Review of the dinoflagellate cyst *Subtilisphaera? inaffecta* (Drugg, 1978) Bujak & Davies, 1983 and *S.? paeminosa* (Drugg, 1978) Bujak & Davies, 1983

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ABSTRACT – Research carried out on the Upper Jurassic dinoflagellate cyst assemblages of the Sub-Tethyan marine realm, show that populations of the dinoflagellate cysts *Subtilisphaera? inaffecta* and *S.? paeminosa* are predominant in shallow water marginal marine or brackish environments. The distribution of groups of dinoflagellate cysts, micrhystridid acritarchs and variations of terrestrial inputs represented by phytoclasts are presumed parameters of the salinity balance during such Late Jurassic depositional environments. In this context, the shagreenate to faintly granulate *S.? inaffecta* appears to be an opportunistic taxon with an ability to prosper in brackish environments. In contrast, the coarsely granulate to pustulate *paeminosa* form is seemingly less eurytopic and flourishes with success in shallow, marginal marine, environments. SEM studies reveals that the two morphotypes possess transapical archaeopyle sutures on what is usually considered the antapex. Following these observations the cysts are interpreted in a reverse sense. Consequently, the attribution to the genus *Subtilisphaera* becomes inappropriate. The two morphotypes, interpreted as variants of a single species, are attributed to the genus *Corculodinium* Batten & Lister, 1988 for which a new emendation is proposed. The specific epithet *inaffecta* is considered legal over *paeminosa*. *J. Micropalaeontol.* **19**(2): 165–175, December 2000.

INTRODUCTION

Research carried out on the Kimmeridgian and Tithonian dinoflagellate cyst assemblages in the Sub-Tethyan (Sub-Mediterranean) marine realm, record populations of *Subtilisphaera* specimens that are commonly predominant. The two Late Jurassic species are *S.? inaffectum* and *S.? paeminosa*, both erected by Drugg (1978). The *Subtilisphaera* populations described herein come from the Loches section (Aude) and the Solen Well (Lot); Fig. 1. These two sections yielded diverse dinoflagellate cyst and sporomorph populations plus large amounts of phytoclast debris or amorphous organic matter (AOM). Phytoclast particles are dominant in the Kimmeridgian samples and AOM is occasionally abundant in the Tithonian samples. Miospores are, in general, well preserved, presumably due to their more robust nature compared with the thinner-walled dinoflagellate cysts. The latter show symptoms of physical degradation; they are colourless and residues are commonly composed of fragmented dinoflagellate cysts. Skolochorate cysts markedly are exceptionally well preserved, most specimens having damaged or twisted processes.

The dinoflagellate cyst assemblages considered in this paper accord well, in terms of stratigraphical distribution, with the published accounts of Kimmeridgian and Tithonian dinoflagellate cysts from Europe. Concerning the Boreal realm these are: Downie (1957), Gitmez (1970), Gitmez & Sarjeant (1972), Ioannides *et al.* (1976), Raynaud (1978), Fisher & Riley (1980), Norh-Hansen (1986), Cox *et al.* (1987), Lord *et al.* (1987), Riding (1987a,b), Riding & Thomas (1988), Baron (1989), Poulsen (1993, 1994a, b, 1996). Riding & Thomas (1992) have published revised stratigraphic charts for the British Isles, with good applicability to NE. Poulsen (1996) modified some of the dinoflagellate cyst zones revised by Riding & Thomas (1992). In the Tethyan and Sub-Tethyan realm the important publications are those of Gitmez (1970), Gitmez & Sarjeant (1972), Ioannides *et al.* (1988), Brenner (1988), Dürr (1988), Courtinat (1989), Kunz (1990) and Dodekova (1992, 1994). The studies of Gitmez (1970), Gitmez & Sarjeant (1972) and Dodekova (1992) are stratigraphically broadly based; these range data have not been
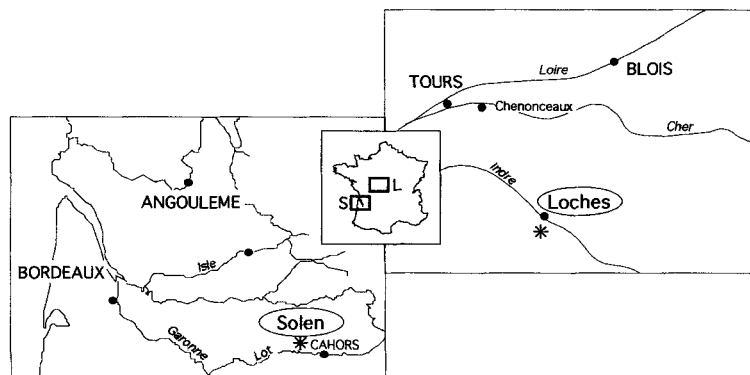
Fig. 1. Location map of the Loches section (L) and the Solen well (S). The Loches section is located in the Aude Department (France), on the edge of the Paris Basin. The Upper Jurassic sediments, which represent a large Kimmeridgian lagoon, are poorly exposed in this area. The Solen well (Lot Department) is situated near Cahors, on the Aquitaine margin, corresponding to the Tithonian Charentes gulf.

considered. The work of Courtinat (1989) is discounted because the lithostigraphical scheme that supported the dinoflagellate cyst zones is now obsolete and requires revision.

The studied material has been obtained applying standard preparation techniques. Quantitative palynological analysis of the overall kerogen composition was carried out on sieved unoxidized material and without application of ultrasonic methods. A series of traverses across the slide to reach a standard number of 220 phytoclast particles made the kerogen counts. In counting the 220 phytoclast particles all the observed palynomorphs registered [maximum 506, average count 266, minimum 156]. The data generated by the counting procedure are relative percentage particle abundances. Slides are housed in the University Claude-Bernard collections.

The objectives of the present study are to review the Kimmeridgian species formerly attributed to the genus *Subtilisphaera*, to discuss their palaeoecology and to present a new point of view on their systematic attribution.

PALAEOCOLOGICAL INTERPRETATIONS

In term of relative abundance the upper Jurassic dinoflagellate cyst assemblages studied (Appendix) present obvious differences between both northern and southern European assemblages. Dürr (1988) has established that Kimmeridgian dinoflagellate cyst microfloras of southern Germany (central Tethyan realm) are dissimilar in overall species content to those from more northerly (Boreal) areas but not in relative abundance. For example, proximate (*Apteodinium*, *Cribroperidinium* and *Kallosphaeridium* groups), proximochorate (*Barbatacysta* and *Epiplosphaera* groups) and skolochorate cysts (*Systematophora* group) are abundant and diverse in the Lower Kimmeridgian of Germany as well as in the British Isles. All these forms are cosmopolitan species.

In common with European assemblages (Boreal and Tethyan realms), species of *Subtilisphaera* in the studied sections proved to be dominant constituents in some instances (up to 65% of palynomorphs; 16% of kerogen). Furthermore, the *Micrhystridium* group were occasionally present in obviously significant proportions (up to 40%) together with the *Prasinophyceae* group (up to 25% of palynomorphs). The abundance of cavate cysts, especially forms of the genus, *Subtilisphaera* have been reported in the upper part of the *Eudoxus* ammonite Zone of Quercy by Ioannides *et al.* (1988). Dürr (1988) noticed the abundant population of *S.? inaffecta* and *S.? paeminosa* in the Late Kimmeridgian ξ2 Zone) of Germany and Poulsen (1996) also mentions a rich flora in the Late Kimmeridgian of Denmark and Poland.

Poulsen (1996) emphasized the particular environment that favoured the abundance of *Subtilisphaera* forms. They appear to indicate shallow water, and probably restricted, low energy depositional environments.

