The palynology of the Lower and Middle Toarcian (Early Jurassic) in the Lusitanian Basin, western Portugal

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ABSTRACT

The uppermost Lower Jurassic (Lower and Middle Toarcian) succession of the northern Lusitanian Basin in western Portugal was examined for palynomorphs. Two localities, the Maria Pares and the Vale das Fontes sections, were sampled. The material spans the *Dactylioceras polymorphum*, *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones. The samples produced relatively low diversity dinoflagellate cyst floras which are typical of those from coeval European successions; the most abundant species is *Luehndea spinosa*. The other forms encountered were *Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Mendicodinium spinosum* subsp. *spinosum*, *Mendicodinium* sp., *Nannoceratopsis ambonis*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex*. Dinoflagellate cysts typically dominate throughout the *Dactylioceras polymorphum* ammonite biozone; they significantly decreased in relative proportions in the overlying *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones. The low diversity *Luehndea-Nannoceratopsis* dinoflagellate cyst flora of the Lusitanian Basin is characteristic of the Sub-Boreal region of Europe. This is a transitional region, intercalated between the Boreal and Tethyan realms. The Toarcian Oceanic Anoxic Event (T-OAE) in the Lusitanian Basin is characterised by a sudden decline in palynomorph abundance and diversity, including the virtual absence of acritarchs and dinoflagellate cysts. Following the T-OAE, *Mancodinium semitabulatum* and *Mendicodinium* spp. were the only dinoflagellate cysts recorded. This 'blackout' of dinoflagellate cysts during the T-OAE, and their partial recovery following the event, is indicative that the benthic anoxia was extremely high in intensity throughout the Lusitanian Basin.

1. Introduction

This aim of this study is to document the Lower Jurassic (Lower and Middle Toarcian) palynomorphs from the Figueira da Foz and Rabaçal areas in the northern part of the Lusitanian Basin in western Portugal, and to examine the response of dinoflagellate cysts and other marine microplankton to the Toarcian Oceanic Anoxic Event (T-OAE). Two successions were studied, the Maria Pares and Vale das Fontes sections which are located between Figueira da Foz and Rabaçal (Fig. 1).

The T-OAE occurred at c. 182 Ma, and is the oldest of the three major Mesozoic-Cenozoic oceanic anoxic events (Jenkyns, 2010, fig. 1). These events were amongst the most profound palaeoenvironmental perturbations during the Phanerozoic. The T-OAE was characterised by rapid rises in marine extinctions, marine stratification, oxygen reduction and seawater temperatures (Cohen et al., 2007; Suan et al., 2008a,b; 2010; 2011). Oceanic Anoxic Events were global palaeoenvironmental phenomena, and the T-OAE was likely to have been caused by a massive carbon injection into the atmosphere from gas hydrates and/or methane release from sedimentary rocks due to intrusive vulcanism (Hesselbo et al., 2000; Kemp et al., 2005; McElwain et al., 2005; Svensen et al., 2007; Hesselbo and Pieńkowski, 2011).

A distinctive prominent negative carbon isotope excursion ($\delta^{13}C$), recorded in marine carbonates and sedimentary organic matter, characterises the T-OAE. In the Lusitanian Basin, the T-OAE has been confidently identified using carbon isotope evidence (Hesselbo et al., 2007; Suan et al., 2008a,b; Pittet et al., 2014). The distribution of dinoflagellates is influenced by factors such as benthic oxygen levels, light, nutrients, ocean currents, salinity, temperature and water depth (Dale, 1996). Hence Toarcian dinoflagellate populations would have been profoundly affected by the T-OAE (Bucefalo Palliani et al., 2002).

Previous studies on the Jurassic palynology of the Lusitanian Basin are Davies (1985), Mohr and Schmidt (1988), van Erve and Mohr (1988), Smelror et al. (1991), Bucefalo Palliani and Riding (1999a; 2003), Barrón and Azerêdo (2003), Oliveira et al. (2007) and Barrón et al. (2013). Only three of these included material from the Toarcian (Davies, 1985; Oliveira et al., 2007; Barrón et al. 2013). However dinoflagellate cysts were not discussed in detail by these authors; Davies (1985) is a purely biostratigraphical study, and Oliveira et al. (2007) and Barrón et al. (2013) mainly discussed pollen and spores.

2. Geological background

The Lusitanian Basin is a marginal marine depocentre located in central western Portugal, and is oriented NE-SW (Fig. 1). It is 300 km long and 150 km wide, with a maximum basin fill of 5 km. The sediments are mainly Jurassic, but range from Upper Triassic to Paleogene. Its formation and evolution was related to the breakup of Pangaea during the opening of North Atlantic. Structurally, the Lusitanian Basin is divided into the northern, central and southern sectors, all of which are bounded by Variscan faults. Four rifting phases occurred between the Late Triassic and the Cretaceous (Azerêdo et al., 2003; Kullberg et al., 2013).

Throughout the Lusitanian Basin, most of the Toarcian comprises the São Gião Formation. This unit spans the *Dactylioceras polymorphum* to the lowermost *Dumortieria meneghinni* ammonite biozones, and is subdivided into five members (Fig.

2; Duarte and Soares, 2002; Duarte, 2007). The type section of the São Gião Formation is the Maria Pares succession in the Coimbra-Rabaçal region, located in the northern part of the Lusitanian Basin (Fig. 1). This section exposes a continuous Toarcian–Aalenian succession which yields ammonite faunas throughout (Henriques, 1992; 1995).

During the Early Jurassic, marine carbonate ramps rapidly formed in the Lusitanian Basin. Consequently Lower Jurassic strata are extensive, and are represented by a richly fossiliferous Pliensbachian and Toarcian interbedded marl-limestone succession (Comas-Rengifo et al., 2013; Mattioli et al., 2013; Henriques et al., 2014). However, the Lower Toarcian carbonate-dominated succession exhibits different facies (Duarte, 1997; Duarte and Soares, 2002; Azerêdo et al., 2014). The lowermost beds are fossiliferous grey marl and limestone couplets, belonging to the *Dactylioceras polymorphum* ammonite biozone (Azerêdo et al., 2003). The lower *Hildaites levisoni* ammonite biozone is represented by the Chocolate Marls, which are carbonate and sparsely fossiliferous; this unit is absent in the Maria Pares section. The middle *Hildaites levisoni* ammonite biozone normally comprises bioclastic limestones often rich in brachiopods. Marl-limestone alternations, similar to the lowermost Toarcian, constitute the upper *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones (Duarte, 1995).

