The Early Jurassic palynostratigraphy of the Lusitanian Basin, western Portugal

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Abstract

A comprehensive investigation of the Early Jurassic stratigraphical palynology of the Lusitanian Basin in western Portugal was undertaken, with most emphasis placed on dinoflagellate cysts. A total of 214 samples, from an upper Sinemurian to upper Toarcian composite section based on six successions, were examined. The Sinemurian material examined was barren of dinoflagellate cysts, however the Pliensbachian and Toarcian successions are characterised by relatively low diversities. *Luehndea spinosa, Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Nannoceratopsis gracilis, Nannoceratopsis senex* and *Scriniocassis priscus* were relatively common, and are biostratigraphically significant. *Luehndea spinosa* dominates the lowermost

Toarcian (*Dactylioceras polymorphum* ammonite Biozone), and is an index species. At the base of *Hildaites levisoni* ammonite Biozone, the effects of the Toarcian-Oceanic Anoxic Event (T-OAE) caused *Luehndea spinosa* to become extinct. At the same time, dinoflagellate cyst abundance and diversity markedly decreased. After the T-OAE, during the middle and late Toarcian, phytoplankton recovery was prolonged and slow in the Lusitanian Basin. The *Luehndea spinosa* and *Mendicodinium microscabratum* dinoflagellate cyst biozones were defined, both of which are subdivided into two dinoflagellate cyst subbiozones.

Keywords: biostratigraphy, palynomorphs, dinoflagellate cysts, Lower Jurassic, Lusitanian Basin, Portugal.

1. Introduction

The Lusitanian Basin of central western Portugal is an important Mesozoic depocentre, and the calcareous microfossil biostratigraphy of the Lower Jurassic succession has been well studied recently (e.g., Perilli and Duarte, 2006; Oliveira et al., 2007a; Pinto, 2008; Reggiani et al., 2010; Henriques and Canales, 2013; Mattioli et al., 2013; Cabral et al., 2014, 2015; Henriques et al., 2014; Ferreira et al., 2015; Rita et al., 2016). By contrast, the Jurassic palynology of this significant sedimentary basin has received relatively little attention. Previous studies on the Jurassic palynobiotas 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. (2007b), Barrón et al. (2013) and Correia et al. (2017a,b). Davies (1985) is a reconnaissance biostratigraphical study, and Oliveira et al. (2007b) and Barrón et al. (2013) are mainly on pollen and spores. Correia et al.

(2017a,b) discussed the palynology of the uppermost Pliensbachian to middle Toarcian interval at Maria Pares, Peniche and Vale das Fontes.

The present contribution is a detailed study of the Lower Jurassic palynology of key Sinemurian, Pliensbachian and Toarcian reference sections in the Lusitanian Basin (e.g., Duarte, 2007; Duarte et al., 2014b), with emphasis on dinoflagellate cysts because they are of the greatest regional biostratigraphical significance (Riding and Thomas, 1992; Poulsen and Riding, 2003). Specifically, the main aims are to document the upper Sinemurian to upper Toarcian palynomorphs from São Pedro de Moel, Brenha, Peniche, Fonte Coberta, Maria Pares and Vale das Fontes (Fig. 1), and to erect a dinoflagellate cyst biozonation.

2. Geological background

The Lusitanian Basin is a marginal marine depocentre 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 (Kullberg et al., 2013). The origin and evolution of this sedimentary basin are related to the breakup of Pangaea and the opening of the North Atlantic Ocean. The fill is mainly Jurassic but ranges from Middle? –Upper Triassic to Upper Cretaceous, and comprises four first order sedimentary cycles (Wilson et al., 1989). A clear Atlantic influence is evident from the ammonite faunas throughout most of the Lower Jurassic succession of the Lusitanian Basin (Mouterde et al., 1979). However, mixed Boreal and Tethyan faunas in the upper Pliensbachian to Toarcian interval indicate intermittent communication between the two realms (Elmi et al., 1989; Terrinha et al., 2002).

The lithostratigraphy of the Lower Jurassic of the Lusitanian Basin is summarised in Fig. 2. During the Early Jurassic, marine carbonate ramps formed rapidly in the

Lusitanian Basin (Soares et al., 1993; Azerêdo et al., 2003, 2014; Duarte, 2007). The upper Sinemurian, especially in the western area, at Figueira da Foz, Peniche and São Pedro de Moel, mainly comprises marl-limestone couplets with ammonite-bearing black shales of the Água de Madeiros Formation (Duarte et al., 2010, 2012). The type section is at São Pedro de Moel in the central western part of the basin (Fig 1; Duarte and Soares, 2002; Duarte et al., 2014a,b). The overlying Pliensbachian and Toarcian hemipelagic deposits are rich in benthic and nektonic faunas; these are the Vale das Fontes, Lemede, São Gião, base of Cabo Carvoeiro and Póvoa da Lomba formations (Fig. 2; e.g., Duarte and Soares, 2002; Duarte et al., 2001, 2010, 2014b; Duarte, 2007). The Vale das Fontes Formation is Pliensbachian in age, ranges from the *Uptonia jamesoni* to *Amaltheus margaritatus* ammonite biozones and is subdivided into three informal members, the last one particularly enriched in organic mater (e.g., Silva et al., 2015; Silva and Duarte, 2015; Fig. 2). The succeeding Lemede Formation is upper Pliensbachian to lowermost Toarcian and spans the upper *Amaltheus margaritatus* to the lower *Dactylioceras polymorphum* ammonite biozones. The Toarcian of the Lusitanian Basin largely comprises the São Gião Formation, that spans the *Dactylioceras polymorphum* to the lower *Dumortieria meneghinni* ammonite biozones, and is subdivided into five informal members (Fig. 2; Duarte and Soares, 2002; Duarte, 2007). The type section of the São Gião Formation is at Maria Pares in the northern part of the Lusitanian Basin (Fig. 1). This locality exposes a continuous ammonite-bearing upper Pliensbachian to Aalenian succession (Mouterde et al., 1964-65; Henriques, 1992, 1995).

At Peniche, in the southwest of the Lusitanian Basin, a thick succession of Pliensbachian limestone-marl alternations overlain by the Toarcian Cabo Carvoeiro Formation which comprises at the top ooidal limestone-siliciclastic interbeds (Wright and Wilson, 1984; Duarte, 1997; Duarte et al., 2017). The type sections of the Vale das Fontes and Lemede formations are at Peniche, and this succession was recently formalised as the Toarcian Global Stratotype Section and Point (GSSP) (Rocha et al., 2016).

3. Material and methods

In this work, 214 samples collected from six Lower Jurassic successions in the Lusitanian Basin were analysed, involving the lithostratigraphical units described above. The loclities are São Pedro de Moel, Brenha, Peniche, Fonte Coberta, Maria Pares and Vale das Fontes (Figs. 1–9; Correia et al., 2017a,b). Twelve samples (prefixed PM) were collected from the upper Sinemurian Polvoeira Member of the Água de Madeiros Formation at Polvoeira, which forms the lowest part of the São Pedro de Moel composite section (Fig. 3). Herein, we refer to this section as “São Pedro de Moel”, although the succession studied corresponds to the Polvoeira section of Duarte et al. (2012, 2014a). At Brenha, 22 samples were taken from a Pliensbachian composite section. The lower part of this section comprises the Vale das Fontes Formation (samples prefixed Br), and the upper part is the Lemede Formation (samples prefixed BrLem). The succession between these two formations is not continuous (Figs 2, 4). These two lithostratigraphical units and the Cabo Carvoeiro Formation were also sampled at Peniche, where 72 samples (numbered P-34 to P38) were collected (Fig. 5; Correia et al., 2017b). At Fonte Coberta, in the Rabaçal area, five samples (prefixed FC) from the upper Pliensbachian Vale das Fontes and Lemede formations were collected (Fig. 6). The section at Maria Pares comprises the lower, middle and upper Toarcian São Gião and Póvoa da Lomba formations. Eighty-nine samples (numbered PZ1 to PZ89) were collected (Figs. 7–9; Correia et al., 2017a). The type section of the São

Gião Formation is at Maria Pares, and the lower Toarcian was previously studied by Correia et al. (2017a). The latter authors also examined 14 samples (numbered PVF1 to PVF14) from the lower Toarcian part of the São Gião Formation at Vale das Fontes (Correia et al., 2017a, fig. 5).

The samples were all prepared using standard palynological techniques (Wood et al., 1996), but the organic residues were not oxidised. All the residues were sieved using a 15 µm mesh. The palynomorph concentrates were stained with Safranin to enhance the visibility of morphological features. 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. Palynological results

4.1. Introduction

In this section, new reports on the Lower Jurassic palynofloras of the five sections studied are described. The data from 14 samples from the São Gião Formation at Vale das Fontes section were included in Correia et al. (2017a). The data presented by Correia et al. (2017a,b) on Maria Pares and Peniche are also considered here. Most emphasis is placed on the dinoflagellate cysts, due their biostratigraphical significance. Selected palynomorphs are figured in Figs. 10–12. The overall percentages of all taxa from each section are depicted in supplementary Tables 1–5, and the relative abundances of the six main palynomorph groups are plotted in supplementary Figures 1–5. The palynomorph taxa that were recorded herein, or mentioned in the text, are listed in the Appendix.

