panthalassic oceans, and the Boreal Sea. In the north, the Viking
576Corridor, which at times provided a marine connection from the EES to the Boreal Sea
577(Figure 6), was largely blocked during the Aalenian due to magmatic doming in the North
578Sea area (Korte et al., 2015). The Hispanic Corridor to the west, which opened as a marine
579connection between Gondwana and Laurentia during the Early Jurassic (Figure 6), was
580affected by changes in relative plate motion and spreading rate between Africa and North
581America (Labails et al., 2010). These changes drove a widening and deepening of the
582Hispanic Corridor during the Bajocian (Aberhan, 2001; Labails et al., 2010; Dera et al.,
5832014). This was accompanied by increased seafloor spreading in the Alpine Tethys (Bill et

584al., 2001). Dera et al. (2014) reported a marked positive shift in neodymium isotopes during
585the Aalenian–Bathonian. These authors suggested this may have been forced by a stronger
586influence of radiogenic Tethyan waters in the European Epicontinental Seaway driven by the
587widening of the Hispanic Corridor and the restriction of the Viking Corridor, which may have
588promoted enhanced upwelling along the Tethyan margin.

589 Giraud et al. (2016) argued these changes in ocean circulation drove the turnover in
590*Watznaueria* through ocean fertilisation. These authors noted that cool seawater temperatures
591in Europe prevailed during the earliest Bajocian (*H. discites* and *W. laeviuscula* ammonite
592biozones), consistent with cool, upwelling water masses. Recently, however, Aguado et al.
593(2017) argued against the upwelling hypothesis. These authors demonstrated that the
594expansion of *Watznaueria* through the Early Bajocian was concomitant with a decline in the
595coccolith *Crepidolithus crassus* (Figure 4). This species is characterised by thick, robust
596coccoliths, which has been interpreted as reflecting a deep-dwelling ecological strategy, as
597the thick coccoliths act to ballast the coccosphere, while increasing the refractive index with
598water, and thus allowing a greater amount of light to pass into the cell (Bour et al., 2010;
599Reggiani et al., 2010; Aguado et al., 2017). As such, Aguado et al. (2017) argued that the
600decline in the abundance of this deep-dwelling species is inconsistent with nutrients being
601supplied by upwelling deepwaters, as upwelling would fertilise the photic zone from the
602bottom up. Instead, Aguado et al. (2017) argued the decline of *C. crassus* is more consistent
603with an increased supply of continentally derived nutrients which drove a shallowing of the
604nutricline.

605 The Early Bajocian eutrophication event has not previously been considered in the
606context of dinoflagellate ecology and evolution. However, given the diversification and
607ecological dominance of *Dissiliodinium* in several regions, it is possible that this pattern also
608reflects a response to elevated nutrient levels, particularly as the acme of this genus in the

609 Early Bajocian is synchronous with the positive carbon isotope excursion (Figure 13). The
610 palaeoenvironmental distribution and palaeoecological preferences of *Dissiliodinium* may
611 indicate that there was an increase in the supply of nutrients to proximal depositional areas in
612 the mid-palaeolatitudes during the Early Bajocian. In Europe, *Dissiliodinium giganteum*
613 appears to have thrived in palaeoenvironments which were in close proximity to terrestrial
614 discharge (Wiggan et al., 2017). Moreover, this species is typified by a large size (~100 µm).
615 As such, *Dissiliodinium giganteum* may have proliferated under high-nutrient conditions
616 (Wiggan et al. 2017), as large phytoplankton cells require high nutrient levels due to the
617 diffusion limitation of nutrient uptake (Marañón, 2015). Moreover, *Dissiliodinium caddaense*
618 is also typified by a large size (~150 µm; Helby et al., 1987) and is recorded in abundance
619 from the Athol and Cadda formations of north-western and western Australia, which were
620 deposited in nearshore depositional settings (Riding et al., 2010b). These data suggest that,
621 like *Dissiliodinium giganteum*, *Dissiliodinium caddaense* was adapted to high nutrient levels,
622 and could tolerate lowered salinities. Similarly, *Dissiliodinium psilatum* appears to show
623 similar morphological and ecological adaptations. In the Early Bajocian of Argentina,
624 *Dissiliodinium psilatum* dominated assemblages in the marginal/deltaic palaeoenvironments
625 of the Neuquén Basin (Stukins et al., 2013). *Dissiliodinium psilatum* is of comparable
626 morphology to *Dissiliodinium giganteum* and, although slightly smaller, is still relatively
627 large with an average width of 80 µm (Prauss, 1989). The abundance of this species in
628 nearshore and deltaic deposits indicates it could have tolerated reduced salinities, and the
629 proximity to terrigenous discharge and its relatively large size indicate an adaptation to high
630 nutrient levels. The proliferation of *Dissiliodinium* in palaeoenvironments close to sources of
631 terrestrial discharge through the Early Bajocian could have been driven by enhanced runoff
632 from increased continental weathering. However, the Early Bajocian was marked by sea level
633 rise in Europe, South America, and Australia (Hallam, 2001; Riding et al., 2010a). Rising sea

634level can trap nutrients in marginal marine regions, yet can also introduce nutrient-rich
635deepwaters into more proximal areas (Arthur and Sageman, 2005). The latter phenomenon
636seems incompatible with the shallowing nutricline hypothesis of Aguado et al. (2017). As
637such, further documentation from other Lower Bajocian successions is required to fully
638resolve of this interval of Early Bajocian palaeoenvironmental change.

639

6403.3.2. *The Bajocian radiation of dinoflagellates*

641To date, few works have attempted to link the Bajocian dinoflagellate radiation to wider
642Middle Jurassic climatic or oceanographic changes. Feist-Burkhardt and Götz, (2016)
643suggested that the Bajocian radiation may have been related to opening of the Atlantic Ocean,
644and changes in ocean circulation. Recently, Wiggan et al. (2017) argued that the pattern of
645dinoflagellate cyst first appearances in northwest Europe was controlled by transgression.
646These authors noted that, in the Swabian Basin of southern Germany, the main influx of first
647appearances was associated with a palaeoenvironmental trend to more distal, offshore
648conditions. In turn, this palaeoenvironmental trend reflects a major episode of sea level rise
649during the Bajocian. In Europe, this took the form of the T7 second-order transgression,
650which lasted from the Late Aalenian to the Early Bathonian (Jacquin et al., 1998). This
651second-order transgression was comprised of a series of third-order cycles. In the Boreal
652realm, this transgression had two pulses, the first lasting from the Late Aalenian to Early
653Bajocian and the second from the latest Early Bajocian to Early Bathonian (Figure 14). In the
654Tethyan realm, this transgression comprised one pulse, which lasted from the Late Aalenian
655to Early Bathonian (Figure 14). Maximum transgression of the T7 cycle as a whole
656corresponds to the maximum flooding surface above Bj5 of the Early Bathonian
657(*Zigzagiceras zigzag* ammonite biozone) (Jacquin et al., 1998). Hallam (2001) argued that

658this transgression was eustatic, as there is evidence of sea level rise in Europe, South America
659and the Himalayas.

660We have compared dinoflagellate cyst stratigraphic data from Europe to sequence stratigraphic
661records. These data demonstrate a correlation between the increase in dinoflagellate cyst
662diversity and sea level rise through the Bajocian in Europe (Figure 14). At a zonal level, the
663large number of appearances recorded from the *Stephanoceras humphriesianum* and
664*Parkinsonia parkinsoni* ammonite biozones correspond to pronounced third-order
665transgressive pulses (Figure 14). Appearances of taxa through the Late Aalenian to Early
666Bathonian could therefore have been brought into the European Epicontinental Seaway by
667transgressive waters, as indicated by the correlation between large numbers of appearances
668and transgressive pulses around the *Stephanoceras humphriesianum* and *Parkinsonia*
669*parkinsoni* ammonite biozones. Further, in addition to sea-level rise, changes in ocean
670circulation related to the widening of the Hispanic Corridor and thermal doming in the Viking
671Corridor may have influenced the pattern of dinoflagellate cyst appearances. Due to the
672restriction of the Viking Corridor, the main path for the passive dispersal of dinoflagellates
673would have been to the south, from the northwest Tethys Ocean, and the Hispanic Corridor.
674The widening of the Hispanic Corridor, and rise in sea level may have driven a rapid influx of
675gonyaulacacean taxa into Europe during the Bajocian, as intervals of higher sea level can
676promote the interconnectivity and floral interchange between ocean basins (van de
677Schootbrugge et al., 2005). As such, enhanced water-mass transfer may have increased floral
678interchange between the European Epicontinental Seaway, the northwestern Tethys and the
679Panthalassa Ocean via the Hispanic Corridor. This idea is supported by the occurrence of
680dinoflagellate cyst taxa, such as *Dissiliodinium psilatium* in both Europe and Argentina
681(Stukins et al., 2013). Additionally, climatic factors may have also influenced the pattern of
682appearances in Europe. A brief interval of warming occurred in the *Stephanoceras*

683*humphriesianum* ammonite biozone in Europe. As this zone also corresponds to a major
684influx of gonyaulacacean taxa, warmer seawater temperatures, coupled with sea-level rise,
685could have promoted the spread of taxa from lower palaeolatitude Tethyan regions into the
686European Epicontinental Seaway. Further, the temporal coincidence between climatic
687warming and transgression in the *Stephanoceras humphriesianum* ammonite biozone may
688indicate a common cause via a glacioeustatic control on third-order sea level oscillations.