The Loches section

In the Kimmeridgian Loches section (Figs. 1, 2), (*Eudoxus* Ammonite Zone), the *Subtilisphaera* population reaches a maximum of 40% (expressed as the total of organic micro-fossils); *S.? inaffecta* is significantly more abundant than *S.? paeminosa*. The *Subtilisphaera* population presents maxima of abundance associated to minima of the dinoflagellate cyst:spor-omorph ratio (Fig. 3) and low dinoflagellate cyst diversity (Fig. 3). The dinocystic:sporomorph ratio generally declines sharply onshore and is especially low in deltaic areas or above the tidal limit (Tyson, 1995). These patterns reflect partial dilution by the high sporomorph and sediment influx. In the *S.? inaffecta* maximum of the Loches section, grains of pollen identified as *Spheripollenites* belonging to the Cheirolepidacean–Taxodiacean conifers are over-dominant. Mesozoic inhabitants of swamp environments comparable to mangroves produce these pollen. The *Subtilisphaera* population maxima of the Loches section probably reflects the most nearshore depositional environments for the samples we have analysed.

The acanthomorph acritarch *Micrhystridium* is well-represented and is occasionally abundant (Fig. 3). Many studies have regularly established that a relative abundance of small micrhystridid acritarchs is most representative of shallow water marginal marine conditions (Erkmen & Sarjeant, 1980; Schrank, 1984; Prauss, 1989). In the Loches section, samples M03, M07–MO8 and M13 show an abundance peak of short spined *Micrhystridium*. The M03 and M07 peaks are associated with a slight increase in the percentages of the elongated or needle-like phytoclasts (PM 1T, PM4Tm and PM4Tn; Fig. 3). These palynomacerals are presumed to possess an elevated buoyancy and are deposited under low energy conditions (Courtinat & Rio, in preparation). The M13 peak is associated with high relative frequencies of phytoclasts (exclusively the PM1E particles), an increase in the relative abundance of the prasinophytes and a low dinocyst diversity. As for the precedent peaks, the M13 'event' appears related to brackish marginal facies. This contention is supported by the general trend of decreasing energy conditions, relatively large inputs of phyto-clasts induced by freshwater arrivals, and decrease in the dinoflagellate cyst diversity.

In the Loches section the *Prasinophyceae* group shows an increasing richness from base to top. This group is known to be an important element of the modern phytoplankton in high latitude seas (Bird & Karl, 1992). A general association or affinity with cold waters for fossil prasinophytes is questionable. Most, but not all, of these occurrences are reported in what are interpreted as dysoxic–anoxic facies. The samples we have analysed from the Loches section show no discernible dysoxic-anoxic event. The pyrolysis data and the absence of true AOM support this assumption. Many workers have regarded the fossil prasinophytes as indicators of brackish surface water conditions. Tyson (1995) demonstrates that the brackish hypothesis is an apparent general agreement based on an uncritical accep-tance of earlier interpretations or on the brackish and freshwater occurrence of some modern motile prasinophytes. His recom-mendation is that this hypothesis is not applied to all occurrences. The brackish hypothesis presumes major fresh-water inputs in the marine surface layer. In this case, prasinophytes are associated with high sporomorph and phytoclast contents. These trends are observed in the Loches section for the phytoclasts (Fig. 3) and for the sporomorphs; although the opposite hypothesis of a hypersaline environment has been assumed (Bernier & Courtinat, 1979; Kunz, 1990). It is realistic to suggest that the prasinophytes are opportunistic forms occupying ecological niches deserted by phytoplankton communities when ecological stress of variable nature occurs.
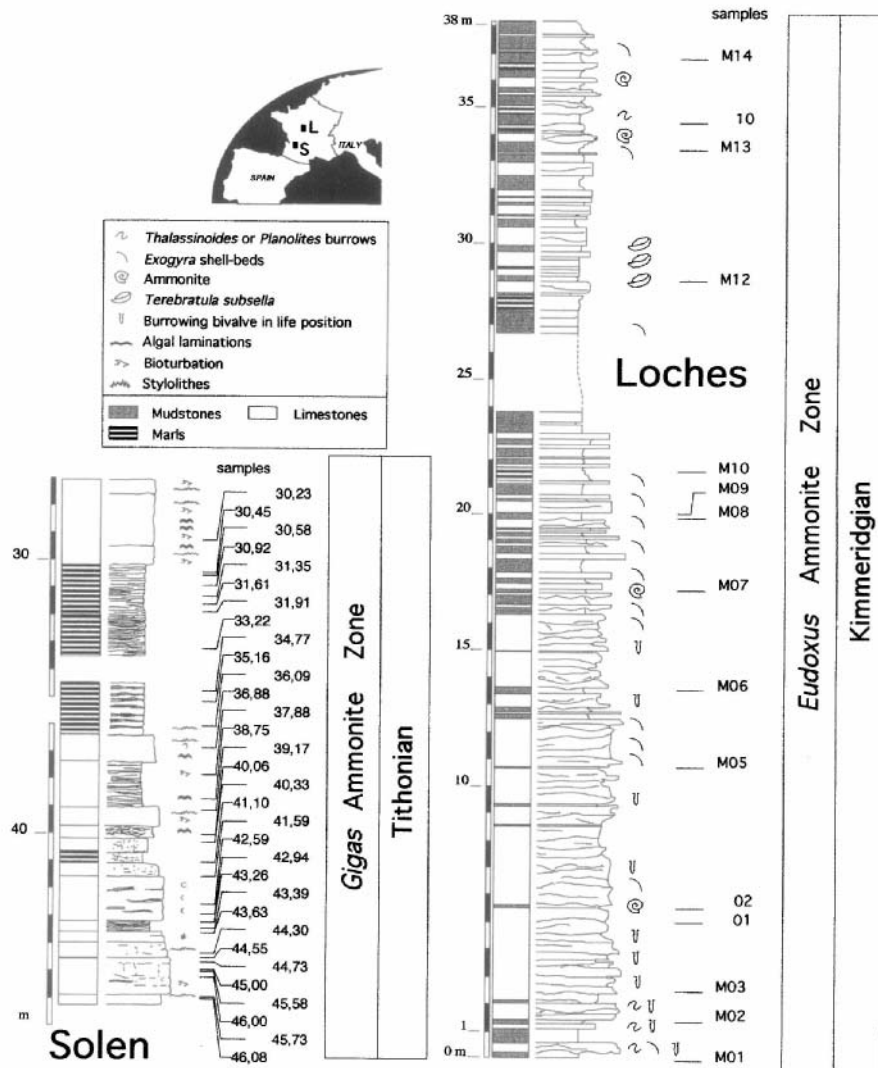
Fig. 2. Lithological log of the Loches section and the Solen well.

The Solen well

The Tithonian samples examined from the Solen Well (*Gigas* Ammonite Zone; Quercy; Figs 1, 2) yielded low diversity assemblages of dinoflagellate cysts and sporomorphs plus large amounts of phytoclast particles (mainly abundant in pure limestones) and amorphous organic matter (AOM; chiefly abundant in marly limestones). The *Subtilisphaera* population represents 65% of the palynomorphs (Fig. 4). The black, equidimensional, polygonal woody particles are common in all lithologies. The relationship between the variations in the *Subtilisphaera* population and other data is different from that observed in the Loches section. The *Subtilisphaera* peaks are unrelated to palynomaceral particles, dinocyst diversity or any other palynofacies parameters. This is due to the particular context favouring deposition of AOM (Courtinat & Hantzpergue; in prep.).

