

Palynology of the Late Berriasian to Early Hauterivian of the Tethyan Realm in SE France: biostratigraphy and taxonomy of the Vergol (Montbrun-les-Bains) and La Charce (Serre de l'Âne) sections, Vocontian Basin

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ABSTRACT: Quantitative palynofloral analysis of late Berriasian to early Hauterivian aged sediments from the Vocontian Basin of southeast France has involved fifty-four outcrop samples from Vergol (Montbrun-les-Bains) and twenty-seven from La Charce (Serre de l'Âne). All samples were marls except for two from the early Valanginian Barrande layers, thin black layers rich in organic carbon. Sampling was focused particularly on the Berriasian/Valanginian, early/late Valanginian and Valanginian/Hauterivian boundaries with two of these particularly important as La Charce is the GSSP for base Hauterivian and Vergol is a GSSP candidate for base Valanginian. Although little has been previously published on the palynology of the Vocontian Basin, this study has benefitted from many previous multi-disciplinary studies in the area; the numerous palynofloral events recorded are tied closely to the standard ammonite zonation. Analyses were mainly focused on the dinocysts, but miospores have also been considered in terms of their palaeoenvironmental response, allowing broad assessment of relative sea level changes. Some linkage between peaks in coastal/lowland ratios, the $\delta^{13}\text{C}$ curve through the Weissert carbon isotope excursion (CIE) and the *Muderongia* group (possible reduced salinity) have been shown. A new dinocyst zonation scheme is proposed, involving twelve zones, eight of which cover the Valanginian; previous schemes are briefly discussed. Two genera, twenty-three species and five subspecies of stratigraphically-significant dinoflagellate cysts are described as new, two genera have been emended and thirteen new combinations have been proposed. The diagnosis of one acritarch genus has been emended and two new combinations effected.

Keywords: Palynology, taxonomy, biozonation, dinocysts, miospores, Berriasian, Valanginian, Hauterivian, Vocontian Basin, Vergol, La Charce.

INTRODUCTION and BACKGROUND

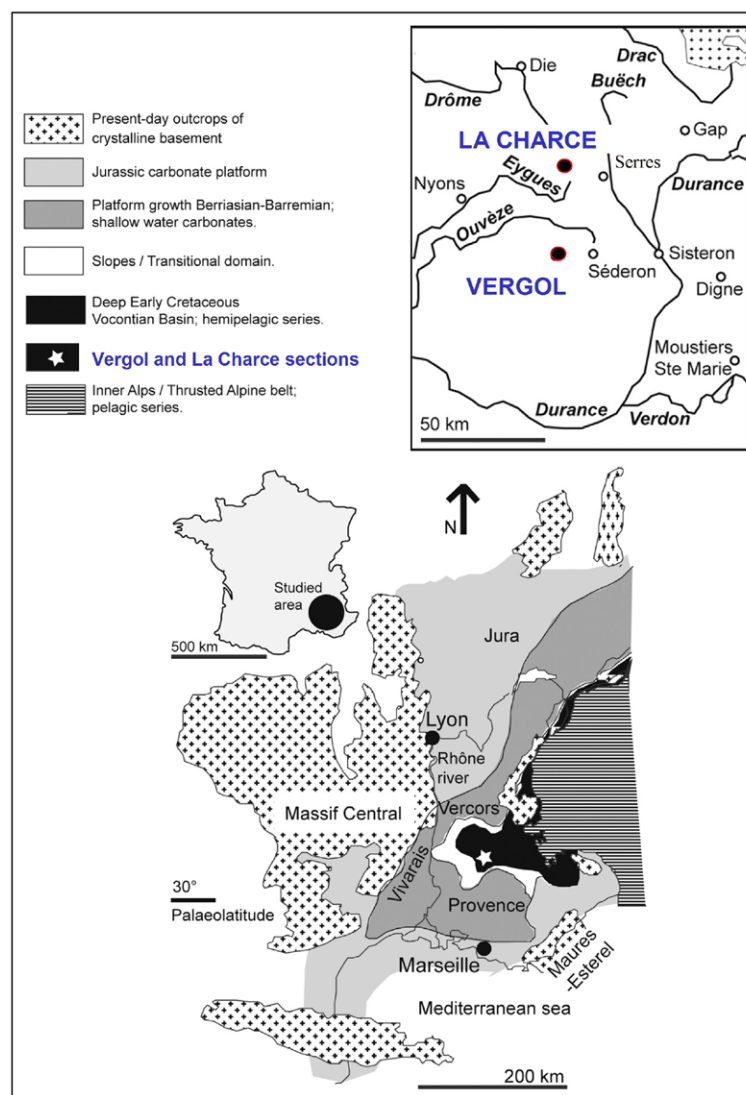
This study describes the palynoflora of an upper Berriasian to lower Hauterivian interval in southeast France, using samples from the Vergol and La Charce sections (text-fig. 1); this encompasses the whole of the Valanginian. Its aim is essentially descriptive, although comments are made on the potential local stratigraphic value of individual taxa, on previous work in the area and on observed ranges in more northerly settings, at the Speeton outcrop and in the UK Central North Sea (Duxbury 1977; 1980; 2018; 2023). Both Vergol and La Charce are situated within the Vocontian Basin (text-fig. 1), an area which was surrounded by an isolated carbonate platform system open to the Western Ligurian Tethys Ocean to the east (Masse 1993).

Macrofossils, mainly ammonites, are abundant in the Vocontian Basin, and an ammonite-based stratigraphical framework has been developed over several decades. Contributions by many workers have developed the ammonite zonation into a robust scheme. The latest, "standard zonation" (Reboulet et al. 2018) is applied here, updated according to the 2022 Warsaw meeting of the Kilian Group and modified around the Berriasian/Valanginian boundary after Kenjo (2014) and Kenjo et al. (2021) (text-fig. 2). For the younger section it is based on Reboulet (1996), Reboulet et al. (2003) and Reboulet and Rard (2008).

Sedimentation throughout the studied interval consists of alternating limestone/marl couplets which are largely continuous within this basin and so can be correlated over a large area (Cotillon et al. 1980). They have been interpreted as the result of calcareous nannoplankton production cycles caused by climatic fluctuations of Milankovitch frequency (Cotillon et al. op. cit.; Giraud 1995). Duchamp-Alphonse et al. (2007) also considered variations in the limestone/marl ratio to be due to fluctuations in nannofossil productivity, but in this case driven by nutrient levels ultimately associated with varying levels of atmospheric CO_2 .

Climatic variations at a Milankovitch scale were also inferred (but for England and Germany) by Mutterlose and Ruffell (1999) who explained alternations of pale layers and dark clay levels as deposited respectively under warm, oligotrophic surface waters and cooler, eutrophic conditions.

Reboulet et al. (2003) proposed a model of dilution cycles through the export of carbonate mud from the surrounding shallow platforms to the Vocontian Basin and Gréselle et al. (2011, p. 51) stated, that "the Valanginian marl-limestone alternations of the Vocontian Basin resulted from changes in the amount of platform derived carbonate mud shed into the basin" as "sea level fluctuations controlled the distal-to-proximal migration of facies belts from offshore to shoreface environments".



TEXT-FIGURE 1

Location map of the Vergol and La Charce sections (Montbrun-les-Bains and Serre de l'Âne, Drôme, France) and palaeogeographic map of the Vocontian Basin (after Ferry 1991).

Reduction in limestone production, particularly in the *verrucosum* Zone, is associated with the Weissert Event, a positive excursion in the $\delta^{13}\text{C}$ curve discussed by many authors, including Bornemann and Mutterlose (2008), Charbonnier et al. (2014), Cotillon and Rio (1984), Duchamp-Alphonse et al. (2007), Erba et al. (2004), Gréselle et al. (2011), Mattioli et al. (2014), McArthur et al. (2007), Reboulet (2015) and Weissert (1989). The consensus appears to be that this $\delta^{13}\text{C}$ excursion is a consequence of Paraná-Etendeka volcanic activity (flood basalts associated with the break-up of Pangaea), triggering a significant increase in atmospheric CO_2 (Martinez et al. 2015; Peate 1997), although McArthur et al. (2007, p. 413) stated, "We conclude, given the available evidence, that the carbon-isotope excursions seen in our sections are not related to Paraná-Etendeka volcanism".

Duchamp-Alphonse et al. (2007), considering this positive excursion, stated that, "In such a scenario, nitrification is a domi-

nant factor controlling neritic and hemipelagic biocalcification. However, one cannot exclude that the global increase of atmospheric CO_2 could generate chemical changes of the sea-surface waters, acting with the nitrification, to modify the biocalcification of the carbonate producers".

Although the limestone/marl alternations are often monotonous, some bed groupings stand out including the "Otopeta bundle" within the *alpillensis* Zone and the "Faisceau Médian" of Cotillon et al. (1980), within the *peregrinus* Zone (text-figs. 3, 4), allowing some regional lithological correlation.

A section towards the base of the *inostranzewi* Zone, has four centimetre-scale black beds (text-fig. 3) termed the Barrande layers (B1 to B4; Reboulet 2001; 2015; Reboulet et al. 2003; Janssen 2021) which are discussed below.

Reboulet et al. (2003) undertook a detailed, multidisciplinary

STAGES		ZONES	SUBZONES	HORIZONS
HAUTERIVIAN	upper	<i>"Pseudothurmannia ohmi"</i>	<i>Pseudothurmannia picteti</i>	
			<i>Pseudothurmannia catulloi</i>	
			<i>"P. ohmi"</i>	
		<i>Balearites balearis</i>	<i>Spathicrioceras seitzii</i>	
			<i>Crioceratites krenkeli</i>	
			<i>Binelliceras binelli</i>	
	lower	<i>Plesiospitidiscus ligatus</i>	<i>B. balearis</i>	
		<i>Subsaynella sayni</i>		<i>Subsaynella begudensis</i>
				<i>Cruasicerias cruasense</i>
		<i>Lyticoceras nodosoplicatum</i>		<i>Olcostephanus (Olcostephanus) variegatus</i>
VALANGINIAN	upper	<i>Criosarasinella furcillata</i>	<i>Teschenites callidiscus</i>	
			<i>C. furcillata</i>	
		<i>Neocomites peregrinus</i>	<i>Olcostephanus (Olcostephanus) nicklesi</i>	
			<i>N. peregrinus</i>	
	lower	<i>Saynoceras verrucosum</i>	<i>Karakaschiceras pronecostatum</i>	
			<i>S. verrucosum</i>	
		<i>Karakaschiceras inostranzewi</i>	<i>Neocomites platycostatus</i>	
			<i>K. inostranzewi</i>	
		<i>Neocomites neocomiensiformis</i>	<i>Busnardoites campylotoxus</i>	
			<i>Neocomites neocomiensiformis</i>	
		<i>"Thurmanniceras" pertransiens</i>	<i>Neolissoceras (Vergolicerias) salinarium</i>	
			<i>Neocomites premolicus</i>	
BERRIASIAN	upper	<i>Tirnovella alpillensis</i>	<i>"Thurmanniceras" otopeta</i>	
			<i>T. alpillensis</i>	
		<i>Fauriella boissieri</i>	<i>Berriasella picteti</i>	
			<i>Malbosiceras paramimoumum</i>	
	middle	<i>Subthurmannia occitanica</i>	<i>Dalmasiceras dalmasi</i>	
			<i>Berriasella privasensis</i>	
			<i>Subthurmannia subalpina</i>	
	lower	<i>Berriasella jacobi</i>		

TEXT-FIGURE 2

The ammonite zonation scheme applied to the study area, conforming to the standard zonation of the IUGS Kilian group (Reboulet et al. 2018), updated during their last meeting held in Warsaw (August 2022).

study over a 4.5 m interval at Vergol (see also Reboulet 2015) to, "quantify the pelagic carbonate fraction produced by nannofossils in order to test if nannoplankton productivity was the main mechanism for the formation of the marl-limestone alternations recorded in the Vocontian Basin". They concluded that:

- Nannofossils did not produce the bulk of carbonates in the limestone beds.
- Dilution by allochthonous carbonate mud was probably the main factor controlling the marl-limestone formation and nannofossil abundance.
- Nannofossil abundance decreases with increasing carbonate content.
- Peaks in nannofossil abundance are very often linked to periods

of reduced sediment accumulation rate.

- Dilution could partly explain the variation in abundance of the macrofauna which is generally greater in marls than in limestones. Dilution by imported carbonates seems to be much more important than dilution by clays.

Vergol (Montbrun-les-Bains)

Vergol (05°25'01"E - 43°12'27"N) is situated to the north of Montbrun-les-Bains, Drôme and upper Berriasian and Valanginian rocks are particularly well-exposed in the area. Details of bed numbers can be found in Reboulet (1996; 2015; 2017a; 2017b), McArthur et al. (2007), Janssen (2009; 2021), Kenjo (2014) and Kenjo et al. (2021).

The position of the Berriasian/Valanginian boundary at Vergol has been a matter of debate - for full discussion of this see Reboulet (2015) and Kenjo et al. (2021). Essentially, Kenjo et al. (2021) re-assessed the base of the "*T. pertransiens* ammonite Zone at Vergol, placing it deeper than previously defined, and they included the "*T. otopeta* ammonite Sub-zone in the Berriasian (text-fig. 2). This is important as schemes used previously by various dinocyst workers including Monteil (1992a, b; 1993) and Leereveld (1997a) included the "*T. otopeta* Sub-zone in the Valanginian. Also, the numbering of beds at Vergol uses two prefixes, "B" and "V" for "Berriasian" and "Valanginian" respectively (text-fig. 3), but because of subsequent re-positioning of the boundary, beds B136 to B151 are now within the early Valanginian.

The sedimentation at Vergol is predominantly limestone in the late Berriasian (*alpillensis* Zone) and early Valanginian (*pertransiens* Zone), with the latest Berriasian characterised by a limestone-dominated interval of 12 calcareous beds, B118 to B129, the "Otopeta bundle", located just below the Berriasian/Valanginian boundary (Kenjo 2014; Kenjo et al. 2021) (text-fig. 3). It becomes more clayey above and is predominantly marl in the interval around the early/late Valanginian boundary. The lithological succession becomes predominantly limestone again in the *peregrinus* Zone, with the Faisceau Médian at the base of that zone (text-figs. 3, 4).

Two slumps have been recorded at Vergol (text-fig. 3), one c.12m thick between Beds V43 and V45 (Kenjo 2014) and one c.8m thick between Beds V96 and V98 (Reboulet 1996). Regionally, analysis of contemporaneous but undisturbed sections can mitigate the "missing" section caused by slumping (see Kujau et al. 2013, fig. 2 and Janssen 2021, fig. 4).

La Charce (Serre de l'Âne)

The La Charce section is located in the La Charce commune, Drôme, about 70 km southeast of Valence and approximately 35 km south of Die (text-fig. 1). La Charce was proposed as the Hauterivian stratotype by Thieuloy (1977) who defined the base of the stage there by the first occurrence (FO) of the ammonite genus *Acanthodiscus*. After considerable discussion (see Mutterlose et al. 2021), The Global Boundary Stratotype Section and Point (GSSP) for the base of the Hauterivian Stage has been defined at the base of La Charce Bed 189 (Reboulet et al. 1992; Mutterlose et al. 2021).

La Charce is close to Vergol (text-fig. 1) and to some extent there is overlap between the two sections, allowing detailed bed by bed correlation of the similar marl/limestone couplets deposited in a relatively deep environment.

The Hauterivian Stage was designated by Renevier (1874) at Hauterive, near Neuchâtel, Switzerland, a section with sometimes condensed beds, poor exposure and rare ammonites (Rawson et al. 1978; Mutterlose et al. 1996). Debelmas and Thieuloy (1965) recommended the erection of a paras-tratotype in the Hautes-Alpes (Vocontian Basin) of southeast France, and a modified ammonite zonation was presented by Moullade and Thieuloy (1967) - see Duxbury 2023, Table 1. That scheme has seen minor modification subsequently and it remains unchanged for that part of the section analysed here (text-fig. 2).

Various advantages and disadvantages to using *Acanthodiscus* to mark the base of the Hauterivian were listed by Mutterlose

et al. (2021, p. 130), including its absence or rarity in various sub-realms. In northwest Europe the first appearance of *Endemoceras* has been taken to mark the base of the Hauterivian, although as noted by Kemper et al. (1981, p. 307), "As the earliest *Acanthodiscus* so far known from the *Endemoceras* Beds is from the upper part of the *amblygonium* Zone it is possible that the lower *amblygonium* Zone is late Valanginian".

However, Bulot et al. (1993, p. 39) considered the German specimens to be forms of *Acanthodiscus* comparable to those from the middle of the *radiatus* Zone in southeast France, consistent with placement of the base of the Hauterivian at the base of the *amblygonium* Zone.

Mutterlose (1996, p. 19) felt that, "The value of *Acanthodiscus* lies in its presence in shallow water facies both in the Tethys and the Boreal Realm, though it is rare in the deeper-water facies", although this genus is absent from the marginal marine Speeton section below Bed C9C (mid *regale* Zone). Rawson et al. (1978, p. 12) argued that the *Endemoceras amblygonium* Zone at Speeton (Unit D2) appears to be entirely Hauterivian on microfaunal evidence (Neale 1960; Fletcher 1973). For further comments on the Hauterivian at Speeton, see Duxbury (2023, p. 114, 115).

The La Charce succession analysed in the current work complements the Vergol material, extending the studied section across the Valanginian/Hauterivian boundary, with a small overlap as old as the *verrucosum* Zone (text-figs. 3, 4). The marly *verrucosum* Zone underlies the Faisceau Médian (also present at the top of the studied Vergol section) which is again clearly defined. Above the Faisceau Médian, the rest of the upper Valanginian is marly, becoming more limestone-rich before a significant increase in limestones at the base of the Hauterivian.