689 The correlation between the increase in dinoflagellate cyst diversity and sea level rise
690suggests that an increase in the area of epicontinental seas may have directly driven the
691radiation of dinoflagellates, via an increase in available ecospace. Indeed, cyst-forming
692dinoflagellates predominantly inhabit shallow seas as cyst formation is most viable in water
693depth of <200 m (Fensome et al., 1996). However, while the preceding Aalenian was a
694largely regressive interval in Europe, sea level was relatively high globally (Hallam, 2001),
695yet gonyaulacaceans were low in diversity through the Aalenian (Feist-Burkhardt and Pross,
6962010). As such, it does not appear that sea level directly drove the diversification of
697gonyaulacacean dinoflagellates. Furthermore, the Late Pliensbachian was a critical interval of
698dinoflagellate evolution even though it was a time of widespread regression (van de
699Schootbrugge et al., 2005). Similarly, the earliest Jurassic was marked by a widespread
700marine transgression during the Hettangian, yet dinoflagellate cysts were extremely low in
701diversity through this interval (Figure 1; Hallam, 2001; van de Schootbrugge et al., 2013).

702 Dinoflagellates appear to have diversified markedly during cool intervals of the
703Jurassic (Riding and Michoux, 2013). The major pulse of dinoflagellate diversification during
704the Late Pliensbachian was linked to a phase of climatic cooling, which may have increased
705upper-ocean turbulence and enhanced vertical mixing, with an increase in bottom-water
706ventilation, creating conditions ideal for cyst-forming dinoflagellates (van de Schootbrugge et
707al., 2005). Although there may have been a switch to a warmer, more humid climate in during

708the Early Bajocian, overall the Aalenian–Bathonian was a time of predominantly cool
709temperatures in Europe (Korte et al., 2015). This given, it is possible that climatic cooling
710may have driven dinoflagellate evolution in the Bajocian as it appears to have done during
711the Late Pliensbachian., However, the Late Pliensbachian was marked by the incursion of
712high palaeolatitude Boreal taxa into Europe (Bucefalo Palliani and Riding, 1997). In contrast,
713in the Bajocian, gonyaulacaceans appear to have formed a comparatively minor component
714of dinoflagellate cyst floras in the high palaeolatitudes (Figure 10; Davies, 1983).
715Furthermore, there is a ~5 myr gap between the cooling across the Early–Middle Jurassic
716transition and the diversification of gonyaulacaceans in the Bajocian. Thus, there is no
717obvious temporal link between cooling climate and the diversification of gonyaulacaceans
718which suggests that climate did not drive the diversification of gonyaulacacean
719dinoflagellates during the Middle Jurassic.

720 Palaeoclimatic and palaeoceanographic changes appear to have controlled the
721stratigraphic pattern of the Bajocian radiation, as well as influencing palaeoecological patterns
722seen within dinoflagellate cyst floras. However, these factors do not appear to form the
723underlying driver of diversification. It is notable, however, that the diversity of
724dinoflagellates and coccolithophores through the Early–earliest Middle Jurassic broadly
725mirrors that of benthic and pelagic metazoans, suggesting a coupling between phytoplankton
726and metazoan evolution (Figure 15). The Mesozoic oceans were characterised by the
727escalatory evolution of predators and their prey, encapsulated in the concept of the Mesozoic
728Marine Revolution (Vermeij, 1977; 1987; 2008). Although the concept of the Mesozoic
729Marine Revolution was originally applied to the Cretaceous, it has since been realised that
730many of the escalation-related adaptations appeared through the Late Triassic to Early Jurassic
731(Harper et al., 1998; Vermeij, 2008). Notably, during the Middle Jurassic, important
732ecological and evolutionary changes occurred in planktivorous metazoans. The trophic guild

733of giant suspension feeding fishes first appeared in the Middle Jurassic, and the earliest fossil
734evidence of this group comes from the Bajocian (Friedman et al., 2010). Within other nekton,
735the Late Aalenian to Early Bajocian was characterised by the extinction of ammonite families
736that dominated Early Jurassic ammonite faunas, and their replacement by families that
737dominated through the Middle Jurassic (Figure 15; Sandoval et al., 2001). Moreover, the
738Bajocian was marked by the first appearance of heteromorph ammonites (O’Dogherty et al.,
7392006). Evidence from buccal morphology and fossilised food remains indicates that diet of
740both planispiral and heteromorph ammonites included mesozooplankton (Jäger and Fraaye,
7411997; Kruta et al., 2011). Given the turnover within ammonites, and the appearance of giant
742suspension feeding fishes, these patterns may indicate that important evolutionary and
743ecological changes occurred within mesozooplankton communities. Although the fossil
744record of mesozooplankton is extremely sparse (Selden et al., 2010), it is notable that many
745of the gonyaulacacean dinoflagellate cyst taxa that appeared through the Bajocian were
746characterised by thick walls and/or an ornament of sutural crests/spines e.g. *Acanthaulax*,
747*Aldorfia*, *Ctenidodinium*, *Gonyaulacysta* and *Meiourogonyaulax* (Figure 11); perhaps such
748morphological developments served as defensive adaptations (Sarjeant et al., 1987).
749Additionally, the presence of dinoflagellate cysts in zooplankton fecal pellets suggests that
750their predation, although, little-considered, may be an important factor in dinoflagellate
751ecology (Persson, 2000; Montresor et al., 2003). Given the temporal coincidence between
752phytoplankton diversification and groups of planktivorous cephalopods and fishes, these
753phenomena may reflect an underlying ecological driver to the Bajocian radiation, with
754connecting links provided by the mesozooplankton. Viewed in this light, the Middle Jurassic
755dinoflagellate radiation might represent a largely-overlooked component of the Mesozoic
756Marine Revolution.

7584. Conclusions

759 Both dinoflagellates and coccolithophores underwent a major radiation through the
760 Middle Triassic to Middle Jurassic. Within this longer-term radiation, important short-term
761 intervals of ecological and evolutionary change can be recognised. The Bajocian was
762 characterised by a major ecological transition in coccoliths and the rapid diversification of
763 gonyaulacacean dinoflagellate cysts. The rise to ecological dominance of the coccolith genus
764 *Watznaueria* during the Early Bajocian appears to have been driven by an increase in nutrient
765 levels. These changes in coccolith floras were paralleled among dinoflagellate cysts by the
766 ecological dominance of the genus *Dissiliodinium* in several mid-palaeolatitude epicratonic
767 basins. An increase in nutrient levels may have been driven by enhanced continental
768 weathering and run off, or changes in ocean circulation. The proliferation of *Dissiliodinium*
769 in proximal palaeoenvironments in the mid-palaeolatitudes during the Early Bajocian may
770 indicate an increase in the supply of continentally derived nutrients. However, the interval of
771 Early Bajocian palaeoenvironmental changes has so far only been documented from Europe
772 and North Africa, which during the Jurassic were located on the northwestern border of the
773 Tethys Ocean. Thus, the global extent and driving mechanisms of these phenomena remains
774 unclear. Future work could focus on documenting the Bajocian carbon isotope record from
775 areas that lay outside of the northwestern Tethys region to accurately assess whether there
776 was a global shift in the carbon cycle during the Early Bajocian. Moreover, the generation of
777 high resolution osmium and strontium isotope records for the Early Bajocian would provide
778 insight into the extent of weathering increase through this interval, in much the same way that
779 these tracers have been employed for examining hydrological cycling during the Toarcian
780 OAE.

781 The Bajocian was marked by a significant increase in the diversity of gonyaulacacean
782 dinoflagellate cysts, marking the transition to ecological dominance of the Gonyaulacaceae

783within cyst-forming dinoflagellates. Thus, the Bajocian represents an important ecological
784transition for dinoflagellates as well as for coccolithophores. However, this radiation remains
785poorly documented outside of Europe and Australia. Within Europe, the stratigraphic pattern
786of the radiation of dinoflagellate cysts appears to have been controlled by sea level, with
787rising sea level and changes in ocean circulation bringing newly emerging taxa into the
788European Epicontinental Seaway, by a combination of enhanced water-mass transfer and the
789spread of marine palaeoenvironments. However, whereas oceanographic changes may have
790controlled the pattern of dinoflagellate cyst appearances in Europe, they may not have been
791the underlying driver of diversification. The preceding Aalenian was marked by large
792volumes of flooded continental area, yet gonyaulacacean diversity was low. Moreover, while
793gonyaulacaceans appear to have diversified during a ‘cool mode’ of Jurassic climate, there is
794a ~5 my gap between rapid cooling through the Early–Middle Jurassic transition and the
795radiation of gonyaulacaceans during the Bajocian. Furthermore, the Gonyaulacaceae do not
796appear to have formed a large component of dinoflagellate cyst floras at high palaeolatitudes
797during the Bajocian. While climatic and oceanographic factors do not appear to have driven
798the diversification of gonyaulacaceans, the temporal coincidence between the radiation of
799dinoflagellates, coccolithophores and multiple trophic levels of benthic and pelagic
800metazoans may point towards an underlying ecological driver. Knoll and Follows (2016)
801suggested that the radiation of mixotrophic dinoflagellates through the Mesozoic may have
802provided a bottom-up mechanism to the Mesozoic Marine Revolution, by enhancing primary
803production. However, many of the morphological features to appear in dinoflagellate cysts
804through the Bajocian could be interpreted as defensive mechanisms, which might reflect a co-
805evolutionary escalation between the primary producers and their immediate consumers, the
806micro- and mesozooplankton. As such, the radiation of dinoflagellates during the Bajocian
807might represent an important, but largely overlooked component of the Mesozoic Marine

808 Revolution. Although mesozooplankton represent the most important trophic link between
809 the phytoplankton and higher trophic levels, they have an extremely sparse fossil record.
810 However, ‘zooclasts’, fragments of metazoans, particularly arthropods, are relatively
811 common in Phanerozoic palynomorph assemblages (e.g. Tyson, 1995). Whereas these small
812 carbonaceous fossils have provided a wealth of palaeobiological insight into the Proterozoic–
813 Phanerozoic transition (e.g. Butterfield and Harvey, 2012), including the first record of the
814 copepods (Harvey et al., 2012; Harvey and Pedder, 2013), they are a relatively unexplored
815 source of micropaleontological data for the Mesozoic and Cenozoic. In part, this is because
816 traditional palynological processing methods may destroy these comparatively delicate
817 organic microfossils (Butterfield and Harvey, 2012). Future work may more closely compare
818 the fossil record of phytoplankton with that of pelagic metazoans such as ammonites and fish,
819 and examine Mesozoic rocks for small carbonaceous fossils in order to link the
820 phytoplankton record to that of the zooplankton, which in turn could be linked to higher
821 trophic levels.