Gradation between the two AOM types observed, sheath-like and diffuse-edged or well-delimited aggregates, and woody particles indicates that the AOM aggregates are amorphous terrestrial humic matter. High frequencies of *Circumpolles*, low and fluctuating dinoflagellate cyst and spore diversities and quasi-absence of bisaccate pollen are in agreement with the suggestion of a nearshore environment, subject to salinity variations and tidal-wave influences where continental run-off alternates with shallow marine conditions. The role of bioturbation, the diurnal–nocturnal activity of cyanobacterian communities and their trapping effect can explain the weak oxidation and, ultimately, the preservation of the sedimentary organic matter. Rhythms marked by palynofacies devoid of aggregates in association or not with sheath-like AOM are observed. These unequal rhythms are thought to be related to the vigour of oxic degradation and salinity balance, depending on turbulence and desalinization events of the surface waters by wind-driven currents, tides and run-off and presence of bioelements favoured by salinity and water depth modifications. The variations in the Jurassic *Subtilisphaera* population are presumably signs of
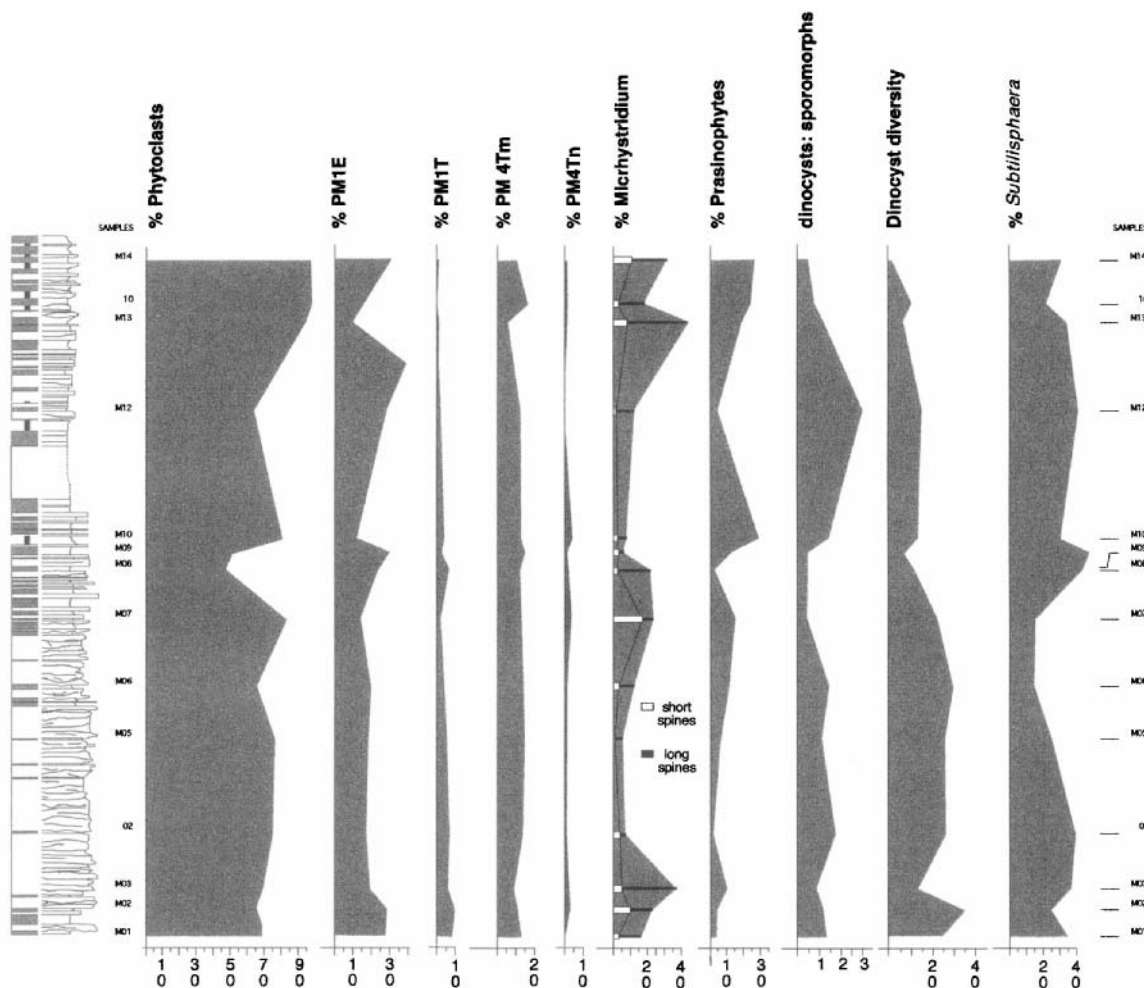
Fig. 3. Distribution of significant palynofacies indicators in the Loches section compared to the *Subtilisphaera* population.

salinity modifications.

In conclusion, the whole of the data show that the late Jurassic *Subtilisphaera*-rich depositional environments were shallow water marginal marine or brackish. Variable distribution of groups of dinoflagellate cysts, micrhystridid acritarchs and prasinophytes are associated with variations of terrestrial inputs represented by phytoclasts that are supposed parameters of the salinity balance prevailing during the *Eudoxus* Ammonite zone at Loches section and the *Gigas* Ammonite Zone of the Solen well. In this context, *S.? inaffecta* appears to have a propensity to flourish in brackish waters (low salinities) and *S.? paeminosa* to favour increased marine waters (normal salinity). The two forms are assumed to be two variants of a single morph (ecophenotypes). The shagreenate or weakly granulate morphotype is presumably eurytopic with a good adaptability for brackish environments. The coarsely granulate sculptured morphotype is seemingly stenotopic and an inhabitant of shallow marginal marine environments. The possibility that the laevigate/granulate ratio could be a palaeosalinity marker is important. The concept of ecophenotype rarely receives attention in palynological studies. Monteil (1991), in a very detailed

work dealing with the plexus *Muderongia*/*Phoberocysta*, proposed for each so-called smooth ecotype (*Muderongia* species) four ecotypes with processes (*Phoberocysta* species). Smooth species (*Muderongia*) are dominant in outer shelf sediments, whereas forms bearing processes (*Phoberocysta*) are more abundant in inner shelf sediments. In a similar way, Feist-Burkhardt & Pittet (1996) have considered that the increase or decrease of surface ornamentation of some Jurassic forms attributed to the *Mendicodinium*/*Ctenidodinium* complex are the result of environmental factors.

SYSTEMATIC AND MORPHOLOGICAL BACKGROUNDS

Drugg (1978), during a Jurassic sampling programme to gain stratigraphically controlled material for palynological research, describes two new cavate forms in the Kimmeridgian of England and Germany. The major particular attribute of these species remains the difficulty in recognizing an archeopyle.

