The effects of the Jenkyns Event on the radiation of Early Jurassic dinoflagellate cysts

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Abstract

This contribution is an overview of the Early Jurassic dinoflagellate cysts of the Lusitanian Basin in Portugal, with particular emphasis on the effects of the Jenkyns Event (Toarcian Oceanic Anoxic Event – T-OAE) on the evolution of this planktonic group. We review and discuss data from 214 samples from six Lower Jurassic successions (upper Sinemurian—upper Toarcian) in the Lusitanian Basin. The late Pliensbachian radiation of dinoflagellate cysts was well recognised in this basin. The pre-Jenkyns Event interval is highly productive, with maximum abundance and species richness values. However, this palaeoenvironmental perturbation severely affected the evolution of this group for the remainder of the Early Jurassic. The prolonged recovery of the dinoflagellates in the Toarcian following the Jenkyns Event is not typical of the northern regions (Arctic and Boreal realms), where new species began to evolve earlier compared with southern European basins.

Keywords: dinoflagellate cysts; evolution; Lusitanian Basin; palaeobiology; palaeogeography; Toarcian Oceanic Anoxic Event

Dinoflagellates, together with coccolithophores and diatoms, comprise the bulk of the marine eukaryotic phytoplankton and are extremely significant primary producers. The bioproductivity and distribution of dinoflagellates are influenced by, for example, light, nutrients, ocean currents, salinity, temperature and water depth. As part of their life cycle, many dinoflagellates form resting cysts, and these have a rich fossil record from the Late Triassic onwards (e.g. Dale 1983; Fensome et al. 1996a,b,c; Falkowski et al. 2004). Dinoflagellate cysts are used as biostratigraphical markers, and palaeoclimatological and palaeoecological proxies (e.g. Stover et al. 1996; Riding and Hubbard 1999; Sluijs et al. 2005).

This contribution is a review of how dinoflagellate cysts responded to a major Early Jurassic global environmental perturbation, the Toarcian Oceanic Anoxic Event (T-OAE), currently renamed the Jenkyns Event (Müller et al. 2017; Reolid et al. 2020). However, the present authors proposed to use "T-OAE" only for marine deposits with oxygen-depleted conditions and the term "Jenkyns Event" for general Early Toarcian global palaeoenvironmental changes. This event, which occurred at ~183 Ma, was characterised by marine anoxia–euxinia, global warming and the extensive burial of organic matter. It was probably caused by greenhouse gas release linked to volcanism from the Karoo-Ferrar large igneous province, and it was accompanied by major changes in global geochemical cycles with a rapid negative shift in organic-carbon isotope records. The rise in palaeotemperatures increased the hydrogeological cycle. Consequently, the concomitant more intense weathering regime contributed elevated levels of nutrients, thereby promoting higher bioproductivity and hence more carbon burial. Studies on this palaeoenvironmental change are extensive, and it has been documented worldwide (e.g. Jenkyns 1988; Hesselbo et al. 2000, 2007; Kemp et al. 2005, 2019; Them et al. 2017; Xu et al. 2017; Fantasia et al. 2018a,b; Fonseca et al. 2018; Izumi et al., 2018; Rodrigues et al. 2019, 2020a,b,c; Jin et al. 2020; Krencker et al. 2020; Ruebsam et al. 2020a,b).

Specifically, we herein review regional trends in the Early Jurassic dinoflagellate cyst record based mostly on the Lower Jurassic (upper Sinemurian to upper Toarcian) reference sections in the Lusitanian Basin, Portugal, and compared with published data from elsewhere. The main emphasis is on the characterization of the pre-and-post-Jenkyns Event dinoflagellate cyst assemblages and the impact of the associated palaeoenvironmental changes on dinoflagellate evolution.

The geological setting of the Lusitanian Basin

The Lusitanian Basin is a critical Mesozoic depocentre, especially for the Jurassic, located in central-western Portugal, and oriented northeast-southwest (Fig. 1). It is 300 km long and 150 km wide, with a maximum basin fill of 5 km. The origin and evolution of this significant sedimentary basin are related to the breakup of Pangaea and the opening of the North Atlantic Ocean. The fill is mainly composed of marine strata, ranging in age from Middle?–Late Triassic to the latest Early Cretaceous (Kullberg et al. 2013). Although the ammonite record of the Lower Jurassic succession of the Lusitanian Basin indicates a strong Atlantic influence (Mouterde et al. 1979), mixed Boreal and Tethyan faunas in the upper Pliensbachian to Toarcian interval suggest intermittent communication between the two biotal realms (Elmi et al. 1989; Terrinha et al. 2002). Marine carbonate ramps formed rapidly in the Lusitanian Basin during the

Early Jurassic, largely comprising marl-limestone alternations (Azerêdo et al. 2003, 2014; Duarte 1997, 2007; Duarte et al. 2010).

Palynological data from the six Lower Jurassic successions (upper Sinemurian–upper Toarcian) in the Lusitanian Basin discussed in this work were first published by Correia et al. (2017a,b, 2018). The first is the São Pedro de Moel composite succession, comprising the Polvoeira Member of the Água de Madeiros Formation at Polvoeira (upper Sinemurian). Herein, we refer to this section as 'São Pedro de Moel', although the succession studied corresponds to the Polvoeira section of Duarte et al. (2012, 2014). The others are: the Brenha and Fonte Coberta sections, comprising the Vale das Fontes and Lemede formations (lower to upper Pliensbachian); the Peniche section, consisting of the Vale das Fontes, Lemede and Cabo Carvoeiro formations (lower Pliensbachian–lower Toarcian); and the Vale das Fontes and Maria Pares sections, comprising the São Gião and Póvoa da Lomba formations (lower to upper Toarcian). These lithostratigraphical units and the stratigraphical logs for each section were described and depicted by Correia et al. (2017a,b, 2018).