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

826

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836 **References**

837 Aberhan, M., 2001. Bivalve palaeobiogeography and the Hispanic Corridor: time of opening
838 and effectiveness of a proto-Atlantic seaway. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 165,
839 375–394.

840 Aguado, R., O'Dogherty, L., Sandoval, J., 2017. Calcareous nannofossil assemblage turnover
841 in response to the Early Bajocian (Middle Jurassic) palaeoenvironmental changes in the
842 Subbetic Basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 472, 128–145.

843 Arthur, M.A., Sageman, B.B., 2005. Sea-level control on source-rock development:
844 perspectives from the Holocene Black Sea, the mid-Cretaceous Western Interior Basin of
845 North America, and the Late Devonian Appalachian Basin.

846 Bartolini, A., Cecca, F., 1999. 20 My hiatus in the Jurassic of Umbria-Marche Apennines
847 (Italy): carbonate crisis due to eutrophication. *Comptes Rendus Académie Sci. - Ser. IIA -*
848 *Earth Planet. Sci.* 329, 587–595.

849 Bartolini, A., Baumgartner, P., Hunziker, J., 1996. Middle and Late Jurassic carbon stable-
850 isotope stratigraphy and radiolarite sedimentation of the Umbria-Marche Basin (Central
851 Italy). *Eclogae Geol. Helvetiae* 89, 811–844.

852 Bartolini, A., Baumgartner, P.O., Guex, J., 1999. Middle and Late Jurassic radiolarian
853 palaeoecology versus carbon-isotope stratigraphy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
854 145, 43–60.

855Bill, M., O'Dogherty, L., Guex, J., Baumgartner, P.O., Masson, H., 2001. Radiolarite ages in
856Alpine-Mediterranean ophiolites: Constraints on the oceanic spreading and the Tethys-
857Atlantic connection. *Geol. Soc. Am. Bull.* 113, 129–143.

858Blackburn, T.J., Olsen, P.E., Bowring, S.A., McLean, N.M., Kent, D.V., Puffer, J., McHone,
859G., Rasbury, E.T., Et-Touhami, M., 2013. Zircon U-Pb geochronology links the end-Triassic
860extinction with the Central Atlantic Magmatic Province. *Science* 340, 941–945.

861Bodin, S., Hönig, M.R., Krencker, F.-N., Danisch, J., Kabiri, L., 2017. Neritic carbonate
862crisis during the Early Bajocian: Divergent responses to a global environmental perturbation.
863*Palaeogeogr. Palaeoclimatol. Palaeoecol.* 468, 184–199.

864Bogus, K., Mertens, K.N., Lauwaert, J., Harding, I.C., Vrielinck, H., Zonneveld, K.A.,
865Versteegh, G.J., 2014. Differences in the chemical composition of organic-walled
866dinoflagellate resting cysts from phototrophic and heterotrophic dinoflagellates. *J. Phycol.* 50,
867254–266.

868Bonis, N., Kürschner, W., Krystyn, L., 2009. A detailed palynological study of the Triassic–
869Jurassic transition in key sections of the Eiberg Basin (Northern Calcareous Alps, Austria).
870*Rev. Palaeobot. Palynol.* 156, 376–400.

871Bougeault, C., Pellenard, P., Deconinck, J.-F., Hesselbo, S.P., Dommergues, J.-L., Bruneau,
872L., Cocquerez, T., Laffont, R., Huret, E., Thibault, N., 2017. Climatic and
873palaeoceanographic changes during the Pliensbachian (Early Jurassic) inferred from clay
874mineralogy and stable isotope (C-O) geochemistry (NW Europe). *Glob. Planet. Change* 149,
875139–152.

876Bornemann, A., Mutterlose, J., 2006. Size analyses of the coccolith species *Biscutum*
877*constans* and *Watznaueria barnesiae* from the Late Albian “Niveau Breistroffer”(SE France):
878taxonomic and palaeoecological implications. *Geobios* 39, 599–615.

879 Bour, I., Mattioli, E., Pittet, B., 2007. Nannofacies analysis as a tool to reconstruct
880 paleoenvironmental changes during the Early Toarcian anoxic event. *Palaeogeogr.*
881 *Palaeoclimatol. Palaeoecol.* 249, 58–79.

882 Boussaha, M., Pittet, B., Mattioli, E., Duarte, L., 2014. Spatial characterization of the late
883 Sinemurian (Early Jurassic) palaeoenvironments in the Lusitanian Basin. *Palaeogeogr.*
884 *Palaeoclimatol. Palaeoecol.* 409, 320–339.

885 Bown, P.R., 1987. The structural development of early Mesozoic coccoliths and its
886 evolutionary and taxonomic significance. *Abh Geol B-A* 39, 33–49.

887 Bown, P.R., 2005. Calcareous nannoplankton evolution: a tale of two oceans.
888 *Micropaleontology* 51, 299–308.

889 Bown, P. R., Young, J. R. 1998. Introduction. In: Bown, P. R. (eds.). *Calcareous Nannofossil*
890 *Biostratigraphy*. British Micropalaeontological Society Series. Chapman and Hall/Kluwer
891 Academic Publishers, London, 1–15.

892 Bown, P. R., Cooper, M. K. E. 1998. Jurassic. *In*: Bown, P. R. (eds). *Calcareous Nannofossil*
893 *Biostratigraphy*, British Micropalaeontological Society Series. Chapman and Hall/Kluwer
894 Academic Publishers, London, 86–131.

895 Bown, P.R., Lees, J.A., Young, J.R., 2004. Calcareous nannoplankton evolution and diversity
896 through time, in: *Coccolithophores*. Springer, Berlin, Heidelberg, pp. 481–508.

897 Bralower, T.J., Bown, P.R., Siesser, W.G., 1992. 25. Upper Triassic calcareous
898 nannoplankton biostratigraphy, Wombat Plateau, northwest Australia. *Proceedings of the*
899 *Ocean Drilling Program, Scientific Results*, 122, 437–451.

900 Brazier, J.M., Suan, G., Tacail, T., Simon, L., Mattioli, E., Martin, J.E., Balter, V., 2015.
901 Calcium isotope evidence for dramatic increase of continental weathering during the

902Toarcian Oceanic Anoxic Event (Early Jurassic). *Earth and Planetary Science Letters* 411,
903164-176.

904Brigaud, B., Durllet, C., Deconinck, J.-F., Vincent, B., Pucéat, E., Thierry, J., Trouiller, A.,
9052009. Facies and climate/environmental changes recorded on a carbonate ramp: A
906sedimentological and geochemical approach on Middle Jurassic carbonates (Paris Basin,
907France). *Sediment. Geol.* 222, 181–206.

908Brittain, J.M., Higgs, K.T. and Riding, J.B. 2010. The palynology of the Pabay Shale
909Formation (Lower Jurassic) of SW Raasay, northern Scotland. *Scottish Journal of Geology*
91046(1), 67–75.

911Brownlee, C., Taylor, A., 2004. Calcification in coccolithophores: A cellular perspective, in:
912Coccolithophores. Springer, Berlin, Heidelberg, pp. 31–49.

913Bucefalo Palliani, R., Riding, J., 1997. The influence of palaeoenvironmental change on
914dinoflagellate cyst distribution-An example from the Lower and Middle Jurassic of Quercy,
915southwest France. *Bull. Cent. Rech. Explor.-Prod. Elf Aquitaine* 21, 107–123.

916Bucefalo Palliani, R., Mattioli, E., Riding, J.B., 2002. The response of marine phytoplankton
917and sedimentary organic matter to the early Toarcian (Lower Jurassic) oceanic anoxic event
918in northern England. *Mar. Micropaleontol.* 46, 223–245.

919Bujak, J.P., Williams, G.L., 1977. Jurassic palynostratigraphy of offshore eastern Canada.
920*Dev. Palaeontol. Stratigr.* 6, 321–339.

921Butterfield, N., Harvey, T., 2012. Small carbonaceous fossils (SCFs): A new measure of early
922Paleozoic paleobiology. *Geology* 40, 71–74.