The Lower and Middle Jurassic ammonite faunas of the Lusitanian Basin indicate a Sub-Boreal (Atlantic) affinity (Mouterde et al., 1979). However, mixed ammonite faunas indicate periodic communication between the Boreal and Tethyan realms (Terrinha et al., 2002). The earliest Toarcian *Dactylioceras polymorphum* ammonite biozone of the Mediterranean region is broadly coeval with the *Dactylioceras tenuicostatum* ammonite biozone of the Subboreal and Submediterranean realms (Fig. 3). Succeeding this, the Mediterranean *Hildaites levisoni* ammonite biozone is the age equivalent of the *Harpoceras falciferum* ammonite biozone of northwest Europe and the *Harpoceras serpentinum* ammonite biozone of southern Europe (Fig. 3; Page, 2003).

3. Material and methods

In this study, two Toarcian successions from the northern part of the Lusitanian Basin were sampled. The most extensive of these is the Maria Pares section near Rabaçal, where fifty-four samples (prefixed PZ) were collected (Figs. 1, 4). This is the type section of the São Gião Formation, and four members were sampled. These are the Marly Limestones with *Leptaena* Facies (MLLF), the Thin Nodular Limestones (TNL), the Marls and Marly Limestones with *Hildaites* and *Hildoceras* (MMLHH), and the Marls and Marly Limestones with Sponge Bioconstructions (MMLSB) members. The other section examined was at Vale das Fontes, near the coast at Boa Viagem Mountain in the Cape Mondego region. Here, fourteen samples (prefixed PVF) were taken from the base of the São Gião Formation (Figs. 1, 5). They are all from the MLLF and the lowermost TNL members. The samples therefore span the *Dactylioceras polymorphum*, *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones. Pittet et al. (2014) located the T-OAE in the equivalent of sample PZ9 in the Maria Pares section and sample PVF14 in the Vale das Fontes section (Figs. 6, 7).

The samples were all prepared using standard palynological techniques comprising acid digestion (Wood et al., 1996), however the organic residues were not oxidised. All residues were sieved using a 15 µm mesh sieve. When possible, a minimum of 300 palynomorphs were counted for each sample. The samples, aqueous residues, microscope slides and figured specimens are all curated in the collections of the LNEG (Portuguese Geological Survey), São Mamede de Infesta, Portugal.

4. Palynology

4.1. Introduction

In this section, the Lower and Middle Toarcian palynofloras from the Maria Pares and the Vale das Fontes successions are described, interpreted and the relevant horizons related to the T-OAE. The percentages of the principal dinoflagellate cysts, and the overall dinoflagellate cyst associations are illustrated in Figs. 6 and 7. Additionally, the relative abundances of the six major palynomorph groups are documented (Figs. 8, 9,). The aggregated percentages of the four groups of marine palynomorphs (i.e. acritarchs, dinoflagellate cysts, foraminiferal test linings and prasinophytes) are depicted in Figs. 10 and 11. Selected palynomorphs are illustrated in

Plates I and II, and Tables 1 and 2 are comprehensive palynomorph datasets for each of the two sections. In tables 1 and 2, all the palynomorphs which were identified are documented, and the data are presented as percentages of the respective overall palynoflora. The palynomorph taxa at and below species level which were recorded herein, or were mentioned in the text, are listed in Appendix 1 with their respective author citations. Appendix 2 is included to document our taxonomic concepts of the dinoflagellate cyst species *Nannoceratopsis gracilis* and *Nannoceratopsis senex*.

4.2. The Maria Pares section

Fifty-four samples were studied from four members of the São Gião Formation at the Maria Pares section in the Coimbra-Rabaçal region (Figs. 1, 4). The samples are assigned to the Lower and Middle Toarcian *Dactylioceras polymorphum*, *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones of the Mediterranean scheme (Figs. 2–4; Mouterde et al., 1964-1965; Elmi et al., 1989). Two of the samples, PZ14 and PZ37, proved entirely barren of palynomorphs (Fig. 8, Table 1). However, eight dinoflagellate cyst taxa were encountered throughout this section. These are: *Luehndea spinosa*; *Mancodinium semitabulatum*; *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum*; *Mendicodinium* sp.; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis*; and *Nannoceratopsis senex* (Fig. 6, Plate I, Table 1).

Luehndea spinosa was recorded from samples PZ1 to PZ8 (Table 1). All these occurrences are in the MLLF Member within the *Dactylioceras polymorphum* ammonite biozone. Due to the known range of *Luehndea spinosa,* the Maria Pares succession is no older than Late Pliensbachian (*Amaltheus margaritatus* ammonite biozone), and no younger than earliest Toarcian (*Dactylioceras polymorphum* ammonite biozone) by comparison with elsewhere in Europe (Morgenroth, 1970; Riding, 1987; Bucefalo Palliani and Riding, 1997a,b; 2000; 2003; Bucefalo Palliani et al., 1997a). The presence of *Luehndea spinosa* in the Maria Pares section is consistent with Davies (1985), who also recorded this species, as *Luehndea* sp. A, at Brenha, Peniche and Zambujal in the Lusitanian Basin between the Late Pliensbachian (*Emaciaticeras emaciatum* ammonite biozone) and the Early Toarcian (*Dactylioceras polymorphum* ammonite biozone).

In the Maria Pares section, the inceptions of *Mancodinium semitabulatum, Nannoceratopsis gracilis* and *Nannoceratopsis senex* are all in sample PZ1.

Mancodinium semitabulatum ranges throughout the entire succession, but *Nannoceratopsis ambonis, Nannoceratopsis gracilis* and *Nannoceratopsis senex* are confined to the MLLF, TNL and the lowermost MMLHH members (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) (Table 1). In Europe, the consistent range bases of *Mancodinium semitabulatum, Nannoceratopsis ambonis, Nannoceratopsis gracilis* and *Nannoceratopsis senex* are all Late Pliensbachian (Morgenroth, 1970; Woollam and Riding, 1983; Bucefalo Palliani and Riding, 2003; Poulsen and Riding, 2003). *Mancodinium semitabulatum* ranges from the Pliensbachian to the Early Bajocian (Riding, 1984a; Feist Burkhardt and Wille 1992; Riding and Thomas 1992), and *Nannoceratopsis ambonis* extends from the Late Pliensbachian to the Late Bajocian (Riding, 1984b). The overall ranges of *Nannoceratopsis gracilis* and *Nannoceratopsis senex* are Late Pliensbachian to Early Bajocian (Feist Burkhardt and Monteil, 1997; Poulsen and Riding, 2003). The presence of these four species is hence entirely consistent with an Early Toarcian age for the succession studied herein.