Material and methods

In this work, we review and discuss dinoflagellate cyst data from 214 samples from these six Lower Jurassic sections in the Lusitanian Basin (Fig. 1; Correia et al. 2018, fig. 2). Twelve samples (prefixed PM) were collected from the upper Sinemurian (*Oxynoticeras oxynotum* and *Echioceras raricostatum* biozones) of São Pedro de Moel (Correia et al. 2018, fig. 3). At Brenha, 22 samples were taken from a Pliensbachian composite section (*Uptonia jamesoni* to *Emaciaticeras emaciatum* biozones). The lower part of this section comprises the Vale das Fontes Formation (samples prefixed Br), and the upper part is the Lemede Formation (samples prefixed BrLem; Correia et al. 2018, fig. 4). A total of 72 samples (P-34 to P38) were collected from the lower Pliensbachian to lower Toarcian (*Tragophylloceras ibex* to *Hildaites levisoni* biozones) succession at Peniche (Correia et al. 2017b, fig. 3; Correia et al. 2018, fig. 5). At Fonte Coberta, in the Rabaçal area, five samples (prefixed FC) from the upper Pliensbachian (*Amaltheus margaritatus* and *Emaciaticeras emaciatum* biozones) were analysed (Correia et al. 2018, fig. 6). The section at Maria Pares comprises the lower, middle and upper Toarcian (*Dactylioceras polymorphum* to *Pleydellia aalensis* biozones) and 89 samples (numbered PZ1 to PZ89) were collected (Correia et al. 2017a, fig. 4; Correia et al. 2018, figs. 7–9). In the Vale das Fontes section, we examined 14 samples (numbered PVF1 to PVF14) from the lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* biozones; Correia et al. 2017a, fig. 5). Correia et al. (2017a,b, 2018) presented detailed palynostratigraphical data on these successions. The different thicknesses of the ammonite biozones from the Lower Jurassic of the Lusitanian Basin, represented herein in Figures 2 and 4, are proportional to the number of samples studied within each biozone.

The samples were processed using traditional demineralisation techniques for carbonate rocks, with hydrochloric acid followed by hydrofluoric acid (Riding and Warny 2008; Riding 2021). Because some palynomorphs are relatively light, the oxidation step was not undertaken. The swirling technique was performed for palynomorph concentration, and heavy liquids were not used. All residues were sieved using 15 µm mesh. The final concentrates used for the microscope slides production were stained with Safranin O, to improve the body colour of the palynomorphs. When possible, 300 palynomorphs was counted for each sample; if not, the maximum number of specimens from two microscope slides were assumed. The unused sample material, aqueous organic residues and microscope slides are all curated in the collections of LNEG (Portuguese Geological Survey), São Mamede de Infesta, Portugal.

The Early Jurassic dinoflagellate cyst palaeobiology of the Lusitanian Basin

A palynological overview

The upper Sinemurian succession at São Pedro de Moel proved entirely barren of dinoflagellate cysts (Fig. 2). The late Sinemurian marker dinoflagellate cyst *Liasidium variabile*, a thermophilic taxon and the index for the Liasidium Event (Riding et al. 2013; Hesselbo et al. 2020), was not recorded in this study. By contrast, the five Pliensbachian and Toarcian sections from the Lusitanian Basin yielded dinoflagellate cysts. Fifteen forms were identified, these are: *Dapsilidinium*? *deflandrei*; *Luehndea spinosa*; *Mancodinium semitabulatum*; *Maturodinium*? *inornatum*; *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum*; *Mendicodinium* sp.; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis*; *Nannoceratopsis senex*; *Nannoceratopsis* sp.; *Scriniocassis priscus*; *Scriniocassis weberi*; *Sentusidinium* sp.; and *Valvaeodinium* sp. (Figs 2, 3; Correia et al. 2017a,b, 2018). These relatively low diversity dinoflagellate cyst assemblages, and their stratigraphical ranges, are generally typical of the European Lower Jurassic (e.g. Riding 1984; Riding et al. 1991; Bucefalo Palliani and Riding 2003; Baranyi et al. 2016; Goryacheva 2017), and are consistent with previous investigations of the Lower Jurassic palynology in the Lusitanian Basin (Davies 1985; Oliveira et al. 2007; Barrón et al. 2013).