4.2. São Pedro de Moel

Twelve samples, PM1 to PM12, were studied from the upper Sinemurian Polvoeira Member of the Água de Madeiros Formation at São Pedro de Moel area. These horizons span the *Oxynoticeras oxynotum* and *Echioceras raricostatum* ammonite biozones (Figs. 2, 3). All the 12 samples proved productive, but the palynomorphs were generally poorly preserved and no dinoflagellate cysts were observed. The assemblages are low in diversity and are dominated (normally >95%) by the gymnosperm pollen *Classopollis classoides* (Fig. 12/6). The prasinophyte genus *Tasmanites* (Fig. 12/4) is present throughout, reaching 19% of the palynoflora in PM12. Other palynomorphs are present in low abundances and include acritarchs (*Micrhystridium* spp.), foraminiferal test linings, pollen (*Alisporites* spp. and *Cerebropollenites macroverrucosus*) and spores (*Cyathidites* spp. and *Kraeuselisporites reissingeri*) (supplementary Fig. 1; supplementary Table 1).

4.3. Brenha

The Lower Jurassic composite section at Brenha spans the Pliensbachian, and all five ammonite biozones are represented (Fig. 4). Twenty two samples (Br 1–20 and BrLem 1 and 2) were collected, and all except Br6 proved to be palynologically productive. The palynomorph assemblages are moderately well preserved, and exhibit higher diversites than the Sinemurian of São Pedro de Moel (supplementary Tables 1, 2).

Three dinoflagellate cyst species were encountered in the upper Pliensbachian; these are *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex* (Figs. 4, 10, 11). These species are present in both the *Amaltheus margaritatus* and the *Emaciaticeras emaciatum* ammonite biozones, corresponding to the MLOF member of the Vale das Fontes Formation, and the middle part of the Lemede Formation. *Luehndea spinosa* was not found in this succession. Dinoflagellate cysts in samples Br14 to Br20, within the *Amaltheus margaritatus* ammonite Biozone, are present in very low proportions, dominantly less than 1% of the palynoflora. However, the relative proportions of dinoflagellate cysts increased markedly in the Lemede Formation (*Emaciaticeras emaciatum* ammonite Biozone). All three species are present in significant numbers in samples BrLem1 and BrLem2; they represent 22.5% of the overall palynoflora in the latter sample (supplementary Table 2).

Other marine palynomorphs present at Brenha comprise foraminiferal test linings, *Halosphaeropsis liassica,* indeterminate acritarchs and prasinophytes, *Micrhystridium* spp., and *Tasmanites* spp. Foraminiferal test linings were only present in the upper Pliensbachian succession. However overall, these miscellaneous marine palynomorphs, like the dinoflagellate cysts, are most common in the *Emaciaticeras emaciatum* ammonite Biozone. Clearly, samples BrLem1 and BrLem2 exhibit the greatest marine influence in this succession (supplementary Fig. 2; supplementary Table 2).

The pollen grain *Classopollis classoides* is the most abundant palynomorph species throughout, with relative abundances between 27.0% and 94.5%. The bisaccate pollen genus *Alisporites* is also sporadically common, and other pollen present, normally in low proportions, are *Araucariacites australis*, *Cerebropollenites macroverrucosus* and *Spheripollenites* spp. The spores *Cyathidites* spp. and *Kraeuselisporites reissingeri,* together with indeterminate forms, are present throughout the succession. *Leptolepidites rotundus* and *Lycopodiacidites rugulatus* were sporadically identified in the upper Pliensbachian samples (supplementary Table 2).

4.4. The Pliensbachian and lower Toarcian succession at Peniche

A total of 72 samples were collected from the lower Pliensbachian to lower Toarcian (*Tragophylloceras ibex* to *Hildaites levisoni* ammonite biozones) succession at Peniche (Fig. 1; supplementary Table 3). These were studied herein, and by Correia et al. (2017b). Twenty-seven samples, P-34 to P-8, were collected from the Pliensbachian Vale das Fontes and Lemede formations (Figs. 2, 5). Correia et al. (2017b) reported on 45 samples (P-7 to P38), from the overlying uppermost Lemede Formation and the lowermost Cabo Carvoeiro Formation (uppermost Pliensbachian–lower Toarcian). Fourteen samples from the upper Pliensbachian and lower Toarcian succession proved entirely devoid of palynomorphs (supplementary Table 3). The remaining 58 samples yielded reasonably abundant palynomorph assemblages which are moderately well preserved.

Eight forms of dinoflagellate cyst were recognised. The most stratigraphically extensive species are *Luehndea spinosa*, *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex*. *Mendicodiniuim microscabratum*, *Nannoceratopsis ambonis*, *Nannoceratopsis* sp. and *Scriniocassis weberi* occurred sporadically, and in low numbers (Figs. 5, 10, 11; supplementary Table 3). In the Pliensbachian part of this succession, between the upper *Prodactylioceras davoei* to lowermost *Emaciaticeras emaciatum* ammonite biozones (samples P-29 to P-13,) dinoflagellate cysts are especially sparse and comprise only *Luehndea spinosa*, *Mancodinium semitabulatum*, *Nannoceratopsis senex* and *Nannoceratopsis* sp. (supplementary Fig. 3). The latter form represents a single specimen found in sample P-20 in the *Amaltheus margaritatus* ammonite Biozone. It has two subequal antapical horns, and does not precisely conform to any of the formalised species of this genus (Fig. 10/4). The lowermost occurrence of *Mancodinium semitabulatum* is at the top of *Prodactylioceras davoei* ammonite

Biozone, in sample P-29, where it is relatively sparse. *Luehndea spinosa* is only present, again in very low proportions, in samples P-26 and P-23 from the *Amaltheus margaritatus* ammonite Biozone. Stratigraphically above these records, *Mancodinium semitabulatum,* reappeared in the *Emaciaticeras emaciatum* ammonite Biozone (samples P-12 to P-10) in significantly greater proportions, up to 5.9% of the overall palynoflora. A similar occurrence pattern was exhibited by *Nannoceratopsis senex*. This species is rare in the *Amaltheus margaritatus* ammonite Biozone (samples P-28 to P-21), and became more frequent in the *Emaciaticeras emaciatum* ammonite Biozone (samples P-12 and P-10).

Therefore, the consistent occurrence of relatively common *Mancodinium semitabulatum* is in sample P-12. From this horizon in the *Emaciaticeras emaciatum* ammonite Biozone to the top of *Dactylioceras polymorphum* ammonite Biozone (sample P14; see Table 3), dinoflagellate cysts are abundant to common. *Luehndea spinosa* has two prominent acmes in the *Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ammonite biozones (Correia et al., 2017b). *Mancodinium semitabulatum* is also common at the *Emaciaticeras emaciatum-Dactylioceras polymorphum* ammonite Biozone transition. *Nannoceratopsis* spp. were also prominent in sample P6 in the *Dactylioceras polymorphum* ammonite Biozone (supplementary Table 3). In the Lusitanian Basin, the beginning of the Toarcian Oceanic Anoxic Event (T-OAE) corresponds to the base of *Hildaites levisoni* ammonite Biozone (Hesselbo et al., 2007; Suan et al., 2008; Pittet et al., 2014; Correia et al., 2017a,b). This anoxic event (samples P15 to P24) badly affected the dinoflagellates due to profound benthic palaeoenvironmental stress (Correia et al., 2017b), and the assemblages had not recovered at the level of sample P38 in the *Hildaites levisoni* ammonite Biozone. The only survivors were sparse and sporadic *Mancodinium semitabulatum* and *Mendicodiniuim microscabratum* (supplementary Table 3).

Miscellaneous marine palynomorphs were recorded throughout this succession. They include acritarchs (indeterminate forms, *Micrhystridium* spp. and *Polygonium jurassicum*), foraminiferal test linings and prasinophytes (*Cymatiosphaera* sp. cf. *C. pachytheca, Halosphaeropsis liassica*, indeterminate forms and *Tasmanites* spp.). Generally, these occurrences are in small proportions (<1–2% of the palynoflora); foraminiferal test linings and *Tasmanites* spp are the most consistently observed (supplementary Fig. 3; supplementary Table 3). Foraminiferal test linings and *Tasmanites* spp. are sporadically relatively frequent between samples P-32 and P-26 (*Tragophylloceras ibex* to *Amaltheus margaritatus* ammonite biozones), and in the productive part of the *Emaciaticeras emaciatum* ammonite Biozone (samples P-12 to P-10) (supplementary Table 3). The interval between samples P-25 and P-7 is relatively sparse in miscellaneous microplankton. Unlike dinoflagellate cysts, miscellaneous microplankton are present in relatively moderate proportons in the T-OAE interval (samples P15 to P24). Foraminiferal test linings are most prominent in this interval, and these dominate the palynobiotas above the T-OAE. In sample P36, these palynomorphs attain 71.9% of the assemblage (supplementary Table 3).