Mendicodinium was recorded sporadically, and in low abundances, between samples PZ16 and PZ54 at Maria Pares (Table 1). This interval spans the *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones. Three representatives were recognised. These are *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum* and *Mendicodinium* sp. Representatives of the typically, but not exclusively, southern European genus *Mendicodinium* are not present in the *Dactylioceras polymorphum* ammonite biozone herein (Table 1). This is inconsistent with the records from the lowermost Toarcian *Dactylioceras tenuicostatum* ammonite biozone reported by Bucefalo Palliani et al. (1997b) from central Italy, and the occurrences from the earliest Pliensbachian to the Early Toarcian (*Hildoceras bifrons* ammonite biozone) of the Lusitanian Basin documented by Davies (1985) and Bucefalo Palliani and Riding, 2003).

In the Maria Pares section, the relative abundance of dinoflagellate cysts decreased markedly at the T-OAE in the lower part of the *Hildaites levisoni* ammonite biozone (sample PZ9). From that point, the occurrences of dinoflagellate cysts remained low throughout the remainder of the *Hildaites levisoni* ammonite biozone and in the *Hildoceras bifrons* ammonite biozone (Figs. 6, 8, Table 1).

In the *Dactylioceras polymorphum* ammonite biozone, *Luehndea spinosa* dominates the dinoflagellate cyst assemblages. In samples PZ5, PZ6 and PZ7, this species represents 90.8%, 68.2% and 76.7% of the palynoflora respectively (Fig. 6,

Table 1). It is possible that this abundance peak represents a transgressive event (Pittet et al., 2014). *Nannoceratopsis gracilis* and *Nannoceratopsis senex* are also relatively common in the *Dactylioceras polymorphum* ammonite biozone, however they each never exceed 20% of the overall palynoflora (Fig. 6). *Nannoceratopsis ambonis* is rare, and is only present in sample PZ8 (Table 1). *Mancodinium semitabulatum* is present throughout the *Dactylioceras polymorphum, Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones, and is the only species present in all three of these biozones. The range top of consistent *Nannoceratopsis* is in sample PZ8, in the *Dactylioceras polymorphum* ammonite biozone. Hence in the majority of the *Hildaites levisoni* ammonite biozone, and throughout the *Hildoceras bifrons* ammonite biozone, *Mancodinium semitabulatum* is present persistently in low numbers, occasionally co-occurring with sparse representatives of *Mendicodinium* spp. (Table 1).

Marine palynomorphs are significantly partitioned in the Maria Pares section. Dinoflagellate cysts dominate the palynomorph assemblages in the middle and upper part of the *Dactylioceras polymorphum* ammonite biozone. By contrast, small clumps of prasinophytes and dispersed specimens of this group dominate throughout the *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones (Figure 8, Table 1). The small clumped prasinophytes are probably referable to *Halosphaeropsis liassica*. Acritarchs, largely *Micrhystridium* spp., and foraminiferal test linings are also frequently present throughout this succession.

Pteridophyte spores such as *Cyathidites* spp., *Ischyosporites variegatus* and *Leptolepidites* spp., and the pollen grains *Alisporites* spp. and *Classopollis classoides*, also dominate in certain samples. However, these terrestrially-derived palynomorphs do not exhibit any coherent or specific trends (Fig. 8). The two lowermost samples from the *Dactylioceras polymorphum* ammonite biozone (PZ1 and PZ2) are especially rich in pollen and spores, notably *Alisporites* spp. and *Classopollis classoides* (Table 1). In contrast, between samples PZ3 and PZ9, marine palynomorphs consistently dominate. Stratigraphically higher than sample PZ9, some samples exhibit a relatively high terrestrial influence. However marine palynomorphs dominate most of these samples but, as previously stated, with no coherent and sustained patterns (Figs. 6, 8, Table 1).

In terms of palynomorph abundance and diversity during the T-OAE (sample PZ9), acritarchs, dinoflagellate cysts and foraminiferal test linings are entirely absent. The only marine palynomorphs present are prasinophytes; small clumps of prasinophytes dominate the assemblage. Together with dispersed specimens of

Tasmanites spp., prasinophytes comprise 94.9% of the overall palynoflora in sample PZ9 (Table 1). This dominance of prasinophytes, largely in the absence of dinoflagellate cysts, is typical of the T-OAE of northern and southern Europe (Wille, 1982a,b; Loh et al., 1986; Prauss; 1989; 1996; Prauss and Riegel 1989; Prauss et al., 1991; Bucefalo Palliani and Riding, 1999b; 2000; Bucefalo Palliani et al., 2002). Pteridophyte spores, including *Cyathidites* spp. and *Leptolepidites* spp., are present in low proportions in sample PZ9 (5.1%), but no pollen grains were encountered (Table 1).

4.3. The Vale das Fontes section

Fourteen samples from the Lower Toarcian MLLF and TNL members of the São Gião Formation succession at Vale das Fontes, Boa Viagem Mountain were studied herein (Figs. 1, 5). They all proved palynologically productive, and are correlated with the *Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones of the Mediterranean scheme (Figs. 2, 3, 5; Table 2; Elmi et al., 1989; Mouterde et al., 1964-1965). Five dinoflagellate cyst species were recorded, these are: *Luehndea spinosa*; *Mancodinium semitabulatum*; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis*; and *Nannoceratopsis senex* (Fig. 7, Table 2, Plate 1). This dinoflagellate cyst association is substantially similar to those from the coeval part of the Maria Pares section, however represenatatives of *Mendicodinium* were not found at Vale das Fontes. Dinoflagellate cysts are relatively common in the middle and upper part of the MLLF Member (*Dactylioceras polymorphum* ammonite biozone, samples PVF1-PVF13), but they are absent in the TNL Member (*Hildaites levisoni* ammonite biozone, sample PVF14) (Figs. 7, 9; Table 2).

As in the Maria Pares section, *Luehndea spinosa* was found throughout the MLLF Member/*Dactylioceras polymorphum* ammonite biozone at Vale das Fontes. It is the most abundant dinoflagellate cyst in most of the samples (PVF4, PVF6–PVF9, PVF11–PVF13). In the middle and upper part of this unit/biozone, in samples PVF8, PVF9, PVF12 and PVF13, *Luehndea spinosa* attains 70.9%, 89.1%, 70.0% and 75.3% of the palynoflora respectively (Fig. 7; Table 2). As at Maria Pares, this major acme may represent a transgressive event (Pittet et al., 2014). The acme and the pattern of occurrences of this species at Vale das Fontes is, somewhat unsurprisingly, virtually identical to that at Maria Pares. The main acme of *Luehndea spinosa* underlies the T-OAE, and has two distinctive peaks with an intervening ‘swallow tail’ (Figs. 6, 7). The presence of this species confirms that the MLLF Member is no younger than earliest Toarcian (subsection 4.2).