Other palynomorph groups such as acritarchs (e.g. *Micrhystridium* spp.) and prasinophytes (e.g. *Halosphaeropsis liassica, Tasmanites* spp.), spores, (e.g. *Cyathidites* spp., *Kraeuselisporites reissingeri*, *Leptolepidites* spp.) and pollen (e.g. *Alisporites* spp., *Araucariacites australis*, *Classopollis classoides*) were also identified (Correia et al. 2017a,b, 2018). Clumps of small and spherical palynomorphs, questionably assigned to the prasinophyte *Halosphaeropsis liassica* (see van de Schootbrugge et al. 2005, 2013) were significantly more common in the Jenkyns Event interval than in the overlying successions. *Halosphaeropsis liassica* is characteristic of the early Toarcian and is used as a marker for this event (Mädler 1968; Bucefalo Palliani and Riding 2000; van de Schootbrugge et al. 2019; Slater et al. 2019). The gymnosperm pollen species *Classopollis classoides* is the most abundant palynomorph throughout the Lower Jurassic of the Lusitanian Basin. The non-dinoflagellate cyst taxa encountered exhibit no noticeable or repeatable trends and are not discussed further here.

Dinoflagellate cyst bioevents and evolutionary constraints

Prior to the Jenkyns Event

In the Lusitanian Basin, the lowest dinoflagellate cyst appearance is recorded at the base of upper Pliensbachian (*Amaltheus margaritatus* Biozone), corresponding to the late Pliensbachian radiation event of this group (Figs 2, 4). We identified the inceptions of *Mancodinium semitabulatum* and *Luehndea spinosa*, both cosmopolitan species (e.g. Bucefalo Palliani and Riding 2003) and representing the family Mancodiniaceae, together with *Nannoceratopsis ambonis, Nannoceratopsis gracilis* and *Nannoceratopsis senex*, which belong to the family Nannoceratopsiaceae. This family is confined to the Jurassic, and the genus *Nannoceratopsis* is the only representative. Although cosmopolitan, *Nannoceratopsis* is more abundant in the Boreal and Arctic realms and here has diversified into morphologically complex species (Poulsen 1996; Bucefalo Palliani and Riding 1999a, fig. 6; van de Schootbrugge et al. 2019). Both the

Mancodiniaceae and Nannoceratopsiaceae are extinct and exhibit unusual archaeopyle types (Morgenroth 1970; Piel and Evitt 1980; Fensome et al. 1993). In terms of abundances, dinoflagellate cysts are moderately rare in the *Amaltheus margaritatus* Biozone, but were much more frequent and numerous during the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* biozones (Fig. 2). *Luehndea spinosa* strongly dominates the palynofloras in the uppermost Pliensbachian–lower Toarcian interval (upper *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* biozones) in the Lusitanian Basin. Nevertheless, *Mancodinium semitabulatum* and *Nannoceratopsis* spp. are relatively common in this basin (Figs. 5a, 6). Both dinoflagellate cyst abundances and taxonomic richness increased in the earliest Toarcian, except for the base of this stage (*Dactylioceras polymorphum* Biozone) where a brief warming event has been identified. These trends were consistently observed in the Toarcian sections at Vale das Fontes, Maria Pares and Peniche (Figs 2, 4). These acmes may reflect local optimal abiotic conditions, such as ideal oxygen concentrations, high seawater levels and high salinities (van de Schootbrugge et al. 2005), increased nutrient levels (Pieńkowski et al. 2016; Fantasia et al. 2019; Rodrigues et al. 2020b) and, mostly, relatively cold temperatures (<20°C; Suan et al. 2008; Correia et al. 2017b, fig. 3). The transgressive event during the early Toarcian in the Lusitanian Basin may have enhanced the dominance of dinoflagellate cysts during the middle and upper parts of *Dactylioceras polymorphum* Biozone (Duarte et al. 2004, 2007; Duarte 2007; Pittet et al. 2014).

During the Jenkyns Event

Above the *Dactylioceras polymorphum* Biozone, overall dinoflagellate cyst abundances and richness became markedly reduced (Figs 2, 4). The negative carbon isotope excursion (CIE) in the Lusitanian Basin is expressed at the base of *Hildaites levisoni*

Biozone (Duarte et al. 2004, 2007; Hesselbo et al. 2007; Pittet et al. 2014; Fantasia et al. 2019) and this level is characterised by the extinction of *Luehndea spinosa* together with a general dinoflagellate cyst 'blackout' event, especially the disappearance of *Nannoceratopsis* (Fig. 2). These bioevents were caused by the palaeoenvironmental changes associated with the Jenkyns Event, particularly the sudden rise of seawater temperatures (>20°C; Suan et al. 2008; Correia et al. 2017b, fig. 3). The probable decrease of nutrients and salinity levels (van de Schootbrugge et al. 2005) may also have contributed to this blackout episode. Although anoxic conditions at the sea bottom were not documented in the Lusitanian Basin, dysoxic conditions occurred during the Jenkyns Event (Fantasia et al. 2019; Reolid et al. 2019; Rodrigues et al. 2020b). Dinoflagellates are planktonic, but during their life cycle, the cyst-producing species have a benthic phase, i.e. the resting cyst itself (Dale 1983). Because the dinoflagellate cyst is non-motile, it slowly sinks to the sediment-water interface or close to it. The cell will be killed immediately during the excystment process if the environment is oxygen-deficient (Wille and Gocht 1979; Wille 1982). Moreover, Müller et al. (2020), recently analysed boron isotopes in brachiopods from the Peniche section, and reported ocean acidification episodes during the early Toarcian, which likely contributed to the dinoflagellate crisis. Other research in the Adriatic Platform (Ettinger et al. 2020) also documented ocean acidification during the Jenkyns Event, as well as anoxia in the photic zone.