All the palynologically productive samples yielded terrestrially-derived palynomorphs in substantial proportions. The pollen grains *Alisporites* spp., *Araucariacites australis*, *Cerebropollenites macroverrucosus, Classopollis classoides, Exesipollenites* spp. and *Spheripollenites* spp. were recognised. *Classopollis classoides* is normally the most abundant palynomorph below sample P5 in the lowermost Toarcian, with overall percentages up to 97.4% in sample P-21. The bisaccate genus *Alisporites* was relatively frequent in the upper Pliensbachian. Most pollen declined at the T-OAE, however *Exesipollenites* spp. and *Spheripollenites* spp. are more frequent in this succession than below the T-OAE (supplementary Table 3). Pteridophyte spores were recorded in relatively low numbers throughout the succession. *Cyathidites* spp., indeterminate spores, *Kraeuselisporites reissingeri* and *Leptolepidites* spp. were the most consistently present. Other forms were encountered rarely; these include *Concavisporites granulosus*, *Ischyosporites vaerigatus*, *Lycopodiacidites rugulatus* and *Plicifera delicata*. Unlike most pollen taxa, spores generally were slightly more frequent during the T-OAE and above it (supplementary Fig. 3; supplementary Table 3).

4.5. Fonte Coberta

Five palynologically productive samples, FC1 to FC5, were collected from the upper Pliensbachian section at Fonte Coberta, near Rabaçal in the northern part of the Lusitanian Basin (Fig. 1, supplementary Table 4). The samples are from the top of the Vale das Fontes and Lemede formations, and span the *Amaltheus margaritatus* and *Emaciaticeras emaciatum* ammonite biozones (Figs. 2, 6).

The palynomorphs from Fonte Coberta are of low diversity and are moderately well preserved. Three dinoflagellate cysts, *Luehndea spinosa*, *Mancodinium semitabulatum* and *Nannoceratopsis senex,* were identified (Figs. 6, 10). The latter occurred in low numbers throughout the succession. By contrast, *Mancodinium semitabulatum* and *Luehndea spinosa* are confined to the *Emaciaticeras emaciatum* ammonite Biozone. The former was recorded in low proportions, but *Luehndea spinosa* was the most abundant palynomorph in samples FC3 (85.2%) and FC5 (62.4%) (supplementary Fig. 4; supplementary Table 4). This abundance of *Luehndea spinosa* at the Pliensbachian-Toarcian transition in the Lusitanian Basin was also observed by Correia et al. (2017a,b).

Miscellaneous marine palynomorphs are present in relatively low numbers in all the samples except FC4. These comprise acritarchs (indeterminate forms and *Micrhystridium* spp.), foraminiferal test linings and prasinophytes (indeterminate forms and *Tasmanites* spp.). The most significant occurrence is the relatively high levels of foraminiferal test linings in the *Emaciaticeras emaciatum* ammonite Biozone (supplementary Table 4).

In samples FC1, FC2 and FC4, by the most abundant palynomorph was the pollen grain *Classopollis classoides*; it is also abundant in FC5. It represented >90% of the palynoflora in samples FC1 and FC4. There is an apparently inverse relationship between the abundances of *Classopollis classoides* and the dinoflagellate cyst *Luehndea spinosa* (supplementary Fig. 4; supplementary Table 4). Other pollen grains present in low proportions are *Alisporites* spp., *Araucariacites australis* and *Cerebropollenites macroverrucosus.* The spores recorded were *Cyathidites* spp., indeterminate forms and *Kraeuselisporites reissingeri* (supplementary Table 4).

4.6. The lower to upper Toarcian succession at Maria Pares

Eighty nine samples were taken from the lower, middle and upper Toarcian at Maria Pares, in the Rabaçal area of the eastern sector of the basin (Fig. 1, supplementary Table 5). This material is from the São Gião and Póvoa da Lomba formations, and the samples span the *Dactylioceras polymorphum* to the *Pleydellia aalensis* ammonite biozones (Figs. 2, 7–9). This material was studied herein, and also by Correia et al. (2017a) who reported on the lowermost 54 samples PZ-1 to PZ54 from the São Gião Formation (lower and middle Toarcian). The overlying 35 samples PZ55 to PZ89, from the middle and upper Toarcian were part of this study only. All but five of the samples proved palynologically productive, with moderately well presered palynobiotas. Three samples from the upper Toarcian *Pleydellia aalensis* ammonite Biozone proved entirely devoid of palynomorphs (supplementary Table 5).

Thirteen dinoflagellate cyst forms were identified. These are: *Dapsilidinium*? *deflandrei*; *Luehndea spinosa*; *Mancodinium semitabulatum*; ?*Maturodinium inornatum*; *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum*; *Mendicodinium* sp.; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis;* *Nannoceratopsis senex*; *Scriniocassis priscus*; *Sentusidinium* sp.; and *Valvaeodinium* sp. (Figs. 10, 11; supplementary Table 5). As in other sections, the most consistently occurring dinoflagellate cyst throughout is *Mancodinium semitabulatum,* the range top of which is in the *Dumortieria meneghinii* ammonite Biozone. *Luehndea spinosa* is dominant in the upper part of the *Dactylioceras polymorphum* ammonite Biozone. *Mancodinium semitabulatum* is also common in this ammonite biozone and around the lower-middle Toarcian transition (samples PZ27 and PZ51; see supplementary Table 5). The range base of consistent *Mendicodinium microscabratum* and *Scriniocassis priscus* is PZ554 in the *Hildoceras bifrons* ammonite Biozone. The stratigraphically highest record of *Scriniocassis priscus* is in the *Hammatoceras speciosum* ammonite Biozone. The maximum abundance of *Mendicodinium microscabratum* is 27.3% in sample PZ56 in the *Hildoceras bifrons* ammonite Biozone, with the stratigraphically highest record in *Hammatoceras speciosum* ammonite Biozone. *Nannoceratopsis* spp. did not recover following the T-OAE, but *Nannoceratopsis senex* is sporadically present in the *Dumortieria meneghinii* and *Pleydellia aalensis* ammonite biozones. In the *Pleydellia aalensis* ammonite Biozone, *Nannoceratopsis senex* was the only dinoflagellate cyst species present, with 10.3% of the overall palynoflora in sample PZ88. *Dapsilidinium*? *deflandrei,* ?*Maturodinium inornatum*, *Mendicodinium spinosum* subsp. *spinosum,* *Mendicodinium* sp., *Nannoceratopsis ambonis, Sentusidinium* sp. and *Valvaeodinium* sp. were extremely rare (supplementary Table 5). For example, only one and two specimens each respectively of *Dapsilidinium*? *deflandrei* (samples PZ57) and ?*Maturodinium inornatum* (samples PZ58 and PZ77) were encountered (supplementary Table 5).

Other marine palynomorphs encountered throughout this succession were foraminiferal test linings, *Halosphaeropsis liassica,* indeterminate acritarchs and prasinophytes, *Micrhystridium* spp. and *Tasmanites* spp. These palynomorphs were dominated by acanthomorph acritarchs, foraminiferal test linings and prasinophytes. Indeterminate acritarchs and *Micrhystridium* spp. are normally most prevalent in the lower and lowermost middle Toarcian, and foraminiferal test linings and indeterminate prasinophytes are most abundant in the upper Toarcian samples (supplementary Fig. 5). Clumps of *Halosphaeropsis liassica* increased their abundance from the *Hildaites levisoni* ammonite Biozone (sample PZ9, 89.7%, see supplementary Table 5; supplementary Fig. 5).

All the palyniferous samples produced pollen-spore floras in significant numbers. The pollen comprises *Alisporites* spp., *Araucariacites australis*, *Callialasporites dampieri, Callialasporites turbatus*, *Cerebropollenites macroverrucosus, Classopollis classoides, Classopollis* sp., *Cycadopites* sp. *Exesipollenites* spp., *Inaperturopollenites* sp., indeterminate forms and *Spheripollenites* spp. The diversity is greatest in the uppermost middle and upper Toarcian, and the dominant and consistent elements are *Alisporites* spp., *Araucariacites australis* and *Classopollis classoides* (supplementary Table 5). The latter is present throughout, and is the most abundant species, reaching a maximum of 50% of the palynoflora in sample PZ85 (*Dumortieria meneghinii* ammonite Biozone). The range top of *Araucariacites australis,* and the inception of *Callialasporites* spp., are in the middle Toarcian

(*Brodiela gradata* ammonite Biozone). The spores were relatively high in diversity, but only *Cyathidites* spp., indeterminate spores, *Ischyosporites variegatus* and *Leptolepidites spp.* were consistent and relatively frequent.

5. Discussion of the Lower Jurassic palynofloras of the Lusitanian Basin

5.1. Introduction

In this section, the palynological data outlined in section 4 are discussed and interpreted, primarily in terms of their biostratigraphical significance. A biostratigraphical scheme for the Pliensbachian and Toarcian of the Lusitanian Basin based on key dinoflagellate cysts bioevents is presented as Figure 13, and a formal biozonation is outlined in section 6.