In the opinion of the author, the two species are closely related. Both are primarily epicavate to bicavate cysts with a pentagonal to elliptical outline. The pericoel can be restricted at one extremity where the periphragm forms a bulge (an apical
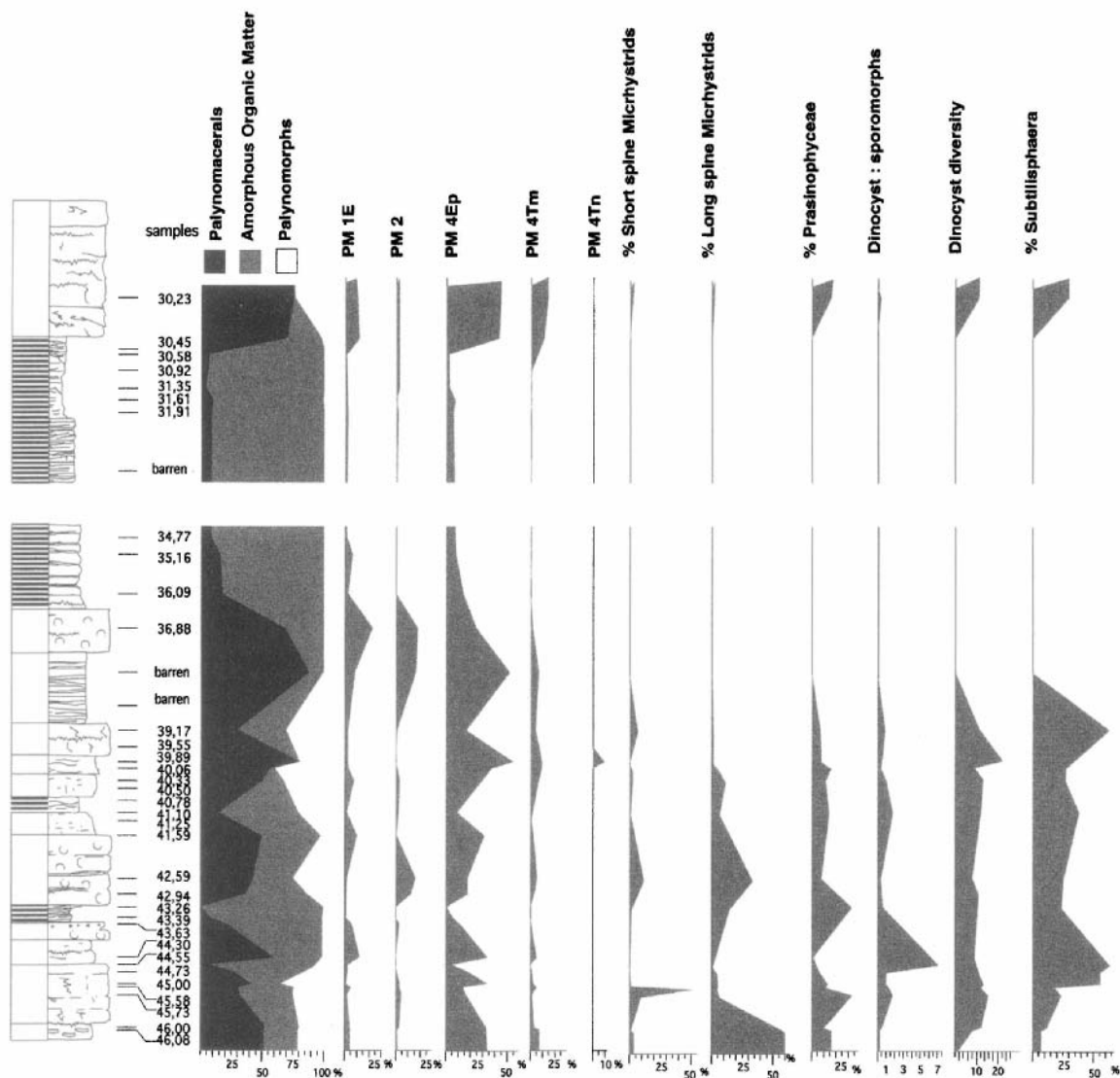
Fig. 4. Distribution of the major components of palynofacies in the Solen well compared to the *Subtilisphaera* population.

horn from the Drugg's assumption conferring the aspect of an epicavate cyst) or at the two opposite extremities (bicavate cysts; with interpreted cone-shaped apical horn and roundish to sub-angular antapical horn). Endocysts are circular to elliptical, smooth-, granulate- or pustulae/verrucae-walled. The only perceptible paratabulation elements are two low transverse ridges delineating a paracingulum. Bujak & Davies (1983) transfer the two species to the genus *Subtilisphaera*. These new assignments are based on the interpretation of a transverse archeopyle (Bujak & Davies, 1983: 'Specimens illustrated by Drugg [1978] as *S. inaffecta* and *S. paeminosa* from the Kimmeridgian of England and Germany, ... appear to have the same transverse archeopyle type.'). The expression 'the same transverse archeopyle type' refers to a transverse archeopyle suture present between the apical and intercalary series developed on cysts with a bipesoid paratabulation. This

interpretation is not accepted by Lentin & Williams (1985) as the illustrations of Drugg (1978; pl. 3, figs 5–12) show neither evidence of transverse archeopyle nor indication of a bipesioid paratabulation. They questionably retained the two species in *Subtilisphaera*. For most authors, Lentin and Williams are the authority on this subject. Evitt (1985) suggests that the genus *Subtilisphaera* is an archeopyle-less *Alterbidinium* Lentin & Williams, 1985 emend. Khowaja-Ateequzzaman *et al.*, 1991.

All these opinions postulate that the epitheca is bell-shaped and that the hypotheca possesses one or two undeveloped antapical horns. These points of view converge towards an apparent consensus based on an uncritical acceptance of a standard morphology of cysts looking like the P-Cysts of Evitt (1985), i.e. cysts that would be referable to living *Peridinium*, *Protoperidinium*, or closely similar genera on the basis of their morphology. However, in this case, neither *S.? inaffecta* nor *S.*
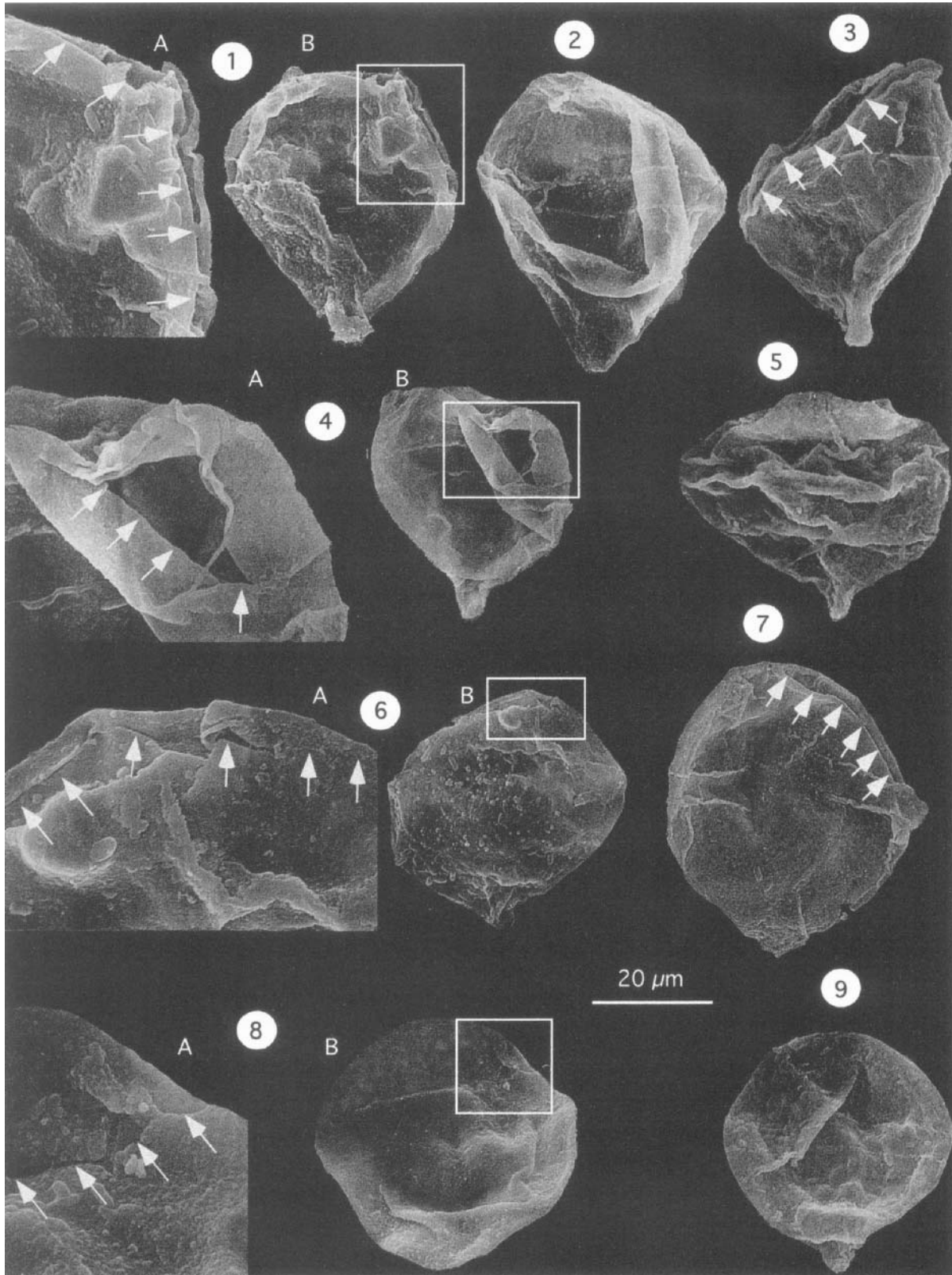
?paeminosa present a full morphology that looks like a peridinoid one.