There are two prominent slumps in the early Hauterivian at La Charce, at the top of the *radiatus* Zone (text-fig. 4) and at the *lo-ryi/nodosoplicatum* ammonite zone boundary (Reboulet 1996). Only the older of these was within the studied section here. As with Vergol, these slumped intervals can be "reconstructed" using adjacent, undisturbed sections.

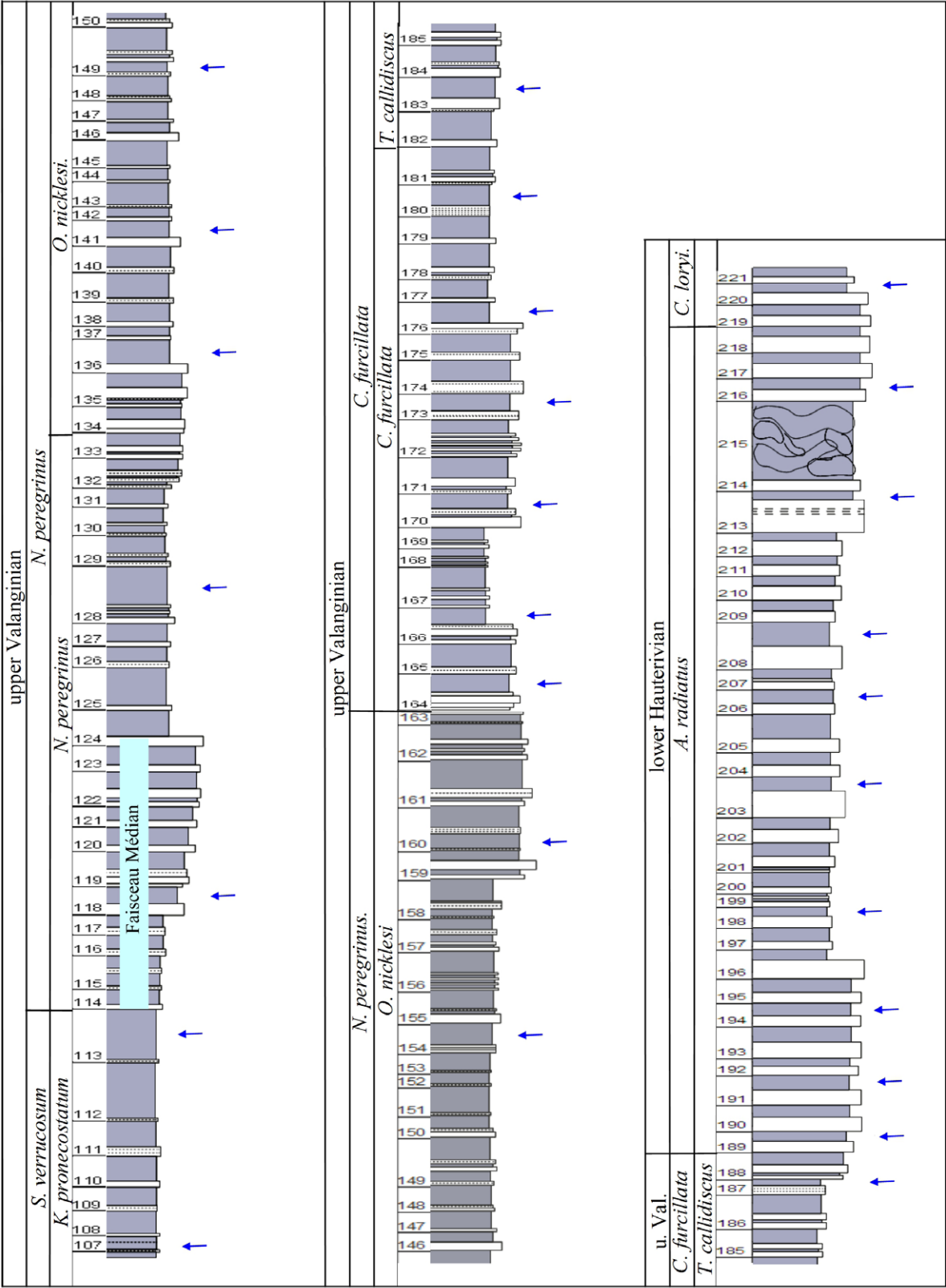
Two different bed numbering systems exist at La Charce, one after Reboulet et al. (1992), the other after Bulot et al. (1993). For simplicity, only the first has been used here.

The Barrande layers (see also Appendix 3)

The early Valanginian Barrande layers are clearly exposed at Vergol within the *inostranzewi* Zone, *inostranzewi* Sub-zone (text-figs. 5A, B). These thin black layers have undisturbed lamination, are rich in organic carbon (TOC from 1.9% to 3.7%), "and are located at the base (or just before) the Weissert isotopic event" (Reboulet 2015). Kujau et al. (2012) suggested that the Barrande layers pre-date their carbon isotope excursion (CIE) Segment II by approximately 180K years (see Kujau et al. 2012, fig. 2A). Barrande layers B1, B2 and B3 are included in Vergol Bed V87 and layer B4 is in Bed V88 (text-fig. 3).

According to Kujau et al. (2012), fine-scale lamination, "can be interpreted to reflect unfavourable conditions for bottom-dwelling detritivores". However, Courtinat (1998) commented that, "Mesozoic scolecodonts in black shales argue for suboxic deposits. Their presence is evidence of benthic life.

The stratigraphy of the Vergol section showing the alternation between limestones (white) and marl (dark) beds and the positions of the Otopeta bundle, Barrande layers, la Tétrade (T) and Faisceau Médian. Samples analysed are indicated by arrows.



TEXT-FIGURE 4
The stratigraphy of the La Charce section showing the alternation between limestones (white) and marl (dark) beds and the position of the Faisceau Médian. Samples analysed are indicated by arrows.

Errantida polychaete annelids rework sediment, though they have in some cases been found in laminated sediments devoid of bioturbation. The burrows of such organisms may disappear after compaction and thus the presence of scolecodonts is not incompatible with the apparent absence of microbioturbation (Courtinat and Howlett 1990)".

Reboulet et al. (2003) concluded that:

- The Barrande layers, except B2, probably correspond to unfavourable conditions for the nannoplankton.
- The high abundance and dominance of bochianitids (orthocone ammonoids) in layer B4 may reflect a deep-nektonic, possibly nektobenthic, mode of life, including feeding incursions to bottom waters when trophic resources were higher there than in surface waters.
- High trophic conditions at the sea bed during deposition of layer B4 were confirmed by abundant benthic macrofauna.

Reboulet et al. (op. cit.) recorded various differences between layers B1 to B3 and layer B4, including, "Bioturbation of organic carbon-rich layer B4 is more developed and exhibits a diversified assemblage" and "The ichnofauna of B4 is more diversified and larger than in the other organic carbon-rich layers, and may be the result of relatively more oxygenated conditions in the sediment (upper dysaerobic)".

Mattioli et al. (2014) studied the Barrande interval as part of a detailed analysis of mid-Valanginian nannoplankton, applying principal component analysis (PCA) to process and interpret nannofossil assemblages. They concluded that:

- Maximum values of the pristane/phytane ratio characterise the interval containing the Barrande layers and may indicate enhanced stratification of the water column.
- Water stratification likely produced poor ventilation of the basin and favoured the development of dysoxic/anoxic conditions.
- Organic matter preservation in the Barrande layers was mainly due to water mass stratification, as attested by high pristane/phytane ratios and peaks in the abundance of robust coccoliths when the nutricline was deep.
- All parameters indicate that a major crash in primary production occurred during deposition of the Barrande layers. Nannofossil abundance and richness are especially low in this interval, as well as dinosterane/regular sterane attesting for low productivity of the major phytoplanktonic groups.

In this, Mattioli et al. appear to contradict some of the conclusions of Reboulet et al. (2003), particularly the last authors' record of abundant benthic macrofauna (highly trophic sea bed conditions) in layer B4. They also imply low dinoflagellate productivity (low dinosterane levels) which did not appear to be the case for layers B1 and B4, the only Barrande layers analysed in the present study - although see Appendix 3.

Kujau et al. (2012) cited less-oxygenated bottom waters and enhanced productivity during the formation of the Barrande layers but stated that the environment of deposition did not reach euxinic conditions. They also stated (op. cit., p. 100), "Since diatoms did not diversify significantly until the Late Cretaceous (Round et al., 1990) dinosterane can be assigned to dinoflagellate input in this case" and that (p. 101), "In the Barrande layers the contribution of dinoflagellates to the eukaryotic community is reduced according to the ratio of dinosterane to regular steranes, pointing

to unfavourable conditions for this group of organisms. The observed biomarker pattern favours a scenario with increased eukaryotic algal and cyanobacterial contribution and limited dinoflagellate productivity for the four organic-rich Barrande layers". They also found that, "no distinct difference between the four layers can be observed with respect to the biomarker patterns". Neither Mattioli et al. nor Kujau et al. analysed organic-walled microplankton directly.

In the present study, analysis of Barrande layers B1 and B4 allows the following observations:

- there was a marked contrast in the palynofloras of layers B1 and B4 although dinoflagellate cysts predominated in both.
- the most common dinocyst taxa in layer B1 were *Circulodinium hirtellum*, *Muderongia simplex*, *M. extensiva* and *Systematophora? cf. scoriacea*.
- the most common dinocyst taxa in layer B4 were *Batioladinium cf. varigranulosum*, *Chlamydomphorella* spp., *Cribroperidinium* spp. and *Dapsiladinium warrenii*.
- dinocyst diversity increased significantly between layers B1 and B4 from 42 to 59 taxa and there was an associated reduction in the proportion of coastal:lowland miospores from 70:30 to 27:73.
- miospores were abundant in layer B4, dominated by bisaccate pollen but including common *Cyathidites* spp. They were relatively rare in layer B1.
- scolecodonts were present in layer B4 but not in layer B1.

Wilpshaar and Leereveld (1994) noted that high abundances of their *Muderongia* Group have been reported in sediments representing variable salinity conditions (e.g., Lister and Batten 1988). It may be the case therefore that high numbers representing that group in layer B1 may reflect conditions of relatively reduced surface water salinity or derivation from such a setting.

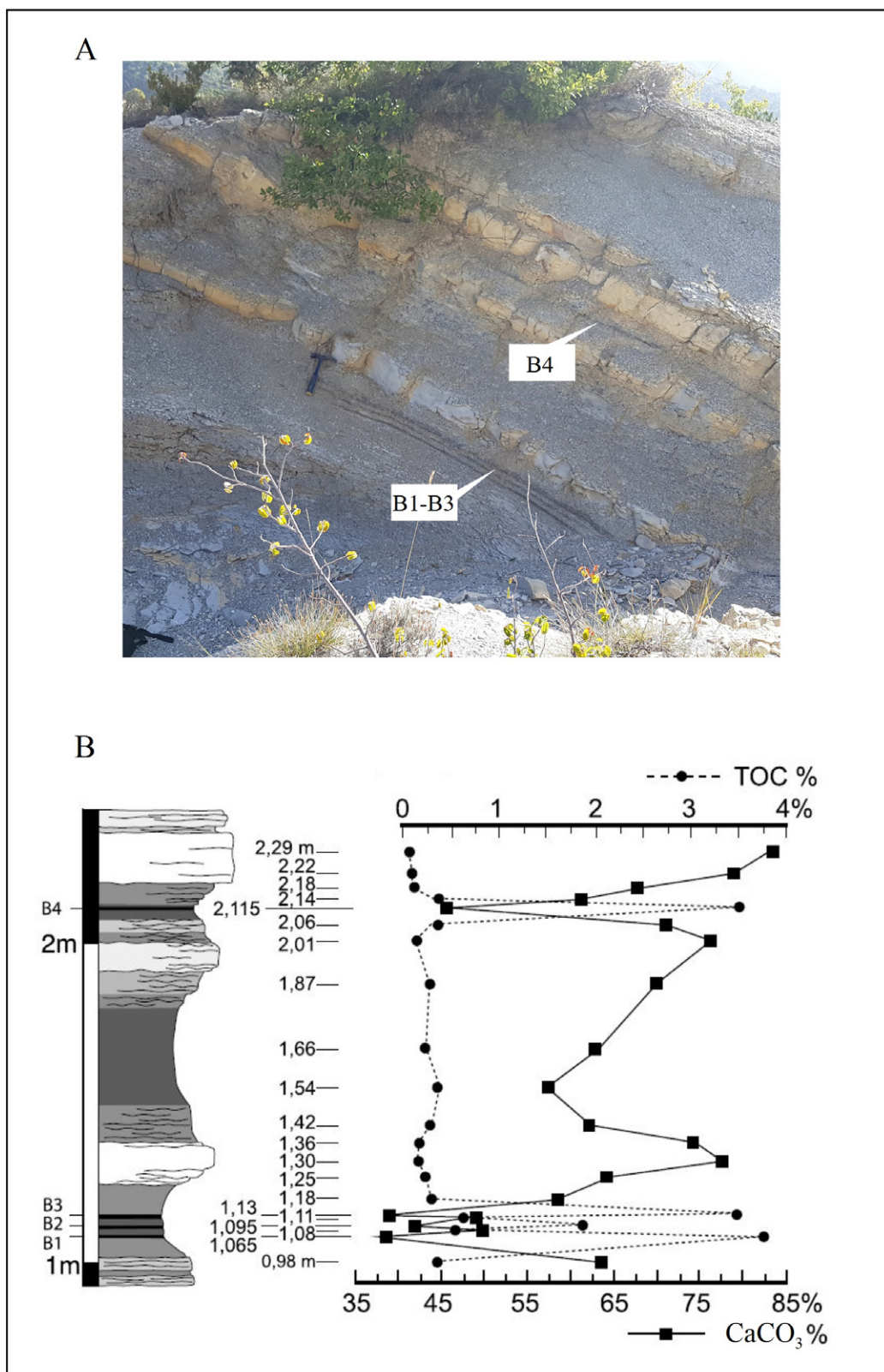
However, for reasons fully discussed in Abbink (1998), the relationship between coastal and lowland miospores can also be taken as a proxy for sea level change. This is mainly because of the relative loss of lowland habitat during sea level rise and the opposite effect during regressions. This might suggest a sea level fall between layers B1 and B4, counter-intuitive to the presence of high numbers of lower-salinity forms at the older level.

Palynofloral results from Barrande layers B1 and B4 do not support Kujau et al.'s (2012) conclusions that the Barrande layers were deposited under unfavourable conditions for dinoflagellates or that distinct differences between the four layers can not be observed.

Neither do they fully support Mattioli et al. (2014). There are clearly significant differences between these layers, as already described by Reboulet et al. (2003).

MATERIALS and METHODS

Fifty-four samples from the Vergol outcrop were palynologically analysed in the present study between the late Berriasian, *alpillensis* Zone and the late Valanginian, *peregrinus* Zone and twenty-seven were analysed from La Charce, between the late Valanginian, *verrucosum* Zone and the early Hauterivian, *loryi* Zone, thereby covering the entire Valanginian interval and its boundaries. Sample spacing was adjusted to give added emphasis to stage and substage boundaries. Sampling was restricted to marls in order to optimise palynomorph recovery, and in the following discussions samples are referred to with prefixes "V" for



TEXT-FIGURE 5

The Barrande layers, four highly carbonaceous centimetre-scale black horizons towards the base of the *K. inostranzewi* Zone at Vergol. 5A the outcrop (from Janssen 2021) and 5B percentages of CaCO₃ and TOC through the Barrande interval (from Reboulet et al. 2003).

Vergol and "LCH" for La Charce, and the suffix "M" for marl. Exceptions are samples from Barrande layers B1 and B4, which are referred to as V87 and V88 respectively.

All samples were prepared according to standard palynological methods: disaggregation of the sediments, removal of carbonates and silicates with HCl and HF respectively, sieving and separation of organic material, oxidising with fuming nitric acid and/or Schultze reagent (as necessary) and preparation of slides. A combined count of 500 specimens per sample was made of all palynomorphs observed (dinocysts, acritarchs, miospores, etc.), allowing a marine percentage to be calculated. The count of marine taxa was then increased to 500 per sample, allowing better resolution of this important sub-set. Rich, diverse dinocyst assemblages were present throughout the sections analysed and these dominated the palynofloras.

Fully quantitative analysis has allowed some assessment of the relative abundance of individual taxa through time and compared to others. Comments are included below on the first occurrences (FO's), last occurrences (LO's) and relative abundances of individual species. The terms FO and LO are used here in preference to FAD and LAD (first and last appearance datums) because of the significant differences observed between some of these events and similar events in Boreal settings so that many true first and last appearances remain to be confirmed. Key dinocyst events were plotted against the lithostratigraphy and the standard ammonite scheme (text-fig. 2) in text-figs. 6 and 7.

Individual miospore taxa tend to be long-ranging but prone to palaeoenvironmental control so that, although not particularly valuable individually, analysis of assemblage changes can provide some insights, as outlined in the Sporomorph EcoGroup (SEG) approach of Abbink (1998). This approach has been applied here and incorporated into various discussions below.

SYSTEMATICS

Several previously undescribed and stratigraphically valuable dinocyst taxa were recorded during the present study, and the following section includes descriptions of two new genera, twenty-three new species and five new subspecies. Two dinocyst genera have been emended and thirteen new combinations have been effected. The diagnosis of one acritarch genus has been emended together with two new combinations. Taxa are treated alphabetically below under their respective groupings.