5.2. Upper Sinemurian palynology

The upper Sinemurian succession at São Pedro de Moel proved entirely devoid of dinoflagellate cysts, confirming the findings of Duarte et al. (2012) and Poças Ribeiro et al. (2013). The late Sinemurian marker dinoflagellate cyst *Liasidium variabile* was not recovered. This distinctive species is characteristic of the upper Sinemurian of northwest Europe, and is a proven thermophilic taxon (Riding and Hubbard, 1999; Brittain et al., 2010; Riding et al., 2013). *Liasidium variabile* thrived, and *Classopollis classoides* was extremely abundant, during a brief palaeoenvironmental perturbation in the late Sinemurian (~194 Ma) of northwest Europe. This was characterised by a significant oceanic and atmospheric injection of isotopically-light carbon, global warming and organic shale deposition (Riding et al., 2013). Organic-rich facies, resulting from anoxic/dysoxic intervals, occurred during the late Sinemurian in the western sectors of the Lusitanian Basin (Duarte et al., 2010, 2012; Boussaha et al., 2014; Plancq et al., 2016). *Classopollis classoides* was extremely abundant in the upper Sinemurian of São Pedro de Moel, and this represents the acme for the entire sucesson examined (supplementary Tables 1–5). The absence of *Liasidium variabile* at São Pedro de Moel may indicate that this species had specific palaeoenvironmental preferences, and did not migrate south of ~30° latitude at this time (Riding et al., 2013, fig. 1).

5.3. Pliensbachian and Toarcian palynology

The five Pliensbachian and Toarcian successions studied herein, and by Correia et al. (2017a,b), are Brenha, Peniche, Fonte Coberta, Maria Pares and Vale das Fontes (Figs. 1–9); all these sections produced dinoflagellate cyst assemblages. Fifteen forms were recorded; these are: *Dapsilidinium*? *deflandrei*; *Luehndea spinosa*; *Mancodinium semitabulatum*; ?*Maturodinium inornatum*; *Mendicodinium microscabratum*; *Mendicodinium spinosum* subsp. *spinosum*; *Mendicodinium* sp.; *Nannoceratopsis ambonis*; *Nannoceratopsis gracilis*; *Nannoceratopsis senex*; *Nannoceratopsis* sp.; *Scriniocassis priscus*; *Scriniocassis weberi*; *Sentusidinium* sp.; and *Valvaeodinium* sp. (supplementary Tables 1–5).

Other aquatic palynomorphs observed comprise acanthomorph acritarchs, foraminiferal test linings and prasinophytes (supplementary Tables 1–5; Correia et al., 2017a,b). Pollen and spores are also present in relatively high relative proportions. The gymnospermous pollen species *Classopollis classoides* is the most abundant terrestrially-derived palynomorph in the Lower Jurassic of the Lusitanian Basin. Other pollen taxa present in significant numbers are *Alisporites* spp., *Araucariacites australis* and *Cerebropollenites macroverrucosus*. The spores *Cyathidites* spp., *Ischyosporites* *variegatus*, *Leptolepidites* spp. and *Kraeuselisporites reissingeri* were also frequently encountered throughout. The miscellaneous marine microplankton, pollen and spores are relatively conservative in their occurrences through this composite Sinemurian to Toarcian succession, and are consistent with an Early Jurassic age (Srivastava, 1987; 2011; Weiss, 1989; Ziaja, 2006; Quattrocchio et al., 2011; Bomfleur et al., 2014).

These relative low diversity dinoflagellate cyst assemblages are broadly typical of upper Pliensbachian to Toarcian successions throughout Europe and adjacent areas (Riding, 1984a; Riding et al., 1991; 1999; Koppelhus and Nielsen, 1994; Bucefalo Palliani and Riding, 1997a,b; 1999a; 2000; 2003; Baranyi et al., 2016). Furthermore, the dinoflagellate cyst association reported herein is consistent with previous research on the Lower Jurassic palynology of the Lusitanian Basin (Davies, 1985; Oliveira et al., 2007b; Barrón et al., 2013). For example, Davies (1985), Oliveira et al. (2007a) and Barrón et al. (2013) also recorded *Luehndea spinosa, Mancodinium semitabulatum*, *Mendicodinium* sp., *Nannoceratopsis senex*, *Nannoceratopsis gracilis, Nannoceratopsis* sp. *Scriniocassis weberi* and *Scriniocassis priscus* from this area.

The dinoflagellate cyst diversity in the upper Pliensbachian of the Lusitanian Basin is relatively low, with only *Luehndea spinosa*, *Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Nannoceratopsis senex*, *Nannoceratopsis gracilis* and *Nannoceratopsis* sp. present. In terms of abundances, dinoflagellate cysts are relatively rare in the *Amaltheus margaritatus* ammonite Biozone, but increased markedly within the *Emaciaticeras emaciatum* ammonite Biozone (supplementary Tables 2, 3). Both abundances and diversity increased in the earliest Toarcian *Dactylioceras polymorphum* ammonite Biozone. *Luehndea spinosa* dominates the palynofloras at the Pliensbachian–Toarcian transition (upper *Emaciaticeras emaciatum* and lower *Dactylioceras polymorphum* ammonite biozones), at Peniche, Fonte Coberta, Maria Pares and Vale das Fontes (Fig. 6; supplementary Tables 3–5; Correia et al., 2017a,b). For example, this species attained a maximum of 96.2% of the overall palynoflora in sample P11 at Peniche (supplementary Table 3). At Peniche, Maria Pares and Vale das Fontes, the abundance curves of *Luehndea spinosa* in the *Dactylioceras polymorphum* ammonite Biozone exhibit a characteristic double peak signature (Correia et al., 2017a,b). These acmes may reflect pulses of an early Toarcian transgressive event prior to the start of the T-OAE in the lowermost *Hildaites levisoni* ammonite Biozone (Duarte et al., 2004, 2007; Pittet et al., 2014).

The Toarcian dinoflagellate cyst assemblages above the base of *Hildaites levisoni* ammonite Biozone are dominated by *Mancodinium semitabulatum* and *Mendicodinium* spp. During the Toarcian, *Dapsilidinium*? *deflandrei,* ?*Maturodinium inornatum*, *Mendicodinium spinosum* subsp. *spinosum*, *Mendicodinium* sp., *Nannoceratopsis ambonis*, *Scriniocassis priscus, Scriniocassis weberi, Sentusidinium* sp. and *Valvaeodinium* sp. had their inceptions (supplementary Tables 3, 5). Despite the somewhat moderate increase in diversity in the Toarcian, above the *Dactylioceras polymorphum* ammonite Biozone, overall dinoflagellate cyst abundances markedly reduced due to the palaeoenvironmental perturbations caused by the T-OAE and the recovery from this event (Correia et al., 2017a,b). Only *Mancodinium semitabulatum* is consistently relatively common. *Mendicodinium microscabratum* and *Nannoceratopsis senex* were only sporadically present in reasonable proportions, and other forms were extremely rare (supplementary Tables 3, 5).

Hence the recovery of dinoflagellates after the T-OAE at Maria Pares and Peniche was extremely slow and somewhat indistinct (supplementary Tables 3, 5). A good example is the reappearance of *Nannoceratopsis senex* following the T-OAE. In northwest Europe, this species was typically suppressed only for part of the *Harpoceras* *exaratum* ammonite Subbiozone of the *Harpoceras serpentinum* ammonite Biozone in the early Toarcian (Bucefalo Palliani and Riding, 2000, fig. 3; Bucefalo Palliani et al., 2002, figs. 3, 13). In northern Siberia, this species was apparently unaffected by the T-OAE (Riding et al., 1999, fig. 11). By contrast, in the Lusitanian Basin, *Nannoceratopsis senex* reappeared in the late Toarcian (*Dumortieria meneghinnii* ammonite Biozone, supplementary Table 5). This slow dinoflagellate recovery in southern Europe was also illustrated by Correia et al. (2017a, fig. 10). The apparently unaffected dinoflagellate cyst associations of the high northerly latitudes and a slow recovery in southern Europe, with an intermediate region (northwest Europe) intercalated between these, appears to be a coherent trend. Despite intense Early Toarcian anoxia in northwest Europe, the palaeoenvironment in Italy and Portugal was far slower to recovery (Bucefalo Palliani et al., 2002; van de Schootbrugge et al., 2005; Jenkyns et al., 2010; Correia et al., 2017a,b). This may have been linked to the reestablishment of marine circulation patterns at this time.

In northwest Europe and in the Boreal Realm, part of the dinoflagellate recovery following the T-OAE in the mid Toarcian to earliest Aalenian is a minor radiation of a plexus of small genera placed in the Family Heterocapsaceae and termed the '*Parvocysta* complex' (Riding, 1984a; Riding et al., 1991; 1999; Butler et al., 2005; Feist-Burkhardt and Pross, 2010). This association is absent throughout the Lusitanian Basin, where the only significant dinoflagellate cyst inceptions in the middle Toarcian are those of *Mendicodinium microscabratum* and *Scriniocassis priscus* (Fig. 13). Furthermore, typical Tethyan species, such as *Mendicodinium brunneum*, *Mendicodinium umbriense*, *Umbriadinium mediterraneense* and *Valvaeodinium hirsutum* are also absent in central western Portugal (Bucefalo Palliani and Riding, 1997a, c; 1999a,b; 2003; Bucefalo Palliani et al., 1997a).

