The palynological response to the Toarcian Oceanic Anoxic Event (Early Jurassic) at Peniche, Lusitanian Basin, western Portugal

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ABSTRACT

The uppermost Pliensbachian and lower Toarcian (Lower Jurassic) succession exposed at Peniche in the central part of the Lusitanian Basin, western Portugal, was examined for palynomorphs. The 45 samples span the *Emaciaticeras emaciatum, Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones (ABs), and the succession includes the Global Stratotype Section and Point (GSSP) for the Toarcian Stage and the Toarcian Oceanic Anoxic Event (T-OAE). A low diversity dinoflagellate cyst flora, typical of the Sub-Boreal Realm, was recovered from the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs. The dominant element is the cold water species *Luehndea spinosa*, which is an index for the Pliensbachian to earliest Toarcian, and is thought to have migrated from the more northerly Boreal Realm. Prior to the T-OAE, dinoflagellates thrived in the Lusitanian Basin, except during a brief warm period in the earliest Toarcian. Despite the latter, the recovery from this event was relatively rapid and was characterised by a return to relatively cool temperatures. The *Hildaites levisoni* AB at Peniche represents the T-OAE and the overlying strata, and is characterised by a profound reduction in dinoflagellate cyst relative abundances. This dinoflagellate cyst ‘blackout’, and the associated rise of prasinophytes, reflects significant environmental stress, such as marine anoxia, elevated temperatures and reduced salinity, with the former two probably being most important. The low proportions of dinoflagellate cysts following the T-OAE indicates a protracted recovery phase from the bottom and water column anoxia developed throughout the Lusitanian Basin.

Keywords: palaeobiology; palynomorphs; provincialism; Toarcian Oceanic Anoxic Event (T-OAE); Lusitanian Basin, Portugal

1. Introduction

This study is a documentation of the palynology of the uppermost Pliensbachian and lower Toarcian (Lower Jurassic) strata at Peniche in the southern Lusitanian Basin, western Portugal. The principal aim was to investigate the response of marine microplankton to the Toarcian Oceanic Anoxic Event (T-OAE).

The Peniche section is located at Ponta do Trovão, on a peninsula close to Peniche (Fig. 1). An exceptionally expanded, well exposed and well preserved Pliensbachian-Toarcian transition is part of this coastal succession, which was chosen as the Global Boundary Stratotype Section and Point (GSSP) for the Toarcian Stage (Elmi, 2006; Rocha et al., 2016). The Pliensbachian-Toarcian boundary is primarily based on a relative abundance of the ammonite *Dactylioceras* and secondarily on the inceptions of several calcareous nannofossils. These bioevents define the base of Toarcian Stage at the base of Bed 15e (Rocha et al., 2016).

The palynology of the upper Pliensbachian and lower Toarcian strata at Peniche was previously studied by Davies (1985), Oliveira et al. (2007) and Barrón et al. (2013). Abundant dinoflagellate cysts were recently recorded from the lower Toarcian in the northern Lusitanian Basin by Correia et al. (2017). The present study is chiefly on the dinoflagellate cyst floras of Peniche, and it is hoped that these data will help to further characterise the Toarcian GSSP here. Pliensbachian and Toarcian calcareous nannofossils of the Peniche section were studied by Perilli & Duarte (2006), Oliveira et al. (2007), Mattioli et al. (2008, 2013) and Reggiani et al. (2010).

The Peniche section includes one of the major Phanerozoic environmental perturbations, the T-OAE. This was the earliest of the major Mesozoic-Cenozoic oceanic anoxic events (Jenkyns, 2010). The T-OAE is global and caused marine extinction and stratification, anoxia, and a rapid increase in seawater temperatures at ~182 Ma (e.g. Harries and Little, 1999; Cohen et al., 2007; Suan et al., 2008a, b; 2010; 2011; Al-Suwaidi et al., 2010; 2016; Gómez and Arias, 2010; Izumi et al., 2012; Danise et al., 2013; Xu et al, 2017). This event is characterised by a negative carbon isotope excursion ($\delta^{13}C$), recorded in marine carbonates and sedimentary organic matter. This characteristic geochemical signal has been confidently recognised in the Lusitanian Basin (Duarte et al., 2004, 2007; Hesselbo et al., 2007; Suan et al., 2008a; Pittet et al., 2014). The T-OAE may have been caused by a massive carbon injection into the atmosphere from oceanic gas hydrates, and/or methane release from sedimentary rocks due to intrusive volcanism (Hesselbo et al., 2000; Kemp et al., 2005; McElwain et al., 2005; Svensen et al., 2007; Hesselbo and Pieńkowski, 2011; van de Schootbrugge et al., 2013). It may have been terminated by fire-feedbacks to atmospheric oxygen concentrations (Baker et al., 2017). The more recent Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma) was also a short-lived interval of elevated temperatures caused by an injection of greenhouse gases into the atmosphere. However, the PETM only caused relatively minor and localised marine anoxia in comparison to the T-OAE (Cohen et al., 2007; Kender et al., 2012).

The distribution and growth of dinoflagellates, which are planktonic organisms, are influenced by factors such as light, nutrients, ocean currents, oxygen levels, salinity, temperature and water depth (Taylor and Pollingher, 1987; Dale, 1996). Toarcian marine plankton populations would therefore have been significantly affected by the T-OAE. Hence, research on Toarcian dinoflagellate cysts and other marine microplankton will help the understanding of this major environmental perturbation (e.g. Prauss, 1996; Prauss et al., 1991; Bucefalo Palliani et al., 2002).

2. Geological background

The Lusitanian Basin is a major marginal marine depocentre on the Atlantic coastal margin in western central Portugal (Fig. 1). This basin is oriented NE-SW, and is 300 km in length and 150 km wide. The depocentre is filled by a maximum thickness of 5 km of Mesozoic (Middle–?Upper Triassic to Upper Cretaceous) strata, but most of the succession is Jurassic (Rasmussen et al., 1998; Kullberg et al., 2013). Its initiation and evolution were associated with the fragmentation of Pangaea during the opening of the North Atlantic.

Lower Jurassic strata are well developed in the Lusitanian Basin, especially in the Peniche area (Duarte et al., 2017). Here, the upper Pliensbachian and lower Toarcian are represented by an expanded succession of interbedded fossiliferous limestones, marls and calcarenites (Wright and Wilson, 1984; Duarte, 1997, 2007; Duarte and Soares, 2002). The upper Pliensbachian comprises the uppermost part of the Vale das Fontes Formation and the majority of the Lemede Formation. The Vale das Fontes and Lemede formations represent the *Almatheus margaritatus*, *Emaciaticeras emaciatum* and lowermost *Dactylioceras polymorphum* ammonite biozones (ABs) (Fig. 2). The Vale das Fontes Formation is composed of interbedded relatively thick (ca. 10 cm–1 m) marls and thinner (<10 cm) limestones, both of which are abundantly fossiliferous (Duarte et al., 2010; Silva et al., 2011, 2015). The overlying Lemede Formation is heavily bioturbated and also cyclic; it comprises interbedded relatively thick (~10 cm–40 cm) limestones and thinner (<10 cm) marl interbeds. Both lithotypes are richly fossiliferous (Duarte and Soares, 2002; Comas-Rengifo et al., 2016). In this study, only the uppermost Lemede Formation was studied (Figs. 2, 3).

The Toarcian of the Peniche region is represented by the Cabo Carvoeiro Formation, which is subdivided into five members (Duarte and Soares, 2002). These are numbered and prefixed with Cabo Carvoeiro, but are frequently abbreviated (i.e. CC1–CC5; Fig. 2). In this study only the CC1, CC2 and lowermost CC3 members were analysed, and this succession is correlated to the *Dactylioceras polymorphum* and *Hildaites levisoni* ABs (Figs. 2, 3). The CC1 member is a succession of fossiliferous greyish marls and marly limestones. By contrast, the CC2 member comprises interbedded relatively fine-grained conglomerates and sandy limestones/marls, and is sparsely fossiliferous. The CC3 member is dominated by marly limestone and greyish marls with rare brachiopods (Fig. 3; Duarte and Soares, 2002).

The Lower and Middle Jurassic ammonite faunas of the Lusitanian Basin are indicative of a Sub-Boreal (Atlantic) affinity (Mouterde et al., 1979). However, occasional diverse and mixed ammonite associations are suggestive of sporadic communication between the Boreal and Tethyan realms (Terrinha et al., 2002). The earliest Toarcian *Dactylioceras polymorphum* AB of the Tethyan region is broadly coeval with the *Dactylioceras tenuicostatum* AB in the Sub-Boreal and Sub-

Mediterranean provinces. Succeeding the Tethyan *Dactylioceras polymorphum* AB, the *Hildaites levisoni* AB is equivalent to the *Harpoceras serpentinum* AB of the Sub-Mediterranean and Sub-Boreal provinces (Elmi et al., 1989; Page, 2003; Simms et al., 2004).