Mancodinium semitabulatum, Nannoceratopsis gracilis and *Nannoceratopsis senex* are also consistently present throughout the MLLF Member at Vale das Fontes. These species are persistent and relatively common, but they never exceed 16% (Table 2). Like with *Luehndea spinosa*, the profiles for *Mancodinium semitabulatum* and *Nannoceratopsis* spp. appear to be similar to those at Maria Pares. There are minor acmes of *Mancodinium semitabulatum* and *Nannoceratopsis* spp. stratigraphically below the abundance peak of *Luehndea spinosa* (Figs. 6, 7; Table 2). *Nannoceratopsis ambonis* is rare, as in the Maria Pares section. This species is sparsely present only in samples PVF2 and PVF5 in the lower part of the *Dactylioceras polymorphum* ammonite biozone (Table 2). The occurrence of *Mancodinium semitabulatum* and *Nannoceratopsis* spp. is compatible with an Early Toarcian age for this succession (subsection 4.2).

Only samples PVF1 and PVF4 in the lower part of the *Dactylioceras polymorphum* ammonite biozone at Vale das Fontes exhibit more terrestrial influence than marine, due mainly to the abundance of *Classopollis classoides* (Table 2). However, in the middle and upper *Dactylioceras polymorphum* ammonite biozone (samples PVF7–PVF13), marine influence dominates. This reaches a maximum of 94.7% marine palynomorphs in sample PVF9, largely due the abundance of *Luehndea spinosa* (Fig. 9, Table 2). As in the Maria Pares section, this marine acme is virtually all due to abundant dinoflagellate cysts stratigraphically below the T-OAE. There are five dinoflagellate cyst abundance peaks in samples PVF7, PVF8, PVF9, PVF12 and PVF13, (Fig. 7; Table 2). The pre-T-OAE dinoflagellate cyst acme is twin-peaked in both sections examined, with a ‘swallow-tail’ underlying a thick limestone bed (Figs. 6, 7).

Acritarchs (*Micrhystridium* spp.), foraminiferal test linings and prasinophytes are present in all the samples. Spores, such as *Cyathidites* spp. and *Kraeuselisporites reissingeri,* are also consistently present, generally in low percentages. Gymnospermous pollen, largely *Classopollis classoides* and *Alisporites* spp., is relatively common throughout (Table 2). There is a general decrease in the relative abundance of pollen up-section, but no other obvious coherent trends in the non-dinoflagellate cyst palynomorphs (Fig. 9). During the T-OAE (sample PVF14), no acritarchs or dinoflagellate cysts were recorded. This relatively sparse assemblage is dominated by indeterminate spores; foraminiferal test linings, pollen and prasinophytes are also present (Table 2).

4.4. Overview of the palynology of the two successions studied

The Maria Pares and Vale das Fontes Toarcian sections studied herein yielded abundant and moderately well-preserved palynofloras. The dinoflagellate cysts recognised comprise: *Luehndea spinosa*; *Mancodinium semitabulatum*; *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum*; *Mendicodinium* sp.; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis*; and *Nannoceratopsis senex* (Plate I, Tables 1, 2). This association is typical of the Lower and Middle Toarcian throughout Europe and adjacent regions (Wille, 1982a; Riding, 1984c; 1987; Davies, 1985; Riding et al., 1991; 1999; Koppelhus and Nielsen, 1994; Bucefalo Palliani and Riding, 1997a,b; 1999a,b; 2000; 2003; Bucefalo Palliani et al., 1997b). *Luehndea spinosa* is confined to the MLLF Member, and is by far the most abundant species, followed by *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* (Figs 6, 7; Tables 1, 2). *Nannoceratopsis ambonis* was recorded occasionally in low numbers, and *Mendicodinium* is only sparsely present above the T-OAE in the Maria Pares section (Table 1). Dinoflagellate cysts dominate the palynomorph assemblages throughout the *Dactylioceras polymorphum* ammonite biozone (Figs 8, 9). *Luehndea spinosa* is the most stratigraphically significant species. The relative abundances of *Luehndea spinosa, Mancodinium semitabulatum* and *Nannoceratopsis* spp. are substantially similar in both sections, and it seems likely that the abundance peaks of *Luehndea spinosa* represent transgresssive events (Figs. 6, 7; Pittet et al., 2014).

These dinoflagellate cyst records are generally consistent with previous research on the palynology of the Lower Toarcian of the Lusitanian Basin (Davies, 1985; Oliveira et al., 2007; Barrón et al., 2013). Davies (1985) identified *Luehndea spinosa, Mancodinium semitabulatum*, *Mendicodinium* spp., *Nannoceratopsis senex* and *Scriniocassis weberi*. The latter species was not recorded in this study. The Ponta do Trovão section, near Peniche is the Toarcian Global Stratotype Section and Point (GSSP), in the Peniche area (Elmi et al., 2007). *Mancodinium semitabulatum, Nannoceratopsis gracilis* and *Nannoceratopsis* sp. were identified from this important succession by Oliveira et al. (2007) and Barrón et al. (2013).

Pollen, prasinophytes and spores are also present in relatively high proportions. The pollen grains largely comprise *Alisporites* spp., *Araucariacites australis*, *Cerebropollenites macroverrucosus*, *Classopollis classoides* and *Perinopollenites elatoides*. The spores are chiefly *Cyathidites* spp., indeterminate forms and *Kraeuselisporites reissingeri* (Tables 1, 2). Most of the prasinophytes are either large, dispersed specimens of *Tasmanites* or clumps of small (c. 20 μm diameter) bodies which are referable to *Halosphaeropsis liassica* (see Mädler 1968; Bucefalo Palliani and Riding, 2000, fig. 7I). By contrast, acritarchs and foraminiferal test linings are relatively sparse (Figs. 8, 9, Tables 1, 2). All the non-dinoflagellate cyst palynomorphs are entirely consistent with an Early Jurassic age (Srivastava, 1987; 2011; Weiss, 1989; Ziaja, 2006). The consistent presence of significant levels of marine palynomorphs indicates a sustained marine depositional setting relatively close to the sources of the terrestrially-derived palynomorphs.