923Calbet, A., 2008. The trophic roles of microzooplankton in marine systems. *ICES J. Mar. Sci.*
924*J. Cons.* 65, 325–331.

925Cohen, A.S., Coe, A.L., Harding, S.M., Schwark, L., 2004. Osmium isotope evidence for the
926regulation of atmospheric CO₂ by continental weathering. *Geology* 32, 157–160.

927Conway, B.H., 1990. Palynostratigraphy of the Jurassic succession in the subsurface of Israel.
928Geological Survey of Israel Bulletin 82, 1–39 pp.

929Correia, V.F., Riding, J.B., Fernandes, P., Duarte, L.V., Pereira, Z., 2017a. The palynology of
930the lower and middle Toarcian (Lower Jurassic) in the northern Lusitanian Basin, western
931Portugal. *Rev. Palaeobot. Palynol.* 237, 75–95.

932Correia, V.F., Riding, J.B., Fernandes, P., Duarte, L.V. and Pereira, Z. 2017b. The
933palynological response to the Toarcian Oceanic Anoxic Event (Early Jurassic) at Peniche,
934Lusitanian Basin, western Portugal. *Marine Micropalaeontology*, in press.

935Crudeli, D., Young, J.R., Erba, E., Geisen, M., Ziveri, P., de Lange, G.J., Slomp, C.P., 2006.
936Fossil record of holococcoliths and selected hetero-holococcolith associations from the
937Mediterranean (Holocene–late Pleistocene): Evaluation of carbonate diagenesis and
938palaeoecological–palaeoenographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
939237, 191–212.

940Dale, B., 1983. Dinoflagellate resting cysts: 'benthic plankton'. In: *Surviv. Strateg. Algae*.
941Phycological Society of America.

942Davies, E.H., 1983. The dinoflagellate oppel-zonation of the Jurassic-Lower Cretaceous
943sequence in the Sverdrup Basin, arctic Canada. *Geological Survey of Canada Bulletin*.

944De Kaenel, E., Bergen, J., 1993. New Early and Middle Jurassic coccolith taxa and
945biostratigraphy from the eastern proto-Atlantic (Morocco, Portugal and DSDP Site 547 B).
946*Eclogae Geol. Helvetiae* 86, 861–907.

947de Vargas, C., Aubry, M., Probert, I., Young, J., 2007. Origin and evolution of
948coccolithophores: from coastal hunters to oceanic farmers. *Evol. Prim. Prod. Sea* 12, 251–
949285.

950de Vernal, A., Marret, F., 2007. Chapter Nine Organic-Walled Dinoflagellate Cysts: Tracers
951of Sea-Surface Conditions, in: Vernal, C.H. and A.D. (eds.), *Developments in Marine*
952*Geology, Proxies in Late Cenozoic Paleooceanography*. Elsevier, pp. 371–408.

953Delwiche, C., F., 2007. CHAPTER 10 - The Origin and Evolution of Dinoflagellates In:
954Falkowski, P. G., Knoll, A.H. (eds.), *Evolution of Primary Producers in the Sea*. Academic
955Press, Burlington, pp. 191–205.

956Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P.,
957Joachimski, M.M., Durlet, C., 2011. Climatic ups and downs in a disturbed Jurassic world.
958*Geology* 39, 215–218.

959Dera, G., Prunier, J., Smith, P.L., Haggart, J.W., Popov, E., Guzhov, A., Rogov, M., Delsate,
960D., Thies, D., Cuny, G., Pucéat, E., Charbonnier, G., Bayon, G., 2014. Nd isotope constraints
961on ocean circulation, paleoclimate, and continental drainage during the Jurassic breakup of
962Pangea. *Gondwana Res.* 27, 1599–1615.

963Dera, G., Toumoulin, A., De Baets, K., 2016. Diversity and morphological evolution of
964Jurassic belemnites from South Germany. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 457, 80–
96597.

966Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst–Theca Relationship, Life Cycle, and Effects
967of Temperature and Salinity on the Cyst Morphology of *Gonyaulax Baltica* Sp. Nov.
968(dinophyceae) from the Baltic Sea Area1. *J. Phycol.* 38, 775–789.

969Evitt, W.R., 1985. Sporopollenin Dinoflagellate Cysts: Their Morphology and Interpretation.
970Amer Assn of Stratigraphic, Dallas, Tex.

971

972Falkowski, P.G., Knoll, A.H. (eds). 2007. The evolution of primary producers in the sea.
973Elsevier Academic Press.

974Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., Taylor,
975F.J.R., 2004a. The Evolution of Modern Eukaryotic Phytoplankton. *Science* 305,

976Falkowski, P.G., Schofield, O., Katz, M.E., Van de Schootbrugge, B., Knoll, A.H., 2004b.
977Why is the land green and the ocean red?, in: *Coccolithophores*. Springer, pp. 429–453.

978Feist-Burkhardt, S., 1990. Dinoflagellate cyst assemblages of the Hausen coreholes (Aalenian
979to early Bajocian), southwest Germany. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine* 14,
980611–633.

981Feist-Burkhardt, S., 2009. Palynology of the Sinemurian/Pliensbachian boundary (Lower
982Jurassic) in the Wutach area, SW Germany: dinoflagellate cyst systematics, biostratigraphy
983and heterotrophic character of *Liasidium variabile*. *Neues Jahrb. Für Geol. Paläontol.-Abh.*
984254, 293–313.

985Feist-Burkhardt, S., Götz, A.E., 2016. Ultra-High-Resolution Palynostratigraphy of the Early
986Bajocian Sauzei and Humphriesianum Zones (Middle Jurassic) from Outcrop Sections in the
987Upper Rhine Area, Southwest Germany, in: *Stratigraphy & Timescales*. Elsevier, pp. 325–
988392.

989Feist-Burkhardt, S., Wille, W., 1992. Jurassic palynology in southwest Germany — state of
990the art. *Cah. Micropaléontologie Nouv. Sér.* 7, 141–156.

991Feist-Burkhardt, S., Monteil, E., 1997. Dinoflagellate cysts from the Bajocian stratotype
992(Calvados, Normandy, western France). *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine* 21,
99331–105.

994Feist-Burkhardt, S., Pross, J., 2010. Dinoflagellate cyst biostratigraphy of the Opalinuston
995Formation (Middle Jurassic) in the Aalenian type area in southwest Germany and north
996Switzerland. *Lethaia* 43, 10–31. doi:10.1111/j.1502-3931.2009.00170.x

997Fensome, R.A., MacRae, R.A., Moldowan, J.M., Taylor, F.J.R., Williams, G.L., 1996. The
998early Mesozoic radiation of dinoflagellates. *Paleobiology* 22, 329–338.

999Fensome, R.A., Saldarriaga, J.F., Taylor, “Max” F. J. R., 1999. Dinoflagellate phylogeny
1000revisited: reconciling morphological and molecular based phylogenies. *Grana* 38, 66–80.

1001Fensome, R.A., Taylor, F., Norris, G., Sarjeant, W., Wharton, D., Williams, G., 1993. A
1002classification of living and fossil dinoflagellates.

1003Ferreira, J., Mattioli, E., Van de Schootbrugge, B., 2017. Palaeoenvironmental vs.
1004evolutionary control on size variation of coccoliths across the Lower-Middle Jurassic.
1005*Palaeogeogr. Palaeoclimatol. Palaeoecol.* 465, 177–192.

1006Fraguas, Á., Comas-Rengifo, M.J., Gómez, J.J., Goy, A., 2012. The calcareous nannofossil
1007crisis in Northern Spain (Asturias province) linked to the Early Toarcian warming-driven
1008mass extinction. *Mar. Micropaleontol.* 94, 58–71.

1009Friedman, M., Shimada, K., Martin, L.D., Everhart, M.J., Liston, J., Maltese, A., Triebold,
1010M., 2010. 100-Million-Year Dynasty of Giant Planktivorous Bony Fishes in the Mesozoic
1011Seas. *Science* 327, 990–993.

1012Gardin, S., Krystyn, L., Richoz, S., Bartolini, A., Galbrun, B., 2012. Where and when the
1013earliest coccolithophores? *Lethaia* 45, 507–523.

1014Giraud, F., Mattioli, E., López-Otálvaro, G.E., Lécuyer, C., Suchéras-Marx, B., Alméras, Y.,
1015Martineau, F., Arnaud-Godet, F., de Kænel, E., 2016. Deciphering processes controlling mid-
1016Jurassic coccolith turnover. *Mar. Micropaleontol.* 125, 36–50.

1017Gedl, P., 2008. Organic-walled dinoflagellate cyst stratigraphy of dark Middle Jurassic
1018marine deposits of the Pieniny Klippen Belt, West Carpathians. *Stud. Geol. Pol.* 131, 7–227.

1019Guinot, G., Cavin, L., 2015. ‘Fish’ (Actinopterygii and Elasmobranchii) diversification
1020patterns through deep time: ‘Fish’ diversification patterns through deep time. *Biol. Rev.*
1021Hallam, A., 1976. Stratigraphic distribution and ecology of European Jurassic bivalves.
1022*Lethaia* 9, 245–259.

1023Hallam, A., 2001. A review of the broad pattern of Jurassic sea-level changes and their
1024possible causes in the light of current knowledge. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
1025167, 23–37.

1026Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., De Graciansky, P.-C., Vail, P.R. (eds)
10271998. Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins.
1028SEPM Special publication no. 60.Harding, I.C., 1986. Archaeopyle variability in Early
1029Cretaceous dinocysts of the partiform gonyaulacoid genus *Druggidium* Habib. *J.*
1030*Micropalaeontology* 5, 17–26.