Earlier suggestions of a different interpretation rely on studies of the Kimmeridgian and Portlandian strata of Jura where *Subtilisphaera* forms are sometimes dominant in the palynomorph assemblages. As a rule, *Subtilisphaera* specimens are commonly damaged on what is the antapex in the current interpretation. Following these observations the suggestion that the cysts could be interpreted upside down has been postulated. A presumed relation with the genus *Saeptodinium* Harris, 1974 has been suggested but without solid argument (Courtinat, 1989). Recent SEM observations render this conjecture (interpretation of the cysts in reverse sense) worthy of further consideration.

Although Lentin & Williams (1985) recorded *S. inaffecta* and *S. paeminosa*, with some doubts in the genus *Subtilisphaera*, their emendation of this generic taxon is questionable because of the nature of the archeopyle of the type species.

The original diagnosis of the genus *Subtilisphaera* Jain & Millepied, 1973 (p. 27) is:

'Shell pentagonal-ovoid, test cavate to bicavate non-tabulate, asymmetrical; cingulum (girdle) well developed, dividing the shell into almost equal halves. Epitract broadly rounded with pointed to broadly obtuse apical horn; hypotract rounded having one prominent antapical horn and second undeveloped or only as a slight projection placed away from median axis (non-axial). Periphragm smooth to granulate, thin, delicate. Endophragm well developed, smooth, thin, delicate; capsule circular, filling periphragm completely, or leaving a small pericoel. Archeopyle mostly not seen, if present intercalary.'

The emended diagnosis of *Subtilisphaera* by Lentin & Williams (1976) reported the transverse archeopyle (?AIP) resulting from separation along a transapical suture. For the authors, the operculum, which may include paraplates 3', 1–3a and 3'''–5'', remains attached along the posterior parasuture (operculum adnate). The type species *Subtilisphaera senegalensis* Jain & Millepied 1976 shows no archeopyle. Stover & Evitt (1978) and Below (1981) have questioned the use of such a negative character and have stressed the uncertainties of the catch-all *Subtilisphaera* genus. Stover & Evitt (1978) assumed the distinctions of the *Geiselodinium* Krutzsch, 1962, *Subtilisphaera*, *Saeptodinium* and *Teneridinium* Krutzsch 1962 genera are disputable. The opinion of Evitt (1985) is to consider that

Geiselodinium and *Teneridinium* genera are apparently freshwater cysts, whose thin and folded walls leave details of morphology quite unclear, while *Subtilisphaera* is a more distinctive marine cyst. The consideration of the mode of life in the distinction of undiscriminating peridinoid cysts is a possible way forward that merits attention.

SEM OBSERVATIONS – SYSTEMATIC IMPLICATIONS

Observed under transmitted light microscope or in SEM, 70% of the studied *Subtilisphaera* forms present a break (Pl. 1, figs 1, 3, 4 and 6). Under transmitted light microscope this fracture is not interpretable. By contrast, SEM analysis shows that the rupture is not a mechanical split but probably has a structural origin because of the presence of accessory sutures (Pl. 1, figs 6 and 8). The principal suture extends adapically from one side of the paracingulum to the other and traverses the apex (Pl. 1, figs 1 and 4). This tear is interpreted as a transapical archeopyle suture. This interpretation renders the half valve that supports the archeopyle suture equivalent to an epicyst. By opposition, the horn would be antapical in position. In addition to the archeopyle suture and the associated accessory sutures, the paracingulum and some paraplate sutures complete the paratabulation. Paraplate sutures are perceivable on the paracingulum (Pl. 1, figs 2 and 7), the apex (Pl. 1, fig. 2) and the antapex (Pl. 1, fig. 7). On some specimens an opisthopyle is present (Pl. 1, fig. 1). The laevigate to faintly granulate *inaffecta* morph (Pl. 1, fig. 4) grades into the more coarsely ornamented *paeminosa* morph (Pl. 1, fig. 5). The separation of the two ornamentation types is not appreciated under SEM. The retention of the two distinct taxa seems irrelevant since the ornamentation is the major criterion of differentiation. The forms that exhibit a coarse ornamentation generally have a more polygonal epicyst and cone-shaped hypocyst (Pl. 1, figs 2 and 7). By comparison, those with the lesser-ornamented periphragm usually have a circular epicyst and a pointed antapex (Pl. 1, fig 9).

The SEM observations, confirmed by those performed under transmitted light microscope, that indicate the orientation of the two forms *S.? inaffecta* and *S.? paeminosa* has been misinterpreted. The more probable exact orientation, instituted on the common assumption that all the transverse archeopyles are epicystal, is to consider the horn as an antapical one. As a consequence, the two morphotypes have characters that are not

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Explanation of Plate 1

Corculodinium inaffectum (Drugg, 1978). **Fig. 1A.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph; enlargement of the specimen figured in 1B. Detail, indicated by arrows, of sutures of the archeopyle. **Fig. 1B.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph. Entire specimen with coarse ornaments and marks of paracingulum. **Fig. 2.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov., a heart-shaped specimen with a well developed parcingulum. Intermediate specimen regarding ornamentation. **Fig. 3.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *inaffectum* morph. Detail, indicated by arrows, of sutures of the archeopyle. **Fig. 4A.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *inaffectum* morph; enlargement of the specimen figured in 4B. Detail, indicated by arrows, of sutures of the archeopyle. **Fig. 4B.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *inaffectum* morph. A four-sided specimen with a pointed antapical horn. **Fig. 5.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph. A wrinkled specimen with a pointed antapical horn. Note the coarse ornamentation. **Fig. 6A.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph, enlargement of the specimen figured in 6B. Detail, indicated by arrows, of accessory sutures of the archeopyle. **Fig. 6B.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph. A subcircular specimen with a faint development of a paracingulum. Note the sparse coarse grana. **Fig. 7.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph. Position of the archeopyle is indicated by arrows. A specimen with an intermediate ornamentation, a well-developed paracingulum and marks of the parasulcus on the antapical area. **Fig. 8A.** *Corculodinium inaffectum* (Drugg 1978) comb. nov.; *inaffectum* morph; enlargement of the specimen figured in 8B. Detail, indicated by arrows, of accessory sutures of the archeopyle. **Fig. 8B.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *inaffectum* morph. A circular specimen without marks of paracingulum. **Fig. 9.** *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; *paeminosum* morph. A circular specimen with traces of paracinculum and a pointed antapical horn.

	Corculodinium	
	uniconicum Batten & Lister, 1988	*inaffectum* (Drugg, 1978) comb. nov
Shape	heart-shaped; epicyst broader than hypocyst; antapical horn	heart-shaped to circular; epicyst broader than hypocyst; antapical horn or mamelon-like protusion
Wall relationsip	two closely adpressed layers	pericoel regularly developed or restricted at the antapex
Wall features	endophragme densely and minutely granulate; periphragm shagreenate	endophragme sacbre or densely and minutely granulate; periphragm smooth to faintly granulate
Paratabulation	suggest formula: ?1–4', ?1–3a, 7", 0c, 5''', 2''''	unknown; only indicated by paracingulum, parasulcus, accessory sutures and weakly developed paraplate sutures
Archeopyle	combination apical/intercalary (tAtI)a/(tAtI)a	transapical or combination apical/intercalary; unknown formula; ventrally adnate
Paracingulum	occasionally faintly suggested by creases	low transverse ridges
Parasulcus	not observed	not observed; occasionally faint ridges
Size	range of maxium diameter 23–35 μm	range of maximum dimension 40–69 μm
Variants	unknown	*paeminosum* morph differs by its coarsely granulate to verrucate periphragme.