In the Lusitanian Basin, representatives of other fossil groups became extinct during the Jenkyns Event, including brachiopods (Comas-Rengifo et al. 2013, 2015) and metacopinid ostracods (Cabral et al. 2013, 2020). More generally, some microfossil groups were profoundly reduced in abundance and/or diversity by the hostile environmental conditions associated with this climatic change, such as calcareous nannofossils (Mattioli et al. 2008, 2013; Ferreira et al. 2019) and foraminifera (Rita et al. 2016; Reolid et al. 2019). There are also recent reports of size reduction of belemnite rostra (Rita et al. 2019) and bivalves and brachiopod shells (Piazza et al. 2019) before the T-OAE, suggesting that reductions in body size may be one of the first ecological responses to the abiotic stressors. By contrast, Ullmann et al. (2020) documented abundant occurrences of the brachiopod *Soaresirhynchia,* a genus with low metabolic rate, at the end of the Jenkyns Event. These findings, together with the palynological data, suggest that apparently, the rapid palaeotemperatures rise is the major factor causing these bioevents. However, the other aforementioned abiotic factors may also play a role in this rapid realignment of marine life.

After the Jenkyns Event

The recovery of dinoflagellate cysts after the Jenkyns Event in the Lusitanian Basin was prolonged and somewhat indistinct; this planktonic group continued to be in crisis during the remainder of the Toarcian (Figs. 2, 4). The overall abundance of dinoflagellate cysts is consistently very low. Only *Mancodinium semitabulatum* is always relatively common, and the reappearance of *Nannoceratopsis* occurred only during the upper Toarcian in the *Hammatoceras speciosum* Biozone (Fig. 2). Moreover, only four new taxa were identified, all with sparse occurrences and low proportions. These are *Mendicodinium* spp. (uncertain), *Scriniocassis priscus* (Scriniocassiaceae), *Valvaeodinium* sp. (Comparodiniaceae) and *Sentusidinium* sp. (Gonyaulacaceae) (Figs. 2, 4). Hence, the Jenkyns Event in this basin strongly affected the cyst-forming dinoflagellate populations and their radiation during the Early Jurassic. However, the upper Toarcian (*Hammatoceras bonarellii* Biozone) of the Lusitanian Basin included an important evolutionary episode, namely the emergence of the first representative of the Gonyaulacaceae, due to the appearance of *Sentusidinium* (Fig. 2; see next section), which possibly migrated from the Arctic and Boreal provinces (Figs. 5b, 6; van de Schootbrugge et al. 2019). The family Gonyaulacaceae continued their diversification and became the most abundant family of cyst-forming dinoflagellates in the fossil record (Wiggan et al. 2017, 2018). Correia et al. (2019) also recognised a recovery of dinoflagellate cysts, both in taxonomic richness and abundance, in the early Bajocian in the Lusitanian Basin.

Global dinoflagellate cyst evolution with emphasis on the Triassic, Early Jurassic and the Jenkyns Event

Background

The evolutionary trajectory of the dinoflagellates has been the subject of considerable debate (e.g. Bujak and Williams 1981; Fensome et al. 1996a,b,c; van de Schootbrugge et al. 2005; Medlin and Fensome 2013). Only around 15% of living dinoflagellate species, mostly marine forms, produce fossilisable cysts and it is generally assumed that a similar percentage formed resistant organic-walled cysts in the geological past (Head 1996; Riding and Lucas Clarke 2016).

There is substantial cytological, geochemical and molecular clock evidence that the dinoflagellates are a relatively ancient lineage, with origins in the Neoproterozoic (Moldowan et al. 1996; Moldowan and Talyzina 1998; Medlin and Fensome 2013). However Janouškovec et al. (2017, fig. 2C) contended that triaromatic dinosteranes, which are macrobiomolecules typical of the dinoflagellates, emerged during the Triassic and not the late Precambrian as previously supposed. It is possible that any pre-Triassic dinoflagellates may have been affected by a decline in preservable phytoplankton during the Carboniferous and Permian, related to factors such as carbon dioxide concentrations, oceanic nutrient fluxes, redox and seawater chemistry (Mullins and Servais 2008; Riegel 2008; Strother 2008, fig. 1).

However, based on the body fossil record, dinoflagellate cysts appeared in the Middle Triassic, possibly triggered by a much-delayed biotic recovery from the end-Permian mass extinction and/or by the Carnian Pluvial Event (Simms and Ruffell 1989; Riding et al. 2010; Dal Corso et al. 2020). They diversified markedly during the Late Triassic (Bujak and Fisher 1976; Bucefalo Palliani and Buratti 2006; Mangerud et al. 2019; Mantle et al. 2020). The dominant cause of this radiation was probably endosymbiosis (Fensome et al. 1996a; Delwiche 1999; Falkowski et al. 2004). At this time, the main dinoflagellate families were the Rhaetogonyaulacaceae (*Dapcodinium* and *Rhaetogonyaulax*) and the Suessiaceae (e.g. *Beaumontella*, *Suessia*, *Wanneria*; see Mantle et al. 2020). Genera such as *Hebecysta, Heibergella* and *Sverdrupiella* were not assigned to established dinoflagellate families by Fensome et al. (1993).