3. Material and methods

In this study, 45 samples were collected from the upper Pliensbachian to lower Toarcian succession at Ponta do Trovão, near Peniche in the southwest Lusitanian Basin (Fig. 1). These horizons are within the *Emaciaticeras emaciatum*, *Dactylioceras polymorphum* and *Hildaites levisoni* ABs (Figs. 2, 3). The reference datum used here (0 m) was the boundary between the Lemede and Cabo Carvoeiro formations (Fig. 3). The sample numbers are all prefixed 'P' referring to Peniche. The seven samples below the datum boundary include a minus sign (e.g. P-7), however the sample numbers above this horizon only comprise the number (e.g. P34).

The samples were prepared using standard palynological techniques (Wood et al., 1996), however the organic residues were not oxidised. The post-mineral acid residues were sieved through a 15 μm mesh sieve. All the final palynomorph concentrates were stained with Safranin to increase body colour. If possible, at least 300 palynomorphs were counted for each sample; if not, the maximum number of specimens from two microscope slides were used. It should be noted that in the *Hildaites levisoni* AB, palynomorphs were extremely sparse, and this number could not be achieved (Supplementary table 1). All the remaining raw sample material, aqueous residues, microscope slides and figured specimens are curated in the collections of LNEG (Portuguese Geological Survey), São Mamede de Infesta, Portugal.

4. Palynology, biostratigraphy, palaeobiology and palaeoecology

4.1. *Introduction*

In this section, the palynobiota is documented, together with biostratigraphical and palaeobiological/palaeoecological interpretations based largely on dinoflagellate cysts. The overall palynomorph dataset is included as Supplementary table 1; the palynomorphs are therefore depicted as percentages of the entire palynobiota. Supplementary tables 2 and 3 illustrate the marine and terrestrial palynobiota respectively, including percentage data. Six horizons, P1, P15, P18, P21, P26 and P27 proved barren of palynomorphs. The relative proportions of the principal marine dinoflagellate cyst taxa and the four marine palynomorphs groups are depicted in Figures 3 and 4, respectively. Supplementary figure 1 illustrates the variation of the marine and terrestrial palynomorphs throughout the succession examined. Selected palynomorph specimens are illustrated in Figures 5 and 6. The palynomorph taxa at and below species level are listed in the Appendix with their respective author citations.

The response of dinoflagellate cysts to environmental change is one of the main aims of this research, with most emphasis placed on the T-OAE. Four plankton phases were recognised (Fig. 7; Table 1). The dinoflagellate cyst record is analysed, and interpreted in conjunction with previous studies on Early Jurassic calcareous nannofossils, temperature records, sequence stratigraphy and stable isotopes (Fig. 3).

4.2. Palynostratigraphy

The relatively low diversity dinoflagellate cyst assemblage is entirely consistent with a late Pliensbachian to early Toarcian age (Supplementary tables 1, 2; Woollam and Riding, 1983; Feist-Burkhardt and Wille, 1992; Riding and Thomas, 1992; Bucefalo Palliani and Riding 2003; Poulsen and Riding 2003). The most abundant, and stratigraphically diagnostic, species was *Luehndea spinosa* which occurs throughout the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs (Supplementary table 2). Its range is late Pliensbachian to earliest Toarcian (e.g. Poulsen and Riding, 2003, fig. 3). This occurrence confirms the age of the uppermost Lemede Formation and the CC1 member. *Luehndea spinosa* was also recorded from the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs of the Lusitanian Basin by Davies (1985) and Correia et al. (2017).

Nannoceratopsis spp. were also confined to the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs (Supplementary table 2). This is compatible with the results of Correia et al. (2017) and the three species recorded here range from the Pliensbachian to Bajocian (e.g. Morgenroth, 1970; Wiggan et al., 2017). By contrast, *Mancodinium semitabulatum* was present throughout the entire succession here (Supplementary table 2). This is also consistent with Correia et al. (2017). This species has a Pliensbachian to Bajocian range in Europe (Woollam and Riding, 1983; Feist-Burkhardt and Götz, 2016; Wiggan et al., 2017). The non-dinoflagellate cyst palynomorphs are entirely consistent with an Early Jurassic age (e.g. Srivastava, 1987; 2011; Weiss, 1989; Ziaja, 2006).

4.3. The Emaciaticeras emaciatum *AB (plankton phase 1; samples P-7 to P-1)*

4.3.1. The palynology of plankton phase 1

Seven samples were analysed from the uppermost part of the Lemede Formation of latest Pliensbachian age, and are referable to the uppermost *Emaciaticeras emaciatum* AB (Fig. 3). All proved palynologically productive. The dinoflagellate cyst species *Luehndea spinosa*, *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* were recorded. *Luehndea spinosa*, where present, was the most abundant species; it attained 92% of the overall palynobiota in sample P-6, where it was the only dinoflagellate cyst recorded. It comprised 86.3% and 73.3% in samples P-7 and P-1 respectively, and was the most common dinoflagellate cyst in sample P-2 (13.0%). However, this distinctive taxon was absent in samples P-5 to P-3 (Supplementary table 1).

Mancodinium semitabulatum, Nannoceratopsis gracilis and *Nannoceratopsis senex* were also recorded in all the horizons except P-6. These species were present in relatively low percentages. *Mancodinium semitabulatum* was most prominent, attaining 17.1% of the overall assemblage in sample P-3. By contrast, *Nannoceratopsis* spp. proved relatively sparse, representing 0.3% to 2.4% in all the samples except P-6 and P-3 (Supplementary table 1). Other marine palynomorphs encountered were acritarchs, mainly *Micrhystridium* spp. and *Polygonium jurassicum*, foraminiferal test linings and prasinophytes. These groups were present in relatively low proportions, but foraminiferal test linings represented a high relative abundance in sample P-4 (Fig. 4, Supplementary table 2). The records of the distinctive acritarch *Polygonium jurassicum* (Fig. 6/1-3) in the *Emaciaticeras emaciatum* to lower *Hildaites levisoni* ABs (Supplementary table 2) extend the known range of this species. It was previously known from the earliest Toarcian of southern Europe (Bucefalo Palliani et al., 1996; Bucefalo Palliani and Mattioli, 1998).

The pteridophyte spores *Cyathidites* spp., *Ischyosporites variegatus*, *Kraeuselisporites reissingeri* and *Leptolepidites* spp. were recorded throughout in minor proportions (0.3% to 3.5%), except in sample P-6 (Supplementary table 1). *Kraeuselisporites reissingeri* has a range of Late Triassic to Aalenian. Here it is consistently present throughout the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs, with occasional occurrences in the *Hildaites levisoni* AB (samples

P16 and P33; Supplementary tables 1, 3). This distribution is similar to that in the northern Lusitanian Basin, where it is confined to the *Dactylioceras polymorphum* AB (Correia et al., 2017).

Gymnosperm pollen were also present in higher proportions than trilete spores. The most common form was *Classopollis classoides* which represented 85.0% of the association in sample P-5. *Alisporites* spp., *Araucariacites australis* and *Cerebropollenites macroverrucosus* were also identified; these forms comprised between 0.3% in P-6 and 6.0% in P-4 (Supplementary table 1). The middle part of the uppermost *Emaciaticeras emaciatum* AB (samples P-5 to P-2) was dominated by gymnospermous pollen. This is largely due the high relative abundances of *Classopollis classoides* in this interval. *Classopollis classoides* was the most abundant continental palynomorph throughout (Supplementary tables 1, 3). This xerophytic and thermophilic genus is typical of the Lower Jurassic worldwide (Srivastava, 1976; Helby et al., 1987; Quattrocchio et al., 2011). By contrast, samples P-7, P-6 and P-1 exhibited high levels of marine influence (Supplementary figure 1), largely due the dominance of *Luehndea spinosa* (Figs. 3, 4; Supplementary table 2).

4.3.2. The palaeobiology of plankton phase 1

In this interval, the most prominent dinoflagellate cyst in the uppermost Pliensbachian was *Luehndea spinosa*. Two relative abundance peaks were present, and these represented the majority of the marine influence (Supplementary table 2). Mattioli et al. (2008) studied coeval calcareous nannofossils from the section, and found that the upper *Emaciaticeras emaciatum* AB is characterised by abundant biota. These include prominent *Schizosphaerella*, a probable calcareous dinoflagellate cyst genus (Bown, 1987), which exhibited three relative abundance peaks (Fig. 7). Therefore, plankton phase 1 is termed the ‘latest Pliensbachian plankton abundance’ (Fig. 7; Table 1).