The most abundant continental palynomorph recorded throughout both sections was *Classopollis classoides* (Tables 1, 2). *Classopollis* is a gymnosperm pollen genus produced by plants belonging to the extinct Mesozoic conifer family Cheirolepidiaceae (Francis, 1983). These were thermophilic and xerophytic conifers that tolerated semiarid conditions, and lived in both low-lying water margin and upland environments (Pocock and Jansonius, 1961; Batten, 1975; Filatoff, 1975; Srivastava 1976). These plants covered large areas, but their abundance declined sharply with increasing palaeolatitude (Vakhrameev, 1981; Riding et al. 2013). *Classopollis* has been reported from the Lower Jurassic of the Lusitanian Basin (Davies, 1985; Oliveira et al., 2007; Barrón et al., 2013). The presence of *Classopollis classoides,* and the absence of *Callialasporites*, is a characteristic of the Late Sinemurian to Early Toarcian interval (Helby et al. 1987; Quattrocchio et al., 2011). The bryophyte spore *Kraeuselisporites ressingeri* is present only in the *Dactylioceras polymorphum* ammonite biozone in the successions studied herein (Tables 1, 2). The range of this species is Late Triassic to Early Jurassic (Rhaetian–Early Sinemurian) of northwest Europe according to Morbey (1978) and Morbey and Dunay (1978). However, Barrón et al. (2010) reported *Kraeuselisporites ressingeri* from the Toarcian–Aalenian GSSP at Fuentelsaz, Spain.

The effects of the T-OAE are markedly evident in samples PZ9 and PVF14, due to the sharp decline in palynomorph diversity and numbers. Furthermore, acritarchs and dinoflagellate cysts are absent (Figs 6, 7; Tables 1, 2). Clumps of the small prasinophyte

Halosphaeropsis liassica dominate sample PZ9, indicating a strong marine trend (Figs. 8, 10). By contrast, spores dominate sample PVF14 from the Chocolate Marls (Fig. 9).

5. Comparison of the Lusitanian Basin marine palynofloras with other studies

Fossil biotas, including dinoflagellate cysts, have allowed the characterisation of two distinct palaeogeographical areas in Europe. These are the northern Boreal Realm and the southern Tethyan Realm (Figure 12). They are separated by an intermediate Sub-Boreal region with mixed faunal/floral characteristics. This area comprises southern France, southern Germany, Hungary and Portugal (Bucefalo Palliani and Riding, 1997b; 2003).

During the Pliensbachian and Early Toarcian, dinoflagellate cyst associations from the Boreal Realm are dominated by *Luehndea spinosa, Mancodinium semitabulatum* and *Nannoceratopsis* spp. (Riding, 1987, fig. 3; Riding et al., 1999, fig. 11; Bucefalo Palliani and Riding, 2000, fig. 3). The range base of the *Parvocysta* suite is in the *Hildoceras bifrons* ammonite biozone (Wille, 1982, fig. 2; Riding et al., 1991, fig. A2), however most of the constituent species of this group are typically Late Toarcian (Riding, 1984c, fig. 3). The northern area typically exhibits markedly higher species diversities than the Tethyan Realm (Bucefalo Palliani and Riding, 2003, figs. 2, 3). This appears to be a sustained trend as this phenomenon was continued significantly later in the Jurassic (Riding and Michoux, 2013).

By contrast, Pliensbachian and Lower Toarcian successions of the Tethyan Realm yield lower diversity floras, including *Mancodinium semitabulatum* and relatively high levels of *Mendicodinium* spp. (Bucefalo Palliani and Riding, 2003, fig. 3). *Mendicodinium* is also prominent in the Early Jurassic of Australia (Riding and Helby, 2001), hence appears to be a characteristically circum-Tethyan genus. However this genus is also present, in low proportions, in Denmark and northern England in the Boreal Realm (Poulsen, 1996; Bucefalo Palliani and Riding, 2000, fig. 3). Furthermore, in the Tethyan Realm, *Luehndea spinosa* and *Nannoceratopsis* spp. are never as prominent as they are further north, and the *Parvocysta* complex is virtually absent.

Nannoceratopsis is entirerely absent throughout this interval in central Italy (Bucefalo Palliani and Riding, 2003).

The Early/Middle Toarcian dinoflagellate cyst floras recorded herein from the Lusitanian Basin are of relatively low diversity. *Luehndea spinosa* is the dominant species, followed by *Nannoceratopsis gracilis, Nannoceratopsis senex* and *Mancodinium semitabulatum*; *Mendicodinium* spp. proved rare (Tables 1, 2). Other forms reported from this interval in the Lusitanian Basin and Hungary such as *Scriniocassis weberi, Umbriadinium mediterraneense* and *Valvaeodinium* spp. were not encountered herein (Baldanza et al., 1995; Davies, 1985; Bucefalo Palliani and Riding, 2003). Moreover, the genus *Valvaeodinium,* which is present elsewhere in the Northern Hemisphere, is entirely absent. Unfortunately, the nearby Algarve Basin of southern Portugal, which is within the Submediterranean Province of the Tethyan Realm (Azerêdo et al., 2003), has not yielded any marine palynomorphs from the Lower Jurassic (Borges et al., 2011).

However, the levels of species richness recorded and the taxa encountered in the Lusitanian Basin are broadly similar with coeval floras from northern Europe and Russia (Wille, 1982a, fig. 2; Riding, 1984c. fig. 3; 1987, fig. 3; Feist-Burkhardt and Wille, 1992, fig. 2; Poulsen, 1996, fig. 12; Riding et al., 1999, fig. 11; Bucefalo Palliani and Riding, 2000, figs. 3, 4; Bucefalo Palliani et al., 2002, figs. 3, 9, 13). The dominance of *Luehndea spinosa*, *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* throughout the Early Toarcian is therefore relatively constant from northern Siberia through the North Sea southwards to the Lusitanian Basin.

Overall therefore, this low diversity *Luehndea-Nannoceratopsis* dominated flora of the Lusitanian Basin is more characteristic of the Boreal than the Tethyan Realm. However, the principal difference between the Boreal Realm and the Lusitanian Basin is the consistent presence of several species of *Nannoceratopsis* and the genus *Scriniocassis* in the former. For example *Nannoceratopsis deflandrei* subsp. *anabarensis*, *Nannoceratopsis spiculata*, *Nannoceratopsis raunsgaardii* and *Nannoceratopsis triceras* are confined to the Boreal Realm (Bucefalo Palliani and Riding, 2003). Furthermore, the high diversity levels of *Mendicodinium,* and forms such as *Luehndea cirilliae*, *Umbriadinium mediterraneense* and *Valvaeodinium hirsutum* characteristic of the Tethyan Realm (Bucefalo Palliani and Riding, 1997c; Bucefalo

Palliani et al., 1997a), are not present in central west Portugal. It therefore appears that, unsurprisingly, the low diversity dinoflagellate cyst assemblage recorded from the Lusitanian Basin is most typical of the intermediate Sub-Boreal region (Davies, 1985; Bucefalo Palliani and Riding, 2003; Olivera et al., 2007; Barrón et al., 2013).