However the dinoflagellates, based on the cyst record, were exceptionally badly affected by the end-Triassic mass extinction at ~201 Ma (van de Schootbrugge et al. 2013), but slowly recovered. There is an enigmatic occurrence of a single species, *Liasidium variabile*, in the late Sinemurian (~193 Ma) as described by Hesselbo et al. (2020 and references therein). Notwithstanding the brief appearance of *Liasidium variabile*, the main dinoflagellate re-diversification occurred ~14 million years after the end-Triassic mass extinction during the late Pliensbachian (Early Jurassic) when the families Mancodiniaceae (e.g. *Mancodinium semitabulatum*, *Luehndea*) and Nannoceratopsiaceae (*Nannoceratopsis*) emerged (Morgenroth 1970; Woollam and Riding 1983; Riding and Thomas 1992). The Jenkyns Event occurred at ~182 Ma, around 50 million years after the inception of unequivocal dinoflagellate cyst body fossils during the Triassic. This significant palaeoenvironmental perturbation appears to have disrupted dinoflagellates and their evolution because recovery from this event was again relatively slow (Bucefalo Palliani et al. 2002; Baranyi et al. 2016). The families Scriniocassiaceae (*Scriniocassis*) and Heterocapsaceae (e.g. *Moesiodinium, Parvocysta*, *Susadinium*) diversified in the middle and late Toarcian after the Jenkyns Event (Riding 1984; Poulsen and Riding 2003; van de Schootbrugge et al. 2019). The next evolutionary radiation episode was ~14 million years after the Jenkyns Event, during the Bajocian (Middle Jurassic) with the occurrence of around 40 new species, largely members of the family Gonyaulacaceae (e.g. *Acanthaulax crispa*, *Batiacasphaera*/*Sentusidinium* spp.*;* *Ctenidodinium* spp., *Dissiliodinium* spp., *Durotrigia* spp., *Korystocysta* spp., *Meiourogonyaulax* spp.; Feist-Burkhardt and Götz 2016; Wiggan et al. 2017; 2018).

The emergence of the dinoflagellate family Gonyaulacaceae

Despite the relatively low absolute numbers involved, inarguably the most significant dinoflagellate cyst event during the latest Pliensbachian and Toarcian is that of the emergence of the family Gonyaulacaceae. This is one of the two dominant dinoflagellate families, the other being the family Peridiniaceae (Fensome et al. 1999). We report a specimen confidently assignable to the Gonyaulacaceae (*Sentusidinium* sp.) from the upper Toarcian of Portugal herein (Fig. 3.12).

A recent major regional study, van de Schootbrugge et al. (2019), proposed that the family Gonyaulacaceae emerged during the latest Pliensbachian in the high northerly latitudes. Furthermore these authors commented that this phenomenon was much later, during the mid Toarcian, in northwest Europe (van de Schootbrugge et al. 2019, fig. 12). Additionally, the inception of the *Parvocysta-Phallocysta* complex (i.e. *Dodekovia, Moesiodinium raileanui*, *Parvocysta, Phallocysta* and *Susadinium*; all characterised by simple intercalary archaeopyles and originally described by Bjaerke 1980) occurs in the Arctic during the early Toarcian, coincident with the onset of the negative CIE (*Harpoceras falciferum* Biozone). This is earlier than in Europe, where the first representatives of this group occurred in the middle Toarcian (*Hildoceras bifrons* Biozone; Poulsen 1992; Riding and Thomas 1992; Poulsen and Riding 2003; van de Schootbrugge et al. 2019). Based on these records, and other occurrences (herein synthesised in Fig. 6), van de Schootbrugge et al. (2019) concluded that the Jenkyns Event was not so severe in the high northerly latitudes ('Arctic Realm' column of Fig. 6), and that this region was the evolutionary cradle of the early dinoflagellates. This contention is supported by Mantle et al. (2020), who identified Arctic North America as a major evolutionary hotspot for dinoflagellates during the Triassic.

The genera *Batiacasphaera*/*Sentusidinium* and *Dissiliodinium* were collectively termed 'proto-gonyaulacoids' by van de Schootbrugge et al. (2019). The preservation of the proto-gonyaulacoid material figured by these authors is not consistently optimal, for example the specimen of *Batiacasphaera* in their fig. 8g has a smooth principal archaeopyle suture. This important feature should be distinctly angular, reflecting the angularity of the anteriormost side of the precingular plates, even if accessory archaeopyle sutures are not developed (Wood et al. 2016). The other specimen of *Batiacasphaera*, from the lower Toarcian of the Kelimyar River section S16 in northern Siberia, is substantially more convincing, with precingular plates with definite angular tops (van de Schootbrugge et al. 2019, fig. 8h). The single specimen of *Dissiliodinium* sp., again from the lower Toarcian of northern Siberia, appears to be a reliable identification (van de Schootbrugge et al. 2019, fig. 8i).

The two specimens of *Sentusidinium* figured by Riding (1984, figs 4J, 4K) from the mid Toarcian (*Haugia variabilis* Biozone) of Yorkshire, as the junior synonym

Escharisphaeridia, are assuredly assignable to the former genus and hence the family Gonyaulacaceae. These specimens with apical archaeopyle are relatively smooth and broad, and the principal archaeopyle sutures indicate the presence of six precingular plates, with the 1'', 3'', 5'' and 6''plates having angular anterior margins (Evitt 1985). Independent researchers have re-examined these specimens and concur that they are indeed unequivocally referable to *Sentusidinium* (e.g. Wolfgang Wille, personal communication 1983). The *Sentusidinium* specimen in this study has the same morphological features described above, also with prominent accessory archaeopyle sutures, characteristic of this genus (Wood et al., 2016), but this form is more granulate (Fig. 3.12). *Sentusidinium* continued to be a rare component, and difficult to determine the species, among assemblages dominated by *Nannoceratopsis* during the Aalenian and earliest Bajocian (Riding 1983, plate 18.6). This is, of course, prior to the explosive radiation of the family Gonyaulacaceae during the middle Bajocian (Wiggan et al. 2017; 2018).