5.4. Pliensbachian and Toarcian palynomorph biostratigraphy of the Lusitanian Basin

In this subsection, the biostratigraphical significance of the principal palynomorphs, with the emphasis on dinoflagellate cyst taxa, are discussed. *Dapsilidinium*? *deflandrei* was found in the *Hildoceras bifrons* ammonite Biozone at Maria Pares (supplementary Table 5). This species is very rare in the Middle Jurassic of northwest Europe (Valensi, 1947; Davey and Riley, 1978), and this is the first report from the Early Jurassic.

Luehndea spinosa ranges from the upper Pliensbachian to the lowermost Toarcian (*Amaltheus margaritatus* to *Dactylioceras polymorphum* ammonite biozones) in the Lusitanian Basin (Fig. 13). This range is consistent with the extent of this distinctive and widespread species in Europe and elsewhere (Morgenroth, 1970; Riding, 1987; Bucefalo Palliani and Riding, 1997a,b; 2000; 2003; Bucefalo Palliani et al., 1997b). The range base of *Luehndea spinosa* in the Lusitanian Basin is represented by sparse and sporadic occurrences close to the base of the *Amaltheus margaritatus* ammonite Biozone at Peniche (Fig. 5; supplementary Table 3). These occurrences of *Luehndea spinosa* in the *Amaltheus margaritatus* ammonite Biozone, together with *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex,* confirms the late Pliensbachian age of the uppermost MLOF member of the Vale das Fontes Formation. *Luehndea spinosa* was not recorded in the coeval strata at Brenha (Fig. 4), possibly because the Brenha section is more proximal than Peniche (Fig. 1). *Luehndea cirilliae* is present in the upper Pliensbachian and lower Toarcian of Hungary (Baldanza et al., 1995; Bucefalo Palliani et al., 1997b; Baranyi et al., 2016). This species was also reported in the Pliensbachian of Brenha by Bucefalo Palliani and Riding (2003), but this taxon was not found in this study, or by Correia et al. (2017a,b).

Mancodinum semitabulatum (Fig. 11/9–12) is present in the Pliensbachian-Toarcian successions at Brenha, Peniche, Fonte Coberta, Maria Pares and Vale das Fontes (supplementary Tables 2–5; Correia et al., 2017a). This species has a consistent range of late Pliensbachian to early Bajocian (Riding, 1984b; Feist Burkhardt and Wille 1992; Riding and Thomas 1992; Wiggan et al., 2017). The stratigraphically lowest record of *Mancodinum semitabulatum* in the Lusitanian Basin is at the top of *Prodactylioceras davoei* ammonite Biozone at Peniche (sample P-29, see Fig. 5; supplementary Table 3). At Brenha, *Mancodinum semitabulatum* was identified at the base of the *Amaltheus margaritatus* ammonite Biozone, in the MLOF member of the Vale das Fontes Formation (Fig. 4; supplementary Table 2). This species became much more common and consistent in the uppermost Pliensbachian and lowermost Toarcian (*Emaciaticeras emaciatum* and *Dactylioceras polymorphum* ammonite biozones) throughout the Lusitanian Basin (supplementary Tables 2, 3; Correia et al., 2017a,b). *Mancodinum semitabulatum* was significantly suppressed by the T-OAE, and is sparse for the remainder of the Toarcian in the Lusitanian Basin, between the *Hildaites levisoni* and the *Dumortieria meneghinii* ammonite biozones (Fig. 13; supplementary Table 5). Rare, questionable specimens of *Maturodinium inornatum* were observed in the middle and upper Toarcian at Maria Pares (supplementary Table 5). This species was previously believed to be confined to the upper Pliensbachian (Morgenroth, 1979; Feist-Burkhardt and Wille, 1992).

At Peniche and Maria Pares, *Mendicodinium microscabratum* was recorded between the *Hildaites levisoni* and the *Hammatoceras speciosum* ammonite biozones (Fig. 13; supplementary Tables 3, 5). This is inconsistent with the range of

Mendicodinium spp., including *Mendicodinium microscabratum,* in the *Dactylioceras polymorphum* ammonite Biozone equivalent of central Italy reported by Bucefalo Palliani et al. (1997a). Thus, the records of *Mendicodinium microscabratum* in the middle and upper Toarcian in the Lusitanian Basin are the youngest known occurrences.

The oldest occurrences of the genus *Nannoceratopsis* in the Lusitanian Basin are the records of *Nannoceratopsis gracilis* and *Nannoceratopsis senex* at the base of the *Amaltheus margaritatus* ammonite Biozone at Brenha and Peniche (Figs. 4; 5). This range base is consistent with records from northwest Europe (Morgenroth, 1970; Woollam and Riding, 1983; Bucefalo Palliani and Riding, 2003; Poulsen and Riding, 2003). The range tops of consistent occurrences of *Nannoceratopsis gracilis* and *Nannoceratopsis senex* are in the lower Bajocian *Stephanoceras humphriesianum* ammonite Biozone (Poulsen and Riding, 2003, p. 124; Wiggan et al., 2017, table 2a). *Nannoceratopsis ambonis* is present in the *Dactylioceras polymorphum* ammonite Biozone at Maria Pares, Peniche and Vale das Fontes, and an isolated occurrence in the upper Toarcian (*Hammatoceras speciosum* ammonite Biozone) at Maria Pares (supplementary Tables 3, 5; Correia et al., 2017a). *Nannoceratopsis gracilis* and *Nannoceratopsis senex* occur consistently, and in relatively high proportions, throughout the *Dactylioceras polymorphum* ammonite Biozone at Maria Pares, Peniche and Vale das Fontes. The genus disappeared at the base of *Hildaites levisoni* ammonite Biozone in these three lower Toarcian successions (supplementary Tables 3, 5; Correia et al., 2017a). This event is interpreted to be a result of the palaeoenvironmental perturbations associated with the T-OAE in the Lusitanian Basin (e.g., Duarte et al., 2004; Hesselbo et al., 2007; Suan et al., 2008, 2010; Pittet et al., 2014; Correia et al., 2017a,b). *Nannoceratopsis ambonis* and *Nannoceratopsis senex* reappeared in the upper

Toarcian (*Hammatoceras speciosum* to *Pleydellia aalensis* ammonite biozones) at Maria Pares (supplementary Table 5).

The distinctive gonyaulacacean species *Scriniocassis weberi* and *Scriniocassis priscus* were encountered, normally in low proportions, in the Toarcian of the Lusitanian Basin (Fig. 13; supplementary Tables 3, 5). *Scriniocassis weberi* ranges throughout the late Pliensbachian to early Aalenian, and *Scriniocassis priscus* is confined to the middle Toarcian to Aalenian, in northwest Europe (Riding, 1984a,b; Prauss, 1989; Feist-Burkhardt, 1990; Feist-Burkhardt and Wille, 1992; Feist-Burkhardt and Pross, 2010). At Peniche, *Scriniocassis weberi* was found in small numbers in the middle part of the *Dactylioceras polymorphum* ammonite Biozone (supplementary Table 3; Correia et al., 2017b). By contrast, *Scriniocassis priscus* was sporadic, yet relatively common where present, between the Toarcian *Hildoceras bifrons* and *Hammatoceras speciosum* ammonite biozones at Maria Pares, and apparently can be used as a marker for this interval in the Lusitanian Basin (Fig. 13).

The pollen-spore floras are generally not as biostratigraphically important as the dinoflagellate cysts. However, there are several miospore datums in the Maria Pares section which are noteworthy. The range base of *Callialasporites* spp. is in the *Brodieia gradata* ammonite Biozone of the middle Toarcian (supplementary Table 5). This biovent is consistent with other reports that the inception of this distinctive pollen genus is in the latest early Toarcian (Riding et al., 1991). Apparently, the range top of the spore *Kraeuselisporites reissingeri* is in sample P33, within the *Hildaites levisoni* ammonite Biozone. This bioevent is broadly consistent with the findings of Morbey (1978, fig. 1). The distinctive spore *Kekryphalospora distincta* was encountered in sample PZ82 (*Dumortieria meneghinii* ammonite Biozone) at Maria Pares (supplementary Table 5). This occurrence is well within the known range of late Pliensbachian to early Bajocian (Fenton and Riding, 1987).

6. The Pliensbachian–Toarcian dinoflagellate cyst biozonation of the Lusitanian Basin

6.1. Introduction

Due their relatively short ranges, many Jurassic dinoflagellate cysts are reliable stratigraphical markers, and several biozonation schemes have been defined based on them (Woollam and Riding, 1983; Helby et al., 1987; Riding and Thomas, 1992; Poulsen and Riding, 2003; Riding et al., 2010). A new dinoflagellate cyst biozonation for the upper Pliensbachian to upper Toarcian of the Lusitanian Basin is summarised in Fig. 13, and compared with the schemes of Riding and Thomas (1992) and Poulsen and Riding (2003).