1031Harper, E.M., Forsythe, G.T., Palmer, T., 1998. Taphonomy and the Mesozoic marine
1032revolution; preservation state masks the importance of boring predators. *Palaios* 13, 352–360.

1033Harvey, T.H., Pedder, B.E., 2013. Copepod mandible palynomorphs from the Nolichucky
1034Shale (Cambrian, Tennessee): Implications for the taphonomy and recovery of small
1035carbonaceous fossils. *Palaios* 28, 278–284.

1036Harvey, T.H., Vélez, M.I., Butterfield, N.J., 2012. Exceptionally preserved crustaceans from
1037western Canada reveal a cryptic Cambrian radiation. *Proc. Natl. Acad. Sci.* 109, 1589–1594.

1038Head, M., 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansonius, J.,
1039McGregor, D.C. (Eds.), *Palynology: Principles and Applications 3*. American Association of
1040Stratigraphic Palynologists, Dallas, Texas, pp. 1197–1248.

1041Helby, R., Morgan, R., Partridge, A., 1987. A palynological zonation of the Australian
1042Mesozoic. *Mem. Assoc. Australas. Palaeontol.* 4, 1–94.

1043Hesselbo, S.P., Gröcke, D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Bell, H.S.M.,
1044Green, O.R., 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic
1045event. *Nature* 406, 392–395.

1046Hesselbo, S.P., Morgans-Bell, H.S., McElwain, J.C., Rees, P.M., Robinson, S.A., Ross, C.E.,
10472003. Carbon-cycle perturbation in the Middle Jurassic and accompanying changes in the
1048terrestrial paleoenvironment. *J. Geol.* 111, 259–276.

1049Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R.,
1050Kump, L., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer, D.L.,
1051Barker, S., Marchitto, T.M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L., Williams, B.,
10522012. The Geological Record of Ocean Acidification. *Science* 335, 1058–1063.
1053doi:10.1126/science.1208277

1054Hostettler, B., Reisdorf, A.G., Jaeggi, D., Deplazes, G., Bläsi, H., Morard, A., Feist-
1055Burkhardt, S., Waltschew, A., Dietze, V., Menkveld-Gfeller, U., 2017. Litho- and
1056biostratigraphy of the Opalinus Clay and bounding formations in the Mont Terri rock
1057laboratory (Switzerland). *Swiss J. Geosci.* 110, 23–37.

1058Ibrahim, M.I., Aboul Ela, N.M., Kholeif, S.E., 2002. Dinoflagellate cyst biostratigraphy of
1059Jurassic-Lower Cretaceous formations of the North Eastern Desert, Egypt. *Neues Jahrb. Für*
1060*Geol. Paläontol.-Abh.* 255–319.

1061Ibrahim, M., Kholeif, S., Al-Saad, H., 2003. Dinoflagellate cyst biostratigraphy and
1062paleoenvironment of the Lower-Middle Jurassic succession of Qatar, Arabian Gulf. *Rev. Esp.*
1063*Micropaleontol.* 35, 171–194.

1064Jacquin, T., Dardeau, G., Durllet, C., de Graciansky, P.-C., Hantzpergue, P., 1998. The North
1065Sea cycle: an overview of 2nd-order transgressive/regressive facies cycles in western Europe.
1066In: de Graciansky, P.C., Hardenbol, J., Jacquin, T., Vail, P.R. (Eds.), *Mesozoic and Cenozoic*
1067*Sequence Stratigraphy of European Basins*. SEPM Special Publication. 60, pp. 445–466.

1068Jäger, M., Fraaye, R., 1997. The diet of the Early Toarcian ammonite *Harpoceras falciferum*.
1069*Palaeontology* 40, 557–574.

1070Janouškovec, J., Gavelis, G.S., Burki, F., Dinh, D., Bachvaroff, T.R., Gornik, S.G., Bright,
1071K.J., Imanian, B., Strom, S.L., Delwiche, C.F., Waller, R.F., Fensome, R.A., Leander, B.S.,
1072Rohwer, F.L., Saldarriaga, J.F., 2017. Major transitions in dinoflagellate evolution unveiled
1073by phylotranscriptomics. *Proc. Natl. Acad. Sci.* 114, 171–180.

1074Jenkyns, H.C., Jones, C.E., GrÖcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002.
1075Chemostratigraphy of the Jurassic System: applications, limitations and implications for
1076palaeoceanography. *J. Geol. Soc.* 159, 351–378.

1077Kemp, D.B., Coe, A.L., Cohen, A.S., Schwark, L., 2005. Astronomical pacing of methane
1078release in the Early Jurassic period. *Nature* 437, 396.

1079Knoll, A.H., Follows, M.J., 2016. A bottom-up perspective on ecosystem change in Mesozoic
1080oceans. *Proc. R. Soc. B Biol. Sci.* 283, 20161755.

1081Knoll, A.H., Summons, R.E., Waldbauer, J.R., Zumberge, J.E., 2007. The geological
1082succession of primary producers in the oceans. In: Falkowski, P.G., Knoll, A.H. (eds) *Evol.*
1083*Prim. Prod. Sea* 133–163.

1084Korte, C., Hesselbo, S.P., Ullmann, C.V., Dietl, G., Ruhl, M., Schweigert, G., Thibault, N.,
10852015. Jurassic climate mode governed by ocean gateway. *Nat. Commun.* 6, 10015.
1086doi:10.1038/ncomms10015

1087Kruta, I., Landman, N., Rouget, I., Cecca, F., Tafforeau, P., 2011. The role of ammonites in
1088the Mesozoic marine food web revealed by jaw preservation. *Science* 331, 70–72.

1089Kuerschner, W.M., Bonis, N.R., Krystyn, L., 2007. Carbon-isotope stratigraphy and
1090palynostratigraphy of the Triassic–Jurassic transition in the Tiefengraben section—Northern
1091Calcareous Alps (Austria). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 244, 257–280.

1092Labails, C., Olivet, J.-L., Aslanian, D., Roest, W.R., 2010. An alternative early opening
1093scenario for the Central Atlantic Ocean. *Earth Planet. Sci. Lett.* 297, 355–368.

1094Lees, J.A., Bown, P.R., Mattioli, E., 2005. Problems with proxies? Cautionary tales of
1095calcareous nannofossil paleoenvironmental indicators. *Micropaleontology* 51, 333–343.

1096MacRae, R.A., Fensome, R.A., Williams, G.L., 1996. Fossil dinoflagellate diversity,
1097originations, and extinctions and their significance. *Can. J. Bot.* 74, 1687–1694.

1098Mantle, D.J., Riding, J.B., 2012. Palynology of the Middle Jurassic (Bajocian–Bathonian)
1099Wanaea verrucosa dinoflagellate cyst zone of the North West Shelf of Australia. *Rev.*
1100*Palaeobot. Palynol.* 180, 41–78.

1101Marañón, E., 2015. Cell Size as a Key Determinant of Phytoplankton Metabolism and
1102Community Structure. *Annu. Rev. Mar. Sci.* 7, 241–264. doi:10.1146/annurev-marine-
1103010814-015955

1104Mattioli, E., Erba, E., 1999. Biostratigraphic synthesis of calcareous nannofossil events in the
1105Tethyan Jurassic. *Riv Ital Paleontol Strat.* 105, 343–376.

1106Mattioli, E., Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian-
1107Toarcian (Lower Jurassic) coccoliths of the family Biscutaceae: intra- and interspecific
1108variability versus palaeoenvironmental influence. *Mar. Micropaleontol.*, *Calcareous*
1109nannofossil palaeoecology and palaeoenographic reconstructions 52, 5–27.

1110Mattioli, E., Pittet, B., Suan, G., Mailliot, S., 2008. Calcareous nannoplankton changes across
1111the early Toarcian oceanic anoxic event in the western Tethys. *Paleoceanography* 23.

1112Mattioli, E., Plancq, J., Boussaha, M., Duarte, L., Pittet, B., 2013. Calcareous nannofossil
1113biostratigraphy: new data from the Lower Jurassic of the Lusitanian Basin. *Comun.*
1114*Geológicas.*

1115Mattioli, E., Pittet, B., Petitpierre, L., Mailliot, S., 2009. Dramatic decrease of pelagic
1116carbonate production by nannoplankton across the Early Toarcian anoxic event (T-OAE).
1117*Glob. Planet. Change* 65, 134–145.

1118Medlin, L., Sáez, A., Young, J., 2008. A molecular clock for coccolithophores and
1119implications for selectivity of phytoplankton extinctions across the K/T boundary. *Mar.*
1120*Micropaleontol.* 67, 69–86.

1121Moldowan, J.M., Dahl, J., Jacobson, S.R., Huizinga, B.J., Fago, F.J., Shetty, R., Watt, D.S.,
1122Peters, K.E., 1996. Chemostratigraphic reconstruction of biofacies: Molecular evidence
1123linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology* 24, 159–162.

1124Moldowan, J.M., Talyzina, N.M., 1998. Biogeochemical evidence for dinoflagellate
1125ancestors in the Early Cambrian. *Science* 281, 1168–1170.

1126Montresor, M., Nuzzo, L., Mazzocchi, M.G., 2003. Viability of dinoflagellate cysts after the
1127passage through the copepod gut. *J. Exp. Mar. Biol. Ecol.* 287, 209–221.