The specimens of late Pliensbachian and Toarcian age referable to the family Gonyaulacaceae therefore represent the true inception of this very important dinoflagellate lineage. They are not diverse, or indeed common; reports such as Riding et al. (1999) and Goryacheva (2017) did not record them for example. However, these specimens cannot be explained away as aberrant specimens, contamination or misidentifications. This situation where the evolution of lineages may begin sporadically, prior to major radiations, is a familiar one in evolutionary biology (e.g. Darlington 1976).

The regional perspective

In summary, it appears that the palaeoenvironmental changes associated with the Jenkyns Event were substantially more extensive in the Lusitanian Basin, compared with coeval depocentres further north for example in the Arctic, Germany and the UK (Fig. 6). In northern Europe the genus *Nannoceratopsis* was affected slightly and the inception of the *Parvocysta-Phallocysta* complex and *Scriniocassis priscus* occurred after the Jenkyns Event, in the *Hildoceras bifrons* Biozone. Even in southern France, late Toarcian dinoflagellate cyst floras became relatively diverse following the Jenykns Event (Bucefalo Palliani and Riding 1997b, fig. 3). In stark contrast, the dinoflagellate cyst associations of the high northerly latitudes (i.e. the Arctic Realm) were apparently relatively unaffected and the inceptions of representatives of the Gonyaulacaceae and the *Parvocysta-Phallocysta* complex occurred earlier (Fig. 6; van de Schootbrugge et al. 2019). This complex is typical of the Arctic and Boreal realms and is very rare in southern Europe. However, in the early Toarcian of central Italy, the occurrence of *Susadinium scrofoides* was reported within the *Dactylioceras tenuicostatum* (=*Eodactylites mirabilis*) Biozone (Fig. 6; Bucefalo Palliani and Riding 1997a; Bucefalo Palliani and Mattioli 1998), which suggests that this species is relatively cosmopolitan, compared with the other taxa in the *Parvocysta-Phallocysta* complex. In this study, no form belonging to this complex was identified. These bioevents from the Arctic and northern Europe markedly diverge from the southern Europe, with a dinoflagellate cyst blackout and a very prolonged recovery from the Jenkyns Event. The best examples of the latter are Portugal (Correia et al. 2017a,b, 2018) and Italy (Bucefalo Palliani and Riding 1997a, 1999b; Bucefalo Palliani and Mattioli 1998), and this phenomenon appears to be a coherent trend (Fig. 6).

The Lusitanian Basin is located in an intermediate region (the Sub-Boreal Realm), between the Tethyan and Boreal realms (Fig. 5). The Early Jurassic dinoflagellate cyst floras of this basin combine cosmopolitan species (*Luehndea spinosa*, *Mancodinium semitabulatum* and *Nannoceratopsis* spp.) with taxa typical of the Tethyan area (*Mendicodinium* spp., after the *Hildaites levisoni* Biozone) and northern regions (*Scriniocassis* spp. and *Sentusidinium* sp. as an early representative of the Gonyaulacaceae, after the *Hildoceras bifrons* Biozone). This may suggest that the Lusitanian Basin received marine influences from both Boreal and Tethyan provinces, at least in intermittent marine water currents during the Toarcian (Fig. 5). Nevertheless, the southwards moving, cold, low-salinity water current from the Arctic established during the mid Toarcian (*Hildoceras bifrons* Biozone), suggested by van de Schootbrugge et al., 2019, apparently, was not reflected in the Lusitanian Basin in terms of a significant re-colonisation of the dinoflagellate populations after the Jenkyns Event. During the Toarcian, the palaeogeographical position of the Lusitanian Basin was relatively enclosed (Fig. 5). This may have prevented the large-scale re-establishment of marine circulation patterns after this global climatic perturbation and, consequently, the local dinoflagellate recovery and associated evolutionary ‘triggers’ were substantially delayed.

Conclusions

In the Lusitanian Basin, the late Pliensbachian radiation of dinoflagellate cysts is very well documented. The pre-Jenkyns Event interval at the base of Toarcian is highly productive, with maximum abundance and richness values. This group thrived before the Jenkyns Event, probably due to optimal ecological conditions, remarkably relatively low palaeotemperatures. The environmental perturbations associated to the Jenkyns Event drastically affected the morphological experimentation period of this group for the remainder of the Early Jurassic. This is an unusually protracted recovery interval, especially given the abundant floras in this area during the late Pliensbachian and earliest Toarcian. It seems that the severity of the Jenkyns Event in the Lusitanian Basin, coupled with the increase in palaeotemperatures and the enclosed nature of the Lusitanian Basin may have prevented the re-colonisation of this depocentre by the dinoflagellates until the Middle Jurassic (Bajocian).