The late Pliensbachian was a relatively cool interval, with temperatures between 10 and 20°C throughout the Laurasian Seaway in western Europe (Korte and Hesselbo, 2011; Korte et al., 2015, fig. 2). Specifically, in the *Emaciaticeras emaciatum* AB of the Lusitanian Basin, $\delta^{18}O_{brachiopod}$ values from diagenetically resistant material indicate temperatures of ~16°C (Fig. 3; Table 1; Suan et al., 2008a). Moreover, $\delta^{18}O_{belemnite}$ and Mg/Ca data from northern Spain indicate that late Pliensbachian water masses cooled and became significantly more saline (van de Schootbrugge et al., 2005). It therefore appears that *Luehndea spinosa*, the other dinoflagellate cysts and the probable calcareous dinoflagellate cyst *Schizosphaerella* thrived in the relatively cool, saline waters of the Iberian Peninsula at this time. Relatively diverse dinoflagellate cyst assemblages in the Mesozoic and Cenozoic frequently appear to have preferred relatively cool waters (e.g. Head et al., 2001; Bowman et al., 2013; Hennissen et al., 2017). Furthermore, significant migrations towards the equator from high latitudes are known to have occurred during cold intervals (e.g. Sluijs et al., 2005; Prauss, 2006; Riding and Michoux, 2013).

4.4. The Dactylioceras polymorphum *AB (plankton phases 2 and 3; samples P1 to P14)*

4.4.1. The palynology of plankton phases 2 and 3

Fourteen horizons (P1–14) were sampled from the earliest Toarcian *Dactylioceras polymorphum* AB, representing the CC1 member of the Cabo Carvoeiro Formation (Fig. 3). The lowermost sample (P1) proved devoid of palynomorphs. By contrast, the overlying 13 samples all yielded relatively abundant palynomorph associations (Supplementary table 1). The dinoflagellate cyst floras proved similar to those from the underlying *Emaciaticeras emaciatum* AB. However, the high relative abundances (73.3%) of *Luehndea spinosa* observed in the uppermost Lemede Formation (subsection 4.3.1) abruptly decreased to between 1.5% and 3.4% in the lowermost Toarcian (samples P2 to P6; Supplementary table 1). This phenomenon was termed the Pliensbachian-Toarcian boundary event (Littler et al., 2010; Korte et al., 2015). Here, the most abundant dinoflagellate cyst was *Mancodinium semitabulatum,* which attained 28.7% in sample P6. *Nannoceratopsis* spp. also increased in relative abundance in samples P4 to P6; in the latter horizon this genus represented 27%. In sample P7, *Luehndea spinosa* massively increased to 93.8% and this dominance continued to the top of the *Dactylioceras polymorphum* AB (82.7% in sample P14). The latter occurrence represented the range top of this species. The maximum value was 96.2% in sample P11 (Supplementary table 1). The signature of the latter peak occurrence, together with 82.7% in sample P14, is virtually identical to that observed in the northern Lusitanian Basin at Maria Pares and Vale das Fontes (Fig. 8; Correia et al., 2017, figs. 6, 7). Between samples P7 and P14, where *Luehndea spinosa* was dominant, *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* were present in low proportions. *Nannoceratopsis gracilis* exhibited significant intraspecific variability (Fig. 5/4–7), and *Nannoceratopsis ambonis* and *Scriniocassis weberi* were recorded in extremely low numbers in samples P9 and P10 (Supplementary table 1). The latter is a gonyaulacacean species and a marker for the late Pliensbachian to Aalenian (Woollam and Riding, 1983; Davies, 1985; Feist-Burkhardt and Wille, 1992; Riding and Poulsen, 2003).

Miscellaneous marine palynomorphs (i.e. acritarchs, foraminiferal test linings and prasinophytes) in the *Dactylioceras polymorphum* AB were similar to those from the underlying *Emaciaticeras emaciatum* AB. The acritarchs included *Micrhystridium* spp., and *Polygonium jurassicum*, and were sporadically common. Prasinophytes were intermittent and sparse, but slightly more diverse than in the underlying samples, with *Cymatiosphaera* sp. cf. *C. pachytheca,* clumps of *Halosphaeropsis liassica* and *Tasmanites* spp. present. *Halosphaeropsis liassica* is characteristic of the early Toarcian (Mädler, 1968; Bucefalo Palliani and Riding, 2000). Foraminiferal test linings occured throughout in significant proportions in samples P8 and P9 (Fig. 4, Supplementary tables 1, 2).

Pteridophyte spores proved moderately diverse with *Calamospora tener, Concavisporites granulosus, Cyathidites* spp., *Kraeuselisporites reissingeri*, *Leptolepidites* spp. and *Osmundacidites wellmanii* present. These normally occured in low numbers, but *Kraeuselisporites reissingeri* attained 9.5% in sample P2 (Supplementary table 1). The gymnosperm pollen comprised *Alisporites* spp., *Araucariacites australis*, *Cerebropollenites macroverrucosus, Classopollis classoides*, *Exesipollenites* spp. and *Spheripollenites* spp. The latter was present throughout the lower Toarcian and was especially prominent in the *Hildaites levisoni* AB (Supplementary tables 1, 3). This long-ranging pollen genus was also recorded from the Pliensbachian to Aalenian of the Lusitanian Basin (Davies, 1985; Correia et al., 2017). As in the underlying AB, *Classopollis classoides* remained the most abundant terrestrial palynomorph in the lower part of this interval (samples P2 to P6 and P8). The relative abundance decreased in the upper part of the *Dactylioceras polymorphum* AB. Therefore, pollen rapidly diminished upsection due to the decrease in *Classopollis classoides* and the increase of *Luehndea spinosa* (Supplementary tables 1–3).

4.4.2. The palaeobiology of plankton phase 2 (samples P2 to P5)

The uppermost sample (P-1) from the 'latest Pliensbachian plankton abundance', was dominated by the dinoflagellate cysts *Luehndea spinosa* and *Mancodinium semitabulatum*. By contrast, the overlying sample (P1), proved barren. At this horizon, negative $\delta^{13}C$ and $\delta^{18}O$ excursions occur (Fig. 3; Hesselbo et al., 2007; Suan et al., 2008a; Korte et al., 2015). These indicate an abrupt environmental change, including a rise in temperatures, which appear to have adversely affected the dinoflagellates. The calcareous nannofossils were similarly affected (Fig. 7; Mattioli et al., 2008). However, *Luehndea spinosa*, *Mancodinium semitabulatum* and *Nannoceratopsis* spp., reappeared in relatively low relative abundances in the immediately overlying strata in the *Dactylioceras polymorphum* AB (samples P2–P5). This recovery from the brief earliest Toarcian warming in sample P1 was gradual and sustained during the lower part of the *Dactylioceras polymorphum* AB (Figs. 3, 4, 8; Supplementary table 2). The recovery of calcareous nannofossils was more rapid, with a significant relative abundance peak in the lower *Dactylioceras polymorphum* AB (Fig. 7). These increases in plankton appear to have been driven by cooling temperatures (Korte et al., 2015, fig. 2). The abrupt and brief warming immediately above the Pliensbachian-Toarcian boundary apparently triggered a sharp decrease in phytoplankton, but did not cause a general biotal crisis. In the benthic fossil record in the Lusitanian Basin, the Pliensbachian-Toarcian transition is characterised by an increase in the relative abundances of foraminifera and ostracods (Pinto, 2008; Rita et al., 2016, figs. 6, 8). This phase is therefore referred to as 'the recovery of dinoflagellates from the earliest Toarcian warming event' (Fig. 7; Table 1).

4.4.3. The palaeobiology of plankton phase 3 (samples P6 to P14)

In this phase, between sample P6 to the uppermost *Dactylioceras polymorphum* AB (sample P14), there was a pronounced increase in dinoflagellate cyst relative abundances. This was caused by an increase in *Luehndea spinosa* (Fig. 3; Supplementary table 2). This trend is consistent with the northern Lusitanian Basin (Correia et al., 2017) where the relative abundance of *Luehndea spinosa* in the middle and upper *Dactylioceras polymorphum* AB appears to have correlative significance (Fig. 8). This increase is apparently due to the continuing decrease in temperatures during the earliest Toarcian (Korte et al., 2015, fig. 2). As in the *Emaciaticeras emaciatum* AB, the relatively cool conditions favoured *Luehndea spinosa*, which was a typical Boreal, cool-adapted, form (Riding, 1987; Riding and Hubbard, 1999; Riding et al., 1999; Bucefalo Palliani and Riding, 2000). The $\delta^{18}O_{brachiopod}$ of the *Dactylioceras polymorphum* AB at Peniche indicates water temperatures between 16 and 20°C (Fig. 3; Table 1; Suan et al., 2008a). The high relative abundances of *Luehndea spinosa* in the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs of the Lusitanian Basin can be explained by favourable ecological conditions for this species in this region, principally cool seawater. However, salinity fluctuations and the early Toarcian transgressive event may also have been influential. Duarte et al. (2004, 2007), Duarte (2007) and Pittet et al. (2014) identified an early Toarcian transgressive event in the Lusitanian Basin that may have enhanced the dominance of dinoflagellate cysts during the middle and upper parts of *Dactylioceras polymorphum* AB. Mattioli et al. (2008) interpreted the calcareous nannofossils from this interval as cool-adapted.