Table 1. Diagnostic elements of *Corculodinium* species.

those of all the suggested genera (principally *Geiselodinium* and *Subtilisphaera* and, to a lesser degree, *Saeptodinium* and *Teneridinium*). Considering the palaeocological adaptation and the diagnostic characters of the morphotypes, the most adequate genus is *Corculodinium* Batten & Lister, 1988. To accept a transverse archeopyle, forms with two layers, a well-expressed paracingulum, enlarged diversity of wall ornamentation and occasional presence of an opisthopyle, an emendation of the genus *Corculodinium* is proposed.

Division **Pyrrhophyta** Pascher, 1914
Class **Dinophyceae** Fritsch, 1929
Order **Peridiniales** Haeckel, 1894

Genus *Corculodinium* Batten & Lister, 1988 emend
1988 *Corculodinium* Batten & Lister: 350.
Type species. *C. uniconicum* Batten & Lister, 1988: 351–352, figs 3h–k.
Diagnostic elements. See Table 1.
Holotype. *C. uniconicum* Batten & Lister, 1988: 351–352, figs 3h, i.
Locality. Isle of Wight, England.
Age. Weald Clay Group, Vectis Formation, Shepherd's Chine Member, Barremian.
Original description. Small, proximate, heart-shaped cyst; epicyst without apical horn or prominence, usually slightly indented at apex when undehisced, broader than hypocyst which is typically conical. Phragma thin, consisting of two closely adpressed layers, sometimes with a minute antapical pericoel, but periphragm may not be developed in some specimens; when present it is laevigate and endophragm is scabrate to minutely granulate. Paratabulation either undiscernible or partly indicated by archeopyle development and sometimes by crumpling of periphragm, interpreted as peridiniacean. Archeopyle, com-

bination apical/intercalary (tAtI), formed by partial dehiscence of simple operculum which is adnate ventrally, sometimes enlarged by secondary splitting at aperture margin along accessory sutures between some precingular paraplates.
Emended description. Hypocavate to bicavate, unusually circumcavate, circular to heart-shaped cyst. Periphragm and endophragm are frequently closely appressed and when a pericoel is present, the cavity is feeble. Epicyst without apical horn but occasionally with one or two weakly developed bulges. Epicyst broader than the conical hypocyst which typically and constantly presents a low roundish to sub-angular antapical horn. Endocyst circular, elliptical or heart-shaped. Wall surface shagreenate, scabrate, granulate, pustulate or verrucate. Periphragm shagreenate, scabrate or faintly and finely granulate to pustulate. Paratabulation either undiscernible or partly indicated by archeopyle development, sometimes by crumpling of periphragm or two low transverse ridges delineating a level (planar) or weakly levogyre paracingulum. When observed under SEM, some specimens show paraplate sutures but the paratabulation cannot be fully defined. Archeopyle variable, transapical (tAtItP)a/? or combination apical/intercalary (tAtI)a/(tAtI)a, formed by partial dehiscence of simple operculum which is adnate ventrally, sometimes enlarged by secondary splitting at aperture margin along accessory sutures between some precingular paraplates.
Dimensions. Total length 23 to 35 μm.
Stratigraphical range. See Table 2.
Remarks. The original description is enlarged to include: (1) the varibility of the archeopyle; (2) the disconnection of the periphragm and endophragm while formerly *Corculodinium* is described for typically acavate forms; (3) the presence on some specimens of a paracingulum and an opisthopyle; and (4) the extended palette of the ornamentation types of the layer surfaces which evolved from laevigate to pustulate-walled.

Zonation in the Boreal Realm

Kimmeridgian ammonite zones: Baylei, Cymodoce, Mutabilis, Eudoxus, Autissiodorensis, Elegans, Scitulus, Wheatleyensis, Hudlestoni; Barremian.

Corculodinium uniconicum

Citations		Geographical location
Batten and Lister,	1988;	Isle of Wight, England

Corculodinium inaffectum

Citations		Geographical location
Drugg,	1978;	Kimmeridge Bay, Southern England
Riding and Thomas,	1988;	Dorset Coast, Southern England
Ioannides *et al.*,	1988;	Quercy, Southwest France
Baron,	1989;	Helmsdale region, East Sutherland, Scotland
Riding and Thomas,	1992;	British Isles
Feist-Burkhardt and Wille,	1992;	Southwest Germany
Poulsen,	1996;	Denmark and Poland
This paper		France

variant paeminosum

Citations		Geographical location
Drugg,	1978;	Saxony, Germany
Riding and Thomas,	1988;	Dorset Coast, Southern England
Ioannides *et al.*,	1988;	Quercy, Southwest France
Dürr,	1988;	South, Germany
Dürr,	1988;	Pas de Calais, North France
Riding and Thomas,	1992;	British Isles
Feist-Burkhardt and Wille,	1992;	Southwest Germany
Poulsen,	1996;	Denmark and Poland
This paper		France

Zonation in the Tethyan Realm

Ammonite zones — Kimmeridgian: Platynota, Hypselocyclum, Divisum, Acanthicum, Eudoxus, Beckeri; Tithonian: Gigas, Darwini, Semiforme, Fallauxi; Barremian.

Table 2. Stratigraphic ranges of Jurassic species and variants belonging to the genus *Corculodinium*.

Other species: *Corculodinium inaffectum* (Drugg, 1978) comb. nov.; Pl. 1, figs 1–9.
Geiselodinium paeminosum Drugg, 1978: 68–69, pl. 3, fig. 8.
Diagnostic elements. See Table 1.
Holotype. *Geiselodinium inaffectum* Drugg, 1978: 68, pl. 3, fig. 10.
Locality. Kimmeridge Bay, Dorset, England.
Age. Kimmeridgian (*Autissiodorensis* Zone).
Dimensions. Total length 49 to 69 μm.
Stratigraphical range. See Table 2.
Remarks. *Corculodinium inaffectum* possesses an interpreted transapical archeopyle, no apical horn and a central antapical horn. These features are those neither of the *Geiselodinium* nor *Subtilisphaera* genera. These two taxa present one apical horn and either one eccentrically located antapical horn, or two symmetrically located but unequal horns. The most closely satisfactory genus is *Corculodinium* Batten & Lister, 1988 emend. herein.

Geiselodinium paeminosum is presumed a synonym of *Corculodinium inaffectum* because both taxa are only distinguishable by their ornamentation. SEM observations show a constant gradation between shagreenate and granulate-, pustulate-walled. The two taxa were described in the same publication and listed in alphabetical order where *G. inaffectum* is the former.