6.2. The Luehndea spinosa *dinoflagellate cyst Biozone*

Definition: The interval from the range bases of *Luehndea spinosa*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex*, to the range top of *Luehndea spinosa*.

Age: Late Pliensbachian (base of *Amaltheus margaritatus* ammonite Biozone) to earliest Toarcian (top of the *Dactylioceras polymorphum* ammonite Biozone).

Characteristics: The dominance of *Luehndea spinosa* and the relatively consistent and frequent presence of *Mancodinium semitabulatum*, *Nannoceratopsis gracilis* and *Nannoceratopsis senex*. The inception of abundant *Luehndea spinosa* allows the consistent subdivision of this biozone.

Comments: The *Luehndea spinosa* dinoflagellate cyst Biozone of the Lusitanian Basin is coeval with the *Luehndea spinosa* Total Range Biozone of Riding and Thomas (1992,

p. 20–21) and the *Luehndea spinosa* Biozone of Poulsen and Riding (2003), both of northwest Europe (Fig. 13). All these three biozones are defined by the range base of *Luehndea spinosa* and other taxa, such as *Nannoceratopsis senex* or *Nannoceratopsis gracilis* at the base, to the range top of *Luehndea spinosa* at the top. The *Nannoceratopsis senex* and *Luehndea spinosa* subbiozones are broadly equivalent to subbiozones a and b of Riding and Thomas (1992), respectively (Fig. 13).

6.2.1. The Nannoceratopsis senex *dinoflagellate cyst Subbiozone*

Definition: The interval from the range base of *Luehndea spinosa,* to the range base of the abundant presence of this species.

Age: Late Pliensbachian (base of *Amaltheus margaritatus* ammonite Biozone) to latest Pliensbachian (close to the top of the *Emaciaticeras emaciatum* ammonite Biozone.

Characteristics: *Luehndea spinosa* is typically present in relatively low abundances in this Subbiozone.

6.2.2. The Luehndea spinosa *dinoflagellate cyst Subbiozone*

Definition: The interval from the range base of the abundant presence of *Luehndea spinosa,* to the range top of this species.

Age: Latest Pliensbachian (close to the top of the *Emaciaticeras emaciatum* ammonite Biozone) to earliest Toarcian (top of the *Dactylioceras polymorphum* ammonite Biozone).

Characteristics: *Luehndea spinosa* is consistently present, and largely in high abundances.

6.3. The Mendicodinium microscabratum *dinoflagellate cyst Biozone*

Definition: The interval from the range top of *Luehndea spinosa,* to the apparent range top of *Mendicodinium microscabratum*.

Age: Early Toarcian (base of the *Hildaites levisoni* ammonite Biozone) to late Toarcian (top of the *Hammoteceras speciosum* ammonite Biozone).

Characteristics: This biozone typically exhibits low abundances and diversities of dinoflagellate cysts. *Mancodinium semitabulatum*, *Mendicodinium microscabratum* and *Scriniocassis priscus* may be present (Fig. 13).

Comments: This biozone is partially equivalent to the *Nannoceratopsis gracilis* Interval Biozone of Riding and Thomas (1992, p. 21–25), but the latter extends into the early Bajocian in northwest Europe. In the Lusitanian Basin, the top of this biozone is presently not well defined. *Nannoceratopsis gracilis* subbiozones a and b of Riding and Thomas (1992) are correlated with the *Mancodinium semitabulatum* and *Mendicodinium microscabratum* subbiozones herein respectively. Furthermore, the *Mancodinium semitabulatum* and *Mendicodinium microscabratum* subbiozones herein, correspond to the *Mancodinium semitabulatum* and *Parvocysta nasuta* biozones of Poulsen and Riding (2003).

This study represents the youngest record of *Mendicodinium microscabratum* in the the middle and upper Toarcian (Fig. 13). Bucefalo Palliani et al. (1997a) reported this species from the lower Toarcian of Italy. Other coeval sections, and younger strata, should be studied in the Lusitanian Basin and adjacent regions in order to confirm if the range top of this species is at the top of *Hammoteceras speciosum* ammonite Biozone.

Using the apparent range top of *Mendicodinium microscabratum,* and the reappearance of *Nannoceratopsis senex*, the base of another dinoflagellate cyst biozone could possibly be defined at, or close to, the base of the *Dumortieria meneghinnii* ammonite Biozone. Due the lack of information on the latest Toarcian of the Lusitanian

Basin, we opted not to erect another dinoflagellate cyst biozone until more information becomes available.

6.3.1. The Mancodinium semitabulatum *dinoflagellate cyst Subbiozone*

Definition: The interval from the range top of *Luehndea spinosa,* to the range base of *Scriniocassis priscus*.

Age: Early Toarcian (base of the *Hildaites levisoni* ammonite Biozone) to middle Toarcian (close to the top of the *Hildoceras bifrons* ammonite Biozone).

Characteristics: The only dinoflagellate cysts present are rare *Mancodinium semitabulatum* and *Mendicodinium microscabratum*.

6.3.2. The Mendicodinium microscabratum *dinoflagellate cyst Subbiozone*

Definition: The interval from the range base of *Scriniocassis priscus,* to the apparent range top of *Mendicodinium microscabratum*.

Age: Middle Toarcian (close to the top of the *Hildoceras bifrons* ammonite Biozone) to late Toarcian (top of the *Hammoteceras speciosum* ammonite Biozone).

Characteristics: *Mendicodinium microscabratum* is the dominant dinoflagellate cyst species in a very low diversity flora.

7. Conclusions

The Lower Jurassic palynology of the Lusitanian Basin of western Portugal was comprehensively investigated, with the principal emphasis on dinoflagellate cysts. A Sinemurian to Toarcian composite succession from six sections throughout this important depocentre was constructed. The Sinemurian proved entirely devoid of dinoflagellate cysts, but the overlying Pliensbachian and Toarcian succession is characterised by relatively low dinoflagellate cyst diversity; fifteen taxa were encountered. Only seven genera were recorded with certainty, these are *Luehndea, Mancodinium, Mendicodinium, Nannoceratopsis, Scriniocassis, Sentusidinium* and *Valvaeodinium.*

The dinoflagellate cyst succession in the Lusitanian Basin is broadly consistent with other Lower Jurassic sedimentary basins in Europe. However, the reliable Upper Sinemurian dinoflagellate cyst *Liasidium variabile* appears not to have migrated south into the Lusitanian Basin from northwest Europe. *Luehndea spinosa* is the dominant palynomorph in the lowermost Toarcian (*Dactylioceras polymorphum* ammonite Biozone), and is the most age-diagnostic species. At the base of *Hildaites levisoni* ammonite Biozone, *Luehndea spinosa* became extinct, probably due to the effects of the T-OAE. Also at this time, dinoflagellate cyst abundance and diversity sharply decreased. The recovery of phytoplankton during the middle and late Toarcian was relatively slow, following the T-OAE.

Other palynomorph groups such as acanthomorph acritarchs, foraminiferal test linings, pollen and spores, and prasinophytes were also documented. The pollen species *Classopollis classoides* is the most common and abundant palynomorph throughout the Lower Jurassic strata of the Lusitanian Basin. The non-dinoflagellate cyst taxa encountered exhibit no discernible trend, or stratigraphical succession.

By contrast, the dinoflagellate cysts *Luehndea spinosa, Mancodinium semitabulatum*, *Mendicodinium microscabratum*, *Nannoceratopsis gracilis, Nannoceratopsis senex* and *Scriniocassis priscus* were relatively frequent and proved to have biostratigraphical significance. Two dinoflagellate cyst biozones were defined for the succession studied. These are the *Luehndea spinosa* and the *Mendicodinium microscabratum* biozones which are of late Pliensbachian–earliest Toarcian, and earliest–late Toarcian age respectively. These two dinoflagellate cyst biozones are each subdivided into two subbiozones.

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Appendix

This is a list of all the palynomorphs which were recovered from the material studied herein, or mentioned in the text, with full author citations. The seven species 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 Williams et al. (2017). The recommendations of Correia et al. (2017a, appendix 2) regarding the taxonomy of *Nannoceratopsis senex* are followed herein.