The Toarcian species of *Nannoceratopsis* were also typically cold water forms (Riding and Hubbard, 1999; Riding et al., 1999). However, in the Lusitanian Basin, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* were present in both the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs in low relative abundances, compared to *Luehndea spinosa* (Fig. 3; Supplementary table 2). It is possible that the nutrient and salinity levels were not optimal for *Nannoceratopsis* spp., but were favourable for *Luehndea spinosa*. *Mancodinium semitabulatum* was a more cosmopolitan species (Bucefalo Palliani and Riding, 2003; Mantle and Riding, 2012), and hence was apparently not influenced by low temperatures and rising sea levels as the other dinoflagellate cyst taxa were.

The calcareous nannofossil and dinoflagellate cyst records during this interval in the Lusitanian Basin are strikingly similar (Fig. 7; Mattioli et al., 2008). Both were abundant during the middle part of *Dactylioceras polymorphum* AB, before decreasing in the upper part. However, the dinoflagellate cysts did not decline as fast as the calcareous nannofossils in the upper *Dactylioceras polymorphum* AB. Hence we hypothesise that a rise in sea level, with a consequent increase in the area of continental shelf, and relatively low seawater temperatures led to the high bioproductivity of phytoplankton in the Lusitanian Basin at this time. Plankton phase 3 is therefore termed ‘the earliest Toarcian plankton abundance’ (Fig. 7; Table 1).

4.5. The Hildaites levisoni *AB (plankton phase 4; samples P15 to P38)*

4.5.1. The palynology of plankton phase 4

The *Hildaites levisoni* AB was most intensively sampled in this study, with 24 horizons collected from the CC2 and base of CC3 members of the Cabo Carvoeiro Formation (Fig. 3). All of these proved sparse, except P15, P18, P21, P26 and P27 which were barren (Supplementary table 1). The T-OAE is present in this succession, and is represented by samples P15 to P24 (Figs. 3, 4, 7). The dinoflagellate cyst associations were extremely low in diversity and relative proportions throughout the *Hildaites levisoni* AB. Only *Mancodinium semitabulatum* (samples P16 to P38) and *Mendicodinium microscabratum* (samples P23 and P25) were recorded. *Mancodinium semitabulatum* attained 6.7% of the palynobiota in sample P23 in the CC2 member, and was the only dinoflagellate cyst species present in the CC3 member. *Mendicodinium microscabratum* was encountered in low proportions from the middle of the *Hildaites levisoni* AB (Supplementary table 1). Correia et al. (2017) recorded *Mendicodinium microscabratum* from the *Hildaites levisoni* and *Hildoceras bifrons* ABs of the northern Lusitanian Basin. *Mendicodinium microscabratum* is present in the earliest Toarcian of central Italy by Bucefalo Palliani et al. (1997) and in the early Toarcian of Peniche by Davies (1985) as *Mendicodinium* sp. A. *Luehndea spinosa*, *Nannoceratopsis* spp. and *Scriniocassis weberi* were absent throughout the *Hildaites levisoni* AB. This scenario is entirely consistent with coeval successions in the northern Lusitanian Basin (Correia et al., 2017).

The miscellaneous microplankton taxa throughout this succession are rather conservative. The acritarch associations were similar to those in the two underlying ABs. *Micrhystridium* sp. and *Polygonium jurassicum* were present sparsely in the *Hildaites levisoni* AB. However, acritarchs were significantly more frequent in the lowermost T-OAE than in the overlying recovery succession (Fig. 4). In particular, they represented 20.5% of the palynobiota in sample P22 (Supplementary table 1). The prasinophyte associations of the *Hildaites levisoni* AB were similar in taxonomic character to those in the underlying *Dactylioceras polymorphum* AB, except that *Cymatiosphaera* sp. cf. *C. pachytheca* was absent. However, prasinophytes were substantially more prevalent than in either of the two underlying ABs. Within the *Hildaites levisoni* AB these distinctive palynomorphs, which largely comprised *Halosphaeropsis liassica* and *Tasmanites* spp., were markedly more common within the T-OAE interval than in the overlying succession (Fig. 4). They were most common in

P17 (18.5%), P19 (16.2%) and P20 (18.9%) (Supplementary table 1). These relative proportions never attained the very high relative abundances of prasinophytes observed in coeval strata at the Maria Pares section in the northern Lusitanian Basin (Correia et al., 2017). Foraminiferal test linings were present in high relative abundances throughout. The relative proportions were generally higher in the samples above the T-OAE (Fig. 4); the maximum was 71.9% in P36 (Supplementary table 1).

The pteridophyte spores from the *Hildaites levisoni* AB included *Concavisporites granulosus*, *Cyathidites* spp., *Ischyosporites variegatus*, *Kraeuselisporites reissingeri*, *Leptolepidites* spp. and *Todisporites granulatus*. Generally, spores were slightly more common in this AB, for example 34.2% in sample P29 and 28.6% in P31. The gymnosperm pollen comprised the same six taxa recorded in the underlying *Dactylioceras polymorphum* AB. However, *Alisporites* spp., *Araucariacites australis* and *Cerebropollenites macroverrucosus* proved extremely sporadic. By contrast, *Classopollis classoides*, *Exesipollenites* spp. and *Spheripollenites* spp. were much more consistent (Supplementary table 1).

In summary, in the *Hildaites levisoni* AB, dinoflagellate cysts were relatively sparse. However, the relative abundance of foraminiferal test linings and prasinophytes significantly increased; prasinophytes were especially prominent in the T-OAE interval. But overall, the marine influence was diminished in comparison with the underlying *Dactylioceras polymorphum* and *Emaciaticeras emaciatum* ABs (Fig. 4; Supplementary figure 1). The percentages of spores and pollen in the *Hildaites levisoni* AB were markedly higher than in the middle and upper parts of the underlying *Dactylioceras polymorphum* AB, but were lower than in the lowermost part of the overall succession studied (Supplementary tables 1, 3).

4.5.2. The palaeobiology of plankton phase 4 (samples P15 to P38)

The lowermost sample from this phase, P15 (*Hildaites levisoni* AB), entirely lacked palynomorphs (Supplementary table 1). This horizon is coincident with the inception of the T-OAE in the Lusitanian Basin (Hesselbo et al., 2007; Suan et al., 2008b; 2010). This major environmental perturbation lies between samples P15 and P24, as indicated by $\delta^{13}C$ data (Fig. 3; Hesselbo et al., 2007; Suan et al., 2008a). From this point, the relative abundance of dinoflagellate cysts sharply decreased as compared to the progressive increase in the underlying *Dactylioceras polymorphum* AB (Figs. 3, 4, 7, 8).

This dinoflagellate cyst 'blackout' appears to be related to the significant environmental changes associated with the T-OAE. The oxygen reduction close to the sediment-water interface occasionally reached the photic zone (Mattioli et al., 2008), and hence would have profoundly affected plankton productivity. Cyst-forming dinoflagellates are affected by bottom water anoxia, which completely inhibits excystment in the benthic zone. Moreover, hypoxia reduces the rate of germination in modern dinoflagellates (Anderson et al. 1987; Kremp and Anderson 2000). The dinoflagellate cyst 'blackout' during the T-OAE has also been discussed by Loh et al. (1986), Prauss (1989), Prauss et al. (1991), Bucefalo Palliani and Riding (1999b) and Bucefalo Palliani et al. (2002).

Mattioli et al. (2008, 2013) reported that when $\delta^{13}C$ values began to decrease in the T-OAE, the levels of calcareous nannofossils drastically declined, and they remained low during the entire T-OAE interval and above it. Furthermore, Fraguas et al. (2012) described a significal calcareous nannofossil extinction event associated with the temperature increase at the *Dactylioceras tenuicostatum-Harpoceras serpentinum* AB boundary. Hence, the calcareous nannofossil record is analogous and coeval with the response of dinoflagellate cysts to the T-OAE, and these floras are similar to those from the northern Lusitanian Basin (Correia et al., 2017). The calcareous nannofossil abundance decrease during the T-OAE has also been recorded in France, Germany, central Italy and northern Spain (Bucefalo Palliani and Mattioli, 1998; Mattioli et al., 2008; Fraguas et al., 2012). However, in these areas, the abundance of calcareous nannofossils increased after the T-OAE. Throughout Europe, except western Portugal, the recolonisation of calcareous nannofossils after this environmental perturbation coincides with dinoflagellate cyst floras, for which the record became re-established in the *Hildoceras bifrons* AB (Bucefalo Palliani et al., 2002). Calcareous nannoplankton is meroplanktonic, and thus is heavily dependent on conditions in the water column. Thecate (motile) dinoflagellates are largely confined to the photic zone, but their resting cysts are benthic and non-motile (Dale, 1983). This means that cyst-producing dinoflagellates are highly sensitive to the ecology of the benthic zone. It is very significant that, despite their different life cycles, the 'phytoplankton blackout' is recorded by both these planktonic groups, indicating that the profoundly stressed conditions associated with the T-OAE affected both the water column and the sea bed (Bucefalo Palliani et al., 2002). For this reason, plankton phase 4 is named the 'plankton crisis' (Fig. 7; Table 1).