1128Morgenroth, P., 1970. Dinoflagellate cysts from the Lias delta of Lühnde/Germany. *Neues*
1129*Jahrb. Für Geol. Paläontol. Abh.* 136, 345–359.

1130O'Dogherty, L., Sandoval, J., Bartolini, A., Bruchez, S., Bill, M., Guex, J., 2006. Carbon–
1131isotope stratigraphy and ammonite faunal turnover for the Middle Jurassic in the Southern
1132Iberian palaeomargin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239, 311–333.

1133Ogg, J.G., Ogg, G., Gradstein, F.M., 2016. *A Concise Geologic Time Scale: 2016.* Elsevier.

1134Percival, L.M., Ruhl, M., Hesselbo, S.P., Jenkyns, H.C., Mather, T.A., Whiteside, J.H., 2017.
1135Mercury evidence for pulsed volcanism during the end-Triassic mass extinction. *Proc. Natl.*
1136*Acad. Sci.* 201705378.

1137Persson, A., 2000. Possible predation of cysts—a gap in the knowledge of dinoflagellate
1138ecology? *J. Plankton Res.* 22, 803–809.

1139Philippe, M., Puijalon, S., Suan, G., Mousset, S., Thévenard, F., Mattioli, E., 2017. The
1140palaeolatitudinal distribution of fossil wood genera as a proxy for European Jurassic
1141terrestrial climate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 373–381.

1142Piel KM, Evitt WR. 1980. Paratabulation in the Jurassic dinoflagellate genus
1143*Nannoceratopsis* and a comparison with modern taxa. *Palynology* 4:79–104.

1144Plancq, J., Mattioli, E., Pittet, B., Baudin, F., Duarte, L.V., Boussaha, M., Grossi, V., 2016. A
1145calcareous nannofossil and organic geochemical study of marine palaeoenvironmental
1146changes across the Sinemurian/Pliensbachian (early Jurassic, ~191Ma) in Portugal.
1147*Palaeogeogr. Palaeoclimatol. Palaeoecol.* 449, 1–12.

1148Price, G.D., Baker, S.J., VanDeVelde, J., Clémence, M.-E., 2016. High-resolution carbon
1149cycle and seawater temperature evolution during the Early Jurassic (Sinemurian-Early
1150Pliensbachian). *Geochem. Geophys. Geosystems* 17, 3917–3928.

1151Prauss, M., 1989. Dinozysten-Stratigraphie und Palynofazies im Oberen Lias und Dogger
1152von NW-Deutschland. *Palaeontogr. Abt. B* 1–124.

1153Raucsik, B., Varga, A., 2008. Climato-environmental controls on clay mineralogy of the
1154Hettangian–Bajocian successions of the Mecsek Mountains, Hungary: An evidence for
1155extreme continental weathering during the early Toarcian oceanic anoxic event. *Palaeogeogr.*
1156*Palaeoclimatol. Palaeoecol.* 265, 1–13.

1157Raucsik, B., A. Demény, I. Borbély Kiss, and G. Szabó. 2001. Monsoon-like climate during
1158the Bajocian. Clay mineralogical and geochemical study on a limestone/marl alternation
1159(Komló Calcareous Marl Formation, Mecsek Mountains, Southern Hungary). *Hantkeniana* 3,
1160149–176.

1161Reggiani, L., Mattioli, E., Pittet, B., Duarte, L., De Oliveira, L.V., Comas-Rengifo, M., 2010.
1162Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian
1163Basin, Portugal): A clue for palaeoenvironmental reconstructions. *Mar. Micropaleontol.* 75,
11641–16.

1165Ricoz, S., van de Schootbrugge, B., Pross, J., Püttmann, W., Quan, T.M., Lindström, S.,
1166Heunisch, C., Fiebig, J., Maquil, R., Schouten, S., Hauzenberger, C.A., Wignall, P.B., 2012.
1167Hydrogen sulphide poisoning of shallow seas following the end-Triassic extinction. *Nat.*
1168*Geosci.* 5, 662–667.

1169Riding, J.B., 1984. A palynological investigation of Toarcian to early Aalenian strata from
1170the Blea Wyke area, Ravenscar, North Yorkshire. *Proc. Yorks. Geol. Soc.* 45, 109–122.

1171Riding, J.B., Thomas, J.E., 1992. Dinoflagellate cysts of the Jurassic System, in: In: Powell,
1172A.J. A Stratigraphic Index of Dinoflagellate Cysts. Chapman and Hall, London, pp. 7–97.

1173Riding, J.B. and Michoux, D. 2013. Further observations on the Jurassic dinoflagellate cyst
1174*Gonyaulacysta dentata* (Raynaud 1978) Lentin & Vozzhennikova 1990 emended Riding
11752012. *Review of Palaeobotany and Palynology* 196, 51–56.

1176Riding, J.B. and Lucas-Clark, J. 2016. The life and scientific work of William R. Evitt
1177(1923–2009). *Palynology* 40, Supplement 1, 2–131.

1178Riding, J.B., Mantle, D.J., Backhouse, J., 2010a. A review of the chronostratigraphical ages
1179of Middle Triassic to Late Jurassic dinoflagellate cyst biozones of the North West Shelf of
1180Australia. *Rev. Palaeobot. Palynol.* 162, 543–575.

1181Riding, J.B., Westermann, G.E.G., Darbyshire, D.P.F., 2010b. New evidence for the age of
1182the Athol Formation (Middle Jurassic; Bajocian) in the Tusk-1 and Tusk-2 wells, offshore
1183Carnarvon Basin, Western Australia. *Alcheringa Australas. J. Palaeontol.* 34, 21–35.

1184Riding, J.B., Leng, M.J., Kender, S., Hesselbo, S.P., Feist-Burkhardt, S., 2013. Isotopic and
1185palynological evidence for a new Early Jurassic environmental perturbation. *Palaeogeogr.*
1186*Palaeoclimatol. Palaeoecol.* 374, 16–27.

1187Rost, B., Riebesell, U., 2004. Coccolithophores and the biological pump: responses to
1188environmental changes. *Coccolithophores—From Mol. Process. Glob. Impact* 76–99.

1189Ruhl, M., Bonis, N.R., Reichert, G.-J., Damsté, J.S.S., Kürschner, W.M., 2011. Atmospheric
1190Carbon Injection Linked to End-Triassic Mass Extinction. *Science* 333, 430–434.

1191Ruhl, M., Hesselbo, S.P., Hinnov, L., Jenkyns, H.C., Xu, W., Riding, J.B., Storm, M.,
1192Minisini, D., Ullmann, C.V., Leng, M.J., 2016. Astronomical constraints on the duration of

1193the Early Jurassic Pliensbachian Stage and global climatic fluctuations. *Earth Planet. Sci.*
1194*Lett.* 455, 149–165.

1195Sandoval, J., O’Dogherty, L., Guex, J., 2001. Evolutionary Rates of Jurassic Ammonites in
1196Relation to Sea-Level Fluctuations. *PALAIOS* 16, 311.

1197Sarjeant, W.A.S., Lacalli, T., Gaines, G., 1987. The Cysts and Skeletal Elements of
1198Dinoflagellates: Speculations on the Ecological Causes for Their Morphology and
1199Development. *Micropaleontology* 33, 1–36.

1200Scotese, C.R., 2014. Atlas of Jurassic Paleogeographic Maps, PALEOMAP Atlas for
1201ArcGIS, volume 4, The Jurassic and Triassic, Maps 32-42, Mollweide Projection,
1202PALEOMAP Project, Evanston, IL.

1203Schaller, M.F., Wright, J.D., Kent, D.V., 2011. Atmospheric Pco₂ Perturbations Associated
1204with the Central Atlantic Magmatic Province. *Science* 331, 1404–1409.

1205Schoene, B., Guex, J., Bartolini, A., Schaltegger, U., Blackburn, T.J., 2010. Correlating the
1206end-Triassic mass extinction and flood basalt volcanism at the 100 ka level. *Geology* 38,
1207387–390.

1208Selden, P.A., Huys, R., Stephenson, M.H., Heward, A.P., Taylor, P.N., 2010. Crustaceans
1209from bitumen clast in Carboniferous glacial diamictite extend fossil record of copepods. *Nat.*
1210*Commun.* 1, 50.

1211Simmons, M., BouDagher-Fadel, M., Banner, F., Whittaker, J., 1997. The Jurassic
1212Favusellacea, the earliest Globigerinina, in: *The Early Evolutionary History of Planktonic*
1213*Foraminifera*. Springer, pp. 17–51.

1214Stukins, S., Jolley, D.W., McIlroy, D., Hartley, A.J., 2013. Middle Jurassic vegetation
1215dynamics from allochthonous palynological assemblages: An example from a marginal

1216marine depositional setting; Lajas Formation, Neuquén Basin, Argentina. *Palaeogeogr.*
1217*Palaeoclimatol. Palaeoecol.* 392, 117–127.

1218Suan, G., Pittet, B., Bour, I., Mattioli, E., Duarte, L.V., Mailliot, S., 2008. Duration of the
1219Early Toarcian carbon isotope excursion deduced from spectral analysis: consequence for its
1220possible causes. *Earth Planet. Sci. Lett.* 267, 666–679.

1221Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L.V., Philippe, M.,
1222Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian
1223(Jurassic) extreme climate changes. *Earth Planet. Sci. Lett.* 290, 448–458.