Dinoflagellate cysts:

Dapsilidinium? *deflandrei* (Valensi, 1947) Lentin & Williams 1981
**Liasidium variabile* Drugg 1978
**Luehndea cirilliae* Bucefalo Palliani et al., 1997
Luehndea spinosa Morgenroth 1970
Mancodinium semitabulatum Morgenroth 1970

**Mendicodinium brunneum* Bucefalo Palliani et al. 1997

Maturodinium inornatum Morgenroth 1970

Mendicodinium microscabratum Bucefalo Palliani et al. 1997

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

**Mendicodinium umbriense* Bucefalo Palliani et al. 1997

Nannoceratopsis ambonis Drugg 1978

Nannoceratopsis gracilis Alberti 1961

Nannoceratopsis senex van Helden 1977

Scriniocassis priscus (Gocht 1979) Below 1990

Scriniocassis weberi Gocht 1964

**Susadinium scrofoides* Dörhöfer & Davies 1980

**Umbriadinium mediterraneense* Bucefalo Palliani & Riding 1997

**Valvaeodinium hirsutum* Bucefalo Palliani & Riding 1997

Miscellaneous microplankton:

Halosphaeropsis liassica Mädler 1968

Polygonium jurassicum Bucefalo Palliani et al. 1996

Pollen:

Araucariacites australis Cookson 1947 ex Couper 1958

Callialasporites dampieri (Balme 1957) Dev 1961

Callialasporites turbatus (Balme 1957) Schulz 1967

Cerebropollenites macroverrucosus (Thiergart 1949) Schulz 1967

Classopollis classoides (Pflug 1953) Pocock & Jansonius 1961

Spores:

Ischyosporites variegatus (Couper 1958) Schulz 1967

Kekryphalospora distincta Fenton & Riding 1987

Kraeuselisporites reissingeri (Harris 1957) Morbey 1975

Lycopodiacidites rugulatus (Couper 1958) Schulz 1967

Plicifera delicata (Bolchovitina 1953) Bolchovitina 1966

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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 six successions studied herein are indicated by numbers 1 to 6. Successions 1 and 2 are the sections at Maria Pares (40° 3′ 10″N; 8° 27′ 25″W) and Fonte Coberta (40° 3' 44"N; 8° 27' 31"W) respectively; both are close to Rabaçal village. Sections 3 and 4 are Vale das Fontes (40° 12′ 10″N; 8° 51′ 31″W) and Brenha (40° 11' 49"N; 8° 49' 55"W) respectively; both are located north of Figueira da Foz. The São Pedro de Moel composite section (Polvoeira section: 39° 43′ 18″N, 9° 02′ 56″W) is near the village of São Pedro de Moel and is the section number 5. The Peniche section (39° 22′ 15″N; 9° 23′ 07″W) is number 6, close to the town of Peniche.

Fig. 2. The ammonite biostratigraphy and lithostratigraphy of the Lower Jurassic (upper Sinemurian to upper Toarcian) of the eastern and western sectors of the Lusitanian Basin, central-western Portugal, based on Duarte and Soares (2002), Duarte (2007) and Duarte et al. (2014a, 2014b). The light grey shading indicates the lithostratigraphical units studied in the present work, and the dark grey shading indicates material studied by Correia et al. (2017a,b).

Fig. 3. The stratigraphical log of the upper Sinemurian succession in the São Pedro de Moel composite section (= the Polvoeira section of Duarte et al. (2012, 2014a)] adapted from Duarte et al. (2014a), with the positions of the palynomorph samples PM1 to PM12 indicated. No dinoflagellate cyst taxa were identified throughout this succession.

Fig. 4. The lithological log of the lower and upper Pliensbachian succession in the composite section at Brenha, adapted from Silva et al. (2006), with the positions of the palynomorph samples Br1 to Br20 indicated. The uppermost part of this section, the Lemede Formation (samples BrLem1 and BrLem2), was not described by Silva et al. (2006). The ammonite biozones are based on, and modified from, Mouterde et al. (1978) and Elmi et al. (1988).The dinoflagellate cyst occurrences are indicated by black dots.

Fig. 5. The stratigraphical log of the lower and upper Pliensbachian succession in the Peniche section, adapted from Phelps (1985), Duarte et al. (2010), Silva et al. (2011), Bárron et al. (2013) and Comas-Rengifo et al. (2016), with the positions of the palynomorph samples P-34 to P-8 indicated. The dinoflagellate cyst occurrences are indicated by black dots.

Fig. 6. A simplified lithological log of the upper Pliensbachian succession in the Fonte Coberta section. The positions of the palynomorph samples FC1 to FC5 are indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965) and Paredes et al. (2016). The dinoflagellate cyst occurrences are indicated by black dots.

Figs. 7. The lithological log of the middle Toarcian part of the São Gião Formation in the Maria Pares section, adapted from Duarte (1995), with the positions of the palynomorph samples PZ55 to PZ70 indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965) and Elmi et al. (1989). Standard bed numbers 52–59b are given immediately to the left of the lithological ornament. The dinoflagellate cyst occurrences are indicated by black dots.

Fig. 8. The lithological log of the upper Toarcian part of the São Gião Formation in the Maria Pares section, adapted from Duarte (1995), with the positions of the palynomorph samples PZ71 to PZ81 indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965) and Elmi et al. (1989). MMLSB = Marls and Marly Limestones with Sponge Bioconstructions member. Standard bed numbers 60–69S are given immediately to the left of the lithological ornament. The dinoflagellate cyst occurrences are indicated by black dots.

Fig. 9. The lithological log of the upper Toarcian Póvoa da Lomba Formation in the Maria Pares section, adapted from Duarte (1995), with the positions of the palynomorph samples PZ82 to PZ89 indicated. The ammonite biozones are based on, and modified from, Mouterde et al. (1964-1965), Elmi et al. (1989) and Henriques (1992). MMLB = Marls and Marly Limestones with Brachiopods member. Standard bed numbers 70B1–75o are given immediately to the left of the lithological ornament. The dinoflagellate cyst occurrences are indicated by black dots.

Fig. 10. Selected dinoflagellate cysts from the Pliensbachian and Toarcian strata of the Lusitanian Basin, west central Portugal. All the specimens are housed in the collections of LNEG (Portuguese Geological Survey), S. Mamede de Infesta, Portugal. The sample numbers, slide numbers and the England Finder coordinates are quoted; all the scale bars represent 20 μm.

1. *Luehndea spinosa* Morgenroth 1970. Fonte Coberta section, upper Pliensbachian (*Emaciaticeras emaciatum* ammonite Biozone), sample FC5, slide 1, L25/4. Ventral view, high focus.

2. *Luehndea spinosa* Morgenroth 1970. Fonte Coberta section, upper Pliensbachian (*Emaciaticeras emaciatum* ammonite Biozone), sample FC3, slide 1, T32/1. Ventral view, high focus. Note the epicystal archaeopyle.

3. *Luehndea spinosa* Morgenroth 1970. Peniche section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample P-26, slide 1, M35/1.

4. *Nannoceratopsis* sp. Peniche section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample P-20, slide 1, T35/4. Left lateral view. Note the two antapical horns of almost equal length.

5. *Nannoceratopsis gracilis* Alberti 1961. Brenha section, upper Pliensbachian (*Amaltheus margaritatus-Emaciaticeras emaciatum* ammonite biozones), sample BrLem1, slide 1, G34/1. Right lateral view. Note the dorsal horn, which is larger than the ventral horn.

6. *Nannoceratopsis senex* van Helden 1977. Brenha section, upper Pliensbachian (*Amaltheus margaritatus-Emaciaticeras emaciatum* ammonite biozones), sample BrLem1, slide 1, K41/2. Left lateral view. Note the single (dorsal) antapical horn, the subpentagonal lateral outline and the somewhat asymmetrical shape.

7. *Nannoceratopsis senex* van Helden 1977. Fonte Coberta section, upper Pliensbachian (*Emaciaticeras emaciatum* ammonite Biozone), sample FC3, slide 1, L31/4. Left lateral view. Note the dorsal antapical horn and the subpentagonal lateral outline.

8. *Nannoceratopsis senex* van Helden 1977. Brenha section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample Br14, slide 1, G49/3. Left lateral

view. Note the single antapical horn and the symmetrical and very rounded outline; the cingular archaeopyle is visible in the top right of the specimen.

9. *Nannoceratopsis senex* van Helden 1977. Peniche section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample P-25, slide 1, O48/4. Right lateral view. Note the single antapical horn and the symmetrical lateral outline; the cingular archaeopyle is visible in the top left of the specimen.

10. *Nannoceratopsis senex* van Helden 1977. Maria Pares section, upper Toarcian (*Dumortieria meneghinii* ammonite Biozone), sample PZ82, slide 1, P41/3. Left lateral view. Note the single antapical horn and the asymmetrical lateral outline.

11. *Nannoceratopsis ambonis* Drugg 1978. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ81, slide 1, U62/2. Left lateral view. Note the prominent dark sagittal rim.

12. *Nannoceratopsis ambonis* Drugg 1978. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ81, slide 1, X63/1. Right lateral view. Note the prominent dark sagittal rim.

Fig. 11. Selected dinoflagellate cysts from the Pliensbachian and Toarcian strata of the Lusitanian Basin, west central Portugal. All the specimens are housed in the collections of LNEG (Portuguese Geological Survey), S. Mamede de Infesta, Portugal. The sample numbers, slide numbers and the England Finder coordinates are quoted; all the scale bars represent 20 μm.

1. *Valvaeodinium* sp. Maria Pares section, middle Toarcian (*Hildoceras bifrons* ammonite Biozone), sample PZ57, slide 1, Q27/3. Note the relatively sparse cover of short, capitate processes and the combination (apical/intercalary) archaeopyle.