The seawater temperatures in the Lusitanian Basin during the *Hildaites levisoni* AB were generally higher (20–24°C) than in the *Dactylioceras polymorphum* AB (16–21°C) (Table 1; Suan et al., 2008a). The abrupt low levels of dinoflagellate cysts at the base of the *Hildaites levisoni* AB coincide with a rise in temperature (Fig. 3). After the T-OAE, temperatures diminished slightly, but the relative abundances of dinoflagellate cysts remained very low. Van de Schootbrugge et al. (2005) also demonstrated the relationship between dinoflagellate cyst relative abundances with temperature and salinity, using belemnite Mg/Ca and $\delta^{18}O$ from material from northern Spain. These data demonstrate high dinoflagellate cyst relative abundances before the T-OAE in cool and high salinity marine settings. During the T-OAE seawater temperatures rapidly rose, and the salinity and dinoflagellate cyst relative abundances decreased, as in the Lusitanian Basin. In addition to the anoxia and the rise in temperatures, low salinity may be another abiotic factor that helps to explain the dinoflagellate cyst 'blackout'.

Mattioli et al. (2008) suggested that the high levels of the calcareous nannofossil genus *Calyculus* during the T-OAE, together with low relative abundances of calcareous nannofossils, is due to a decrease in salinity. *Calyculus* is an atypical genus because it was characteristic of stressed environments. The relatively low salinities may be due a southward current of low density water from the Arctic into the Tethys (Bjerrum et al., 2001) or increased continental runoff (Röhl et al., 2001). Either or both these factors would have enhanced stratification and, consequently anoxia. The replacement of calcareous nannofossils and dinoflagellates, which were both abundant in the *Dactylioceras polymorphum* AB, for prasinophytes (Bucefalo Palliani et al., 2002; Mattioli and Pittet, 2004; van de Schootbrugge et al., 2005; Correia et al., 2017) also indicates low salinity surface waters. Prasinophytes are an opportunistic group of green algae, which do not necessarily require a sustained benthic phase in their life cycle (Tappan, 1980). The non-motile stage of their life cycle, the phycomata, is typically relatively short (Tappan 1980, p. 809). This gives them a significant competitive advantage (through rapid to exponential reproduction rates) if the benthos is compromised by anoxia, and nutrients are sporadically supplied to the surface waters from deeper levels in the water column. Prasinophytes have been referred to as 'disaster taxa' and first evolved in the less well oxygenated Proterozoic and Palaeozoic ocean surfaces (Falkowski et al., 2004; van de Schootbrugge et al., 2013).

The apparent extinction of the dinoflagellate cyst *Luehndea spinosa* appears to be directly related to the stressed environmental conditions associated with the T-OAE.

The higher relative abundances of this species in the latest Pliensbachian and earliest Toarcian are related to relatively low seawater temperatures (Fig. 3; Table 1). As a typical Boreal species, *Luehndea spinosa* preferred relatively low temperatures and was apparently stressed to extinction by the sudden temperature rise in the *Hildaites levisoni* AB. As for *Luehndea spinosa*, changes in seawater temperature appeared to have caused significant alterations in other planktonic groups. For example, Peti and Thibault (2017) documented small average sizes of *Schizosphaerella* during the T-OAE interval in the Paris Basin. These data suggest that the *Schizosphaerella* size fluctuations are correlated with climatic change, and the smaller average size is a response to the warmer conditions.

Nannoceratopsis was also absent in the *Hildaites levisoni* AB; this is consistent with the northern Lusitanian Basin (Correia et al., 2017, figs. 6, 7). Thus, *Nannoceratopsis* did not recolonise the Lusitanian Basin following the T-OAE in the *Hildaites levisoni* and the *Hildoceras bifrons* ABs. By contrast, Bucefalo Palliani and Riding (2003, fig. 3) documented *Nannoceratopsis gracilis* and *Nannoceratopsis senex* in the *Harpoceras serpentinum* AB, following the T-OAE. This disappearance of *Luehndea spinosa* and *Nannoceratopsis* spp. during this event in the Lusitanian Basin indicates differences between the T-OAE in western Portugal compared to elsewhere in Europe, where the dinoflagellate cyst populations recovered relatively rapidly. The recovery elsewhere was due to the floras recolonising shelfal areas from shallow water intertidal/littoral refugia where tidal action prevented the development of anoxia. It appears that, in the Lusitanian Basin, environmental conditions were especially stressful during the T-OAE. This may have been because the vertical extent of anoxia was more extensive, and that the intensity of benthic anoxia was especially severe. Furthermore, it seems likely that seawater temperatures were very high and/or salinity was lowered more than elsewhere in Europe. Only the cosmopolitan dinoflagellate cyst *Mancodinium semitabulatum* and *Mendicodinium microscabratum,* which had an isolated and sparse occurrence, survived during the T-OAE at Peniche. *Mancodinium semitabulatum* was present, albeit sporadically and in low numbers, throughout the entire succession in the three ABs studied herein and hence appears to be a highly resilient species (see also Correia et al., 2017).

In the Lusitanian Basin, other fossil groups became extinct. These include brachiopods (Comas-Rengifo et al., 2013; 2015), some species of calcareous nannofossils (Perilli and Duarte, 2006) and the metacopinid ostracods (Cabral et al., 2011; 2013). Alternatively, others, such as the calcareous nannofossil *Discorhabdus ignotus* (see Mattioli et al., 2013), were temporarily restricted to refugia, due to the hostile environmental conditions associated with the T-OAE. At Peniche, Rita et al. (2016, fig. 9) reported an interval devoid of benthic foraminifera only at the middle *Hildaites levisoni* AB, coincident with the end of the δ^{13}C negative excursion. In the upper part of the *Hidaites levisoni* AB, after the reestablishment of favourable oxygenated marine environments, the apparent decrease of seawater temperatures, and normal levels of nutrients and salinity, these groups recovered (Pinto, 2008; Comas-Rengifo et al., 2013, 2015; Rita et al., 2016). In this study, the barren interval for foraminifera of Rita et al. (2016) coincides with samples P23 and P24. Both these samples yielded foraminiferal test linings (Supplementary table 2). The reason for this apparent disparity is not obvious. It is possible that the foraminifera here did not attain maturity; foraminiferal test linings only represent small morphotypes which cannot presently be linked to their agglutinated and/or calcareous conterparts (Stancliffe 1996).

Foraminiferal test linings were relatively abundant throughout the *Hildaites levisoni* AB (Fig. 4; Supplementary table 2). This is not deemed to be the result of preservation bias mitigating against the presence of dinoflagellate cysts under anoxic conditions. The reason why foraminiferal test linings are common in this interval may be due to a combination of their adaptability and relative mobility, coupled with the concomitant reduction in dinoflagellate cysts. These remains of benthic foraminifera could have survived the effects of bottom water anoxia by rapid adaptation (Hart et al. 2003; Reolid et al. 2014).

In summary, phytoplankton, i.e. calcareous nannofossils and dinoflagellates, was dramatically adversely affected by anoxia and enhanced temperatures during the T-OAE in the Lusitanian Basin. Both groups declined abruptly in the lowermost part of the *Hildaites levisoni* AB (Figs. 3, 4, 7, 8; Supplementary table 2; Mattioli et al., 2008; Correia et al., 2017). However, unlike the benthic animal groups, and calcareous nannofossils and dinoflagellates elsewhere in Europe, the phytoplankton apparently did not recover after the T-OAE during the upper part of the *Hidaites levisoni* AB. This marked disparity is highly intriguing; plankton groups are generally one of the pioneers in recolonisation following ecological crises (e.g. Eshet et al., 1995). This scenario is somewhat counterintuitive as consumers and predators in the trophic structure require primary producers (i.e. phytoplankton). Nevertheless, it appears that calcareous nannofossils and dinoflagellates were more severely affected by the anoxia, and changes in temperature and salinity, than at least some of the higher trophic levels in the Lusitanian Basin. Of these abiotic factors, in the case of dinoflagellate populations, anoxia is deemed to have been most influential as this entirely inhibits excystment (Anderson et al. 1987; Martindale and Aberhan 2017). Temperature may also have been a highly influential factor, and probably was the major cause of the demise of *Luehndea spinosa*. Dinoflagellates have specific temperature windows where excystment is possible (Kremp and Anderson 2000, fig. 5). Many dinoflagellates may have (or have had) light and salinity preferences, but these factors largely tend only to reduce germination rates (Anderson et al. 1987).

5. The Pliensbachian and Toarcian dinoflagellate cyst floras of the northern hemisphere

5.1. Overview of provincialism during the Pliensbachian and Toarcian

In the Mesozoic of Europe, two palaeogeographical realms are recognised; these are the northerly Boreal Realm and the Tethyan Realm to the south (Arkell, 1956; Hallam, 1969; Reid, 1973). An intermediate area, the Sub-Boreal region, separates these major biotic provinces. This transitional area comprises southern France, Hungary, Portugal and Spain, and it exhibits faunal/floral characteristics of both the Boreal and Tethyan realms (Fig. 9; Bucefalo Palliani and Riding, 1997a; 2003; Correia et al., 2017).