APPENDIX LIST OF SPECIES

Dinoflagellate cysts
Proximate cysts
Acanthaulax venusta (Klement, 1960) Sarjeant, 1968
Atopodinium haromense Thomas & Cox, 1988
Chytroeisphaeridia chytroeides (Sarjeant, 1962) Downie & Sarjeant, 1965
Chytroeisphaeridia pericompsa (Ioannides *et al.* 1976) Davey 1979
Cribroperidinium ? longicorne (Downie, 1957) Lentin & Williams, 1985
Cribroperidinium aceras (Eisenack, 1958) Sarjeant, 1985
Cribroperidinium globatum complex: this complex comprises *C. globatum* Gitmez & Sarjeant, 1972) Helenes, 1984, *Acanthaulax granulatum* (Klement, 1960) Brenner, 1988 and *A. granuligera* (Klement, 1960) Brenner, 1988
Cribroperidinium nuciforme (Deflandre, 1938) Courtinat, 1989
Ctenidodinium chondrum Drugg, 1978
Ctenidodinium panneum (Norris, 1965) Sarjeant, 1969
Dissilodinium globulum Drugg, 1978
Egmontodinium polyplacophorum Gitmez & Sarjeant, 1972
Escharisphaeridia pocockii (Sarjeant, 1968) Erkmen & Sar-

jeant, 1980
Escharisphaeridia psilata Kumar, 1986
Evansia tripartita (Johnson & Hills, 1973) Jansonius, 1986
Gongylodinium sp.
Impletosphaeridium polyacanthum (Gimez, 1970) Islam, 1993
Kallosphaeridium sp.
Leptodinium sp. ? *arcuatum* Klement, 1960
Mendicodinium groenlandicum (Pocock & Sarjeant, 1972) Davey, 1979
Occisucysta balia Gitmez, 1970
Occisucysta monoheuriskos Gitmez & Sarjeant, 1972
Pareodinia brevicornuta Kunz, 1990
Pareodinia ceratophora Deflandre, 1947 emend. Gocht, 1970
Rhynchodinioposis cladophora (Deflandre, 1938) Below, 1981
Valensiella ovula (Deflandre, 1947) Eisenack, 1963
Valensiella reticulata (Davey, 1969) Courtinat, 1989

Proximochorate cysts
Barbatacysta brevispinosum complex: this compex comprises (*B. brevispinosum* Courtinat, 1980, *B. creberbarbata* [Erkmen & Sarjeant, 1980] Courtinat, 1989 and *B. lemoignei* Courtinat, 1989)
Barbatacysta pilosa (Erhenberg 1843 emend. Erkmen & Sarjeant, 1980) Courtinat, 1989
Barbatacysta verrucosa (Sarjeant, 1968) Courtinat, 1989
Epiplosphaera reticulospinosa Klement, 1960
Heslertonia pellucida Gitmez, 1970
Prolixosphaeridium granulosum Deflandre, 1937) Davey *et al.* 1966
Trichodinium erineaceoides Davies, 1983

Chorate cysts
Oligosphaeridium patulum Rinding & Thomas, 1988
Polystephanephorus calathus (Sarjeant, 1961) Sarjeant, 1961 emend. Stancliffe & Sarjeant, 1990
Systematophora areolata Klement, 1960
Systematophora daveyi Riding & Thomas, 1988
Systematophora penicillata (Ehrenberg, 1854) Sarjeant, 1980

Cavate cysts
Chlamydophorella wallala Cookson & Eisenack, 1960
Dingodinium harsveldtii complex: this complex comprises *D. harsveldtii* Hergreen *et al.* 1984, *D. minutum* Dodekova, 1975 and *D. tuberosum* (Gitmez, 1970) Riley 1980 emend. Poulsen, 1996
Endoscrinium anceps Raynaud, 1978
Corculodinium inaffectum (Drugg, 1978) emend. herein.
Glossodinium dimorphum Ioannides *et al.* 1977
Senoniasphaera jurassica (Gitmez & Sarjeant, 1982) Lentin & Williams, 1976
Stephanelytron scarburghense Sarjeant, 1961 emend Stover *et al.* 1977
Tubotuberella apatela (Cookson & Eisenack, 1960) Ioannides *et al.* 1976
Wallodinium krutzschii (Alberti, 1961) Habid, 1972

Acritarchs
Micrhystridium short spines complex: this complex comprises *M. deflandrei* Valensi, 1948 and *M.* cf *deflandrei* Valensi, 1948

of Courtinat, 1989
Micrhystridium long spines complex: this complex comprises *M. fragile* Deflandre, 1947 and *M. rarispinum* Sarjeant, 1960
Solisphaeridium stimuliferum (Deflandre, 1938) Pocock, 1972

Prasinophyceae
Crassosphaera hexagonalis Wall, 1965
Cymatiosphaera cf. *eupeplos* Valensi
Hyalinsphaeridia complex: this complex comprises *H. acorpuscula* Bernier & Courtinat, 1979, *H. hyalina* (Deflandre, 1947) Bernier & Courtinat, 1979 and *Leiosphaeridia nidusiforma* Bernier & Courtinat, 1979.
Pterospermopsis helios Sarjeant, 1959
Tasmanites newtoni Wall, 1965

Chlorococcales
Botryococcus spp.

Spores
Deltoidospora mesozoica (Thiergart, 1949) Schuurman, 1977
Foveosporites foveoreticulatus Döring, 1965
Ischyosporites variegatus (Couper, 1958) Schulz, 1967
Leptolepidites spp.
Retitriletes austroclavatidites (Cookson, 1953) Krutzsch, Mai et Schulz, 1963
Staplinisporites caminus (Balme, 1957) Pocock, 1962
Todisporites minor Couper, 1958

Pollen
Abietineaepollenites microalatus (R. Potonié, 1931) R. Potonié, 1951
Araucariacites spp./*Callialasporites* spp. complex
Cerebropollenites mesozoicus (Couper, 1958) Nilsson, 1958
Classopollis spp.
Ginkgocycadophytus nitidus (Balme, 1957) De Jersey, 1962
Perinopollenites elatoides Couper, 1958
Exesipollenites complex: this complex comprises *E. tumulus* Balme, 1957, *E. scabratus* (Couper, 1958) Pocock, 1970 and *E. scabrosus* Norris, 1969
Vitreisporites pallidus (Reissinger, 1938) Nisson, 1958

REFERENCES
Baron, H. 1989. Dinoflagellate cyst biostratigraphy and palaeoenvironments of Upper Jurassic (Kimmeridgian to basal Portlandian) of the Helmsdale region, east Sutherland, Scotland. *In* Batten, D. J. & Keen, M. C. (Eds), *Northwest European Micropalaeontology and Palynology* 193–213. British Micropalaeontological Society Series Ellis Horwood Ltd, Chichester.
Batten, D. J. & Lister, J. K. 1988. Early Cretaceous dinoflagellate cysts and chlorococcalean algae from freshwater and low salinity palynofacies in the English Wealden. *Cretaceous Research*, **9**: 337–367.
Below, R. 1981. Dinoflagellaten-Zysten aus dem oberen Hauterive bis unteren Cenoman Sud-West-Marokkos. *Palaeontographica*, Abt.B, **176**: 1–145.
Bernier, P. & Courtinat, B. 1979. Le microplancton (*Leiosphaeridae*) et la matière organique des calcaires d'arrière-récif du Kimméridgien supérieur dans le Jura méridional. Systématique, conditions de génèse et d'environnement. *Document du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **75**: 95–117.
Bird, D.F & Karl, D. M. 1992. Prasinophyte bloom in the northern Gerlache Strait. Abstracts 1992 Annual meeting of the Phycological Society of America. *Journal of Phycology*, **28**: 16.
Brenner, W. 1988. Dinoflagellaten aus dem Unteren Malm (Oberer Jura)

von Süddeutschland; Morphologie, Ökologie, Stratigraphie. *Tübinger Mikro-paläontolgische Mitteilungen*, **6**: 1–118.

Bujak J. P. & Davies, E. H 1983. Modern and fossil Peridiniineae. *Americain Association of Stratigraphic palynologists*, Contribution series **13**: 1–203.

Courtinat, B. 1989. Les organoclastes des formations lithologiques du Malm dans le Jura méridonal. Systématique, biostratigraphie et éléments d'interprétations paléoécologique. *Documents des laboratoires de géologie Lyon*, **105**: 1–361.

Cox, B. M., Lott, G. K., Thomas, J. E. & Wilkinson, I. P. 1987. Upper Jurassic chronostratigraphy and age indicators for the UK. *In* Hardman, R. F. P. & Brooks, J. R. V. (Eds), *Tectonic Events Responsible for Britain's Oil and Gas Reserves*, 169–190. Geological Society, London Special Publications **55**.

Dodekova, L. 1992. Dinoflagellate cysts from the Bathonian-Tithonian (Jurassic) of North Bulgaria. II. Taxonomy of Oxfordian and Kimmeridgian dinoflagellate cysts. *Geologica Balcanica*, **22**: 33–69.