This prolonged recovery of the dinoflagellates in the Toarcian following the Jenkyns Event is not typical of further north in Europe. It is the case that late Toarcian dinoflagellate cysts are not as well studied as to their early Toarcian counterparts; however, it is clear that the re-establishment of this group in the Lusitanian Basin following the Jenkyns Event was extremely slow. Given the recent work of van de Schootbrugge et al. (2019), it seems probable that the elevated palaeotemperatures around Iberia at this time were the leading cause of this phenomenon, even given the lowered thermal gradients typical of greenhouse conditions.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

The contribution of Vânia F. Correia represents part of PhD scholarship SFRH/BD/93950/ 2013 awarded by the Portuguese Foundation for Science and Technology (FCT). This work is related to the Project “IGCP 655 – TOAE: Toarcian Oceanic Anoxic Event: Impact on marine carbon cycle and ecosystems (UNESCO-IUGS)”.Vânia F. Correia and Paulo Fernandes also acknowledge the support granted from FCT through the grant UID/MAR/00350/2020 attributed to CIMA of the University of Algarve. James B. Riding publishes with the approval of the Executive Director, British Geological Survey (NERC). Luís V. Duarte was supported by FCT, through the strategic project UID/MAR/04292/2013 granted to the Marine and Environmental Sciences Centre (MARE). We are grateful to the two reviewers, Susanne Feist-Burkhardt and Niels Poulsen, and to the volume editor, Emanuela Mattioli, for providing important comments which significant improved this manuscript.

Appendix A

This is a list of all the dinoflagellate cyst species which were recovered from the Lusitanian Basin, or mentioned in the text, with full author citations. The species listed which were not found in the material from the Lusitanian Basin are asterisked. The taxa are listed alphabetically, and the author citations can be found in Fensome et al. (2019). The recommendations of Correia et al. (2017a, appendix 2) regarding the taxonomy of *Nannoceratopsis senex* are followed herein.

Dinoflagellate cysts:

**Acanthaulax crispa* (Wetzel 1967) Woollam and Riding 1983

Dapsilidinium? *deflandrei* (Valensi 1947) Lentin and Williams 1981

**Liasidium variabile* Drugg 1978

Luehndea spinosa Morgenroth 1970

Mancodinium semitabulatum Morgenroth 1970

Maturodinium? *inornatum* Morgenroth 1970

Mendicodinium microscabratum Bucefalo Palliani et al. 1997

Mendicodinium spinosum Bucefalo Palliani et al. 1997 subsp. *spinosum* (autonym)

Nannoceratopsis ambonis Drugg 1978

Nannoceratopsis gracilis Alberti 1961

Nannoceratopsis senex van Helden 1977

Scriniocassis priscus (Gocht 1979) Below 1990

Scriniocassis weberi Gocht 1964

**Susadinium scrofoides* Dörhöfer and Davies 1980

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Display material captions:

Fig. 1. The location and geological setting of the Lusitanian Basin of western Portugal adapted from Duarte et al. (2010). The six sections studied herein are indicated thus: **P** = Peniche, the Toarcian GSSP, 39°22'15"N, 9°23'07"W; **PM** = São Pedro de Moel composite section, 39° 43' 18"N; 9° 02' 56"W; **VF** = Vale das Fontes, 40°12'10"N, 8°51'31"W; **Br** = Brenha, 40° 11' 49"N; 8° 49' 55"W; **FC** = Fonte Coberta, 40° 3' 44"N; 8° 27' 31"W; and **MP** = Maria Pares, 40°3'10"N, 8°27'25"W.

Fig. 2. A composite dinoflagellate cyst range chart for the Lower Jurassic of the Lusitanian Basin based on selected bioevents and phases. The relative abundance of dinoflagellate cyst is also pictured. The database supporting this chart are those in Correia et al. (2017a,b, 2018). The different thicknesses of the ammonite biozones is proportional to the number of samples studied for each zone, and does not represent the actual rock thickness. Note that the extremities of ranges with horizontal bars represent true range bases and tops (i.e. inceptions and apparent extinctions respectively) as appropriate. The range extremities which lack horizontal bars represent interruptions to

known stratigraphical ranges. The yellow shaded denotes the Jenkyns event interval (negative CIE).

Fig. 3. Selected dinoflagellate cysts from the upper Pliensbachian and Toarcian strata of the Lusitanian Basin. The sample numbers, slide numbers and the England Finder coordinates are quoted. All the scale bars represent 20 µm.

1. *Luehndea spinosa* Morgenroth 1970. Vale das Fontes section, lower Toarcian (*Dactylioceras polymorphum* Biozone), sample PVF8, slide 1, O24. Mid-ventral view, high focus. Note the prominent cingulum, interrupted by the sulcus.
2. *Mancodinium semitabulatum* Morgenroth 1970. Vale das Fontes section, lower Toarcian (*Dactylioceras polymorphum* Biozone), sample PVF1, slide 1, H56/2. Oblique right lateral, ventral view.
3. *Valvaeodinium* sp. Maria Pares section, middle Toarcian (*Hildoceras bifrons* Biozone), sample PZ57, slide 1, Q27/3. Note the relatively sparse cover of short, capitate processes and the combination (apical/intercalary) archaeopyle.
4. *Nannoceratopsis ambonis* Drugg 1978. Peniche section, lower Toarcian (*Dactylioceras polymorphum* Biozone), sample P10, slide 1, T25/3. Left lateral view. Note the prominent dark sagittal rim.
5. *Nannoceratopsis gracilis* Alberti 1961. Peniche section, lower Toarcian (*Dactylioceras polymorphum* Biozone), sample P6, slide 1, G28/3. Right lateral view. Note the dorsal antapical horn.
6. *Nannoceratopsis senex* van Helden 1977. Peniche section, upper Pliensbachian (*Amaltheus margaritatus* Biozone), sample P-25, slide 1, O48/4. Right lateral view. Note the single antapical horn and the "tear-shaped".