6. The effects of the Toarcian Oceanic Anoxic Event

The Toarcian Oceanic Anoxic Event (T-OAE) significantly diminished all biotas, especially benthic ones, due to the effects of the intense bottom water anoxia. This event directly caused some extinctions (Fig. 12; Harries and Little, 1999; Bucefalo Palliani et al., 2002; Caswell et al., 2009; Caswell and Coe, 2012; 2013). The profoundness of the anoxia was greater in the Boreal Realm than in the Tethyan region, and the event was more sustained in the north (Bucefalo Palliani and Riding, 2003). In the Boreal Realm, this event caused the extinction of *Luehndea spinosa* (see Riding, 1987). In the Lusitanian Basin, the T-OAE caused the virtual disappearance of all dinoflagellate cyst taxa within the lowermost part of the *Hildaites levinsoni* ammonite biozone which is consistent with the Boreal Realm (Figs. 6–9, 12). It is therefore clear that the dinoflagellates and their cysts were responding to a major palaeoenvironmental change.

In northern Europe, the dinoflagellate cyst record became re-established in the *Hildoceras bifrons* ammonite biozone by floras returning from refugia in the littoral zone when the marine environments became re-oxygenated (Fig. 12; Bucefalo Palliani et al., 2002). Furthermore, there was significant speciation in northern Europe and surrounding regions at this time (Riding, 1984c; Riding et al., 1991; 1999). This renewal and diversification did not occur in the the Lusitanian Basin and throughout the Tethyan Realm (Fig. 12; Bucefalo Palliani and Riding, 2003). An example of this is that *Nannoceratopsis gracilis* and *Nannoceratopsis senex* are absent immediately above the T-OAE in the Lusitanian Basin (Figs. 6, 12). Further north, these species quickly became re-established in the *Harpoceras falciferum* ammonite biozone (Fig. 12; Riding, 1987, fig. 3; Bucefalo Palliani and Riding, 2000, fig. 3).

The range top of *Luehndea spinosa* throughout Europe is within the *Dactylioceras polymorphum* ammonite biozone or equivalent (Fig. 12). This bioevent was observed slightly stratigraphically higher, in the lowermost part of the *Hildaites levisoni* ammonite biozone, in the Lusitanian Basin (Figs. 6, 12). Apparently, only *Mancodinium semitabulatum* recolonised the Lusitanian Basin in the *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones (Figs. 6, 12; Table 1). Bucefalo Palliani and Riding (2003, fig. A3.4) documented the occurrence of *Nannoceratopsis gracilis* and *Nannoceratopsis senex* in the *Harpoceras falciferum* ammonite biozone, following the T-OAE throughout Europe. However, this cosmopolitan genus did not recolonise the two successions studied here from the Lusitanian Basin (Fig. 12). This was perhaps due to the severe intensity of the T-OAE in central-west Portugal. It therefore appears that *Mancodinium semitabulatum* was more resilient to benthic anoxia and marine stratification than was *Nannoceratopsis*.

7. Conclusions

A palynological study of Lower Toarcian strata at Maria Pares and Vale das Fontes in the Lusitanian Basin of Portugal yielded low diversity dinoflagellate cyst floras typical of the latest Early Jurassic of Europe. The dominant species is *Luehndea spinosa,* and *Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Mendicodinium spinosum* subsp. *spinosum*, *Mendicodinium* sp., *Nannoceratopsis ambonis*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* were also recorded. Dinoflagellate cysts normally dominate the palynofloras in the *Dactylioceras polymorphum* ammonite biozone, but their relative proportions markedly decreased in the *Hildaites levisoni* and *Hildoceras bifrons* ammonite biozones. The Lower Toarcian of the Lusitanian Basin yielded a low diversity *Luehndea-Nannoceratopsis* dominated dinoflagellate cyst flora. This is characteristic of the transitional Sub-Boreal region which is characterised by a flora which appears to be intermediate between the Boreal and Tethyan realms (Bucefalo Palliani and Riding, 2003).

The T-OAE in the Lusitanian Basin is marked by the absence of acritarchs and dinoflagellate cysts, and an abrupt decline in palynomorph abundance and diversity. After the T-OAE, only *Mancodinium semitabulatum* and *Mendicodinium* spp. were recorded. This complete ‘blackout’ of dinoflagellate cysts in the T-OAE, and their limited recovery following this event strongly suggests that the benthic anoxia was of high intensity in the Lusitanian Basin. Other Toarcian successions in the Lusitanian Basin should be studied in order to better understand the palaeobiological effects of the T-OAE on dinoflagellate populations, and to clarify the palaeogeographical affinity of this important depocentre.

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Appendix 1

A list of all palynomorphs which were recovered from the material studied herein, or were mentioned in the text with full author citations. The 18 dinoflagellate cyst taxa listed which were not found in the material from the Lusitanian Basin are asterisked. The taxa are listed alphabetically in four groups. References to the dinoflagellate cyst author citations can be found in Fensome and Williams (2004).

Dinoflagellate cysts:

**Luehndea cirilliae* Bucefallo Palliani et al. 1997
Luehndea spinosa Morgenroth 1970 (Plate I, 7–9)
Mancodinium semitabulatum Morgenroth 1970 (Plate I, 10–12)
**Mendicodinium brunneum* Bucefalo Palliani et al. 1997
Mendicodinium microscabratum Bucefalo Palliani et al. 1997 (Plate I, 5)
Mendicodinium spinosum Bucefalo Palliani et al. 1997 subsp. *spinosum* (autonym) (Plate I, 4)
**Mendicodinium umbriense* Bucefalo Palliani et al. 1997
Mendicodinium sp. (Plate I, 6)
Nannoceratopsis ambonis Drugg 1978 (Plate I, 3)
**Nannoceratopsis deflandrei* Evitt 1961
**Nannoceratopsis deflandrei* Evitt 1961 subsp. *anabarensis* Ilyina et al. 1994