All type and figured specimens, including holotypes and paratypes from Vergol and La Charce are curated at the Muséum d'histoire naturelle (MHN), Route de Malagnou 1, Geneva. A further set of slides covering the entire Vergol and La Charce sections analysed in the current study is stored in the collection of the Marine Palynology and Paleoceanography group, Utrecht University, The Netherlands, under code 000.000.017.384. England Finder (E.F.) references are included for holotypes and paratypes in Type Locality data (below), and for all figured specimens in Appendix 2.

Dinoflagellate Cysts

Notes on some chorate genera

Cleistosphaeridium, *Dapsilidinium*, *Downiesphaeridium*, *Impletosphaeridium* and *Simplicidinium*

Several chorate taxa recorded in the present study are hard to place

generically, not because of poor preservation or morphological novelty, but because of current taxonomic uncertainties. As stated by Fensome et al. (2016, p. 66 - under their genus *Simplicidinium*), "There seems to be considerable confusion currently surrounding the generic assignment of chorate species with non-tabulate spines/processes and a cryptic, or not clearly discernible or consistent archaeopyle". Genera relevant to the current study which are affected by this confusion all have Eocene type species which may or may not be directly related to taxa at Vergol and La Charce. These include:

Cleistosphaeridium Davey et al. 1966 emend. Eaton et al. 2001. Type: Davey et al. 1966, pl. 10, fig. 7, as *Cleistosphaeridium diversispinosum* (Eocene).

Impletosphaeridium Morgenroth 1966 emend. Islam 1993. Type: Morgenroth 1966a, pl. 10, fig. 5, as *Impletosphaeridium transfordum* (Eocene).

Dapsilidinium Bujak et al. (1980). Type: Davey and Williams 1966b, pl. 4, fig. 10, as *Polysphaeridium pastielsii* (Eocene).

Downiesphaeridium Islam 1993 emend. Masure in Fauconnier and Masure 2004. Type: Islam 1983, pl. 2, fig. 1, as *Cleistosphaeridium spinulastrum* (Eocene).

Simplicidinium Fensome et al. 2016. Type: Eaton 1976, pl. 21, fig. 5, as *Impletosphaeridium insolitum* (Eocene).

In describing *Cleistosphaeridium*, Davey et al. (1966, p. 166) included spherical to ovoidal cysts with numerous, distally-closed processes and an apical archeopyle. Islam (1993) reviewed *Cleistosphaeridium* and considered it a junior taxonomic synonym of *Systematophora* Klement 1960. Although the processes of *Systematophora* are arranged in penitabular complexes with, usually, basal connections, those of *Cleistosphaeridium* had been considered essentially non-tabulate. However, Islam concluded that the processes of *C. diversispinosum* were in "arcuate process complexes demonstrating their penitabular distribution".

Williams et al. (1998, p. 119) noted Islam's synonymy of *Cleistosphaeridium* and *Systematophora* and stated (op. cit. p. 333), "*Cleistosphaeridium* is now accepted as a taxonomic junior synonym of *Systematophora*". They consequently transferred *Cleistosphaeridium multifurcillatum* (Prössl 1990 ex. Prössl 1992), a species recorded here (see below), to *Impletosphaeridium*.

Eaton et al. (2001) agreed with Islam that *Cleistosphaeridium* possesses penitabular ridges and felt that *C. diversispinosum* appears to be gradational morphologically with *Systematophora ancylaea* Cookson and Eisenack 1965 and *S. placacantha* (Deflandre and Cookson 1955) Davey et al. 1969, which they termed the "*diversispinosum* complex". Eaton et al. felt that these three Cenozoic species should be brought into a single genus on their close resemblance, but they considered that their inclusion in the "Jurassic-based" genus *Systematophora* was unsatisfactory. They proposed the retention of *Cleistosphaeridium* to accommodate this "*diversispinosum* complex", stating, "Although the typically Cenozoic dinoflagellate cyst genus *Cleistosphaeridium* resembles the Jurassic genus *Systematophora* in its apical archeopyle, skolorate form and the presence of penitabular process complexes, other morphological features indicate that the two genera are not closely related".

Eaton et al. (op cit., p. 134) added, "the use of a generic name (*Impletosphaeridium*) that continues to be used as a "grab bag" is not supported" and, "we believe that the synonymy of *Cleistosphaeridium* and *Impletosphaeridium* is still a possibility... Indeed, the holotypes of *Cleistosphaeridium diversispinosum* and *Impletosphaeridium transfodum* may be conspecific". This would be particularly important, as *Impletosphaeridium* would have priority, although Eaton et al. (op. cit., p. 175) stated, "A formal proposal to conserve *Cleistosphaeridium* against *Impletosphaeridium* is also under consideration" and, "We would further recommend that the scope of *Impletosphaeridium* be restricted to its type, *Impletosphaeridium transfodum*, only, and that other species assigned to *Impletosphaeridium* be treated as questionable until they can be transferred to more appropriate genera".

Having noted that Islam considered *Cleistosphaeridium* a junior taxonomic synonym of *Systematophora*, Fauconnier and Masure (2004, p. 128) nevertheless agreed with Eaton et al. in retaining *Cleistosphaeridium*. Fensome et al. (2016, p. 36) also agreed with Eaton et al. (op. cit.), further stating that, "*Cleistosphaeridium* is considered to be areoligeracean because of the asymmetry in some specimens of the antapex and sulcal notch, and also because it forms a morphological plexus with other areoligeracean genera, including *Glaphyrocysta*, *Enneadocysta*, *Licracysta* and *Cooksonidium*. We include in the genus species in which adjacent processes are medially and distally interconnected".

Although Fauconnier and Masure (2004, p. 337) followed Eaton et al.'s suggestion and considered *Impletosphaeridium* a "problematic genus", this has not been followed consistently; Fensome et al. (2019 - "The Lentin and Williams Index") lists over 40 species positively assigned to *Impletosphaeridium*. Fensome et al. (2009, p. 38) agreed with Islam (1993, p. 84, 85) that the archeopyle of the paratype of *Impletosphaeridium transfodum*, the type species, is "probably apical" and stated, "This genus is useful, if of dubious status, since it serves as a repository for chorate forms whose general morphology accords with a gonyaulacacean dinoflagellate affinity, but whose archeopyle is uncertain". The genus *Impletosphaeridium* has been included below to accommodate *Impletosphaeridium multifurcillatum* (Prössl 1990 ex Prössl 1992) Williams et al. 1998, following Fensome et al. 2019, although in view of the above discussion, this may need to be re-addressed.

Dapsilidinium was described by Bujak et al. (1980, p. 27), as having processes which are, "hollow, open distally, tubiform or tapering" and a tetratabular apical archeopyle. It was erected to accommodate taxa which had previously been assigned to the genus *Polysphaeridium* Davey and Williams 1966b, a genus whose type species, *P. subtile* was subsequently shown to have an epicystal archeopyle (Eaton 1976, p. 280 and Bujak et al. 1980, p. 27, 28, 32, 34).

Dapsilidinium is therefore distinguished by its open-ended processes from *Downiesphaeridium* Islam 1993, which has hollow but distally-closed processes. Masure (in Fauconnier and Masure 2004, p. 195) emended the diagnosis of the latter genus to include species with hollow, acicular processes.

However, Fensome et al. (2016, p. 66) stated, "Islam (1993) proposed *Downiesphaeridium*, purportedly for forms with an apical archeopyle and simple non-tabulate processes. The processes of the type of *Downiesphaeridium* are typical of *Lingulodinium*, and the archeopyle in the type of *Downiesphaeridium* looks precin-

gular; it is thus suggested here that *Downiesphaeridium* may be a taxonomic junior synonym of *Lingulodinium*, but at least should not be used beyond the type".

The genus *Simplicidinium* was described by Fensome et al. (2016, p. 66) to include proximochorate to chorate cysts bearing numerous non-tabulate spines or processes with symmetrical distal terminations, i.e. "a spiny ball with an apical archeopyle". They described the spines or processes as distally closed, although Eaton (1976, p. 308), in his description of the type species, *Simplicidinium* (as *Impletosphaeridium*) *insoluitum* described the processes as solid.

Amphorulacysta, *Cymososphaeridium*, *Hystrichosphaerina*, *Hystrichosphaeridium*, *Oligosphaeridium*, *Palaecysta*, *Perissiasphaeridium* and *Systematophora*

Davey (1982, p. 9) considered that species within the genera *Systematophora*, *Oligosphaeridium* and *Surculosphaeridium*, "have in common that they are all skolochorate, gonyaulacacean cysts having an apical archeopyle and possessing not more than one process or process group per paraplate. Generic differentiation depends on process morphology". Using these criteria, Davey included seven pre-existing genera in a "*Systematophora-Oligosphaeridium-Surculosphaeridium* complex" and he added a further two, *Stiphrosphaeridium* and *Cymososphaeridium*; all were listed and their key characteristics specified in Davey's Table 1. Most of the genera included in his complex were recorded here and brief comments on the morphology of those most relevant to the current study are made where appropriate below.

Genus *Amphorulacysta* Chen 2013 emend. Zotto et al. 1987 and Monteil 1990

Type: Dodekova 1969, pl. 14, figs. 1-3, as *Amphorula metaelliptica*

Remarks: *Amphorulacysta* is a substitute name for *Amphorula* Dodekova 1969, which is illegitimate. Chen (2013, p. 285) compared and contrasted *Palaecysta* and *Amphorulacysta*, as "both expressing the same paraplate tabulation (0-2pr, 4', 6", 6c, 5-6", 1"', 1p, as, ps, 4s) and having arcuate processes in the apical, pre-, and post-cingular paraplates. The differences, however, are that (1) the former is skolochorate (with substantially longer processes and process clusters, which are nearly a quarter of the body diameter) while the latter is proximochorate (septal) and (2), although they both possess a pair of processes per paracingular paraplate, the former lacks while the latter possesses a linked basal ridge base".

In making his comparisons, Chen restricted himself to, "the original concept of '*Amphorula*' *sensu stricto* Dodekova (1969), not including any further expansions in definition and/or in concept by Zotto et al. (1987), Brenner (1988) or Monteil (1990)". Chen's reluctance to accept emendations by Zotto et al. and Monteil was explained by his statement, "It should be stressed that the proposal of including other members that possess closed polygonal and circular septal processes in the precingular and postcingular series such as *Amphorula dodekovae* Zotto et al. (1987; also recorded by Brenner 1988) and Monteil (1990) into *Amphorula* is not accepted. That proposal would destroy the most important and unique characteristic - arcuate process clusters - of the whole group". See comments after *Amphorulacysta metaelliptica*, below.

Amphorulacysta metaelliptica (Dodekova 1969) Williams and Fensome 2016 emend. Monteil 1990
Plate 1, Figures 1-3, 7, 10

Amphorula metaelliptica DODEKOVA 1969, p. 20, pl. 4, figs. 1-6; text-figs. E, F. Holotype: Dodekova 1969, pl. 4, figs. 1-3.
Amphorulacysta metaelliptica (Dodekova 1969). – WILLIAMS and FENSOME 2016, p. 139.

Remarks: All descriptions of *Amphorulacysta* (as *Amphorula*) to date describe proximochorate-septate cysts and in the present study this was also largely the case. However, as in other lineages studied here, there is some variation, and this was also shown by *Amphorulacysta metaelliptica* (Dodekova 1969) Williams and Fensome 2016, here.

The specimen in Plate 1, Figs. 7, 10 is a rare form, considered here to be an "end member" of *A. metaelliptica*, although it is undoubtedly skolochorate. This extreme form might be assigned to *Palaecysta integra* Chen 2013 because of its arcuate processes and isolated cingular features, but it appears to possess at least one annular basal ridge (pl. 1, fig. 10), which is atypical of *Palaecysta*. Specimens illustrated by Leereveld (1997a, fig. 8b-d), also assigned to *Amphorula metaelliptica* by that author, are similar to this form.

Individual, more typical specimens of *A. metaelliptica* recorded here (pl. 1, figs. 1, 2) can have a mixture of annular and arcuate basal ridges, although this is at variance with Monteil's (1990) emended diagnosis ("Acingular septa open, arcuate, semi-elliptical to semicircular, rounded") and of Chen's caution in restricting *Amphorulacysta* to forms with "arcuate process clusters".

According to Monteil (1990, p. 603), the stratigraphic range of *Amphorulacysta metaelliptica* is "earliest Berriasian (Jacobi-Grandis Zone) to the Late Berriasian (Boissieri Zone; Late Piceteti subzone)". Monteil (op. cit.) recognised that *A. metaelliptica* has been reported in the early Valanginian of Romania (Antonescu and Avram 1980) and Germany (Below 1981), but as isolated occurrences, and he considered these early Valanginian occurrences to be insignificant. In the present study, *A. metaelliptica* was recorded rarely but fairly consistently between the base of the studied section, Vergol Bed B97M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) and Bed V88 (early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-Zone), including in 12 samples within the early Valanginian.

Genus *Aprobolocysta* Duxbury 1977 emend Pourtoy 1988

Type: Duxbury 1977; pl. 14, figs. 4, 5; text-fig. 19B, as *Aprobolocysta eilema*

Aprobolocysta extrema Duxbury 2001
Plate 9, Figures 16, 17. Plate 12, Fig. 6

Dinocyst sp. A RILEY and FENTON 1984, p. 685, pl. 2, fig. 9.
Aprobolocysta extrema DUXBURY 2001, p. 99, fig. 2, nos. 1-4. Holotype: Duxbury 2001, fig. 2, no. 1.

Remarks: This species was shown in Duxbury (2018, fig. 10) to range from the latest Berriasian, *albidum* ammonite Zone to the early Valanginian, *Polyptychites* ammonite Zone at Speeton. This species appears to have a shorter range at Vergol, however, entirely within the early Valanginian. It was rare and occurred between

beds B136M, *pertransiens* Zone, *premollicus* Sub-zone to Bed V42, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone. This is the first Tethyan record of this species.

Aprobolocysta humilis n. sp.
Plate 12 Figures 1-3

Holotype: Plate 12, Figures 1, 2

Type Locality: Vergol outcrop, late Berriasian, Bed B129M, *alpillensis ammonite* Zone, *otopeta* Sub-zone. Holotype: Slide B129M(2), E.F. J45.0.

Derivation of Name: From the Latin *humilis*, modest, humble - in reference to the relatively small size of this species.

Diagnosis: A relatively small species of *Aprobolocysta* which is proximochorate, ovoidal and without horns. Both wall layers are smooth and the periphragm is folded, forming a reticulum of approximately even mesh size over the entire cyst surface. There is no clear reflection of tabulation, although the position of the cingulum can be suggested by some alignment of the reticulum. Archeopyle apical, typical of the genus.

Dimensions: Holotype (complete specimen): Length – 53 µm. Width – 46 µm.
Overall: 68 (61) 53 µm × 58 (49) 43 µm.
Specimens measured – 8.

Remarks: This species is most similar to *Aprobolocysta neista* and *A. plicata*, species which have periphragm folds forming a relatively coarse reticulum. Whereas *A. neista* has high, irregular, spiky crests, *A. humilis* and *A. plicata* have lower, distally entire crests of even height over much of the cyst. In addition, *Aprobolocysta plicata* displays a cingulum marked by a row of relatively small fields and can possess a prominent apical horn. In contrast, *Aprobolocysta humilis* has a significantly finer reticulum than *Aprobolocysta neista* and *A. plicata*, is relatively squat, possesses no horns and has only faint reflection of the cingulum, if any.

In some respects, *Aprobolocysta humilis* resembles species of *Cassiculosphaeridia* Davey 1969a and *Valensiella* Eisenack 1963. However, the archeopyle margin in both of those genera is parallel to the cingulum whereas in *A. humilis* it slopes markedly towards the sulcus, a feature typical of *Aprobolocysta* and *Batioladinium* Brideaux 1975.

This species was restricted to an interval spanning the Berriasian/Valanginian boundary at Vergol, beds B121M to B136M, *alpillensis* Zone, *otopeta* Sub-zone to base *pertransiens* Zone, *premollicus* Sub-zone.

Aprobolocysta pustulosa Smith and Harding 2004
Plate 12, Fig. 10

Aprobolocysta pustulosa SMITH and HARDING 2004, p. 359, 361, 363, pl. 1, figs. 1, 2, 9-11. Holotype: Smith and Harding 2004, pl. 1, figs. 1, 2.

Remarks: This species was first described by Smith and Harding (2004) from a single sample at a base Valanginian level at the Volgian lectostratotype section, Kashpir (Volga Basin, Russia - Sample 24 in Smith and Harding op. cit., fig. 8). It was subsequently shown by Duxbury (2018, fig. 10) to range as old as the late Berriasian, *albidum* ammonite Zone. Although not specified

in Duxbury 2018, *A. pustulosa* ranges as high as Bed D4B at Speeton (pers. obs.), early Valanginian, *paratollia* ammonite Zone.

As with other species of *Aprobolocysta*, the presence of *A. pustulosa* at Vergol proves a wide palaeogeographic range, from Boreal to Tethyan settings although, like *A. extrema*, *A. pustulosa* appears to have a shorter range at Vergol than at Speeton. It was restricted to the early Valanginian, *pertransiens* Zone, occurring between beds B147M and V19M, spanning the *premollicus* and *salinarium* Sub-zones. This is the first Tethyan record of this species.

Aprobolocysta reticulata (Stover and Helby 1987a) Duxbury 2018 emend. Duxbury 2018

Batioladinium reticulatum STOVER and HELBY 1987a, pp. 101–103, fig. 1. Holotype: Stover and Helby 1987a, figs. 1E–G.

Aprobolocysta neistosa Duxbury 1980. – DAVEY 1982, pp. 24, 25, pl. 7, figs. 5–7. – IOSIFOVA 1996, pp. 24, 25, pl. 8, figs. 3a–3c.