2. *Dapsilidium*? *deflandrei* (Valensi 1947) Lentin & Williams 1981. Maria Pares section, middle Toarcian (*Hildoceras bifrons* ammonite Biozone), sample PZ57, slide 1, R70/3. Note the covering of short distally-blunt processes.

3. *Sentusidinium* sp. Maria Pares section, upper Toarcian (*Hammatoceras bonarelli* ammonite Biozone), sample PZ71, slide 1, M52/2. Note the apical archaeopyle with deep accessory archaeopyle sutures.

4, 5. *Scriniocassis priscus* (Gocht 1979) Below 1990. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ77, slide 1, C32. 4 - ventral view, high focus. 5 - ventral view, low focus illustrating the dorsal surface. Note the rounded, subhexagonal cyst outline and the infrareticulate wall sculpture which is coarser near the sutures. The distinctive, strongly curved sutures surrounding the sulcus are evident in 4. In 5, the two plate (2´´ and 3´´) precingular archaeopyle, the large, middorsal 4´´´ plate and the sutural crests are clearly visible.

6. *Scriniocassis priscus* (Gocht 1979) Below 1990. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ79, slide 1, W43/2. Dorsal view, high focus. Note the two plate precingular archaeopyle and the sulcus.

7. *Mendicodinium microscabratum* Bucefalo Palliani et al. 1997. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ79, slide 1, G49/2. Ventral view; note the epicystal archaeopyle and the microscabrate autophragm.

8. *Mendicodinium* sp. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ80, slide 1, H47/2. Oblique left lateral view.

9. ?*Maturodinium inornatum* Morgenroth 1970. Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ77, slide 1, X52/1. Note the hypocystal tabulation and the faint cingulum.

10. *Mancodinium semitabulatum* Morgenroth 1970. Maria Pares section, upper Toarcian (*Dumortieria meneghinii* ammonite Biozone), sample PZ82, slide 1, X54/3. Note the well-preserved, partly separated, small epicystal plates which are involved in the formation of the 'disintegration' type archaeopyle, in which all the epicystal plates are individually lost.

11. *Mancodinium semitabulatum* Morgenroth 1970. Brenha section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample Br15, slide 1, T47/4. Ventral view, high focus. Note the presence of some of the small, partially detatched precingular plates.

12. *Mancodinium semitabulatum* Morgenroth 1970. Peniche section, lower Pliensbachian (*Prodactylioceras davoei* ammonite Biozone), sample P-29, slide 1, O37/1. Ventral view, median focus. Note the anterior sulcal plate (the sulcal tongue).

Fig. 12. Selected aquatic and terrestrially-derived palynomorphs from the Sinemurian to Toarcian strata of the Lusitanian Basin, west central Portugal. All the specimens are housed in the collections of LNEG (Portuguese Geological Survey), S. Mamede de Infesta, Portugal. The sample numbers, slide numbers and the England Finder coordinates are quoted; all the scale bars represent 20 μm.

1. *Micrhystridium* sp. (acanthomorph acritarch). Peniche section, lower Pliensbachian (*Tragophylloceras ibex* ammonite Biozone), sample P-34, slide 1, R37.

2. *Micrhystridium* sp. (acanthomorph acritarch). Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ79, slide 1, G46/1.

3. Acanthomorph acritarch indeterminate. Maria Pares section, upper Toarcian (*Dumortieria meneghinii* ammonite Biozone), sample PZ82, slide 1, N30.

4. *Tasmanites* sp. (prasinophyte). São Pedro de Moel section, upper Sinemurian (*Oxynoticeras oxynotum* ammonite Biozone), sample PM2, slide 1, S33.

5. *Kekryphalospora distincta* Fenton & Riding 1987 (spore). Maria Pares section, upper Toarcian (*Dumortieria meneghinii* ammonite Biozone), sample PZ82, slide 2, C36/1.

6. *Classopollis classoides* (Pflug 1953) Pocock & Jansonius 1961 (pollen). São Pedro de Moel section, upper Sinemurian (*Oxynoticeras oxynotum* ammonite Biozone), sample PM2, slide 1, Q36.

7. *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967 (pollen). Brenha section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample Br14, slide 1, E54.

8. *Alisporites* sp. (pollen). Brenha section, upper Pliensbachian (*Amaltheus margaritatus* ammonite Biozone), sample Br17, slide 1, V46/2.

9. *Exesipollenites* sp. (pollen). Maria Pares section, middle Toarcian (*Hildoceras bifrons* ammonite Biozone), sample PZ57, slide 1, M35/2.

10. *Spheripollenites* sp. (a tetrad of pollen grains). Maria Pares section, middle Toarcian (*Hildoceras bifrons* ammonite Biozone), sample PZ58, slide 1, L51/1.

11. *Callialasporites dampieri* (Balme 1957) Dev 1961 (pollen). Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ81, slide 3, K29/4.

12. *Callialasporites turbatus* (Balme 1957) Schulz 1967 (pollen). Maria Pares section, upper Toarcian (*Hammatoceras speciosum* ammonite Biozone), sample PZ81, slide 3, N54.

Fig. 13. A composite dinoflagellate cyst range chart for the Lower Jurassic of the Lusitanian Basin based on selected bioevents. The database supporting this chart are the those herein, and those in Correia et al. (2017a,b). The proposed dinoflagellate cyst biozonation is also depicted on the right, and is compared to two northwest European zonal schemes (Riding and Thomas, 1992 and Poulsen and Riding, 2003).

Online supplementary data:

Figures 1–5:

Supplementary Fig. 1. The relative abundances, expressed as percentages, of the five main palynomorph groups recorded from the upper Sinemurian (*Oxynoticeras oxynotum* and *Echioceras raricostatum* ammonite biozones) succession of the São Pedro de Moel section (samples PM1 to PM12). Note the overwhelming dominance of pollen.

Supplementary Fig. 2. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the Pliensbachian (*Uptonia jamesoni* to *Emaciaticeras emaciatum* ammonite biozones) succession of the Brenha section (samples Br1 to Br20 and BrLem1 and BrLem2). Note the overall dominance of pollen.

Supplementary Fig. 3. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the Pliensbachian (*Tragophylloceras ibex* to *Emaciaticeras emaciatum* ammonite biozones) succession of the Peniche section (samples P-34 to P-10). Note the overwhelming dominance of gymnosperm pollen.

Supplementary Fig. 4. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the upper Pliensbachian (*Amaltheus margaritatus* and *Emaciaticeras emaciatum* ammonite biozones) succession of the Fonte Coberta section (samples FC1 to FC5). Note the dominance of dinoflagellate cysts and gymnosperm pollen.

Supplementary Fig. 5. The relative abundances, expressed as percentages, of the six main palynomorph groups recorded from the middle and upper Toarcian (*Hildoceras bifrons* to *Pleydellia aalensis* ammonite biozones) succession of the Maria Pares section (samples PZ56 to PZ88). Note the dominance of gymnosperm pollen and prasinophytes.

Tables 1–5:

Supplementary Table 1. The palynomorph assemblages from the upper Sinemurian succession of the São Pedro de Moel section (12 samples, numbered PM1 to PM12), subdivided into five groups. The numbers in the cells represent percentages of the specified taxon within the overall palynoflora; blank spaces indicate the absence of the respective form.

Supplementary Table 2. The palynomorph assemblages from the lower and upper Pliensbachian succession of the Brenha section (22 samples, numbered Br1 to Br20, BrLem1 and BrLem2), subdivided into six groups. The numbers in the cells represent percentages of the specified taxon within the overall palynoflora; blank spaces indicate the absence of the respective form. Sample Br6 proved palynologically barren.

Supplementary Table 3. The palynomorph assemblages from the lower Pliensbachian to lower Toarcian succession of the Peniche section (72 samples, numbered P-34 to P-1, and P1 to P38), subdivided into six groups. Note that the new material herein is represented by samples P-34 to P-8, and indicated by the light shading. Samples P-7 to P38 (no shading) were previously studied by Correia et al. (2017b). The numbers in the cells represent percentages of the specified taxon within the overall palynoflora; blank spaces indicate the absence of the respective form. The fourteen barren sample numbers are asterisked.

Supplementary Table 4. The palynomorph assemblages from the upper Pliensbachian succession of the Fonte Coberta section (five samples, numbered FC1 to FC5), subdivided into six groups. The numbers in the cells represent percentages of the specified taxon within the overall palynoflora; blank spaces indicate the absence of the respective form.

Supplementary Table 5. The palynomorph assemblages from the lower, middle and upper Toarcian succession of the Maria Pares section (89 samples, numbered PZ1 to PZ89), subdivided into six groups. Note that the new material herein is represented by samples PZ55 to PZ89, and indicated by the light shading. The underlying samples PZ1 to PZ54 (no shading) were previously studied by Correia et al. (2017a).The numbers in the cells represent percentages of the specified taxon within the overall palynoflora; blank spaces indicate the absence of the respective form. The five barren sample numbers are asterisked.