Nannoceratopsis gracilis Alberti 1961 (Plate I, 1)
Nannoceratopsis magnicornis Bucefalo Palliani & Riding 1997
Nannoceratopsis raunsgaardii Poulsen 1996
Nannoceratopsis senex van Helden 1977 (Plate I, 2)
Nannoceratopsis spiculata Stover 1966
Nannoceratopsis symmetrica Bucefalo Palliani & Riding 2000
Nannoceratopsis triceras Drugg 1978
Scriniocassis weberi Gocht 1964
Susadinium scrofoides Dörhöfer & Davies 1980
Umbriadinium mediterraneense Bucefalo Palliani & Riding 1997
Valvaeodinium hirsutum Bucefalo Palliani & Riding 1997
Valvaeodinium koessenium (Morbey 1975) Below 1987
Valvaeodinium perpunctatum (Wille & Gocht 1979) Below 1987
Valvaeodinium punctatum (Wille & Gocht 1979) Below 1987
Valvaeodinium stipulatum (Wille & Gocht 1979) Below 1987

Miscellaneous microplankton:
foraminiferal test linings (Plate II, 12)
Halosphaeropsis liassica Mädler 1968 (prasinophyte)
Micrhystridium spp. (acritarch) (Plate II, 10)
Tasmanites spp. (prasinophyte) (Plate II, 11)

Spores:
Calamospora tener (Leschik 1955) Mädler 1964
Cibotiumspora juriensis (Balme 1957) Filatoff 1975
Cingutriletes sp.
Conbaculatispora sp.
Concavisporites toralis (Leschik 1955) Nilsson 1958
Concavisporites spp.
Cyathidites spp. (Plate II, 1)
Ischyosporites variegatus (Couper 1958) Schulz 1967 (Plate II, 2)
Kraeuselisporites reissingeri (Harris 1957) Morbey 1975 (Plate II, 3)
Leptolepidites spp. (Plate II, 4)
Lycopodiacidites rugulatus (Couper 1958) Schulz 1967 (Plate II, 5)

Osmundacidites wellmanii Couper 1953

Plicifera delicata (Bolchovitina 1953) Bolchovitina 1966

Retitriletes spp.

Todisporites spp.

Pollen:

Alisporites spp. (Plate II, 6)

Araucariacites australis Cookson 1947 ex Couper 1958 (Plate II, 7)

Cerebropollenites macroverrucosus (Thiergart 1949) Schulz 1967 (Plate II, 8)

Classopollis classoides (Pflug 1953) Pocock & Jansonius 1961 (Plate II, 9)

Exesipollenites spp.

Inaperturopollenites sp.

Perinopollenites elatoides Couper 1958

Appendix 2

In this contribution, we do not follow the taxonomic proposals of Ilyina et al. (1994) with regard to the dinoflagellate cyst species *Nannoceratopsis senex*. These authors changed the status of this taxon from a species to a subspecies of *Nannoceratopsis deflandrei*. Ilyina et al. (1994) placed the newly attributed subspecies *senex,* together with their new subspecies *anabarensis* and the autonym subspecies *deflandrei,* into the species *Nannoceratopsis deflandrei.* This strategy was on the basis that *Nannoceratopsis deflandrei* has a relatively untextured autophragm, in comparison to *Nannoceratopsis gracilis* which has a rough, spongy wall. This difference between the species *Nannoceratopsis gracilis and Nannoceratopsis senex* was also discussed by Piel and Evitt (1980, p. 103). In the present author's view, the principal criteria for speciation in *Nannoceratopsis* should be the lateral outline and the number of hypocystal horns, and not the fine-scale texture of the autophragm. Therefore we maintain the original contention of van Helden (1977), who established *Nannoceratopsis senex* as a distinctly tear-shaped form of this genus with a narrow antapical margin defined by the distal part of the single hypocystal horn (Plate I, 2). This contrasts with *Nannoceratopsis gracilis,* which has a subtriangular lateral outline with a much wider antapical margin (Plate I, 1). *Nannoceratopsis gracilis* is therefore deemed to be a senior synonym of *Nannoceratopsis deflandrei,* as originally envisaged by Evitt (1962).

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Fig. 1. The location and geological setting of the Lusitanian Basin of western Portugal (adapted from Reolid and Duarte, 2014). The sections studied are indicated by the numbers 1 and 2. The Maria Pares section, close to Zambujal village in the Rabaçal area (1) is at 40° 3’ 10’’N, 8° 27’ 25’’W. The Vale das Fontes section in the Figueira da Foz area (2) is at 40° 12’ 10’’N, 8° 51’ 31’’W.

Fig. 2. The ammonite biostratigraphy and lithostratigraphy of the Toarcian of the northern and central parts of the Lusitanian Basin, western Portugal based on Perilli and Duarte (2006). The grey shading indicates the four lithostratigraphical units which were studied herein.

Fig. 3. Correlation of the Lower Toarcian ammonite biozones in the Mediterranean (North Africa, Italy, Portugal, southern Spain), Submediterranean (southern England,

France, Germany, northern Spain) and Subboreal (northern Britain) provinces, adapted from Page (2003).

Fig. 4. The lithological log of the Lower and Middle Toarcian succession in the Maria Pares section (modified from Duarte, 1995), with the positions of the palynomorph samples PZ1–PZ54 indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965) and Elmi et al. (1989). MLLF = Marly Limestones with *Leptaena* Facies Member; TNL = Thin Nodular Limestones Member; MMLHH = Marls and Marly Limestones with *Hildaites* and *Hildoceras* Member; MMLSB = Marls and Marly Limestones with Sponge Bioconstructions Member.

Fig. 5. The lithological log of the Lower Toarcian succession in the Vale das Fontes section (modified from Duarte, 1995), with the positions of the palynomorph samples PVF1–PVF14 indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965) and Elmi et al. (1989). MLLF = Marly Limestones with *Leptaena* Facies Member; TNL = Thin Nodular Limestones Member.

Fig. 6. The relative proportions of the dinoflagellate cysts *Luehndea spinosa, Mancodinium semitabulatum* and *Nannoceratopsis* spp., expressed as a percentage of the overall palynoflora, from the Lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) in the Maria Pares section. *Mendicodinium* spp. are not included. The right hand column illustrates the percentages of all dinoflagellate cyst taxa, including *Mendicodinium* spp. T-OAE = Toarcian Oceanic Anoxic Event.

Fig. 7. The relative proportions of the dinoflagellate cysts *Luehndea spinosa, Mancodinium semitabulatum* and *Nannoceratopsis* spp., expressed as a percentage of the overall palynoflora, from the Lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) in the Vale das Fontes section. *Mendicodinium* spp. are not included. The right hand column illustrates the percentages of all dinoflagellate cyst taxa, including *Mendicodinium* spp. T-OAE = Toarcian Oceanic Anoxic Event.