Aprobolocysta (?) sp. A Pourtoy 1988, pp. 389, 390, pl. 4, figs. 1–3, 6.

Aprobolocysta reticulata (Stover and Helby 1987a). – DUXBURY 2018, pp. 174–176, pl. 5, figs 3, 4, 6, 8, 11, 12.

Remarks: The presence of this species as old as Bed V45M proves an early Valanginian first occurrence similar to that reported at Speeton in Duxbury 2018. The FO's at Speeton and Vergol are therefore younger than its Berriasian-restricted occurrence in Australasia (Stover and Helby 1987a, Helby et al. 1987).

Aprobolocysta reticulata also occurred, rarely but consistently, at La Charce, as high as sample LCH191M, basal Hauterivian, *radiatus* Zone. This is similar to the lower *amblygonium* Zone (palynofloral sub-zone LKP10.3) Boreal LO reported for this species in Duxbury 2018.

A subspecies of *Aprobolocysta reticulata*, *A. reticulata* subsp. *imparilis* is newly described below and, for comparison, *A. reticulata* subsp. *reticulata* Autonym is illustrated in Plate 9, Figs. 8, 9, 13.

Aprobolocysta reticulata (Stover and Helby 1987a) Duxbury 2018 subsp. *imparilis* n. subsp.
Plate 9, Figures 11, 12, 18, 19

Holotype: Plate 9, Figures 11, 12

Paratype: Plate 9, Figure 19

Type Locality: Vergol outcrop, late Valanginian, Bed V112M, *verrucosum* ammonite Zone, *pronecostatum* Sub-zone. Holotype: Slide V112M(1), E.F. F32.4. Paratype: Slide V112M (schulze), E.F. S50.0.

Derivation of Name: From the Latin *imparilis*, odd, different - in reference to markedly different cingular crests.

Diagnosis: A subspecies of *Aprobolocysta reticulata* where the anterior cingular crest is markedly higher than the posterior but which otherwise conforms to other morphological characteristics of this species, including a reticulate periphragm and a prominent apical projection. In some specimens, undulation of the higher cingular crest is particularly clear. The operculum is usually retained.

Dimensions: Holotype (complete): 68 × 51 µm. Paratype (operculum lost): 61 × 48 µm.

Overall – Complete specimens (4): 71 (70) 68 µm × 51 (46) 38 µm. Operculum lost (paratype only): 61 × 48 µm. Specimens measured – 5.

Remarks: The distinctive, high anterior cingular crest displayed by this subspecies and its wavy nature can be reminiscent of the cingular fold in *Aprobolocysta eilema* Duxbury 1977, a significantly younger species (see Duxbury 2023). The presence of a clearly reticulate periphragm and a prominent apical projection distinguish *A. reticulata imparilis*, however.

This subspecies was recorded in the early and late Valanginian at Vergol, beds V45M to V112M, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to *verrucosum* Zone, *pronecostatum* Sub-zone.

Monteil (1985) recorded this subspecies as a rarity, as *Aprobolocysta* aff. *varigranosa* Duxbury 1977, with a similar range (*pertransiens* to *campylotoxum* ammonite zones), and at Angles in the same stratigraphic interval (Monteil 1986).

Aprobolocysta trycheria Pourtoy 1988

Plate 9, Figures 6, 7

Aprobolocysta trycheria POURTOY, 1988, p. 388–389, pl. 1, figs. 1–6, 8; pl. 5, figs. 1–2, 5, 9. Holotype: Pourtoy, 1988, pl. 1, figs. 1–3.

Remarks: This species was described by Pourtoy (1988) from the late Valanginian, *callidiscus* ammonite zone of Switzerland and in his PhD thesis (1989) he quoted a range of late Valanginian to late Hauterivian, *trinodosum* to *balearis* ammonite Zones. In the present study, the oldest occurrence of *A. trycheria* was in sample V94M from the early Valanginian, *inostranzewi* ammonite zone, and the youngest occurrence was in La Charce sample LCH191M (basal Hauterivian, *radiatus* Zone). Duxbury (2023) showed the youngest occurrence of this species at Speeton to be within the late Hauterivian *speetonensis* ammonite zone, similar to Pourtoy's Swiss record.

Genus ***Apteodinium*** Eisenack 1958 emend. Sarjeant 1985 emend. Lucas-Clark 1987

Type: Eisenack 1958, Plate 23, fig. 9, as *Apteodinium granulatum*

Apteodinium deflandrei (Clarke and Verdier 1967) Lucas-Clark 1987

Gardodinium deflandrei CLARK and VERDIER 1967, p. 26–28, pl. 3, figs. 10–12, Text-fig. 10. Holotype: Clarke and Verdier, 1967, pl. 3, fig. 10. – JAN DU CHÊNE et al., 1986a, pl. 8, figs. 10–11.

Aldorfia deflandrei (Clarke and Verdier 1967). – STOVER and EVITT 1978, p. 140.

Remarks: Very rare occurrences of this species were recorded between La Charce samples LCH208M and LCH220M, early Hauterivian, upper *radiatus* to *loryi* Zones. This is a similar level to the early Hauterivian, *regale* Zone FO of this species noted in the Speeton section (Bed C9D) in Duxbury 2023 and appears to indicate an early Hauterivian FO for this species in Boreal and Tethyan settings.

Genus ***Avellodinium*** Duxbury 1977 emend. Backhouse 1988

Type: Duxbury 1977, pl.5, figs.1–2, as *Avellodinium falsificum*

Avellodinium lepidum Backhouse 1988
Plate 14, Figure 8

Avellodinium lepidum BACKHOUSE 1988, p. 75, pl. 19, figs. 3-7; pl. 47, fig. 1. Holotype: Backhouse 1988, pl. 19, figs. 6a-b.

Avellodinium? haterivense PRÖSSL 1990, p. 99, 100, pl. 1, figs. 3, 7, 14, 15 ex Prössl, 1992.

Remarks: As noted in Duxbury (2023, p. 125), the generic diagnosis of *Avellodinium* was emended by Backhouse (1988, p. 75) to include species “with long, dichotomously branched intergonal processes similar in size and shape to the trifurcate gonial processes”, thus separating *Avellodinium lepidum* from *A. falsificum* Duxbury 1977 which lacks intergonal processes. Both species are illustrated here (pl. 14, figs. 8 and 17) to show this.

Avellodinium lepidum is a long-ranging species, observed by Backhouse (op. cit.) no older than the Valanginian. In the current study it was present between the early Valanginian, Vergol Bed V31M (*pertransiens* Zone, upper *salinarium* Sub-zone) and the top of the studied interval, La Charce Bed LCH220M, early Hauterivian, *loryi* Zone.

Genus ***Batioladinium*** Brideaux 1975 emend Pourtoy 1988

Necrobroomea Wiggins 1975, p. 111

Type: Alberti, 1961, pl. 5, fig. 2, as *Broomea jaegeri*.

Remarks: Pourtoy's emendations of *Aprobolocysta* and *Batioladinium* separated taxa having only an autocyst (*Batioladinium*) from those with an autocyst and ectocyst (*Aprobolocysta*). The same approach has been taken here.

Batioladinium inaequalis Duxbury 2023
Plate 9, Figures 10, 14

Batioladinium inaequalis DUXBURY 2023, p. 127-128, pl. 6, figs. 14, 18, 22. Holotype: Duxbury 2023, pl. 6, fig. 18.

Remarks: Rare specimens of this species were recorded here, displaying all key characteristics described in Duxbury (2023). However, although specimens from Speeton usually bear a short, solid, slender spine at the left antapical horn termination, specimens from Vergol did not; the left antapical horn terminations were bluntly rounded.

Batioladinium inaequalis was recovered only from Vergol Bed V132M, late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone and, together with its range at Speeton (early Hauterivian, *amblygonium* Zone - Duxbury 2023), this suggests a very restricted range across the late Valanginian/early Hauterivian boundary. It was absent from all La Charce samples, however.

Batioladinium longicornutum (Alberti 1961) Brideaux 1975
Plate 9, Figure 15

Batioladinium longicornutum (Alberti, 1961, p. 27, 28, pl. 5, figs. 18-21; pl. 6, figs. 1, 2). – BRIDEAUX, 1975, p. 1240. Holotype: Alberti, 1961, pl. 5, fig. 19. – EISENACK and KLEMENT 1964, p. 69. – FENSOME et al. 1996, p. 2205, fig. 1.

Remarks: *Batioladinium longicornutum* is a particularly long-horned, smooth and relatively thick-walled species (Harding

1990, p. 46) with antapical horns of approximately equal length. For comparisons with other long-horned species, see Duxbury (2023, p. 127).

According to Below (1990, p.53), *Batioladinium radiculatum* Davey 1982 is a taxonomic junior synonym of *B. longicornutum*, but this is rejected here, following Poulsen (1996, p. 105). As remarked by Davey (op. cit., p. 22), *B. radiculatum*, “is differentiated from the rather similar species *B. longicornutum* by its generally weaker and shorter antapical horns and by its ornamented hypocyst”. A typical Central North Sea specimen of *B. radiculatum* is included as Pl. 9, Fig. 20 here for comparison. In addition to clear hypocystal ornament, *B. radiculatum* has some merging of the antapical horns proximally, something never seen in *B. longicornutum*.

The contrasting ages of *B. radiculatum* and *B. longicornutum* were also cited by Davey (op. cit), who quoted the LAD of the former as late Ryazanian, and the FAD of the latter as early Hauterivian. From first-hand observations in many Central North Sea wells, the present author agrees with a late Ryazanian (= late Berriasian) LAD for *B. radiculatum*.

Evidence in Duxbury 2018 (fig. 10) suggests that very rare *B. longicornutum* can range as old as the early Valanginian. However, in the present study, *B. longicornutum* was recorded positively only as old as Vergol Bed V124M, late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone, and a questionable specimen was recorded from Bed V112M, *verrucosum* Zone, *pronecostatum* Sub-zone, again from the late Valanginian. This late Valanginian FO is similar to that recorded for *B. longicornutum* by Monteil (1992b, Table 1), also in southeast France, although his records were entirely above the *verrucosum* Zone. Although still in the late Valanginian, the *callidiscus* Sub-zone FO for *B. longicornutum*, illustrated by Habib and Drugg (1983, fig. 3) is younger than in the present study or in Monteil (1992b).

Batioladinium micropodum (Eisenack and Cookson 1960) Brideaux 1975
Plate 10, Figure 18

Broomea micropoda EISENACK and COOKSON 1960, p. 7, 8, pl. 2, figs. 8, 9. Holotype: Eisenack and Cookson 1960, pl. 2, fig. 9.

Batioladinium micropodum (Eisenack and Cookson 1960). – BRIDEAUX 1975, p. 1240.

Remarks: As in Duxbury (2023, p. 128), only specimens with *B. micropodum* type ornament and apical and rudimentary antapical horns have been referred to that species (pl. 10, fig. 18), whereas those with no apical horn have been placed in *B. cf. micropodum* (pl. 10, fig. 13).

Batioladinium varigranosum (Duxbury 1977) Davey 1982
Plate 9, Figures 1-5

Aprobolocysta varigranosa DUXBURY 1977, p. 53–54,). Holotype: Duxbury 1977, pl. 14, fig. 6; text-fig. 20b.

Batioladinium varigranosum (Duxbury 1977) DAVEY 1982, p. 22.

Remarks: As in Duxbury (2023, p. 128, 129), specimens assigned to *Batioladinium varigranosum* are restricted here to those approaching the type material of Duxbury (1977, pl. 14, figs. 6, 7, text-fig. 20a, b) and as illustrated by Duxbury (2018, pl. 19, figs. 13 and 14) and by Duxbury (2023, pl. 4, fig. 7). For further dis-

cussion of the morphology of *Batioladinium varigranosum sensu stricto* see Duxbury (2023, p. 129).

The FO of *Batioladinium varigranosum sensu stricto* at Vergol was in Bed V31M, early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone and at Speeton it ranges as old as Bed D3D (Duxbury 2018, fig. 1), early Valanginian, towards the base of the *Polyptychites* Zone.

The LO of this species at Vergol in Bed V112M, late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone, supports the suggestion by Duxbury (2023, p. 129) that *B. varigranosum sensu stricto* is a Valanginian species, and that specimens (including the type specimens) at the base of the Speeton Clay Hauterivian (Duxbury 1977) may represent reworking immediately above a major hiatus.

Genus ***Bicornus*** Duxbury n. gen.

Type species: *Bicornus obscurus* n. gen. n. sp.

Derivation of Name: From the Latin bi-, two and cornus, horn – in reference to the characteristic spindle shape.

Diagnosis: Spindle-shaped, dorso-ventrally flattened dinocysts composed of autophragm only. A distally rounded apical projection of variable length and a single short, acuminate antapical projection are invariably present. Wall surface smooth to very finely granular with indistinct tabulation marked by narrow, low ridges. No clear archeopyle observed but a large hole is present over much of the dorsal surface, presumed to involve at least plates 3" and 4"; much of the dorsal cingulum is absent.

Remarks: The taxonomic affinity of this genus is unclear. It may be gonyaulaccean, but if so its lack of a clear archeopyle and the presence of an acuminate antapical horn are atypical, the latter perhaps being more typical of peridiniacean taxa. The large hole over much of the dorsal surface may represent the archeopyle but, if so, the involvement of part of the dorsal hypocyst is again unusual.

Bicornus obscurus Duxbury n. sp.

Plate 4, Figures 7-9, 11-13, 15, 16

Holotype: Plate 4, Figures 11, 15

Paratype: Plate 4, Figures 12, 13

Type Locality: Vergol outcrop, early Valanginian, *pertransiens* ammonite Zone, *premolicus* Sub-zone, Holotype: Bed B151M, Slide B151M/1b, E.F. D47.0. Paratype: Bed B138M, Slide B138M/2, E.F. V33.1.

Derivation of Name: From the Latin *obscurus*, indistinct - in reference to the vestigial tabulation of this species.

Diagnosis: As for the genus.

Dimensions: Holotype 76 × 53 µm.

Paratype 91 × 58 µm.

Overall 91 (73) 51 µm × 58 (52) 43 µm.

Specimens measured – 11.

Remarks: The apical horn of *Bicornus obscurus* varies considerably in length, from being equal to the short antapical horn to

being a much longer and stronger feature. In some specimens there appears to be a slight offset of the antapical horn, suggesting that it may be a left antapical feature, with the right antapical suppressed.

Tabulation is present but vestigial, although cingular and hypocyst ridges are usually present, outlining an indistinct pattern. Lateral cingular notching is a common feature.

A large hole occurs over much of the dorsal hypocyst and this suggests itself as a substantial medial thinning of the cyst in transmitted light. Which plates are involved in this feature is unclear but presumably 3" and 4", together with a part of the cingulum. Negative images of the holotype and paratype are included in Pl. 4, Figs. 13, 15 in order to better illustrate the partial tabulation and dorsal hole.

Bicornus obscurus n. gen. n. sp. was observed only towards the base of the early Valanginian at Vergol, between Beds B138M and B151M, restricted to the *pertransiens* ammonite Zone, *premolicus* Sub-zone. However, Monteil (pers. comm.) has, "never observed this species in the Valanginian, *pertransiens/premolicus* Sub-zone" but he did record it (Monteil 1986) from the late Berriasian of the Val de Fier East section (Jura). This discrepancy is unresolved.

Genus ***Biorbifera*** Habib 1972 emend. Below 1987 emend. Riding and Helby 2001b

Type: Habib 1972, pl.10, fig.3, as *Biorbifera johnewingii*.

Biorbifera johnewingii Habib 1972

Plate 10, Figures 4, 8, 12

Biorbifera johnewingii HABIB 1972, p. 377, 378, pl. 10, figs. 2, 3. Holotype: Habib 1972, pl. 10, fig. 3.– FENSOME et al., 1995, p. 1577, fig. 2.

Remarks: The oldest occurrence of this species at Vergol was in Bed B115M, late Berriasian, *alpillensis* Zone, *alpillensis/otopeta* Subzonal boundary level. This is consistent with the late Berriasian base described by Habib and Drugg (1983; 1987), at the base of their "Biorbifera johnewingii Zone". However, in order to construct their "Neocomian Stratotype Zonation", Habib and Drugg (1983) analysed 12 sections, including 9 in southeast France and they placed the FO of *B. johnewingii* within the *dalmasi* ammonite Sub-zone which is now assigned to the top of the Middle Berriasian (text-fig. 2).

In contrast, however, Monteil (1992b, Table 1), also working in southeast France, recorded *B. johnewingii* ranging into the Tithonian, and he described his own "Biorbifera johnewingii Zone" of an early Tithonian to early Berriasian age, which is significantly older than Habib and Drugg's FO of that species. Monteil's evidence suggests that the FO of *B. johnewingii* in the present study is "too high", possibly because of extreme rarity in older Vergol samples.

The reason for the large difference in first occurrences of *B. johnewingii* between the extensive Monteil and Habib and Drugg studies, both in southeast France, is difficult to resolve. Habib and Drugg (1987, p. 755) stated, "value in biostratigraphic dating, especially in the Neocomian (Berriasian-Hauterivian), is evident from ... precise correlation with the corresponding stage stratotype (and ammonite-dated parastratotype) dinoflagellate stratig-

raphy of southeastern France and western Switzerland", but this is exactly the area studied by Monteil.