There are major differences between Pliensbachian and early Toarcian dinoflagellate cyst assemblages from the Boreal and Tethyan realms. In northern Europe, *Luehndea spinosa, Mancodinium semitabulatum* and several species of *Nannoceratopsis* are dominant within relatively diverse assemblages which may also include *Scriniocassis* and *Valvaeodinium* (Fig. 9; Morgenroth, 1970; Riding, 1984; Riding and Thomas, 1992; Riding et al., 1999; Bucefalo Palliani and Riding, 2000; 2003). However, *Nannoceratopsis* is the most prominent genus throughout the Boreal Realm (e.g. Riding et al., 1991; Bucefalo Palliani et al., 2002). The typically late Toarcian *Parvocysta* suite (including *Susadinium scrofoides*) of Riding (1984) had its inception in the *Hildoceras bifrons* AB, and significantly diversified during the remainder of the Toarcian and the early Aalenian (Wille, 1982; Riding et al., 1991; 1999; Butler et al., 2005; Feist-Burkhardt and Pross, 2010).

The Tethyan counterparts are significantly different. The dinoflagellate cysts from Pliensbachian and lower Toarcian successions in this more southerly region, which includes Greece, central Italy and surrounding regions, are relatively low in diversity. *Mancodinium semitabulatum* is present, together with relatively common and diverse *Mendicodinium* spp. and *Valvaeodinium* spp., together with *Umbriadinium mediterraneense* (Fig. 9; Bucefalo Palliani et al., 1997; Bucefalo Palliani and Riding, 1997a; 1999a; 2003, figs. 3, A2.1). While *Mancodinium semitabulatum, Mendicodinium* spp. and *Valvaeodinium* spp. are all cosmopolitan, their occurrence, especially when the latter two genera are diverse and prominent, is characteristically Tethyan. The former is a circum-Tethyan genus (Mantle and Riding, 2012). The *Parvocysta* complex is effectively absent, and genera such as *Luehndea* and *Nannoceratopsis* are relatively scarce and sporadic.

5.2. *The Pliensbachian and Toarcian dinoflagellate cysts of the Sub-Boreal Realm*

Dinoflagellate cysts from the Pliensbachian and Toarcian of the Sub-Boreal region have been studied in southern France, Hungary and Portugal. The palynology of the upper Pliensbachian of Quercy, southwest France was examined by de Vains (1988) and Bucefalo Palliani and Riding (1997a). De Vains (1988, fig. 8) provided presence/absence data from seven samples. She recorded *Luehndea spinosa, Mancodinium semitabulatum, Mancodinium* sp., *Mendicodinium* spp., *Nannoceratopsis* spp. and *Scriniocassis weberi*. Bucefalo Palliani and Riding (1997a) reported semi-quantitative data from the upper Pliensbachian of the Quercy area and a slightly more diverse assemblage. The flora is dominated by *Mendicodinium* spp. and *Nannoceratopsis* spp., together with minor levels of *Luehndea spinosa* and *Mancodinium semitabulatum*.

The first study on the Jurassic dinoflagellate cysts of Hungary was by Baldanza et al. (1995). These authors worked on the phytoplankton from the upper Pliensbachian and lower Toarcian succession of Reka Valley in the Mecsek Mountains of southwest Hungary. They encountered a relatively diverse flora comprising the genera *Luehndea, Mancodinium, Mendicodinium, Nannoceratopsis, Umbriadinium* and *Valvaeodinium* (Baldanza et al., 1995, figs. 4, 6). The two assemblages from the uppermost Pliensbachian were totally dominated by *Luehndea cirilliae, Luehndea spinosa, Nannoceratopsis gracilis* and *Nannoceratopsis senex*, with low proportions (6%) of

Mendicodinium spp. By contrast, the three lower Toarcian samples were more diverse. *Luehndea* spp. (56%) continued their dominance, but *Nannoceratopsis* spp. comprised 16% of the assemblage, considerably less than in the latest Pliensbachian (49%). Also present were *Mendicodinium* spp. (15%), *Valvaeodinium* spp. (10%) and *Umbriadinium mediterraneense* (3%). *Mancodinium semitabulatum* proved rare, and was only observed in the lowermost Toarcian (Baldanza et al., 1995, fig. 4). Bucefalo Palliani and Riding (2003, fig. A2.5) recorded a relatively diverse association from the lower Toarcian of Urkut, Hungary including *Luehndea cirilliae, Luehndea spinosa*, *Mendicodinium* spp., *Nannoceratopsis gracilis*, *Scriniocassis* spp, *Umbriadinium mediterraneense* and *Valvaeodinium* spp. *Mendicodinium* and *Valvaeodinium* were by far the most common genera. Recently, Baranyi et al. (2016) examined 35 samples from the lower Toarcian (*Dactylioceras tenuicostatum* to *Hildoceras bifrons* ABs) of the Reka Valley. In this study, *Luehndea* and *Nannoceratopsis* totally dominated the *Dactylioceras tenuicostatum* AB (assemblages 1 and 2). *Luehndea* spp. were confined to assemblage 1, but *Nannoceratopsis* spp. reappeared in the *Hildoceras bifrons* AB, following the T-OAE.

The earliest research on the Jurassic marine palynology of Portugal was by Davies (1985). This author provided presence/absence data from several localities of the Lusitanian Basin and identified forms such as *Dapcodinium priscum, Luehndea* sp., *Mancodinium semitabulatum, Mendicodinium* spp., *Nannoceratopsis* spp. and *Scriniocassis* spp. Semiquantitative dinoflagellate cyst data were presented for the Pliensbachian to lower Toarcian succession of the Lusitanian Basin by Bucefalo Palliani and Riding (2003). *Luehndea* spp., *Mancodinium semitabulatum* and *Mendicodinium* spp. were reported. However, the most detailed publication on the Lower Jurassic palynology of the Lusitanian Basin is Correia et al. (2017) who researched the lower and middle Toarcian of two sections in the north part of this basin. Only four genera, *Luehndea, Mancodinium, Mendicodinium* and *Nannoceratopsis*, were recorded. Correia et al. (2017) recorded very high proportions of *Luehndea spinosa* in the uppermost part of the *Dactylioceras polymorphum* AB (lowermost Toarcian) at Maria Pares and Vale des Fontes (Fig. 8). The T-OAE badly disrupted the dinoflagellate cyst record, and relatively low numbers of specimens were present following this event. At Maria Pares, *Luehndea spinosa* and *Nannoceratopsis* did not reappear following the T-OAE. However, *Mancodinium semitabulatum* survived and became consistently common throughout most of the overlying *Hildaites levisoni and Hildoceras bifrons* ABs, together with sporadic *Mendicodinium* spp. (Correia et al., 2017, table 1). By comparison with elsewhere in Europe (Morgenroth, 1970; Riding, 1987; Bucefalo Palliani and Riding, 1997a,b; 2000; 2003; Bucefalo Palliani et al., 1997), the youngest occurrence of *Luehndea spinosa* in the Lusitanian Basin is apparently slightly diachronous (Correia et al., 2017, fig. 10). This is probably due to a slight miscorrelation of the Tethyan and Sub-Boreal ammonite zonations. The floras recorded by Correia et al. (2017) are similar in taxonomic content and relative proportions to those described herein.

5.3. Uppermost Pliensbachian and lower Toarcian marine palynofloras of Peniche and the Lusitanian Basin in a regional context

The uppermost Pliensbachian and lower Toarcian dinoflagellate cyst floras recorded herein from Peniche were relatively low in diversity. *Luehndea spinosa* was by far the dominant species, with *Mancodinium semitabulatum* and *Nannoceratopsis* spp. being distinctly subordinate but occasionally relatively common below the T-OAE. *Mendicodinium microscabratum, Nannoceratopsis ambonis* and *Scriniocassis weberi* all proved sporadic and rare (Supplementary table 2). Other taxa which have been reported from coeval strata in the southern part of the Sub-Boreal Realm such as *Mendicodinium spinosum* subsp. *spinosum, Umbriadinium mediterraneense* and *Valvaeodinium* spp. were not encountered herein (e.g. Baldanza et al., 1995; Correia et al., 2017). The floras are broadly comparable with coeval biotas from northern Europe and Russia (e.g. Riding, 1987; Feist-Burkhardt and Wille, 1992; Riding et al., 1999). Hence, the dominance of *Luehndea spinosa*, *Mancodinium semitabulatum* and *Nannoceratopsis* spp. during the late Pliensbachian to early Toarcian appears to be relatively persistent from northern Siberia throughout northern Europe to the Lusitanian Basin. Thus, the low species richness flora dominated by *Luehndea, Mancodinium* and *Nannoceratopsis* in the Lusitanian Basin appears to be more typical of the Boreal than the Tethyan Realm. However, *Nannoceratopsis* is more diverse in the Boreal Realm than further south (Bucefalo Palliani and Riding, 2003). Furthermore, high diversities of *Mendicodinium,* together with characteristically Tethyan species such as *Umbriadinium mediterraneense* and *Valvaeodinium hirsutum*, do not appear to be present in the Lusitanian Basin.