Fig. 8. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the Lower and Middle Toarcian (*Dactylioceras polymorphum*,

Hildaites levisoni and *Hildoceras bifrons* ammonite biozones) of the Maria Pares section (samples PZ1–PZ54). Samples PZ14 and PZ37 are entirely devoid of palynomorphs. Note the dominance of prasinophytes in the T-OAE (sample PZ9). T-OAE = Toarcian Oceanic Anoxic Event.

Fig. 9. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the Lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) of the Vale das Fontes section (samples PVF1–PVF14). T-OAE = Toarcian Oceanic Anoxic Event.

Fig. 10. The relative abundances of marine palynomorphs (i.e. acritarchs, dinoflagellate cysts, foraminiferal test linings and prasinophytes) within the overall palynofloras from the Lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) of the Maria Pares section. Note the peaks at and below the T-OAE (Toarcian Oceanic Anoxic Event).

Fig. 11. The relative abundances of the marine palynomorphs (i.e. acritarchs, dinoflagellate cysts, foraminiferal test linings and prasinophytes) within the overall palynofloras from the Lower Toarcian (*Dactylioceras polymorphum* and *Hildaites levisoni* ammonite biozones) of the Vale das Fontes section. Note the peak in sample PVF9. T-OAE = Toarcian Oceanic Anoxic Event.

Fig. 12. A comparison of the stratigraphical ranges of selected dinoflagellate cysts from the Lower and Middle Toarcian (*Dactylioceras polymorphum* to *Hildoceras bifrons* ammonite biozones or their equivalents) of the major European Basins. In the Tethyan Realm, the ranges are plotted from central Italy and the Lusitanian Basin, Portugal. Data from German and the U.K. are depicted for the Boreal Realm. The position of the major dinoflagellate cyst disappearance event or ‘blackout’ caused by the T-OAE is depicted in yellow. Note how this event appears to be slightly diachronous; it is older in the Tethyan Realm than in the Boreal Realm.

Table 1. The palynomorph assemblages from the Lower and Middle Toarcian of the Maria Pares section near Rabaçal. The numbers represent percentages of the respective

taxon within the overall palynoflora; blank spaces indicate the absence of the respective form.

Table 2. The palynomorph assemblages from the Lower Toarcian of the Vale das Fontes section, north of Figueira da Foz. The numbers represent percentages of the respective taxon within the overall palynoflora; blank spaces indicate the absence of the respective form.

Plate I. Selected dinoflagellate cysts from Toarcian of the Maria Pares and Vale das Fontes sections of the Lusitanian Basin, in west-central 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. *Nannoceratopsis gracilis* Alberti 1961 emend. Evitt 1962. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF10, slide 1, R47/1. Right lateral view. Note the dorsal antapical horn and the microreticulate autophragm.
2. *Nannoceratopsis senex* van Helden 1977. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF2, slide 1, Q57. Right lateral view. Note the single antapical horn and the microreticulate autophragm.
3. *Nannoceratopsis ambonis* Drugg 1978 emend. Riding 1984. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF2, slide 1, Y36/1. Left lateral view. Note the prominent dark sagittal rim and the microreticulate autophragm.
4. *Mendicodinium spinosum* Bucefalo Palliani et al. 1997 subsp. *spinosum* (autonym). Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ26, slide 1, F49/1. Oblique dorsal view. Note the spines and the smooth autophragm.
5. *Mendicodinium microscabratum* Bucefalo Palliani et al. 1997. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ16, slide 1, T36/1. Right lateral view. Note the microscabrate autophragm.
6. *Mendicodinium* sp. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ29, slide 1, M33/3. Oblique left lateral view. Note that this form is larger than most Toarcian specimens of *Mendicodinium*; the width is 40 μm.

7. *Luehndea spinosa* Morgenroth 1970. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF8, slide 1, O24. Mid-ventral view, high focus. Note the prominent cingulum which is interrupted by the sulcus.

8. *Luehndea spinosa* Morgenroth 1970. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF10, slide 1, Y27/3. Dorsal view, high focus. Note the uninterrupted cingulum.

9. *Luehndea spinosa* Morgenroth 1970. Maria Pares section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PZ5, slide 1, O22/2. Oblique dorsal view. Note the antapical (1'''') plate.

10. *Mancodinium semitabulatum* Morgenroth 1970. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ32, slide 1, D42. Oblique ventral-left lateral view. Note the well-preserved precingular plates which are involved in the formation of the 'disintegration' archaeopyle, in which all the epicystal plates are lost, apparently one-by-one. The anterior sulcal plate (the sulcal tongue) is visible; this is clearly not involved in archaeopyle formation.

11. *Mancodinium semitabulatum* Morgenroth 1970. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF1, slide 1, H56/2. Oblique right lateral-ventral view. Note the clearly detached 7'' plate, which is immediately adjacent to the much narrower anterior sulcal plate (sulcal tongue).

12. *Mancodinium semitabulatum* Morgenroth 1970. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ32, slide 1, K39. Slightly oblique dorsal view. Note the anterior sulcal plate (sulcal tongue) and the release of all the epicystal plates during archaeopyle formation.

Plate II. Selected miscellaneous microplanton, pollen and spores from the Toarcian of the Maria Pares and Vale das Fontes sections of the Lusitanian Basin, in west-central 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. *Cyathidites* sp. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ20, slide 1, F50.

2. *Ischyosporites variegatus* (Couper 1958) Schulz 1967. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ19, slide 1, J51.

3. Tetrad of *Kraeuselisporites reissingeri* (Harris 1957) Morbey 1975. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF5, slide 1, E34/3.

4. Tetrad of *Leptolepidites* sp. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF13, slide 1, H28.

5. *Lycopodiacidites rugulatus*(Couper 1958) Schulz 1967. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ19, slide 1, J37/2.

6. *Alisporites* sp. Maria Pares section, Lower Toarcian (*Hildaites levisoni* ammonite biozone), sample PZ15, slide 1, S70/4.

7. *Araucariacites australis* Cookson 1947 ex Couper 1958. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF5, slide 1, O40.

8. *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF1, slide 1, P41.

9. Tetrad of *Classopollis classoides* (Pflug 1953) Pocock & Jansonius 1961. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF2, slide 1, K39/3.

10. *Micrhystridium* sp. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF2, slide 1, E54/3.

11. *Tasmanites* sp. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF10, slide 1, J49/3.

12. Foraminiferal test lining. Vale das Fontes section, Lower Toarcian (*Dactylioceras polymorphum* ammonite biozone), sample PVF7, slide 1, H50.