The LO of *Biorbifera johnewingii* has been variously reported with some agreement between authors. A late Valanginian LO was illustrated by Habib and Drugg (1983, fig. 3) at the top of the *trinodosum* Zone and Monteil (1992b, Table 1) placed it towards the base of that zone. The *trinodosum* Zone straddles the *peregrinus/furcillata* zonal boundary in current usage (text-fig. 2). In the present study, *B. johnewingii* ranged to the top of the Vergol section, sample V132M and was also recorded as a very rare component in La Charce samples LCH107M and LCH113M, suggesting a LO close to the *verrucosum/peregrinus* boundary, similar but probably slightly older than Monteil's evidence and at least one ammonite zone older than indicated by Habib and Drugg (op. cit.).

Stover et al. (1996, p. 673) referred to Haq et al.'s (1987) placement of the LAD of "Tethyan species" *Biorbifera johnewingii* in the basal Hauterivian, and they illustrated this in their text-fig. 24A. On the next page, however, Stover et al. (op. cit., text-fig. 24B) illustrated a LAD for that species within the late Valanginian of southeast France (i.e., Tethyan). In their "Mesozoic-Cenozoic Cycle Chart", Haq et al. (op. cit.) placed the LO of *B. johnewingii* towards the top of the *radiatus* Zone, implying that this species "should" be present throughout the large majority of samples analysed here from La Charce, and this was not the case.

It is considered here that an early Hauterivian LAD of *B. johnewingii* is most unlikely and that the LAD of this species is therefore a useful intra-late Valanginian marker, occurring towards the base of the *peregrinus* Zone, as reported by Monteil.

Genus *Bourkidinium* Morgan 1975 emend. Nøhr-Hansen 1993

Type: Morgan 1975, pl. 2, figs. 2a–c, as *Bourkidinium granulatum*.

Bourkidinium elegans Torricelli 1997

Plate 12, Figure 11

Bourkidinium sp. HABIB and DRUGG 1987, p. 756, pl. 4, fig. 10.

Bourkidinium sp. 2 LEEREVELD 1997a, fig. 10 m, n.

Bourkidinium sp. 2 LEEREVELD 1997b, fig. 7i.

Bourkidinium elegans TORRICELLI 1997, p. 343–345, pl. 2, figs. 1–9. Holotype: Torricelli 1997, pl. 2, fig. 4.

Remarks: This species was noted as a rarity by Habib and Drugg (1987, p. 756) as *Bourkidinium* sp. They stated, "Despite these restricted occurrences, this species may have stratigraphic value, since it is known to occur in the late Hauterivian of France (*Crioceratoides duvali* ammonite Zone to the top of the Hauterivian)". It was subsequently recorded by Leereveld (1997a, b) as *Bourkidinium* sp. 2 from the latest Valanginian (*N. callidiscus* Horizon) to the late Hauterivian of Rio Argos, southeastern Spain.

In his stratigraphic remarks on *Bourkidinium elegans*, Torricelli (1997, p. 343–345) described nannofloral occurrences associated with his Sicilian type material, stating, "According to Channell et al. (1995), this nannoflora assemblage constrains the chronostratigraphic attribution of the studied samples to the lower Hauterivian". Torricelli's illustrated specimens are from his samples VR12 and VR14. However, Torricelli (2001) re-visited his material and re-interpreted his assemblages in terms of Leereveld's (1997a, b) palynofloral zonation, concluding that the FO of *B. elegans*, and samples VR12 and VR14, were within the late Hauterivian.

In the present study, the FO of *Bourkidinium elegans* was in La Charce sample LCH191 and this species was common as old as LCH208 (both samples from the early Hauterivian, *radiatus* ammonite zone). It was not recorded in the Valanginian.

Bourkidinium granulatum MORGAN 1975 emend. Nøhr-Hansen 1993 emend. Torricelli 2000.

Plate 12, Figures 4, 5

Bourkidinium granulatum Morgan 1975, p. 160, 161, pl. 2, figs. 2a–c. Holotype: Morgan, 1975, pl. 2, figs. 2a–c. – FENSOME et al., 1996, figs. 1–3 - p. 2141. – FAUCONNIER and MASURE, 2004, pl. 11, fig. 7.

Tanyosphaeridium magneticum DAVIES 1983, p. 25, pl. 8, figs. 1–8, 11, 12; text-fig. 20. – LEEREVELD 1997a, fig. 7o.

Tanyosphaeridium spp. HARDING 1990, pl. 29, fig. 13 only.

Bourkidinium sp. 1. LEEREVELD 1997a, p. 412, fig. 10d.

Remarks: This species was described by Morgan (1975, p. 160, 161) as a prolate cyst with an apical archeopyle and hollow, distally-flared processes, "arranged in two groups, one at the apical, and the other at the antapical, end". Also, "all, or all but one or two, of the apical group of processes are on the free operculum". The holotype (Morgan op. cit., pl. 2, figs. 2a–c) appears to have no circular or precingular processes.

The generic and specific diagnoses were emended by Nøhr-Hansen (1993, p. 47–50) to include forms with a significantly more complete coverage of processes, the species emendation stating, "The group at the antapex consist of 6–15 processes which, apart from the antapical processes, may include the postcingular and sulcal processes. The group at the apex consists of 4–10 processes including the apical, or the apical and precingular processes".

Davies (1983, p. 25) stated that, in comparison with his new species *Tanyosphaeridium magneticum*, "*Bourkidinium granulatum* has fewer processes (9–15) on each end lacking all precingular and circular processes". Although Nøhr-Hansen did not formally synonymise *T. magneticum* into *B. granulatum*, his emendation appears to encompass it.

Similarly, *Bourkidinium* sp. 1 of Leereveld (1997a, p. 412, fig. 10d) is considered here to fit within Nøhr-Hansen's broader definition of *B. granulatum*. Although Leereveld (op. cit., p. 412) states that *Bourkidinium* sp. 1 differs from *B. granulatum* because the body ornament, "is scabrate rather than granulate", this is considered a poor specific criterion considering the wide morphological range encountered. Also, although Nøhr-Hansen (op. cit., p. 50) stated that, "The body is densely granulate", not all of his figured specimens concur with this, particularly pl. 3, figs. 2, 3, which appear to be smooth or scabrate.

The broader approach to *Bourkidinium granulatum* taken by Nøhr-Hansen is adopted here since wide variations were encountered, as with *Tanyosphaeridium* cf. *variecalamum*.

In the present study, very rare examples of *Bourkidinium granulatum* were recorded as old as Bed B136M, early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone, although it was consistent only as old as Bed V26M (early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone). This first occurrence compares to the Spanish range bases of *Bourkidinium* sp. 1 and *Tanyosphaeridium magneticum* in Leereveld (1997a, fig. 2 - see discussion above). The Boreal range base of *B. granulatum* at Speeton is in the early Valanginian, mid *paratollia* Zone (Duxbury 2018, text-figs 2, 10).

Bourkidinium granulatum ranged to the top of the Vergol section and a major increase in numbers was noted as old as Bed V124M, late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone, where this species was very common to abundant. It ranged throughout the studied interval at La Charce, again being most common in the late Valanginian.

Genus ***Callaiosphaeridium*** Davey and Williams 1966b emend. Duxbury 1980 emend. Below 1981

Hexasphaera Clarke and Verdier 1967, p. 42

Type: Deflandre and Courteville 1939, pl. 4, fig. 1, as *Hystriospheridium asymmetricum*

Remarks: This is a very long-ranging genus, described originally from the Senonian, where it ranges at least as young as the late Campanian (pers. obs.). In the present study, *Callaiosphaeridium* spp. were recorded as deep as Vergol Bed V54M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone; most specimens tended to have short, often parallel-sided cingular processes (pl. 13, fig. 15). No sub-division to species level has been attempted here.

Leereveld (1997a, b) recorded *Callaiosphaeridium* (as *C. asymmetricum*) no older than the Hauterivian at Rio Argos, a similar FO to that of *C. asymmetricum* in Habib and Drugg (1983, fig. 3), Stover et al. (1996, text-fig. 24B) and Duxbury (2023, text-fig. 4); this genus was not included in Monteil (1992b).

Genus ***Cassiculosphaeridia*** Davey 1969a

Type: Davey 1969a, pl. 4, fig. 3, as *Cassiculosphaeridia reticulata*.

Remarks: The similarity of this genus to various others with circular to subcircular outlines, a surface reticulum developed to varying degrees and a tetratabular apical archeopyle was discussed by Duxbury (2019, p. 181, 182) and won't be repeated here. Key features used by various authors in discriminating between them include the presence or absence of a cingulum and/or other reflected tabulation and the number of wall layers. Opinions differ between authors on the presence or absence of an ectophragm and, if it's present, whether the reflected tabulation relates to the autophragm or the ectophragm.

Courtinat (1989, p. 182) considered *Cassiculosphaeridia* to be a taxonomic junior synonym of *Valensiella* Eisenack 1963 emend. Courtinat 1989, although this was rejected by Slimani (1994), based on reworked specimens of the type species, *Valensiella ovulum* (Deflandre 1947) Eisenack 1963, in his own (Campanian to Danian) material.

Cassiculosphaeridia magna Davey 1974 emend. Harding 1990 Plate 7, Figure 17

Cassiculosphaeridia magna DAVEY 1974, p. 46, pl. 1, figs. 3–7. Holotype: Davey 1974, pl. 1, fig. 6.

Remarks: This species is characterised mainly by its relatively large size and its clear reticulum covering the entire surface. Harding (1990, p. 49) stated, "The presence of an ectophragm in this species has not previously been reported. However, study of new topotype material from Bed LB5B at Speeton and abundant

specimens of this striking species from other localities has shown that this is a consistent feature if very mild oxidising agents are used (or oxidation is not performed) to prevent digestion of the ectophragm".

In discussing *Cassiculosphaeridia reticulata* Davey 1969a, Davey (1974, p. 47) remarked on the considerable variation in the, "coarseness of the reticulum, and size and arrangement of the crests", but he did not make similar remarks about *C. magna*. However, Davey's illustrations of the type material (1974, pl. 1, figs. 3–7) again showed significant variation, apparently within individual assemblages - his pl. 1, figs. 4 and 6 (holotype) are both from Speeton Bed LB5B and the first has a notably finer reticulum. Specimens assigned to *Cassiculosphaeridia magna* in the present study are again relatively large and show significant variation in the reticular mesh size.

The stratigraphic range of this species at Vergol was no older than Bed V104M, late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone and it increased in numbers up-section. This range base is significantly younger than that at Speeton, where *C. magna* occurs as old as Bed D7C (late Berriasian, *albidum* Zone). Its range base at Vergol, however, is consistent with that shown for southeast France by Monteil (1992b, Table 1 - *verrucosum* Zone), at the base of Monteil's *Cassiculosphaeridia magna* Zone but is significantly older than Leereveld's (1997a, fig. 2) single record from his top Valanginian *callidiscus* Horizon.

Cassiculosphaeridia reticulata Davey 1969a Plate 8, Figures 14, 16, 19, 20

Cassiculosphaeridia reticulata DAVEY 1969a, p. 142, pl. 3, fig. 7; pl. 4, fig. 3. Holotype: Davey 1969a, pl. 4, fig. 3.

Remarks: The FAD of *Cassiculosphaeridia reticulata* was recorded only to the base of the Valanginian in Duxbury (2018), suggesting that "*Cassiculosphaeridia*-like" taxa as discussed in Duxbury 2019 might be restricted entirely to the Cretaceous and might be better separated from superficially similar, essentially Jurassic species (e.g. some species of *Valensiella*).

As with *Cassiculosphaeridia magna*, the range base of *C. reticulata* was younger at Vergol than at Speeton; consistent occurrences were recorded only as old as Bed V97M (*verrucosum* Zone, *verrucosum* Sub-zone) and sporadically no older than Bed V68M, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone. See also remarks under *Ellipsoidictyum minusculum* Duxbury n. sp., below.

Genus ***Cauca*** Davey and Verdier 1971 emend.

Type: Alberti 1961, pl. 9, fig. 4, as *Hystriochodinium parvum*.

Emended diagnosis: Small, spherical, ellipsoidal to ovoidal cysts with the epicyst equal to or shorter than the hypocyst. The epicyst is rounded triangular in outline, extending into a low apical prominence and the hypocyst outline is semicircular. The endophragm is smooth, scabrate or granular and bears sutural crests marking an apparently gonyaulacoid tabulation and a clear cingulum. Crests usually bear numerous processes. The archeopyle is epicystal, with the operculum normally attached.

Remarks: In their comments on this genus, Davey and Verdier (1971, p. 14) concluded that, "The combination of epitrectal ar-

chaeopyle and long sutural spines distinguish this genus from all previously described ones", and this approach was followed by Duxbury (2023). However, Davey and Verdier's generic diagnosis also stated "cyst without polar structures" and, "Spines long and simple". Other features which appear to be typical of *Cauca* are its relatively small size and a low apical prominence. Although the latter feature was specifically excluded from Davey and Verdier's generic diagnosis (op. cit., p. 14), two of the specimens that they assigned to *Cauca parva* (Alberti 1961) Davey and Verdier 1971 (op. cit., pl. 1, figs. 7 and 9) appear to show it.

Cauca perplexa Duxbury 2023 has long, flat, flexuous, processes which are very complex distally, furcating three or four times, a feature unusual for this genus and again contrary to Davey and Verdier's generic diagnosis. Also, *Cauca redacta* n. sp. possesses low sutural crests which may or may not bear short, flexuous spines, whilst retaining other features typical of *Cauca*, including its small size and an apical prominence.

In order to encompass the wide range of morphological variation now apparent within this genus, as exhibited by *Cauca parva* (Alberti 1961) Davey and Verdier 1971, *C. maculosa* Duxbury 2018, *C. perplexa* Duxbury 2023, *C. rigida* Duxbury 2023 and *C. redacta* n. sp., it has been necessary here to extend Davey and Verdier's concept of this genus.

Duxbury (2023, p. 130) referred to the similarity of the long, blade-like processes of some species of *Cauca* to those in *Hystrichodinium* Deflandre 1935, citing an epicystal archeopyle as definitive of *Cauca*, contrary to Below (1981, p. 120-121). Comparisons might also be made between *Cauca redacta* n. sp. (very reduced spines or none at all) and *Heslertonina* Sarjeant 1966b, particularly as some representatives of *Heslertonina* have significantly reduced crestal height and sometimes very short crestal spines (see *Heslertonina inferior* n. sp., below). In this case it seems to be the relatively small size and rounded-triangular epicyst with a low apical prominence in *Cauca* that sets them apart. Also, there seems to be a continuum in *C. redacta* from specimens with numerous distinct (but short) sutural spines to those with none.

***Cauca maculosa* Duxbury 2018**
Plate 11, Figure 4

Remarks: This species was described in Duxbury 2018, largely within the basal Hauterivian, Subzone LKP10.3, being common in the upper part of its range; the current study confirmed its common occurrence at La Charce. A significantly longer range was recorded here, as old as the late Berriasian, Vergol Bed B115M. Numbers increased up-section as old as Vergol Bed V101M (base late Valanginian) and it was consistently common throughout much of the late Valanginian and early Hauterivian.

The process length of this species varied somewhat, with particularly long-spined specimens more typical of older samples.

***Cauca redacta* Duxbury n. sp.**
Plate 11, Figures 8, 11, 12, 15, 16

Holotype: Plate 11, Figures 11, 12

Paratype: Plate 11, Figure 16

Type Locality: Vergol outcrop, Valanginian. Holotype: early Valanginian, Bed V97M, *inostranzewi* ammonite Zone, *platycostatus*

Sub-zone, Slide V97M(A), E.F. P45.4. Paratype: early Valanginian, Bed V97M, *inostranzewi* ammonite Zone, *platycostatus* Sub-zone, Slide V97M(A), E.F. R37.4.

Derivation of Name: From the Latin redactus, reduced - in reference to the loss of crestal spine height in this species.

Diagnosis: A small, thin-walled species with an ovoidal main body, and with the epicyst smaller than the hypocyst. The epicyst is rounded triangular in outline, extending into a low apical prominence and the hypocyst outline is semicircular. The endophragm bears a cover of granules or is ornament-free. The periphragm bears sutural crests which are low and smooth and which can be distally entire or bear very short acuminate spines. The archeopyle is epicystal, with the operculum attached.

Dimensions: Holotype 41 × 38 µm.

Paratype 38 × 33 µm.

Overall - 43 (41) 38 µm × 38 (35) 33 µm.

Specimens measured – 5.

Remarks: This species is characterised by the small size of its main body and very reduced to absent crestal spines. The endocyst can bear surface granules, although these may be absent, particularly in specimens lacking spines. In some specimens, spines may be restricted to crests fringing the antapex.

Some similarities were observed here between *Cauca redacta* and *Heslertonina inferior* n. sp., a species which also has reduced sutural crests and can bear short crestal spines. This is discussed under *Heslertonina* Sarjeant 1966b, below.

The observed range of this species at Vergol was between samples V45M (early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone) and V124M (late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone), although its consistent occurrence was restricted to the interval between samples V91M and V111M, bracketing the early/late Valanginian boundary.

Genus *Chlamydophorella* Cookson and Eisenack 1958 emend. Duxbury 1983

Chlamydophorella Cookson and Eisenack 1958, p. 56

Gardodinium Alberti 1961 p. 18

Sepispinula Islam 1993, p. 88

Type: Cookson and Eisenack 1958, pl.11, fig.1, as *Chlamydophorella nyei*.

Remarks: *Chlamydophorella* spp. were very common to very abundant throughout the studied interval, as was also noted for the Speeton section in Duxbury 2023 (p. 132). Large numbers of *Chlamydophorella* spp. are therefore typical for both Boreal and Tethyan Early Cretaceous assemblages. Most occurrences of this genus have again been grouped into an informal category, "*Chlamydophorella* spp.", as there appears to be a continuous transition between them, and there appears to be no stratigraphic value in doing otherwise. Particularly distinctive taxa are briefly discussed below, together with a new species, *Chlamydophorella caminus*.