Therefore, unsurprisingly, the Sub-Boreal region appears to be an intermediate area which exhibits biotic aspects of both the Boreal and Tethyan realms. For example, dinoflagellate cyst assemblages are typically more diverse than further southeast in the Tethys, but *Mendicodinium* and *Valvaeodinium* are more prominent than in the Boreal Realm (Bucefalo Palliani and Riding, 1999a). The prominence of *Luehndea spinosa* in the late Pliensbachian and earliest Toarcian of Hungary and Portugal may be geographically controlled in southern Europe, representing a slightly lower latitudinal assemblage than southern France, where it is less common. The floras from the uppermost Pliensbachian at Quercy are dominated by *Nannoceratopsis* (Bucefalo Palliani and Riding, 1997a, fig. 3), which is a typically Boreal phenomenon. An alternative, and probably more plausible, explanation of the striking relative abundance of *Luehndea spinosa* in the upper Pliensbachian to lowermost Toarcian strata, immediately underlying the T-OAE, in the Lusitanian Basin is that it migrated from the Boreal Realm, following southward cold water streams, and thrived in the western part of the Sub-Boreal Realm (Fig. 9). It is also possible that the relatively low diversity associations in the Lusitanian Basin reflect its relatively isolated position from the rest of the Sub-Boreal Realm and Tethys due to the emergent Iberian Massif (Fig. 9). This is supported by the absence of typically Tethyan taxa such as *Umbriadinium mediterraneense* and *Valvaeodinium* spp. This study has also highlighted the fact that *Mancodinium semitabulatum* occurs throughout the Pliensbachian and Toarcian of the northern hemisphere, and appears to have been an effective recoloniser following the T-OAE in the Lusitanian Basin (Fig. 3; Supplementary table 2).

In conclusion, the Boreal dinoflagellate cysts *Luehndea spinosa, Nannoceratopsis senex, Nannoceratopsis gracilis* and *Scriniocassis weberi,* and the Tethyan genus *Mendicodinium,* may have migrated at this time to the intermediate Sub-Boreal Realm, where the Lusitanian Basin and Peniche are located. *Mancodinium semitabulatum* is interpreted as having a very wide biogeographical range. The dinoflagellate cyst assemblage described herein from the Lusitanian Basin is therefore a combination of the aforementioned taxa (Fig. 9).

6. Conclusions

The well exposed uppermost Pliensbachian and lower Toarcian succession at Peniche in the Lusitanian Basin was extensively sampled for palynological analysis; 45

samples were collected from the *Emaciaticeras emaciatum*, *Dactylioceras polymorphum* and *Hildaites levisoni* ABs. Thirty nine of these horizons yielded abundant and well-preserved palynomorph biotas, including low diversity dinoflagellate cyst assemblages.

Seven dinoflagellate cyst species were recognised: *Luehndea spinosa*, *Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Nannoceratopsis ambonis*, *Nannoceratopsis gracilis*, *Nannoceratopsis senex* and *Scriniocassis weberi*. They are largely present in the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs, and the most abundant taxon is *Luehndea spinosa*. The stratigraphically highest occurrence of *Luehndea spinosa* is in sample P14, at the top of *Dactylioceras polymorphum* AB, immmediately before the T-OAE. *Luehndea spinosa* was a cold water taxon. It appears to have tracked the southerly movement of cold water from the Boreal Realm, and thrived in the western Sub-Boreal Realm which was somewhat isolated at this time due to the emergent Iberian Massif. *Luehndea spinosa* is also biostratigraphically significant, and its presence confirms the age of the uppermost Lemede Formation and the CC1 member as established by ammonite faunas. The remainder of the palynoflora is entirely compatible with a latest Pliensbachian to early Toarcian age.

In terms of biotic provincialism, the dinoflagellate cyst floras from Peniche, which is in the Sub-Boreal Realm, unsurprisingly exhibit some characteristics of the Boreal Realm to the north and the Tethyan Realm to the south. The associations from Peniche most closely resemble coeval floras from elsewhere in the Sub-Boreal Realm such as Hungary and the northern Lusitanian Basin, but not southern France.

The principal aim of this work was to analyse the response of marine palynoflora to the T-OAE. Prior to the T-OAE, in the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ABs dinoflagellates thrived throughout the Lusitanian Basin with the exception of the relatively warm earliest Toarcian period. The recovery from this event was relatively rapid, and cool temperatures were re-established. This interval was dominated by the cool water dinoflagellate cyst *Luehndea spinosa*.

The CC2 and lowermost CC3 members sampled here are assigned to the *Hildaites levisoni* AB, and represent the T-OAE and the immediately overlying strata. This sucesssion is characterised by a virtual ‘blackout’ of dinoflagellate cysts, which were largely replaced by opportunistic prasinophytes. Calcareous nannofossils were also badly disrupted at this time. The massive reduction in relative abundance of dinoflagellate cysts, and the rise of prasinophytes, in this interval reflects the effects of the T-OAE, and is termed the plankton crisis. The bottom water and water column anoxia, significantly elevated temperatures, and reduced salinities, badly affected the dinoflagellate life cycle which includes a benthic resting cyst. The prasinophytes do not necessarily need a benthic phase during their life cycle. Of these factors, anoxia is possibly most important as this entirely inhibits the excystment of dinoflagellates. Temperature was also a highly important factor, at least in the specific case of *Luehndea spinosa* extinction, as in this work was effectively evident the correlation between its relative abundance with seawater temperature changes. By contrast to *Luehndea spinosa*, *Mancodinium semitabulatum* was a successful recoloniser. The low numbers of dinoflagellate cysts following the T-OAE strongly indicates a long recovery phase, and suggests that environmental conditions were especially stressful during the T-OAE in the Lusitanian Basin.

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Appendix

This is a list of all palynomorphs at and below species level which were recovered from the material studied herein, or mentioned in the text, with full author citations. The taxa are listed alphabetically in four groups. All six dinoflagellate cyst taxa mentioned herein, but were not found in the material from the Lusitanian Basin are asterisked. References to the dinoflagellate cyst author citations can be found in Williams et al. (2017). The recommendations of Correia et al. (2017, appendix 2) regarding the taxonomy of *Nannoceratopsis senex* are followed herein.

Dinoflagellate cysts
**Dapcodinium priscum* Evitt 1961
**Luehndea cirilliae* Bucefallo Palliani et al. 1997
Luehndea spinosa Morgenroth 1970
Mancodinium semitabulatum 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 weberi Gocht 1964
**Susadinium scrofoides* Dörhöfer & Davies 1980
**Umbriadinium mediterraneense* Bucefalo Palliani & Riding 1997
**Valvaeodinium hirsutum* Bucefalo Palliani & Riding 1997

Miscellaneous microplankton:
Cymatiosphaera pachytheca Eisenack 1957
Halosphaeropsis liassica Mädler 1968
Polygonium jurassicum Bucefalo Palliani et al. 1996

Spores
Calamospora tener (Leschik 1955) Mädler 1964
Concavisporites granulosus Tralau 1968
Ischyosporites variegatus (Couper 1958) Schulz 1967
Kraeuselisporites reissingeri (Harris 1957) Morbey 1975
Osmundacidites wellmanii Couper 1953
Todisporites granulatus Tralau 1968

Pollen
Araucariacites australis Cookson 1947 ex Couper 1958
Cerebropollenites macroverrucosus (Thiergart 1949) Schulz 1967
Classopollis classoides (Pflug 1953) Pocock & Jansonius 1961

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Fig. 1. The location and geological setting of the Lusitanian Basin of western Portugal (adapted from Duarte et al., 2010). The section studied at Peniche, which is the Toarcian GSSP, is near to Peniche city, is indicated by the letter P at 39°22'15''N; 9°23'07''W.

Fig. 2. The ammonite biostratigraphy and lithostratigraphy of the upper Pliensbachian and Toarcian succession of the Peniche area of the Lusitanian Basin, western Portugal based on Duarte (2007) and with the biostratigraphical data of Silva et al. (2011) and Comas-Rengifo et al. (2016). The grey shading indicates the lithostratigraphical units which were studied herein. MLOF = Marly Limestones with Organic Facies member; CC1–5 = Cabo Carvoeiro Formation members 1–5.