1224

1225Suan, G., Nikitenko, B.L., Rogov, M.A., Baudin, F., Spangenberg, J.E., Knyazev, V.G.,
1226Glinskikh, L.A., Goryacheva, A.A., Adatte, T., Riding, J.B., Föllmi, K.B., Pittet, B., Mattioli,
1227E., Lécuyer, C., 2011. Polar record of Early Jurassic massive carbon injection. *Earth Planet.*
1228*Sci. Lett.* 312, 102–113.

1229Suchéras-Marx, B., Guihou, A., Giraud, F., Lécuyer, C., Allemand, P., Pittet, B., Mattioli, E.,
12302012. Impact of the Middle Jurassic diversification of *Watznaueria* (coccolith-bearing algae)
1231on the carbon cycle and $\delta^{13}\text{C}$ of bulk marine carbonates. *Glob. Planet. Change* 86–87, 92–
1232100.

1233Suchéras-Marx, B., Giraud, F., Fernandez, V., Pittet, B., Lécuyer, C., Olivero, D., Mattioli,
1234E., 2013. Duration of the Early Bajocian and the associated $\delta^{13}\text{C}$ positive excursion based
1235on cyclostratigraphy. *J. Geol. Soc.* 170, 107–118.

1236Suchéras-Marx, B., Mattioli, E., Giraud, F., Escarguel, G., 2015. Paleoenvironmental and
1237paleobiological origins of coccolithophorid genus *Watznaueria* emergence during the late
1238Aalenian–early Bajocian. *Paleobiology* 41, 415–435.

1239 Taylor, P.D., Ernst, A., 2008. Bryozoans in transition: The depauperate and patchy Jurassic
1240 biota. *Palaeogeogr. Palaeoclimatol. Palaeoecol., Jurassic Marine Palaeobiology* 263, 9–23.

1241 Tiraboschi, D., Erba, E., 2010. Calcareous nannofossil biostratigraphy (Upper Bajocian–
1242 Lower Bathonian) of the Ravin du Bès section (Bas Auran, Subalpine Basin, SE France):
1243 evolutionary trends of *Watznaueria barnesiae* and new findings of “*Rucinolithus*”
1244 morphotypes. *Geobios* 43, 59–76.

1245 Tremolada, F., Van de Schootbrugge, B., Erba, E., 2005. Early Jurassic schizosphaerellid
1246 crisis in Cantabria, Spain: implications for calcification rates and phytoplankton evolution
1247 across the Toarcian oceanic anoxic event. *Paleoceanography* 20.

1248 Tyson, R.V., 1995. Abundance of organic matter in sediments: TOC, hydrodynamic
1249 equivalence, dilution and flux effects, in: *Sedimentary Organic Matter*. Springer, pp. 81–118.

1250 van de Schootbrugge, B., Bailey, T.R., Rosenthal, Y., Katz, M.E., Wright, J.D., Miller, K.G.,
1251 Feist-Burkhardt, S., Falkowski, P.G., 2005. Early Jurassic climate change and the radiation of
1252 organic-walled phytoplankton in the Tethys Ocean. *Paleobiology* 31, 73–97.

1253 van de Schootbrugge, B., Tremolada, F., Rosenthal, Y., Bailey, T.R., Feist-Burkhardt, S.,
1254 Brinkhuis, H., Pross, J., Kent, D.V., Falkowski, P.G., 2007. End-Triassic calcification crisis
1255 and blooms of organic-walled ‘disaster species.’ *Palaeogeogr. Palaeoclimatol. Palaeoecol.*,
1256 *Triassic-Jurassic Boundary events: problems, progress, possibilities* 244, 126–141.

1257 van de Schootbrugge, B., Bachan, A., Suan, G., Richoz, S., Payne, J.L., 2013. Microbes, mud
1258 and methane: cause and consequence of recurrent Early Jurassic anoxia following the end-
1259 Triassic mass extinction. *Palaeontology* 56, 685–709. doi:10.1111/pala.12034

1260 Vermeij, G.J., 1977. The Mesozoic marine revolution: evidence from snails, predators and
1261 grazers. *Paleobiology* 3, 245–258.

1262 Vermeij, G.J., 1987. Evolution and escalation: an ecological history of life. Princeton
1263 University Press.

1264 Vermeij, G.J., 2008. Escalation and its role in Jurassic biotic history. *Palaeogeogr.*
1265 *Palaeoclimatol. Palaeoecol., Jurassic Marine Palaeobiology* 263, 3–8.

1266 Versteegh, G.J.M., Blokker, P., Wood, G.D., Collinson, M.E., Sinninghe Damsté, J.S., de
1267 Leeuw, J.W., 2004. An example of oxidative polymerization of unsaturated fatty acids as a
1268 preservation pathway for dinoflagellate organic matter. *Org. Geochem., Selected papers from*
1269 *the sixteenth international symposium on environmental biogeochemistry* 35, 1129–1139.

1270 Wall, D., 1965. Microplankton, Pollen, and Spores from the Lower Jurassic in Britain.
1271 *Micropaleontology* 11, 151–190. doi:10.2307/1484516

1272 Wiggan, N.J., Riding, J.B., Franz, M., 2017. Resolving the Middle Jurassic dinoflagellate
1273 radiation: The palynology of the Bajocian of Swabia, southwest Germany. *Rev. Palaeobot.*
1274 *Palynol.* 238, 55–87.

1275 Wood, S.E.L., Riding, J.B., Fensome, R.A. and Williams, G.L. 2016. A review of the
1276 *Sentusidinium* complex of dinoflagellate cysts. *Review of Palaeobotany and Palynology* 234,
1277 61–93.

1278 Xu, W., Ruhl, M., Jenkyns, H.C., Hesselbo, S.P., Riding, J.B., Selby, D., Naafs, B.D.A.,
1279 Weijers, J.W., Pancost, R.D., Tegelaar, E.W., 2017. Carbon sequestration in an expanded
1280 lake system during the Toarcian oceanic anoxic event. *Nat. Geosci.* 10, 129–134.

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1284**Figure Captions:**

1285

1286Figure 1. Dinoflagellate cyst and coccolith species richness throughout the Middle Triassic to
1287Jurassic modified from Wiggan et al. (2017, fig. 1). The timescale is based on Gradstein et al.
1288(2012). The family-level spindle plot for dinoflagellate cysts clearly shows the significant
1289increase in diversity of the family Gonyaulaceae during the Bajocian. Key bioevents for
1290coccolithophores are indicated, notably the evolution of placolith coccoliths in the
1291Pliensbachian, and the ecological transition to the dominance of *Watznaueria* in the Bajocian.
1292The dinoflagellate cyst species richness is taken from MacRae et al. (1996), the spindle plot
1293data is after Fensome et al. (1996) and the coccolith species richness is after Bown et al.
1294(2004).

1295

1296Figure 2. Coccolith abundances and $\delta^{13}\text{C}$ for the Late Aalenian to Early Bajocian marls of
1297the Subalpine Basin, France. Note that the increase in the absolute and relative abundances of
1298*Watznaueria* through the Early Bajocian parallels the increase in $\delta^{13}\text{C}$. There is also a shift in
1299the absolute abundance of coccoliths of around an order of magnitude, from 10^7 – 10^8
1300coccoliths per g in the latest Aalenian to earliest Bajocian, to 10^8 – 10^9 coccoliths per g in the
1301latest Early Bajocian. Modified from Suchéras-Marx et al. (2015, fig. 4).

1302

1303Figure 3. Synthetic relative abundances of three important morphogroups of the
1304coccolithophore genus *Watznaueria* through the Late Aalenian to Early Bathonian from
1305Giraud et al. (2016). Note that at the Aalenian–Bajocian transition, there is an increase in taxa
1306defined by a central cross area. This is then followed by an increase in the abundances of taxa
1307without a central area, and those with a central bar. This increase in the abundance of

1308 *Watznaueria* is concomitant with a long-term decline in the abundance of *Lotharingius*.
1309 Abundances after Giraud et al. (2016, fig. 8) and coccolith morphologies after Giraud et al.
1310 (2016, fig. 2). Ammonite biozone abbreviations: L.m. = *Ludwigia murchisonae*; G.c. =
1311 *Graphoceras concavum*; H.d. = *Hyperlioceras discites*; W.l. = *Witchellia laeviuscula*; S.p. =
1312 *Sonninia propinquans*; S.h. = *Stephanoceras humphriesianum*; S.n. = *Strenoceras niortense*;
1313 G.g. = *Garantiana garantiana*; P.p. = *Parkinsonia parkinsoni*; Z.z. = *Zigzagiceras zigzag*;
1314 P.a. = *Procerites aurigerus*; P.p. = *Procerites progracilis*, T.s. = *Tulites subcontractus*; M.m.
1315 = *Morrisiceras morrisoni*; H.r. = *Hecticoceras retrocostatum*; C.d. = *Clydoniceras discus*.

1316

1317 Figure 4. Coccolith abundances and $\delta^{13}\text{C}$ for the Late Aalenian to Early Bajocian of the
1318 southern Iberian palaeomargin, Spain modified after Aguado et al. (2017, fig. 2). Note the
1319 increase in the absolute abundance of *Watznaueria* which parallels an increase in $\delta^{13}\text{C}$. The
1320 increase in the abundance of *Watznaueria* is concomitant with the decline in the abundance of
1321 *Crepidolithus crassus*, a coccolith which has been interpreted as inhabiting the deep photic
1322 zone.