Chlamydophorella ambigua (Deflandre 1937) Stover and Helby 1987c

Michrhystridium ambiguum DEFLANDRE 1937, p. 81, pl. 16 (al. pl. 13), figs. 8, 9. Holotype: Deflandre 1937, pl. 16 (al. pl. 13), fig. 8. – FAUCONNIER and MASURE 2004, pl. 71, figs. 6, 7.

Polysphaeridium ambigum (sic.) (Deflandre 1937). – YUN 1981, p. 44, pl. 3, fig. 16.

Chlamydophorella ambigua (Deflandre 1937). – STOVER and HELBY 1987c, p. 277.

Hystrichosphaeridium huguoniotii VALENSI 1955, p. 38, 39; text-fig. 2a.

Hystrichosphaeridium ancoriferum COOKSON and EISENACK 1960, p. 8, pl. 2, fig. 11.

Baltisphaeridium huguoniotii (Valensi 1955). – DOWNIE and SARJEANT 1965, p. 91

Chlamydophorella ambigua (Deflandre 1937) Stover and Helby 1987c subsp. ***ambigua*** Autonym
Plate 5, Figures 23, 24, 26

Remarks: All examples of *Chlamydophorella ambigua* recorded in the present study had smooth spines and were assigned to *Chlamydophorella ambigua ambigua*. It is distinguished from other *Chlamydophorella* spp. through its relatively sparse cover of spines which appear to be capitate with no obvious ectophragm. The last feature may be preservational, as the ectophragm of this species appears to be particularly fragile (see comments in Duxbury 2023, p. 132).

Chlamydophorella ambigua ambigua was recorded no older than Vergol sample V82M, early Valanginian, *neocomiensiformis* Zone, *campylotoxus* Sub-zone in the present study (i.e., it was absent from much of the Berriasian and early Valanginian).

Chlamydophorella caminus Duxbury n. sp.
Plate 5, Figures 13, 17

Gardodinium trabeculosum (Gocht 1959) Alberti 1961. – LEEREVELD 1997a, figs. 8e, 9a.

Holotype: Plate 5, Figure 13

Type Locality: Vergol outcrop, Valanginian. Holotype: late Valanginian, Bed V132M, *peregrinus* ammonite Zone, *peregrinus* Sub-zone, Slide V132M/1, E.F. S48.4.

Derivation of Name: From the Latin *caminus*, chimney - in reference to the apical projection.

Diagnosis: A thin-walled, holocavate species of moderate size with an ovoidal, tapering autocyst terminating in a short, distally closed and rounded projection. The hypocyst is semicircular in outline. Short, stout processes link the autophragm and a significantly thinner, very finely reticulo-fenestrate ectophragm. A broad-based, hollow apical horn extends the ectophragm and this is open distally. There is no clear indication of tabulation or dorso-ventral flattening. The archeopyle is apical, with the operculum attached.

Dimensions: Holotype: 63×46 µm.
Overall - 63 (59) 56 µm×48 (45) 43 µm.
Specimens measured – 5.

Remarks: *Chlamydophorella caminus* is similar to *Chlamydophorella pyriformis* (Vozzhennikova 1967) Davey 1978 in having a characteristically ovoidal shape and prominent ectophragmal

apical horn. It differs, however in being significantly smaller, in lacking any indication of tabulation, in bearing less numerous and stouter autophragmal processes and in having a very finely reticulo-fenestrate ectophragm as opposed to the smooth ectophragm of *C. pyriformis*, as described by Lentin and Vozzhennikova (1990, p. 102).

Harding (1996, p. 359) considered *Chlamydophorella pyriformis* to be a questionable taxonomic junior synonym of *Chlamydophorella trabeculosa* (Gocht 1959) Davey 1978 (as *Gardodinium trabeculosum*), although he stated, "The possible synonymy of *G. trabeculosum* and *G. pyriforme* requires further investigation".

Describing his type material for *C. trabeculosa*, Gocht (1959, p. 62) stated (translation), "All are dorso-ventrally flattened", and this seems to be a significant feature of both Gocht's material and that of Alberti 1961 (as *Gardodinium eisenackii*), although Harding (op. cit., p. 361) recognised only, "Moderate primary dorso-ventral compression". Further features observed in Gocht and Alberti's material which seem typical of *Chlamydophorella trabeculosa* include "shoulders", which give some angularity to the epicyst, and clear lateral cingular notches.

All of these features, apparently typical of *C. trabeculosa*, are absent from *C. pyriformis* and on that basis the present author agrees with Lentin (see Harding 1996, p. 364) in her reluctance to believe that these species are conspecific.

The specimens illustrated by Leereveld (1997a, figs. 8e, 9a) as *Gardodinium trabeculosum* are here included in *Chlamydophorella caminus*. Undoubtedly, other authors have also assigned various taxa to *C. trabeculosa* which lack the typical features noted above, but largely without illustration, precluding their re-interpretation. *Chlamydophorella trabeculosa* ranges no older than Bed C7H at Speeton (early Hauterivian, base *inversum* Zone - Duxbury 2023, fig. 4), and it was absent from the current study.

Chlamydophorella caminus is a long-ranging species, recorded from Vergol Bed B142M (early Valanginian, *pertransiens* Zone, *pertransiens* Sub-zone) to the highest sample analysed from La Charce (early Hauterivian, *loryi* Zone). However, its FO is an important marker in being very closely above the Berriasian/Valanginian boundary. At Vergol, there were no *Chlamydophorella* spp. bearing a prominent apical horn pre-Valanginian.

A similar near-base *pertransiens* FO was illustrated for *Chlamydophorella caminus* by Leereveld (1997a, fig. 2, as *Gardodinium trabeculosum*), although that author did not analyse the *otopeta* Zone. Similarly, Monteil (1992b, Table 1) recorded "*Gardodinium trabeculosum*" (without illustration), but only as deep as the uppermost *pertransiens* Zone. This might again be *Chlamydophorella caminus*.

Chlamydophorella ordinalis (Davey 1974) Davey 1978
Plate 18, Figures 17, 18

Gardodinium ordinale DAVEY 1974, p. 51, pl. 3, figs. 5, 6. Holotype: Davey 1974, pl. 3, fig. 6.

Chlamydophorella ordinale (Davey 1974). – DAVEY 1978, p. 893.

Remarks: The "split range" of this species was discussed in Duxbury 2023 (p. 133), with older occurrences being essentially confined to the late Valanginian to early Hauterivian and younger ranges restricted to the late Barremian. The older part of this

range was covered in the present study and this appears to confirm previous records, with *Chlamydophorella ordinalis* recorded only between La Charce samples LCH164M and LCH213M (late Valanginian, *furcellata* Zone, *furcellata* Sub-zone to early Hauterivian, *radiatus* Zone). This species was absent from pre-*furcellata* Zone samples, including all of the Vergol material.

The oldest published record of *Chlamydophorella ordinalis* appears to be that of Leereveld (1997a, figs. 2 and 7j, k) where a single, isolated occurrence was illustrated towards the base of the Valanginian, *pertransiens* Zone. This appears to be anomalously old compared to other records.

Genus *Chytroeisphaeridia* (Sarjeant 1962) Downie and Sarjeant 1965 emend. Pocock 1972 emend. Davey 1979c

Leiosphaeridia subgenus *Chytroeisphaeridia* Sarjeant 1962, p. 492.

Chytroeisphaeridia (Sarjeant 1962, p. 492) Downie and Sarjeant 1965, p. 102

Type: Sarjeant 1962, pl. 70, fig. 13, as *Leiosphaeridia* subgenus *Chytroeisphaeridia chytrooides*.

Chytroeisphaeridia conspicua Duxbury n. sp.
Plate 3, Figures 1-4

Chytroeisphaeridia scabrata Pocock 1972. – LEEREVELD 1997b, fig. 10a.

Holotype: Plate 3, Figure 2

Paratype: Plate 3, Figure 1

Type Locality: Holotype: late Valanginian, Bed LCH164M, base *furcellata* ammonite Zone, *furcellata* Sub-zone, Slide LCH164M/1, E.F. G40.2. Paratype: base Valanginian, Bed B136M, *pertransiens* ammonite Zone, *premolicus* Sub-zone, Slide B136M/R1, E.F. C42.2.

Derivation of Name: From the Latin *conspicuus*, manifest, visible, prominent - in reference to the distinctiveness of this species.

Diagnosis: A relatively large species with an elongate ovoidal body, autocyst only. The epicyst is rounded triangular in outline and the hypocyst may be more broadly rounded or similar to the epicyst. There are no apical or antapical horns and the surface is featureless. Some thinning of the cyst wall is often observed towards the poles. Other than the large single-plate precingular archeopyle (presumed mid dorsal) there is no indication of tabulation.

Dimensions: Holotype $96 \times 58 \mu\text{m}$.

Paratype $68 \times 53 \mu\text{m}$.

Overall - 96 (71) $58 \mu\text{m} \times 61$ (52) $46 \mu\text{m}$.

Specimens measured – 25.

Remarks: This species is characterised by its relatively large size and its elongation. There is an increase in size and degree of elongation throughout its long range (it was observed throughout the Vergol and La Charce sections analysed here), and this seems to be a gradual change. Younger specimens are particularly elongate, approaching spindle-shaped (as in the holotype), and can show some "pinching" towards the antapex so that cysts develop a rounded antapical protrusion (see pl. 3, figs. 2-4).

The more elongate younger specimens are very similar to that illustrated by Leereveld (1997b, fig. 10a), as *Chytroeisphaeridia scabrata* Pocock 1972. Leereveld (op. cit.) recorded "*C. scabrata*" throughout the Hauterivian/Barremian section of Rio Argos but he did not report that species per se in the Rio Argos Tithonian-Valanginian interval (Leereveld 1997a).

Genus *Circulodinium* Alberti 1961 emend. Fensome et al. 2019

Circulodinium Alberti 1961, p. 28

Type: Alberti 1961, pl. 4, fig. 20, as *Circulodinium hirtellum*.

Circulodinium hirtellum Alberti 1961

Plate 13, Figure 7. Plate 17, Figures 4, 7

Cyclonephelium distinctum Deflandre and Cookson 1955. – GOCHT 1959, pl. 4, figs. 16, 18. – DAVEY 1969a, pl. 11, figs. 7, 8. – DUXBURY 1977, pl. 8, figs. 1, 2. – DUXBURY 1980, pl. 8, fig. 1.

Circulodinium hirtellum ALBERTI 1961, p. 28-29, pl. 4, fig. 20. Holotype: Alberti 1961, pl. 4, fig. 20.

Circulodinium deflandrei ALBERTI 1961, p. 29, pl. 4, figs. 7-13. – STOVER and HELBY 1987b, fig. 21D-I.

Cyclonephelium hirtellum (Alberti 1961). – DAVEY 1978, p. 894.

Remarks: See Duxbury (2023) for discussion of this species and of the genera *Cyclonephelium* Deflandre and Cookson 1955 and *Circulodinium* Alberti 1961.

As in previous Early Cretaceous studies, a significant range of sizes, antapical "horn" development and spine types has been recorded in numerous specimens assignable to *Circulodinium hirtellum*; they appear to be part of a continuum. No *Cyclonephelium* spp. were recorded in the current study other than *Cyclonephelium maugaad* Below 1981, an unusual species whose allocation to that genus might be questioned.

Occurrences of *C. hirtellum* were recorded throughout much of the section analysed here, although it was consistently very common between Vergol Bed V82M and La Charce Bed LCH149M (i.e. across the early/late Valanginian boundary, *neocomiensiformis* Zone, upper *campylotoxus* Sub-zone to *peregrinus* Zone, *nicklesi* Sub-zone).

Genus *Codoniella* Cookson and Eisenack 1961 emend. Davey 1979a

Type: Cookson and Eisenack 1960, pl. 3, fig. 1, as *Codonia campanulata*.

Codoniella prisca Duxbury n. sp.

Plate 8, Figures 15-17

Holotype: Plate 8, Figure 17

Paratype: Plate 8, Figure 16

Type Locality: Vergol outcrop, early Valanginian, Bed V97M, *inostranzewi* ammonite Zone, *platycostatus* Sub-zone. Holotype: Slide V97M(A), E.F. K41.2. Paratype: Slide V88B, E.F. K46.3.

Derivation of Name: From the Latin *priscus*, ancient - in reference to its occurrence relative to other members of the genus.

Diagnosis: A fairly thick-walled species of *Codoniella* which lacks cingular tabulation and sutural thickenings between the pre- and post-cingular plates. The crests surrounding the apical and antapical regions are moderately high, forming funnel-like structures which tend to widen distally. The apical structure is normally lower than the antapical, both exhibit microfenestration and some longitudinal striation can occur. The archeopyle is single-plate precingular.

Dimensions: Holotype $51 \times 30 \mu\text{m}$. Paratype $51 \times 33 \mu\text{m}$. Overall 51 (50) $48 \mu\text{m} \times 33$ (32) $30 \mu\text{m}$. Specimens measured – 5.

Remarks: Like the type species, *Codoniella campanulata* (Cookson and Eisenack 1960) Downie and Sarjeant 1965, *C. prisca* n. sp. is characterized by its funnel-shaped, membranous structures extending apically and antapically from a non-tabulate endocyst. It differs, however, in having a thicker cyst wall and lower apical and antapical structures which are microfenestrate and can have longitudinal striations.

Codoniella campanulata was recorded by Cookson and Eisenack (1960) from the Cenomanian to ?Santonian of Western Australia and by Davey (1979a) from the late Albian of IPOD Leg 48, Hole 400A, northern Bay of Biscay. A second species, *Codoniella psygma* Davey 1979a, was recorded by Davey (op. cit.) from the Apto-Albian, and it was also restricted to a near-base Albian sample in DSDP Site 535, Leg 77, Southeastern Gulf of Mexico (Riley and Fenton 1984).

Codoniella prisca n. sp. was restricted to the latest early Valanginian at Vergol, *inostranzewi* ammonite Zone, Beds V88 (*inostranzewi* Sub-zone) to V97M (*platycostatus* Sub-zone), and is therefore significantly older than other representatives of this genus.

Genus *Cribroperidinium* Neale and Sarjeant 1962 emend. Davey 1969a emend. Sarjeant 1982 emend. Helenes 1984

Cribroperidinium Neale and Sarjeant 1962, p. 443
Acanthaulax Sarjeant 1968, p. 227
Millioudodinium Stover and Evitt 1978, p. 173
Meristaulax Sarjeant 1984, p. 160

Type: Neale and Sarjeant 1962, pl. 19, fig. 4; text-fig. 3a–b, as *Peridinium sepimentum*

Remarks: *Cribroperidinium* spp. were very common to abundant throughout the studied intervals and the large majority have been "lumped" into an informal category, "*Cribroperidinium* spp.". Two of the more stratigraphically useful species are included below.

***Cribroperidinium colum* Duxbury 2001**
 Plate 6, Figure 14

Cribroperidinium colum DUXBURY 2001, p. 103, 104, fig. 5, nos. 1–4.
 Holotype: Duxbury 2001, fig. 5, nos. 1, 2.

Remarks: This species was described by Duxbury (2001, p. 103, 104) from the late Hauterivian to "middle" Barremian of the Central North Sea. Its consistent range was extended into the late Valanginian in Duxbury 2018 (p. 204), although recognising that it can range (rarely) into the early Valanginian. This was further

confirmed in the current study, where it was consistent but rare as old as Vergol Bed V111M (late Valanginian, *verrucosum* Zone, upper *verrucosum* Sub-zone) and an isolated occurrence was recorded in Bed V88 (early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone).

***Cribroperidinium sepimentum* Neale and Sarjeant 1962**
 Plate 17, Figures 15, 16

Cribroperidinium sepimentum NEALE and SARJEANT 1962, p. 443–444, pl. 19, fig. 4; text-figs. 3a–b. Holotype: Neale and Sarjeant 1962, pl. 19, fig. 4; text-fig. 3a–b. – JAN DU CHÊNE et al. 1986a, pl. 19, fig. 4.

Remarks: In Duxbury 2018 (p. 205, text-fig. 10), the oldest occurrence of this species was in palynofloral sub-zone LKP8.3, dated in that work as latest early Valanginian but re-interpreted here as mid late Valanginian. In the present study, the FO of *C. sepimentum* was in La Charce Bed LCH141M, late Valanginian, *peregrinus* Zone, lower *nicklesi* Sub-zone, very close to the FO of the nannofossil *Eiffelithus striatus* in Bed LCH141 (Gardin, pers. comm.). It was absent from all Vergol samples.

Cribroperidinium sepimentum was described in Neale and Sarjeant (1962, p. 443, 444) from the Shell West Heselton No. 1 Borehole, at 99.25 m (325 ft 7"); the age of this sample was subsequently listed in Sarjeant (1966a, p. 19) as "Middle Hauterivian" (quoted as 99.25/50 m). In the same volume, Sarjeant (1966c, p. 214) tabulated that sample, but as "Upper Hauterivian". Duxbury (1977, p. 28, text-figs. 2, 21) confirmed a base late Hauterivian LO (Speeton Bed C6) for this species.

Genus *Cyclonephelium* Deflandre and Cookson 1955

Type: Deflandre and Cookson, 1955, Plate 2, fig. 12, as *Cyclonephelium compactum*

Remarks: See Duxbury 2023 for discussion of the genera *Cyclonephelium* Deflandre and Cookson 1955 and *Circulodinium* Alberti 1961.