Dodekova, L. 1994. Dinoflagellate cysts from the Bathonian-Tithonian (Jurassic) of North Bulgaria. III. Tithonian dinoflagellate cysts. *Geologica Balcanica*, **24**: 11–46.

Downie, C. 1957. Microplankton from the Kimmeridge Clay. *Quarterly journal of the Geological Society of London*, **112**: 413–434.

Drugg, W. S. 1978. Some jurassic dinoflagellate cysts from England, France and Germany. *Palaeontographica*, Abt. B, **168**: 61–79.

Dürr, G. 1988. Palynostratigraphie des Kimmeridgium und Tithonium von Süddeutschland und Korrelation mit borealen Floren. *Tübinger Mikro-paläontolgische Mitteilungen*, **5**: 1–159.

Erkmen, U. & Sarjeant, W. A. S. 1980. Dinoflagellate cysts, acritarchs and tasmanitids from the Uppermost Callovian of England and Scotland: with a reconsideration of the '*Xanthidium pilosum*' problem. *Geobios*, **13**: 45–99.

Evitt, W. R. 1985. Sporopollenin Dinoflagellate Cysts: Their Morphology and Interpretation. *Americain Association of Stratigraphic Palynologists Foundation*, 1–333.

Feist-Burkhardt, S. & Wille, W. 1992. Jurassic palynology in southwest Germany – state of the art. 8th International Palynological Congress, Aix-en-Provence. *Cahiers de Micropaléontologie*, **7**: 141–156.

Feist-Burkhardt, S. & Pittet, B. 1996. Dinoflagellate cyst distribution patterns in Upper Oxfordian shallow marine carbonates and marls from the Swiss Jura Mountains. Program and Abstracts. *Ninth International Palynological Congress*, 23–28 June, 1996, Houston, Texas, 42.

Fisher, M. J. & Riley, L. A. 1980. The stratigraphic distribution of dinoflagellate cysts at the boreal Jurassic–Cretaceous boundary. *IVth International Palynological Conference, Lucknow (1976-1977)*, **2**: 313–329.

Gitmez, G. U. 1970. Dinoflagellate cysts and acritarchs from the basal Kimmeridgian (Upper Jurassic) of England, Scotland and France. *Bulletin of the British Museum Natural History (Geology)*, **18**: 233–331.

Gitmez, G. U. & Sarjeant, W. A. S. 1972. Dinoflagellate cysts and acritarchs from the basal Kimmeridgian (Upper Jurassic) of England, Scotland and France. *Bulletin of the British Museum (Natural History) Geology*, **21**: 173–257.

Ioannides, N. S., Colin, J. P. & Jan Du Chéne, R. 1988. A preliminary investigation of Kimmeridgian dinoflagellates and ostracodes from Quercy, Southwest France. *Bulletin des Centres de Recherches Exploitation-Production Elf-Aquitaine*, **12**: 471–491.

Ioannides, N. S., Stavrinos, G. N. & Downie, C. 1976. Kimmeridgian microplankton from Clavell's Hard, Dorset, England. *Micropaleontology*, **22**: 443–478.

Jain, K. P. & Millepied, P. 1976. Cretaceous microplankton from Senegal Basin, N.W. Africa. 1. Some new genera and combinations of dinoflagellates. *Paleobotanist*, **20**: 22–32.

Kunz, R. 1990. Phytoplankton und Palynofazies im Malm NW-Deutschlands (Hannoversches Bergland). *Palaeontographgica*, Abt. B, **216**: 1–105.

Lentin, J. K. & Williams, G. L. 1976. A monograph of fossil peridinoid dinoflagellate cysts. *Bedford Institute of Oceanography*, **Report Series BI-R-75-16**: 1–237.

Lentin, J. K. & Williams, G. L. 1985. Fossil dinoflagellates: index to genera and species, 1985 edition. *Canadian Technical Report of Hydrography and Ocean Sciences*, **60**: 1–449.

Lord, A. R., Cooper, M. K. E., Corbett, P. W. M. *et al.* 1987. Microbiostratigraphy of the Volgian Stage (Upper Jurassic), Volga River, USSR. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1987**: 577–605.

Monteil, E. 1991. Morphology and sytematics of the ceratioid group: a new morphographic approach. Revision and emendation of the genus *Muderongia* Cookson & Eisenack 1958. *Bulletin des Centres de Recherches Exploitation-Production Elf-Aquitaine*, **15**: 461–505.

Norh-Hansen, H. 1986. Dinocyst stratigraphy of the Lower Kimmeridge Clay, Westbury, England. *Geological Society of Denmark Bulletin*, **35**: 31–51.

Poulsen, N. E. 1991. Upper Jurassic dinocyst stratigraphy in the Danish Central Trough. *In* Michelsen, O. & Frandsen, N (Eds), *Jurassic stratigraphy in the southern Central Trough. Geological Survey of Denmark, Ser. B*, **16**: 7–15.

Poulsen, N. E. 1992. Jurassic dinoflagellate cyst biostratigraphy of the Danish Subbasin in relation to sequences in England and Poland; a preliminary review. *Review of Palaeobotany and Palynology*, **75**: 33–52.

Poulsen, N. 1993. Dinoflagellate cyst biostratigraphy of the Oxfordian and Kimmeridgian of Poland. *Acta Geologica Polonica*, **43**: 251–272.

Poulsen, N. E. 1994a. Dinoflagellate cyst biostratigraphy of the late Jurassic of Poland. *Geobios*, spec. mem. **17**: 401–407.

Poulsen, N. E. 1994b. Dinoflagellate cyst biostratigraphy of Rhaetian-Ryazanian (uppermost Triassic–lowermost Cretaceous) deposits from the Danish Subbasin. *Geobios*, spec. mem. **17**: 409–414.

Poulsen, N. 1996. Dinoflagellate cysts from marine Jurassic deposits of Denmark and Poland. *American Association of Stratigraphic Palynologist*, **31**: 1–227.

Prauss, M. 1989. Dinozysten-Stratigraphie und Palynofazies im oberen Lias und Dogger von NW-Deutschland. *Palaeontographica*, Abt. B, **214**: 1–124.

Raynaud, J.-F. 1978. Principaux dinoflagellés charactéristiques du Jurassique supérieur d'Europe du Nord. *Palinologia*, Numero extraordinario, **1**: 387–405.

Riding, J. B. 1987. Dinoflagellate cyst stratigraphy of the Nettleton Bottom Borehole (Jurassic: Hettangian to Kimmeridgian), Lincolnshire, England. *Proceedings of the Yorkshire Geological Society*, **46**: 231–266.

Riding, J. B. & Thomas, J. E. 1988. Dinoflagellate cyst stratigraphy of the Kimmeridge clay (Upper Jurassic) from the Dorset coast, Southern England. *Palynology*, **12**: 65–88.

Riding, J. B. & Thomas, J. E. 1992. Dinoflagellate cysts of the Jurassic system. *In*: Powell, A. J. (Ed.), *A stratigraphic Index of dinoflagellate cysts*, 7–98. Chapman & Hall, London.

Schrank, E. 1984. Organic-walled microfossils and sedimentary facies in the Abu Tartur phosphates (Late Cretaceous, Egypt). *Berliner Geowissenschaftlichen Abhandlungen*, **A50**: 177–187.

Stover, L. E. & Evitt, W. R. 1978. Analyses of Pre-Pleistocene Organic-walled Dinoflagellates. *Stanford University Publications, Geological Sciences*, **15**: 1–300.

Tyson, R. V. 1995. *Sedimentary organic matter. Organic facies and palynofacies*. Chapman & Hall, London, 615pp.

Woollam, R. & Riding, J. B. 1983. Dinoflagellate cyst zonation of the English Jurassic. *Institute of Geological Sciences, Natural Environment Research Council*, **Report 83/2**: 1–41.