Fig. 3. Dinoflagellate cyst relative abundances, the $\delta^{13}C_{carb}$ record, the temperature profile based on $\delta^{18}O$ and the sequence stratigraphy of the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) in the Peniche section, western Portugal. The log is modified from Hesselbo et al. (2007) and Barrón et al. (2013), and indicates the positions of the palynomorph samples P-7 to P38. The ABs are based on, and modified from, Mouterde (1955), Elmi et al. (1989) and Comas-Rengifo et al. (2016). CC1–3 = Cabo Carvoeiro Formation members 1–3. Toarcian GSSP = Toarcian Global Boundary Stratotype Section and Point, immediately above sample P-1. T-OAE = Toarcian Oceanic Anoxic Event, between samples P15 and P24. The first (left hand) column depicts the relative proportions of the dinoflagellate cysts *Luehndea spinosa*, *Mancodinium semitabulatum* and *Nannoceratopsis* spp. expressed as a percentage of the overall marine palynofloras. The second column depicts the carbon isotope ($\delta^{13}C_{carb}$) record of Hesselbo et al. (2007). The third column represents temperature profile inferred from the $\delta^{18}O$ record of Suan et al. (2008a). The fourth (right hand) column illustrates the sequence stratigraphy of Duarte (2007); two second order cycles are illustrated. TP = transgressive phase; RP = regressive phase.

Fig. 4. The relative abundances of the four marine palynomorph groups, expressed as percentages of the total marine palynoflora, from the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and the lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) of the Peniche section, western Portugal. Note that the samples P1, P15, P18, P21, P26 and P27 are entirely devoid of palynomorphs, and were not illustrated here in order to achieve better visualisation of the marine palynobiotas. Toarcian GSSP = Toarcian Global Boundary Stratotype Section and Point.

Fig. 5. Selected dinoflagellate cysts from the uppermost Pliensbachian and lower Toarcian of the Peniche section of the Lusitanian Basin, western Portugal. All specimens are housed in the collections of the LNEG (Portuguese Geological Survey), S. Mamede de Infesta, Portugal. The sample number, slide number and England Finder coordinates are provided. All the scale bars represent 20 μm.

1. *Luehndea spinosa* Morgenroth 1970. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P9, slide 1, X37. Oblique lateral view, high focus. Note the cingulum and the antapical (1'''') plate.
2. *Luehndea spinosa* Morgenroth 1970. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P12, slide 1, N27/4. Dorsal view, high focus. Note the uninterrupted cingulum.
3. *Luehndea spinosa* Morgenroth 1970. Upper Pliensbachian (*Emaciaticeras emaciatum* AB), sample P-6, slide 1, H28/2. Oblique dorsal view, high focus. Note the uninterrupted cingulum and the antapical (1'''') plate.
4. *Nannoceratopsis gracilis* Alberti 1961. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P6, slide 1, D45/4. Left lateral view. Note the rounded ventral antapical horn.
5. *Nannoceratopsis gracilis* Alberti 1961. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P6, slide 1, G28/3. Right lateral view. Note the short dorsal antapical horn and the less pronounced ventral antapical horn.
6. *Nannoceratopsis gracilis* Alberti 1961. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P6, slide 1, G20/4. Right lateral view. Note the long dorsal antapical horn.

7. *Nannoceratopsis gracilis* Alberti 1961. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P10, slide 1, Q20/4. Right lateral view. Note the moderate width, comparing with the specimens in 4, 5 and 6.
8. *Nannoceratopsis ambonis* Drugg 1978. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P10, slide 1, T25/3. Left lateral view. Note the prominent, thick sagittal rim.
9. *Nannoceratopsis senex* van Helden 1977. Upper Pliensbachian (*Emaciaticeras emaciatum* AB), sample P-4, slide 1, M50/3. Left lateral view. Note the single antapical horn.
10. *Mancodinium semitabulatum* Morgenroth 1970. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P6, slide 1, O27/4. Dorsal view, high focus. Note the anterior sulcal plate (the sulcal tongue) and the well-preserved precingular plates (the 1'' and 7'') which are involved in the formation of the 'disintegration' style archaeopyle.
11. *Scriniocassis weberi* Gocht 1964. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P9, slide 1, R36/1. Dorsal view, high focus. Note the coarse reticulum and the 2P archaeopyle.
12. *Mendicodinium microscabratum* Bucefalo Palliani et al. 1997. Lower Toarcian (*Hildaites levisoni* AB), sample P23, slide 1, L24/4. Dorsal view. Note the microscabrate autophragm and the epicystal archaeopyle.

Fig. 6. Selected palynomorphs from the uppermost Pliensbachian and lower Toarcian of the Peniche section of the Lusitanian Basin, western Portugal. All specimens are housed in the collections of the LNEG (Portuguese Geological Survey), S. Mamede de Infesta, Portugal. The sample number, slide number and England Finder coordinates are provided. All the scale bars represent 20 μm.

1. *Polygonium jurassicum* Bucefalo Palliani et al. 1996. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P5, slide 1, J25/3.
2. *Polygonium jurassicum* Bucefalo Palliani et al. 1996. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P6, slide 1, T38.
3. *Polygonium jurassicum* Bucefalo Palliani et al. 1996. Lower Toarcian (*Hildaites levisoni* AB), sample P16, slide 1, G43/2.

4. *Micrhystridium* sp. Lower Toarcian (*Hildaites levisoni* AB), sample P38, slide 1, T46.
5. Indeterminate acritarch. Lower Toarcian (*Hildaites levisoni* AB), sample P17, slide 1, V48.
6. *Cymatiosphaera* sp. cf. *C. pachytheca* Eisenack 1957. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P13, slide 1, F34/3.
7. *Osmundacidites wellmanii* Couper 1953. Lower Toarcian (*Dactylioceras polymorphum* AB), sample P3, slide 1, O64.
8. *Striatella* sp. Lower Toarcian (*Hildaites levisoni* AB), sample P25, slide 1, B33.
9. *Concavisporites granulosus* Tralau 1968. Lower Toarcian (*Hildaites levisoni* AB), sample P16, slide 1, T46/4.
10. *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967. Upper Pliensbachian (*Emaciaticeras emaciatum* AB), sample P-4, slide 1, T35/3.
11. Foraminiferal test lining. Lower Toarcian (*Hildaites levisoni* AB), sample P23, slide 1, N47/4.
12. Foraminiferal test lining. Lower Toarcian (*Hildaites levisoni* AB), sample P23, slide 1, X23/4.

Fig. 7. The total dinoflagellate cysts expressed as a percentage of the overall marine palynobiota plotted against the total calcareous nannofossils per gram of rock (taken from Mattioli et al., 2008) in the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) to the lower Toarcian (*Hildaites levisoni* AB) at Peniche, western Portugal. The four plankton phases described in section 4 are also plotted against the two microfossil records.

Fig. 8. The uppermost Pliensbachian to lower Toarcian dinoflagellate cyst relative abundances, expressed as percentages of the overall palynoflora, observed herein at Peniche, western Portugal (the right hand column). These are compared with the lower Toarcian dinoflagellate cyst relative abundances at Vale des Fontes and Maria Pares (the left hand and central columns respectively) of the northern Lusitanian Basin, western Portugal taken from Correia et al. (2017). The shaded interval denotes the correlation of the maximum relative abundance of dinoflagellate cysts in the upper part

of the *Dactylioceras polymorphum* AB, immediately below the T-OAE in the Lusitanian Basin.

Fig. 9. The Toarcian palaeogeography of the western Tethys region, modified from Thierry and Barrier (2000), with the interpreted dinoflagellate migrations between the Boreal and Tethyan Realms depicted; these are explained in subsection 5.3.

Table 1. A concise summary of the four plankton phases recognised herein, which are described in detail in section 4. The *Emaciaticeras emaciatum, Dactylioceras polymorphum* and *Hildaites levisoni* ABs are abbreviated to *H.l., D.p.* and *H.l.* respectively in column 2. The temperatures are taken from Suan et al. (2008a).

Supplementary figure 1. The relative abundance of marine and terrestrial palynomorphs (blue and brown shading respectively), expressed as percentages of the overall palynoflora from the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) of the Peniche section, western Portugal.

Supplementary table 1. The palynomorph assemblages from the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) of the Peniche section, western Portugal. The numbers represent the percentages of the respective taxon within the overall palynoflora (i.e. marine and terrestrial). Blank spaces indicate the absence of the respective form, and the barren samples are asterisked. The grey shading represents the samples within the T-OAE. The right hand column represents the absolute (overall) numbers of palynomorphs counted.

Supplementary table 2. The marine palynomorph assemblages from the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) of the Peniche section, western Portugal. The numbers represent the percentages of the respective taxon within the overall marine palynoflora (not the overall palynoflora). Blank spaces indicate the absence of the respective form, and the barren samples are asterisked. The grey shading represents the samples within the T-OAE. The right hand column represents the absolute numbers of marine palynomorphs counted.

Supplementary table 3. The terrestrial palynomorph assemblages from the uppermost Pliensbachian (*Emaciaticeras emaciatum* AB) and lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ABs) of the Peniche section, western Portugal. The numbers represent the percentages of the respective taxon within the overall terrestrial palynoflora (not the overall palynoflora). Blank spaces indicate the absence of the respective form, and the barren samples are asterisked. The grey shading represents the samples within the T-OAE. The right hand column represents the absolute numbers of terrestrial palynomorphs counted.