***Cyclonephelium maugaad* Below 1981**
 Plate 8, Figure 24; Plate 15, Figure 4

Cyclonephelium maugaad BELOW 1981, p. 15, pl. 11, figs. 2, 3a–b; pl. 15, fig. 20. Holotype: Below, 1981, pl. 11, fig. 2. – FENSOME et al. 1991, p. 671, fig. 1. – FAUCONNIER and MASURE 2004, pl. 18, fig. 10

Remarks: Some discussion of this unusual species was included in Duxbury (2023, p. 137), including remarks on its similarity to *Atopodinium* Drugg 1978, with possible implications for its taxonomic placement. As in Duxbury 2023, no "true" *Cyclonephelium* spp. were recorded in the current study.

The stratigraphic range quoted for *C. maugaad* by Below (1981) was Hauterivian to Aptian, and it was recorded between Speeton Beds D2D and LB2D (early Hauterivian, *amblygonium* to early Barremian, *fissicostatum* ammonite Zones) by Duxbury (2023). It occurred consistently only as old as Bed C8B (early Hauterivian, *regale* Zone), however, being very rare below that.

In the present study, *C. maugaad* occurred consistently between Vergol Bed V82M to the top of the studied section at La Charce (late Valanginian, *neocomiensiformis* Zone, upper *campylotoxus*

Sub-zone to early Hauterivian, *loryi* Zone). Very rare, isolated occurrences were noted below this, however, to the base of the studied section at Vergol.

Genus *Cymosphaeridium* Davey 1982

Type: Davey 1982, pl. 3, figs. 5, 8, 11, as *Cymosphaeridium validum*.

Cymosphaeridium validum Davey 1982

Plate 1, Figures 9, 13, 14

Cymosphaeridium validum DAVEY 1982, p. 18, 19, pl. 3, figs. 5, 6, 8, 11. Holotype: Davey, 1982, pl. 3, figs. 5, 8, 11. – FENSOME et al. 1995, p. 1875, figs. 1-3. – FAUCONNIER and MASURE 2004, pl. 19, figs. 1-3.

Remarks: This species was long-ranging in the present study, from Vergol Bed B121M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone) to the top of the studied section at La Charce. It was common as old as Vergol sample V76M (early Valanginian, *neocomiensiformis* Zone, *campylotoxus* Sub-zone) and it was very common between La Charce Beds LCH160M and LCH180M (late Valanginian, *peregrinus* Zone, top *nicklesi* Sub-zone to *furcillata* Zone, *furcillata* Sub-zone), peaking in Bed LCH170M.

Some variation in morphology was noted, particularly a form here informally termed *Cymosphaeridium validum* "regulare" which has none of the deeply furcate processes typical of this species and which has processes that are stouter than usual; in these respects, this taxon resembles the Berriasian/early Valanginian species *Oligosphaeridium diluculum* Davey 1982. *Cymosphaeridium validum* "regulare" (pl. 1, fig. 17) was recorded between La Charce Bed LCH118M (late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone) and the top of the studied La Charce section, but it was common only as old as Bed LCH203M (early Hauterivian, *radiatus* Zone).

Genus *Dapsilidinium* Bujak et al. 1980

Type: Davey and Williams 1966b, pl. 4, fig. 10, as *Polysphaeridium pastielsii*.

Remarks: As described by Bujak et al. (1980, p. 27), this genus has processes which are, "hollow, open distally, tubiform or tapering" and a tetratabular apical archeopyle. It is distinguished by its open-ended processes from *Downiesphaeridium* Islam 1993, which has distally closed processes (although see also comments on the latter genus under "Notes on some chorate genera", above).

The distinction between *Dapsilidinium* (open-ended processes) and *Downiesphaeridium* (closed processes) is also the main distinction applied here to the elongate genera *Prolixosphaeridium* Davey et al. 1966 and *Tanyosphaeridium* Davey and Williams 1966b (see comments below under *Prolixosphaeridium*).

Dapsilidinium? deflandrei (Valensi 1947) Lentin and Williams 1981

Plate 10, Figure 21

Hystrichosphaeridium deflandrei VALENSI 1947, p. 817; text-fig. 3. Holotype: Valensi 1947, text-fig. 3. – FAUCONNIER and MASURE 2004, pl. 21, figs. 1-4.

Polysphaeridium? deflandrei (Valensi, 1947). – DAVEY and WILLIAMS

1969, p. 6.

Dapsilidinium? deflandrei (Valensi 1947). – LENTIN and WILLIAMS 1981, p. 69.

Remarks: Occurrences of this species were recorded between Vergol Beds B121M and V124M, late Berriasian to late Valanginian, *alpillensis* Zone, *otopeta* Sub-zone to base *peregrinus* Zone; it was not observed at La Charce. This contrasts with its reported occurrence at Rio Argos (Leereveld 1997a, b), which was consistent within the early Valanginian, *campylotoxus* Zone then sporadic as high as the Barremian. It has also been observed by the present author in the late Hauterivian at Speeton, Beds C6 to C4C.

Dapsilidinium duma (Below 1982c) Lentin and Williams 1985

Plate 19, Figures 3, 9, 10

Polysphaeridium duma BELOW 1982c, p. 28, pl. 2, figs. 9a-b, 10a-b, 11-12; text-fig. 6a. Holotype: Below, 1982c, pl. 2, figs. 9a-b. – FAUCONNIER and MASURE, 2004, pl. 19, figs. 14-15.

Dapsilidinium duma (Below 1982c). – LENTIN and WILLIAMS 1985, p. 92.

Remarks: As discussed and figured by Below (1982c, p. 28, pl. 2, figs. 9-12), this species shows significant variation in central body shape and in the number and distal features of the open-ended, hollow processes. Although Below (op. cit., p. 28) described between 50 and 60 processes, the specimen figured in his pl. 2, figs. 10a, b (a particularly elongate form) appears to have significantly fewer, something noted in Below's plate description. In the present study, examples referred to *Dapsilidinium duma* were most comparable to Below's (op. cit.) pl. 2, fig. 11, with significantly longer processes than the holotype (Below, op. cit., pl. 2, figs. 9a, b). Also, the distal process filaments of some specimens recorded here were longer than on any of the specimens figured by Below.

Dapsilidinium duma ranged from Vergol Bed V31 (early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone) to the top of the studied interval at La Charce (early Hauterivian, *loryi* Zone). Consistent occurrences of this species were recorded only as old as Vergol Bed V84M (early Valanginian, uppermost *neocomiensiformis* Zone), however.

Dapsilidinium warrenii (Habib 1976) Lentin and Williams 1981

Plate 13, Figures 1, 4

Polysphaeridium warrenii HABIB 1976, p. 383, pl. 2, figs. 4, 6a-b. Holotype: Habib 1976, pl. 2, figs. 6a-b.

Dapsilidinium warrenii (Habib 1976). – LENTIN and WILLIAMS 1981, p. 70.

Remarks: Although Habib (1976, p. 383) stated that, "The numerous thin, parallel-sided processes of *Polysphaeridium warrenii* distinguish it from other species in that genus", in comparing *D. warrenii* with *Dapsilidinium multispinosum* (Davey 1974) Bujak et al. 1980, he considered that, "the processes in the latter species terminate distally with a closed, slightly recurved spinate margin (R. J. Davey, personal communication), whereas in *P. warrenii* the processes are open distally in most cases and do not recurve. The two species would otherwise be considered conspecific".

Although Habib (1976, p. 383) commented that *Dapsilidinium warrenii* (as *Polysphaeridium*) has processes which are open "in most cases", his more restrictive species description has, "distally

open cylindrical processes"; Habib didn't qualify this further, and both of the specimens he illustrated (op cit., pl. 2, figs. 4, 6) appear to have distally open processes.

Also, in his plate description of the holotype of *D. warrenii* (op cit., pl. 2, fig. 6), Habib described, "the minutely digitate distal ends" of some processes. This is very similar to Davey's (1974) description of *D. multispinosum*, where, "The distal spines are sometimes reduced and difficult to observe".

It is tempting therefore to consider *Dapsilidinium warrenii* a junior synonym of *Dapsilidinium multispinosum* but, given Davey's poor illustration of the holotype of *D. multispinosum* (Davey 1974, pl. 7, fig. 4), no firm conclusions can be made here; re-examination of the type material might resolve this.

Typical specimens of *Dapsilidinium warrenii* were consistently present in the current study, being particularly common in the late Berriasian and earliest Valanginian interval at Vergol. Some specimens also included here in *D. warrenii* bore significantly shorter processes (pl. 13, fig. 4) and were reminiscent of some species of *Litosphaeridium* Davey and Williams 1966b.

Genus ***Diacanthum*** Habib 1972

Diacanthum Habib 1972, p. 376

Tehamadinium Jan du Chêne et al. 1986b, p. 227

Type: Habib 1972, pl.9, fig.1, as *Diacanthum hollisteri*

Remarks: Below (1981, p. 60) re-interpreted Habib's 1972 (p. 376, 377) description of *Diacanthum hollisteri*, concluding that it had a 2P (2" + 3") archeopyle, not 2P (3" + 4") as stated by Habib (op. cit.) and was therefore a junior synonym of *Occisucysta* Gitmez 1970. *Tehamadinium* was subsequently separated from *Occisucysta* by Jan du Chêne et al. (1986b, p. 21), who stated (translation), "*Occisucysta* differs from *Tehamadinium* by the presence of a differentiated periphragm, by an apical horn formed only from the periphragm and also by details of tabulation". If Below was correct, therefore, in specifying a 2P (2" + 3") archeopyle for *D. hollisteri*, this implies that *Diacanthum* is a senior synonym of *Tehamadinium*.

However, Habib and Drugg (1987) re-described *Diacanthum hollisteri* as having a variable archeopyle, defined as P(3"), 2P(2" + 3"/3" + 4"), 3P(2" + 3" + 4"). Jan du Chêne et al. 1986b (p. 9) stated that they had (translation), "observed very numerous cysts attributed to different species of *Tehamadinium* and we have never observed an archeopyle including plate 4" ". They concluded (op. cit., p. 9) that (translation), "The variability of the archeopyle differentiates *Diacanthum* from species of *Occisucysta* *sensu* Gitmez, 1970 (and therefore from the genus *Tehamadinium*)".

The primacy of archeopyle types in separating genera was discussed by Bailey (1987, p. 91 - 94), who stated, "Strict adherence to this principle has led to the erection of separate genera for otherwise identical forms". Referring to variable archeopyles he further stated, "The often customary separation of genera solely on the basis of differences in the archeopyle is becoming far less rigid. Indeed, Evitt (1985) states that the principle is "unacceptably simplistic" ".

Bailey (op. cit., p. 94) also suggested that, "Because of the ar-

chaeopyle variability, there will be a certain amount of overlap in the generic diagnosis of some forms; e.g., *Dissiliodinium* and *Durotrigia*. In this case, one can utilise other diagnostic features".

In their remarks following their emended diagnosis of *Diacanthum*, Habib and Drugg (1987, p. 762) stated, "The concept of *Diacanthum* is emended to accommodate the variability of archeopyle development observed in the type species. The perforate wall structure is also considered to be diagnostic". However, in their diagnosis of *Tehamadinium*, Jan du Chêne et al. (1986b, p. 21) stated (translation), "The autophragm is often thick, sometimes porous, externally smooth or ornate", so it seems that the only essential difference between *Diacanthum* and *Tehamadinium* is the stated archeopyle type.

In view of the consistent 2" + 3" archeopyle observed in numerous specimens of this species in the current study (see remarks under *D. hollisteri* below), *Diacanthum* is here considered to be a senior synonym of *Tehamadinium* Jan du Chêne et al. 1986b. The variable archeopyle described by Habib and Drugg (1987) was not observed and remains unexplained. Habib and Drugg's interpretation might be partly because of some mis-interpretation of key plates (as noted in Below 1981, p. 60) and as further discussed under *Diacanthum hollisteri* (below). It may also be partly due to mis-interpretation of physical damage to this relatively large species.

Diacanthum hollisteri Habib 1972

Plate 6, Figures 8, 12, 17, 22

Diacanthum hollisteri HABIB 1972, p. 376-377, pl. 9, figs. 1, 3; pl. 10, fig. 1; text-fig. 2. Holotype: Habib 1972, pl. 9, fig. 1. - FENSOME et al., 1995, p. 1547, fig. 1.

Tehamadinium dodekovae JAN DU CHÊNE et al. 1986b, p. 25, 26, pl. 18, figs. 1-9; pl. 19, figs. 1-6; text-fig. 5, nos.1, 2.

Remarks: The "close similarity" between *Tehamadinium dodekovae* and *Diacanthum hollisteri* Habib 1972 was noted by Jan du Chêne et al. (1986b, p. 26). However, they expressed some concerns that because the holotype of *D. hollisteri* was lost and the type palynofloral residue was considered too poor to re-examine, Habib and Drugg (1987, p. 762 - 764) had based their generic and specific emendations on (translation), "study of populations of diverse origins (DSDP sites 105, 534, 603 as well as stratotypes and parastratotypes of the Berriasian and Valanginian of south-east France)".

The specimens of *D. hollisteri* illustrated by Habib and Drugg (1987, pl. 3, figs. 1-4) from southeast France are considered here to be conspecific with material recorded in the present study and in Monteil 1993, pl. 3, figs. 6, 7 (as *D. hollisteri* and *T. dodekovae* respectively). Despite Habib and Drugg's interpretation of a variable archeopyle for this species, none were observed here with anything but a 2P (2" + 3") archeopyle, supporting Below's (1981, p. 60) re-interpretation of this species.

In their discussions of the archeopyle type in *D. hollisteri*, Habib and Drugg (op. cit.) referred to the various involvement of 3 precingular plates, and in plate 3, fig. 4B they described, "Opercular piece representing the second precingular plate remains attached at the cingulum; operculum otherwise absent. Note characteristic outlines of high pentagonal third precingular plate, small quadrate fourth precingular plate". This description of characteristic plate outlines was repeated throughout their account.

The specimen illustrated in Habib and Drugg (op. cit.) as pl. 3, fig. 4 may be best compared with the two specimens in similar orientation illustrated here (pl. 6, figs. 8, 12, 17, 22) which, like other specimens recorded in the current study, allow a different interpretation for these opercular plates. In Habib and Drugg's terms, the operculum, as observed in the current study, consists of a high pentagonal second precingular plate and a small quadrate third precingular plate.

This is consistent with that described by Jan du Chêne et al. 1986b for *Tehamadinium*, including *T. dodekovae* and would suggest that Habib and Drugg's description, "Opercular piece representing the second precingular plate remains attached at the cingulum" must refer to the first precingular plate, which would be most unlikely to be part of the operculum.

To have two genera including more or less identical species with more or less the same stratigraphic range is very unlikely. The remarkable similarity between *D. hollisteri* and *T. dodekovae* is obvious and in the present study they are considered to be the same species. *Diacanthum hollisteri* therefore takes precedence.

The stratigraphic range of this species was poorly-defined by Habib (1972, fig. 1), between an interval "dinoflagellates rare" to "probably Valanginian" in DSDP Leg 11, Site 105. *Diacanthum hollisteri* was also recorded by Habib (op. cit.) at Site 100, core #1 (age not specified by Habib) and Site 99A core #11 (Early Cretaceous or Late Jurassic). Site 100, core #1 is the type horizon for *D. hollisteri*, and an "earliest Cretaceous (Valanginian) age" was assigned on nannoplankton evidence by Bukry (1972), although Luterbacher (1972) considered that, "The calpionellid association found in Core 1 of Site 100 is indicative of a Berriasian age".

A more precise range was illustrated in Habib and Drugg 1987 (fig. 3), between the mid Berriasian, upper *grandis* Zone and the late Valanginian, *trinodosum* Zone.

Subsequent outcrop studies (Monteil 1992b, 1993 and Leereveld 1997a) have further confirmed the range of *D. hollisteri*. Monteil (1993, p. 257) described the FO of this species (as *T. dodekovae*) at the base of his *Dichadogonyaulax bensonii* Zone, early Berriasian, *jacobi-grandis* ammonite zone (pars.) and the LO was indicated by Monteil (1992b, Table 1 - as *T. dodekovae*) towards the base of the late Valanginian, *verrucosum* Zone. The range cited by Leereveld (1997a) from Rio Argos (Spain) was from the top of the middle Berriasian (*dalmasi* Zone - Leereveld's oldest sample) to the late Valanginian, *trinodosum* Zone.

In the current study, *D. hollisteri* was recorded throughout much of the Vergol section (absent only from the youngest sample, Bed V132M) and it was consistently common as high as sample V63M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone. Its highest recorded occurrences here were in Vergol Bed V127M and La Charce Bed LCH118M (both within the Faisceau Médian), late Valanginian, *peregrinus* Zone, *nicklesi* Sub-zone). The LO recorded here is therefore closer to that cited by Leereveld and Habib and Drugg than that cited by Monteil.

Other species

Diacanthum aculeatum (Klement 1960) n. comb.
Gonyaulax aculeatum Klement 1960, p. 42, pl. 5, figs. 6-9; text-fig. 21.
 Holotype: Klement 1960, pl. 5, figs. 6, 7.

Diacanthum brixii (Below 1982a) n. comb.
Occisucysta brixii Below 1982a, p. 29, 30, 32, pl. 2, figs. 3a-b, 4a-b, 5-11, 12a-b, 13a-b; pl. 3, figs. 10-17, 21; textfigs. 5a-d
 Holotype: Below 1982a, pl. 2, figs. 13a-b

Diacanthum coummia (Below 1981) n. comb.
Occisucysta coummia Below 1981, p. 61, pl. 8, figs. 6, 7; pl. 13, figs. 10, 11.
 Holotype: Below 1981, pl. 8, fig. 6

Diacanthum crestatum (Jain 1977) n. comb.
Occisucysta crestata Jain 1977, p. 175, pl. 5, figs. 63-65
 Holotype: Jain 1977, pl. 5, figs. 63-65

Diacanthum daveyi (Jan du Chêne et al. 1986b) n. comb.
Tehamadinium daveyi Jan du Chêne et al. 1986b, p. 24, pl. 16, figs. 1-15; pl. 17, figs. 1-5.
 Holotype: Jan du Chêne et al. 1986b, pl. 16, figs. 1-8.