7. *Mendicodinium microscabratum* Bucefalo Palliani et al. 1997. Maria Pares section, lower Toarcian (*Hildaites levisoni* Biozone), sample PZ16, slide 1, T36/1. Right lateral view. Note the epicystal archaeopyle and the microscabrate autophragm.
8. *Mendicodinium spinosum* Bucefalo Palliani et al. 1997 subsp. *spinosum* (autonym). Maria Pares section, lower Toarcian (*Hildaites levisoni* Biozone), sample PZ26, slide 1, F49/1. Oblique dorsal view. Note the spines and the smooth autophragm.
9. *Mendicodinium* sp. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* Biozone), sample PZ80, slide 1, H47/2. Oblique left lateral view. The width is 42 µm.
10. *Scriniocassis priscus* (Gocht 1979) Below 1990 Maria Pares section, upper Toarcian (*Hammatoceras speciosum* Biozone), sample PZ77, slide 1, C32. Ventral view, low focus. The distinctive strongly curved sutures surrounding the sulcus are evident.
11. *Scriniocassis weberi* Gocht 1964. Peniche section, lower Toarcian (*Dactylioceras polymorphum* Biozone), sample P9, slide 1, R36/1. Dorsal view, high focus. Note the coarse reticulum and the 2P archaeopyle.
12. *Sentusidinium* sp. Maria Pares section, upper Toarcian (*Hammatoceras bonarellii* Biozone), sample PZ71, slide 1, M52/2. Note the apical archaeopyle with deep accessory archaeopyle sutures and six precingular plates, indicating the typical gonyaulacoid tabulation.

Fig. 4. The relative abundances of the dinoflagellate cyst families, expressed as percentages of the entire palynoflora, and the overall species richness of the Lower

Jurassic in the Lusitanian Basin. The different thicknesses of the ammonite biozones is proportional to the number of samples studied for each zone, and does not represent the actual rock thickness. The yellow shading denotes the Jenkyns Event interval. The evolutionary phases of the dinoflagellate cysts during the Early Jurassic in the Lusitanian Basin are also pictured. Note the earliest Toarcian (*Dactylioceras polymorphum* Biozone) dinoflagellate cyst acme, with maximum abundance and species richness, and the prolonged dinoflagellate cyst crisis, during and after the Jenkyns Event, with relatively low abundances and species richness.

Fig. 5. The Toarcian palaeogeography of the western Tethys region with the Boreal, Sub-Boreal and Tethyan Realms indicated (adapted from Correia et al. 2017b, after Thierry and Barrier 2000). In (**a)** the most significant dinoflagellate cyst taxa from the Lusitanian Basin during the uppermost Pliensbachian to lowermost Toarcian (*Dactylioceras polymorphum* Biozone; before the Jenkyns Event) and equivalent occurrences in the Boreal and Tethyan realms are depicted. In (**b)** the re-colonisation of the dinoflagellates in the Lusitanian Basin during the remaining Toarcian, after the Jenkyns Event, with hypothetical migration routes from the Boreal and Tethyan areas are illustrated. Migrations of the genus *Mendicodinium* from the Tethyan region during the early Toarcian (1) and *Scriniocassis priscus* and earliest representatives of Gonyaulacaceae (*Sentusidinium* sp.) from the north-western Europe during the middle and late Toarcian (2) are depicted. Note that, apparently, the origin of the early Gonyaulacaceae was in the northern regions (Arctic and Boreal realms).

Fig. 6. A comparison of the stratigraphical ranges of selected dinoflagellate cysts from the upper Pliensbachian to upper Toarcian (*Amalthues margaritatus* to *Pleydellia aalensis* biozones and their equivalents, adapted from Page 2003; Nikitenko et al. 2008) of the major European and Arctic basins. In the Tethyan Realm, the ranges are based on data from central Italy (Bucefalo Palliani and Riding 1997a; Bucefalo Palliani and Mattioli 1998). Note that the interval below and above the Jenkyns Event in central Italy are devoid of ammonites (i.e. are not dated) and the biozone *Eodactylites mirabilis* is equivalent to *Dactylioceras tenuicostatum*, according with Bilotta et al. 2009. Data from Germany (Prauss et al. 1991; Feist-Burkhardt and Wille 1992; Bucefalo Palliani and Riding 1998) and UK (Riding 1984; Bucefalo Palliani and Riding 2000; Bucefalo Palliani et al. 2002; van de Schootbrugge et al. 2019) are depicted for the Boreal Realm. The dinoflagellate floras from the Lusitanian Basin recorded in Correia et al. (2017a,b, 2018) may indicate an intermediate region between these two realms, Sub-Boreal Realm. The Arctic Realm is also represented with data from the Viking Corridor and Siberia (Riding et al. 1999; Goryacheva 2017; van de Schootbrugge et al. 2019). Note that the dashed lines represent probable occurrences based on known stratigraphical ranges.