1323

1324 Figure 5. Absolute abundances of *Dissiliodinium giganteum* through the Early Bajocian of
1325 borehole B404-2 in southern Germany based on raw data from Wiggan et al. (2017).
1326 *Dissiliodinium giganteum* forms a significant proportion (>80%) of the dinoflagellate cyst
1327 assemblages throughout the *Witchellia laeviuscula* ammonite biozone, but declined in
1328 abundance towards the latest Early Bajocian (*Stephanoceras humphriesianum* ammonite
1329 biozone). Two specimens of *Dissiliodinium giganteum* are shown to the right. The upper
1330 specimen is in apical view; the loss of multiple precingular plates during archaeopyle
1331 formation can be observed. The lower image is in dorsoventral view.

1332

1333Figure 6. Bajocian palaeogeography and the abundance distribution of the dinoflagellate cyst
1334genus *Dissiliodinium* during the Early Bajocian. *Dissiliodinium giganteum* was abundant in
1335basins which bordered the northwest Tethys Ocean on the edge of the European
1336Epicontinental Seaway (EES) (i.e. southern Germany, Poland/northern Slovakia and
1337Switzerland). *Dissiliodinium caddaense* was abundant in the Early Bajocian of Australia, and
1338*Dissiliodinium psilatatum* was prominent in the Early Bajocian of the Neuquén Basin,
1339Argentina. The abundances of *Dissiliodinium giganteum* are based on raw data in Wiggan et
1340al. (2017) and unpublished information. The abundances of *Dissiliodinium caddaense* are
1341based on raw data from Riding et al. (2010b). The abundances of *Dissiliodinium psilatatum* are
1342based on raw data from Stukins et al. (2013). The palaeogeography is modified after Scotese
1343(2014).

1344

1345Figure 7. The stratigraphic ranges of dinoflagellate cysts from the latest Aalenian to the
1346earliest Bathonian of northwest Europe, based on data from Wiggan et al. (2017). Note that
1347there is a relatively continuous pattern of first appearances, but there are numerous first
1348appearances in the *Stephanoceras humphriesianum* ammonite biozone (*S.h.*). The grey fill
1349denotes dinoflagellate cyst taxa which belong to the family Gonyaulacaceae. The ammonite
1350biozone abbreviations are as per Figure 3.

1351

1352Figure 8. The stratigraphic ranges of dinoflagellate cysts from the latest Early Bajocian to the
1353earliest Bathonian of northwest Europe based on data from Wiggan et al. (2017). Note the
1354large number of first appearances in the *Stephanoceras humphriesianum* (*S.h.*) and
1355*Parkinsonia parkinsoni* (*P.p.*) ammonite biozones. First appearances from the *Stephanoceras*

1356*humphriesianum* zone onwards are dominated by gonyaulacacean taxa (grey fill). The
1357ammonite biozone abbreviations are as per Figure 3. F-B & M (1997) = Feist-Burkhardt and
1358Monteil (1997).

1359

1360Figure 9. A dinoflagellate cyst species richness curve from the latest Aalenian to the earliest
1361Bathonian based on stratigraphic data from Wiggan et al. (2017). Note how the increase in
1362diversity is primarily driven by a rise in the number of gonyaulacacean taxa (grey). There are
1363also pronounced increases in species richness in the *Stephanoceras humphriesianum* and
1364*Parkinsonia parkinsoni* ammonite biozones.

1365

1366Figure 10. Percentage of gonyaulacacean dinoflagellate cyst taxa for the Bajocian and
1367Bathonian low-, mid-, and high-palaeolatitude regions. It is clear that gonyaulacaceans
1368formed a larger proportion of the dinoflagellate cyst floras in the low- to mid-palaeolatitudes
1369than the high-palaeolatitudes during the Middle Jurassic. The graph is based on raw data
1370from: Bujak and Williams (1977) (eastern Canada); Davies (1983) (Arctic Canada); Conway
1371(1990) (Israel); Ibrahim et al. (2003) (Egypt); Mantle and Riding (2012) (Australia); Stukins
1372et al. (2013) (Argentina); and Wiggan et al. (2017) (northwest Europe).

1373

1374Figure 11. The diversity and disparity of gonyaulacacean dinoflagellate cyst taxa from the
1375Aalenian and Bajocian. Note how, in the Aalenian, the Gonyaulaceae were represented by
1376four genera, all of relatively simple morphology and largely nontabulate (i.e. not exhibiting
1377tabulation). *Batiacasphaera*, *Kallosphaeridium* and *Sentusidinium* all have apical
1378archaeopyles, whilst *Dissiliodinium* has a multiplate precingular archaeopyle. In the
1379Bajocian, the earliest fully tabulate sexiform gonyaulacaceans appeared, represented by

1380 *Durotrigia daveyi*. Other Bajocian developments included thick, ornamented cyst walls (e.g.
1381 *Acanthaulax*, *Aldorfia*), and prominent sutural crests (e.g. *Ctendidodinium*,
1382 *Meiourogonyaulax*). Moreover, the single-plate precingular archaeopyle appeared in genera
1383 such as *Acanthaulax*, *Aldorfia* and *Gonyaulacysta*, which has remained a prominent
1384 excystment strategy in gonyaulacaceans to the present day. Similarly, the epicystal
1385 archaeopyle type appeared in genera such *Ctendodinium*, *Korystocysta* and *Wanaea*. Note
1386 that *Meiourogonyaulax* and *Rhynchodiniopsis* are each represented by two photographs of the
1387 same specimen taken at different focal depths. The left image of *Meiourogonyaulax* was
1388 taken at the mid-focus, and the right taken at low focus, the latter shows the apical
1389 archaeopyle. The left image of *Rhynchodiniopsis* was taken at the high focus and right at low
1390 focus, the latter shows the one-plate precingular archaeopyle.

1391 Figure 12. Seawater palaeotemperatures based on the $\delta^{18}\text{O}$ of brachiopod and mollusc
1392 carbonate for the Early and Middle Jurassic (Pliensbachian–Bajocian) of Europe, simplified
1393 and redrawn after Korte et al. (2015, fig. 2). It is clear that a shift to cooler
1394 palaeotemperatures of $\sim 10^\circ\text{C}$ occurred through the Early–Middle Jurassic transition. The
1395 pronounced warming pulse in the latest Early Bajocian corresponds to the *Stephanoceras*
1396 *humphriesianum* ammonite biozone.

1397

1398 Figure 13. Carbon isotope and abundances of *Dissiliodinium giganteum* for the Late Aalenian
1399 to Early Bathonian. The central column depicts a composite $\delta^{13}\text{C}$ curve for bulk carbonate
1400 from the Late Aalenian to Early Bathonian of Europe based on raw data from O’Dogherty et
1401 al. (2006) and Suchéras-Marx et al. (2013). Note the $\sim 1.5\text{‰}$ shift to more positive $\delta^{13}\text{C}$
1402 values in the Early Bajocian. The right hand panel illustrates the abundance of the
1403 dinoflagellate cyst *Dissiliodinium giganteum* in the Swabian Basin of southern Germany

1404 taken from Wiggan et al. (2017) and supplemented by unpublished data. Note that the acme
1405 of *Dissiliodinium giganteum* is coeval with the positive shift in $\delta^{13}\text{C}$.

1406

1407 Figure 14. A comparison of sequence stratigraphy, sea level and dinoflagellate cyst species
1408 richness and appearances per zone through the Late Aalenian to Early Bathonian. The
1409 Bajocian was characterised by the T7 second-order transgression, which lasted from the latest
1410 Aalenian *Graphoceras concavum* ammonite biozone to the earliest Bathonian *Zigzagiceras*
1411 *zigzag* ammonite biozone. Maximum transgression is represented by the maximum flooding
1412 surface above third-order boundary Bj5 (the dotted line), which corresponds to a major
1413 flooding event through many European basins (Jacquin et al., 1998; Hallam, 2001). Note how
1414 the increase in species richness roughly parallels the rise in sea level. The large number of
1415 first appearances from the *Stephanoceras humphriesianum* (*S.h.*) and *Parkinsonia parkinsoni*
1416 (*P.p.*) ammonite biozones correspond to the pronounced third-order transgressive pulses Bj2
1417 and Bj5. The ammonite biozone abbreviations are as per Figure 3. The sea level cycles are as
1418 per Figure 12. The stratigraphy and sea level were generated using Timescale Creator v.6.4.2;
1419 the mean sea level curve is based on midpoint of coastal onlap charts of Hardenbol et al.
1420 (1998).

1421

1422 Figure 15. Species richness curves and the appearances of key marine fossil groups for the
1423 Early and Middle Jurassic. It is clear that the species richness curves of coccoliths and
1424 dinoflagellate cysts closely parallel those from higher trophic levels. All groups are plotted
1425 per stage/substage, except for the ammonites which are plotted per ammonite biozone.
1426 Coccolith and dinoflagellate cyst species richness data were taken from Figure 1. The
1427 planktonic foraminifera data are from Simmons et al. (1997). The bivalve data are those of

1428Hallam (1976). Data from bryozoans are from Taylor and Ernst (2008). The elasmobranch
1429diversity is after Guinot and Cavin (2015). The belemnite information is after Dera et al.
1430(2016), and the ammonite data are from Sandoval et al. (2001) and O'Dogherty et al. (2006).
1431The range of giant suspension feeders is after Friedman et al. (2010).

1432