Diacanthum evittii (Dodekova 1969) n. comb.
Gonyaulacysta evittii Dodekova 1969, p. 14, 15, pl. 1, figs. 1-6; pl. 2, figs. 1-12; text-figs. Aa-b
 Holotype: Dodekova 1969, pl. 1, figs. 1, 2

Diacanthum konarae (Dodekova 1992) n. comb.
Tehamadinium konarae Dodekova, 1992, p. 60, 61, pl. 10, figs. 4-8.
 Holotype: Dodekova 1992, pl. 10, figs. 4-7.

Diacanthum mazaganense (Below 1984) n. comb.
Occisucysta mazaganense Below 1984, p. 636, 637, pl. 6, figs. 9A-C; pl. 7, figs. 1A, B; text-fig. 7.
 Holotype: Below 1984, pl. 7, figs. 1A, B

Diacanthum sousense (Below 1981) n. comb.
Occisucysta sousense Below 1981, p. 61, 62, pl. 8, figs. 1a-b, 2
 Holotype: Below 1981, pl. 8, figs. 1a-b

Diacanthum tenuiceras (Eisenack 1958) Stover and Evitt 1978
Gonyaulax tenuiceras Eisenack 1958, p. 389-391, pl. 21, figs. 14, 15; pl. 22, figs. 1-3; pl. 24, fig. 2; text-figs. 4a-c, 5
 Holotype: Eisenack 1958 pl. 21, fig. 15

Diacanthum victorii (Pöthe de Baldis and Ramos 1983) n. comb.
Occisucysta victorii Pöthe de Baldis and Ramos 1983, p. 444, pl. 3, figs. 6, 8
 Holotype: Pöthe de Baldis and Ramos 1983, pl. 3, figs. 6, 8

Genus *Dichadogonyaulax* Sarjeant 1966b emend. Sarjeant 1975 emend. Woollam 1983 emend. Benson 1985

Type: Norris 1965, figs. 8, 9, as *Gonyaulax culmula*.

Dichadogonyaulax bensonii Monteil 1992a
 Plate 2, Figures 14, 15, 18, 19

Dichadogonyaulax bensonii MONTEIL 1992a, p. 274, 276, pl. 1, figs. 1-6; pl. 8, figs. 5-6. Holotype: Monteil 1992a, pl. 1, figs. 1-4

Remarks: This species is superficially similar to *Epitricysta vinckensis* Stover and Helby 1987b in being oblately spherioid with typical polar orientation and relatively high cingular crests which are (in the case of *D. bensonii*) or can be (in the case of *E. vinckensis*) spinose and at least in part fenestrate. Details of the tabulation and the presence or absence of an epicystal cingular crest (as de-

scribed by the defining authors) separate these species. The size ranges quoted by Stover and Helby and by Monteil are very similar. *Epitricysta vinckensis* was not discussed by Monteil (op. cit.).

In the present study, two morphologically similar taxa were recorded, and assigned to *Dichadogonyaulax bensonii sensu stricto* and *D. cf. bensonii*. The former is as described by Monteil, but *D. cf. bensonii* (pl. 2, fig. 5) is smaller and thicker-walled; unfortunately no detailed examination of the tabulation of *D. cf. bensonii* has been possible.

Dichadogonyaulax bensonii was described by Monteil (1992a) from the Berriasian and early Valanginian of southeast France, ranging no younger than the top of the *pertransiens* Zone, a last occurrence confirmed in Monteil 1992b, Table 1. Leereveld (1997a) also recorded this species, but ranging into the *campylotoxus* Zone, slightly higher than Monteil's evidence. In the present study, *Dichadogonyaulax bensonii sensu stricto* was recorded only in the Vergol section, as high as Bed V101M (base late Valanginian, base *verrucosum* Zone), although it was rare and sporadic towards the top of its range.

The observed range of *Dichadogonyaulax cf. bensonii* essentially "follows-on" from that of *Dichadogonyaulax bensonii s.s.* with occurrences recorded between Vergol Bed V97M (top early Valanginian, *inostranzewi* Zone, *platycostatus* Sub-zone) to La Charce Bed LCH 164M (late Valanginian, base *furcellata* Zone). The reference by Duxbury (2018, p. 204) to *Dichadogonyaulax bensonii* ranging as high as palynofloral sub-zone LKP10.3 (basal Hauterivian) refers to *D. cf. bensonii*.

Genus ***Dingodinium*** Cookson and Eisenack 1958 emend. Mehrotra and Sarjeant 1984 emend. Stover and Helby 1987c

Type: Cookson and Eisenack 1958, pl. 1, fig. 10, as *Dingodinium jurassicum*.

Remarks: In their detailed discussion and revised description of *Dingodinium*, Stover and Helby (1987c, p. 281, 282) considered its main distinguishing characteristics to be, "lateral flattening, the prominent ventral pericoel resulting in the camocavate relationship of the cyst bodies and the attached apical archeopyle". They described tabulation, "Generally indicated by archeopyle and paracingulum; other expressions, such as parasutural features, confined to epi-endocyst".

Stover and Helby (op. cit., p. 282) also discounted any tabulation on the hypocyst of *Dingodinium*, "Although Haskell (1969) and Dodekova (1971) provided formulae implying that paratabulation is discernible". They also discounted the presence of any intercalary plates in their specimens or any illustrated specimens, after "Examination of abundant specimens of *D. cerviculum*, additional specimens of *D. jurassicum*, and restudy of published data".

Stover and Helby (op. cit.) contrasted *Dingodinium* with *Belodinium* Cookson and Eisenack 1960, *Boreocysta* Stover and Evitt 1978 and *Gardodinium* Alberti 1961, and they only provisionally accepted *Dingodinium? spinosum* (Duxbury 1977) Davey 1979b, as "Critical features necessary for adequate evaluation are not apparent on illustrations".

In contrast, Pestchevitskaya (2018) reviewed the genus and emended the diagnosis of *Dingodinium* to include a combination archeopyle of type pr[tA₁₋₄]ta. She also provided the full tabula-

tion formula 1pr, 4', 1-3a, 7", 7c, 6", 1p, 1"" sometimes emphasized by folds, crests or arrangement of sculptural features on the pericyst. Pestchevitskaya (op. cit., p. 685) also stated that, "the published detailed morphological studies support the presence of intercalary plates in representatives of the genus *Dingodinium* and their presence in the combination archeopyle of composite type (Stover and Helby, 1987a; Pestchevitskaya, 2010)". This directly contradicts Stover and Helby's (1987c) conclusions.

Also, Pestchevitskaya (op. cit., p.685) stated, "As a result, within the same species, the archeopyle can look intercalary (when only intercalary plates are lost), apical (when all are lost), or combination (when plates are not completely torn off and it is possible to establish the detailed morphology of the operculum)".

Pestchevitskaya (op. cit., p. 683) compared *Dingodinium* with *Ambonosphaera* Fensome 1979, *Sirmiodiniopsis* Drugg 1978, *Senoniasphaera* Clarke and Verdier 1967 and *Scriniodinium* Klement 1957. Both Pestchevitskaya (op. cit.) and Poulsen (1996) accepted the combination *Dingodinium spinosum* unquestioningly, although it remains a questionable assignment (after Stover and Helby 1987c) in Fensome et al. 2019.

Some aspects of both the Stover and Helby and Pestchevitskaya discussions of *Dingodinium* may be questioned:

1/. The stipulation that this genus must display lateral flattening does not appear to cover even the species of *Dingodinium* accepted by Stover and Helby (op. cit.) and certainly not all of those accepted by Pestchevitskaya. Inclusion of this stipulation in their emended diagnosis may reflect their study of abundant specimens of *Dingodinium cerviculum* Cookson and Eisenack 1958, a species known to have such compression, first noted by Haskell (1969, p. 60). However, the type species of this genus is *Dingodinium jurassicum* Cookson and Eisenack 1958 which is not laterally compressed, so that by emphasising this feature, Stover and Helby (op. cit.) effectively excluded the type species. Photographs are included here (pl. 5, figs. 11, 12, 15, 16) of well-preserved specimens of *D. jurassicum* from the Middle Oxfordian (Osmington Oolite Series) of Dorset, England, showing the broad, ovoidal endocyst, which is not laterally flattened.

2/. Stover and Helby excluded tabulation on the hypocyst of *Dingodinium* from their revised generic description, but provisionally accepted *Dingodinium? spinosum* (Duxbury 1977) Davey 1979b, a species illustrated widely with sutural spines and therefore obviously outside their generic definition. Pestchevitskaya took a different approach, stating (op. cit., p. 683), "It is established that the tabulation of the pericyst can be expressed not only by sutural features, but also by crests", and she listed *Dingodinium spinosum* without question.

3/. The inclusion by Pestchevitskaya of intercalary plates as part of the combination archeopyle of *Dingodinium*, the emendation of *Dingodinium albertii* Sarjeant 1966c and *D. tuberosum* (Gitmez 1970) Fisher and Riley 1980 to accommodate this, and the implication of such plates in the type species, *D. jurassicum* ("The pericoel is wide on the ventral side and narrow on the dorsal side; it can be absent, in the zone of intercalary plates" - Pestchevitskaya 2018, p. 688) are difficult to accept without clearer evidence.

The gap in the pericyst interpreted by Pestchevitskaya as "the zone of intercalary plates" was illustrated for *D. albertii* by

Duxbury (1977, p. 29, text-fig. 6) where the archeopyle was described as, "a definite apical archeopyle with the operculum rarely completely detached. A break occurs in the endophragm along a zig-zag line and in the periphragm along a much more irregular one. The operculum remains attached in the ventral area and is "hinged" with the rest of the cyst". Such an archeopyle is illustrated here in pl. 5, figs. 11, 12, 15, 16 for *D. jurassicum* and, like Stover and Helby (op. cit., p. 281), the present author has seen no clear evidence of intercalary plates in this genus.

Neither Stover and Helby (op. cit.) nor Pestchevitskaya (op. cit.) compared *Dingodinium* with *Nelchinopsis* Wiggins 1972 emend Harding 1996, and Harding (op. cit.), in his detailed descriptions and emendations of *Nelchinopsis* and *Gardodinium*, did not compare either genus with *Dingodinium*.

In his re-assessment of *Nelchinopsis kostromiensis* and *Chlamydothorella trabeculosa* (as *Gardodinium trabeculosum*), Harding (1996, p. 351) stated that, "These two taxa are the only fossil dinocysts so far described which show parasutural features developed on ectophragmal wall layers". Subsequently, a third, similar species, *Microdinium? crinitum*, was transferred to *Nelchinopsis* Wiggins 1972 emend. Harding 1996 by Duxbury (2023, p. 149).

A new species, *Dingodinium? globosum* n. sp. was recorded in the present study from the late early and late Valanginian at Vergol. It is questionably assigned to this genus as it appears to be morphologically intermediate between *Dingodinium spinosum* and *Nelchinopsis kostromiensis*, as discussed below.

Dingodinium cerviculum Cookson and Eisenack 1958 emend. Mehrotra and Sarjeant 1984 emend. Khowaja-Ateequzzaman et al. 1990

Plate 5, Figures 10, 14, 22

Dingodinium cerviculum COOKSON and EISENACK 1958, p. 40, pl. 1, figs. 12–14. Holotype: Cookson and Eisenack, 1958, pl. 1, fig. 14.

Remarks: *Dingodinium* spp. occurred through much of the studied section here although they were rare and sporadic below Vergol Bed V101M, close to the base of the late Valanginian, *verrucosum* Zone. There was significant variation in overall size and in the size and density of endocystal ornament, but larger specimens with very fine ornament were recorded no deeper than Bed V101M (base late Valanginian, base *verrucosum* Zone). These have been assigned to *Dingodinium cerviculum* here, although the cavation displayed is significantly less than for the Australasian material (see pl. 5, figs. 10, 14, 22 and Stover and Helby 1987c, fig. 15). The FO of *D. cerviculum* at Vergol corresponds to the lower *verrucosum* Zone first occurrence of this species in Habib and Drugg 1983, fig. 3.

Dingodinium? globosum Duxbury n. sp.

Plate 5, Figures 1–4, 6, 7

Nelchinopsis kostromiensis (Vozzhennikova 1967) Wiggins 1972. – CHAROLLAIS et al. 2023, pl. 11, fig. 6, pl. 12, fig. 6

Holotype: Plate 5, Figures 1, 6

Paratype: Plate 5, Figure 7

Type Locality: Vergol outcrop, early Valanginian, Bed V91M,

inostranzewi ammonite Zone, *inostranzewi* Sub-zone. Holotype: Slide V91M (Schulze), E.F. T.48.4. Paratype: Slide V91M (Schulze), E.F. V54.0.

Derivation of Name: From the Latin *globosus*, round as a ball - in reference to the shape.

Diagnosis: Camocavate cysts with a spheroidal endocyst with no apical projection and a more delicate pericyst produced into a broad-based, distally perforate, rounded apical horn. The endophragm is largely free of ornament but may bear isolated conical or low verrucate ornament. The apical archeopyle involves splitting between apical and precingular plates; the operculum remains attached. Tabulation, apparently gonyaulacoid, is fully developed on the pericyst as indicated by denticulate septa which are higher on the hypocyst. The cingulum is laevorotatory and offset by 1–2 cingular widths; an irregular claustrum in the pericyst represents the sulcus. Gonal areas are raised, creating an angularity to the pericyst.

Dimensions: Holotype 51 × 48 µm. Paratype 53 × 53 µm.

Overall: 53 (50) 48 µm × 53 (47) 43 µm.

Specimens measured – 10.

Remarks: This species is difficult to place taxonomically. Its camocavate nature and archeopyle type suggest *Dingodinium*, and its overall structure, including denticulate crests, is reminiscent of *Dingodinium spinosum* (Duxbury 1977) Davey 1979b. It differs from the last species in its much more rounded outline, in the more complete sutural crest development and in its characteristic, distally perforate "pepper pot" apical horn. Like *D. spinosum*, it is atypical of *Dingodinium* where the large majority of species show significantly greater separation of the cyst walls and where the tabulation, when indicated at all, tends to be restricted to periphragm folds. Also, although *Dingodinium? globosum* can have verrucose endocystal ornament, this is usually reduced and tends to be very irregular, leaving areas of the endocyst smooth.

There is also marked similarity between *Dingodinium? globosum* and *Nelchinopsis kostromiensis* (Vozzhennikova 1967) Wiggins 1972 emend. Harding 1996, a species it resembles in its spheroidal endocyst, its raised gonal areas, its broad-based, low apical horn and its regularly denticulate crests (compare pl. 5, figs. 1–4, 6, 7 and pl. 5, fig. 5). However, in Harding's (1996) re-appraisal of the genus *Nelchinopsis* Wiggins 1972, he described an, "auto-phragm supporting a thin ectophragm on densely-packed, solid, slender processes". This is not the case in *Dingodinium? globosum*.

Specimens referred to *Nelchinopsis kostromiensis* in Charollais et al. 2023 (pl. 11, fig. 6, pl. 12, fig. 6) display the typical "pepper pot" apical horn termination of *Dingodinium? globosum* and are included here. Charollais et al. (2023, p. 39) stated (translation), "*Nelchinopsis kostromiensis*, present in sample AP 644, appears at the base of the *campylotoxus* Zone (Monteil, 1992b)", which is a very similar level to the FO of *D.? globosum* here.

The observed range of this species in the current study was between Beds V45M and V132M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone, although it was consistently recorded only as high as Bed V111. A single specimen was also recorded from La Charce sample LCH113, top *verrucosum* Zone. The absence of this species from higher samples at La Charce may be due to its rarity towards the top of its range.

Genus *Dinogymnium* Evitt et al. 1967 emend. Lentin and Vozzhennikova 1990

Type: Evitt et al. 1967, pl. 1, figs. 21–23; pl. 2, fig. 5; text-figs. 16–18, as *Dinogymnium acuminatum*.

Remarks: The stratigraphical record of this genus was summarised by Londeix, et al. (1996), highlighting its overwhelmingly Late Cretaceous distribution (op. cit., fig. 1). Those authors discussed the tendency in *Dinogymnium* to intra-specific variation and the consequent difficulties in taxonomy. Because of this variability, Londeix et al. (op. cit., p. 375) preferred not to accept "such a restricted definition" of *Dinogymnium* as presented in Lentin and Vozzhennikova (1990), thereby effectively rejecting the genus *Alisogymnium* Lentin and Vozzhennikova 1990, p. 24. Of course, a different approach might be appropriate in the much more diverse Late Cretaceous *Dinogymnium* assemblages.

With its longitudinal "pleats", apparent lack of tabulation and possession usually of pores penetrating the test wall, *Dinogymnium* is an unusual dinocyst genus. Some useful discussion of its possible palaeoenvironmental significance was presented by May (1977, 1980), concluding that this genus may have been adapted to an environment of widely varying and rapidly fluctuating salinity.

Occurrences in the early Cretaceous are relatively very rare, and the oldest outcrop reports to date are from the early Hauterivi-an, *loryi* and *radiatus* Zones of Vergons and Chatel-Saint-Denis, S. E. France and Switzerland respectively (Londeix et al. 1996). Older records were reported offshore in Riley and Fenton 1984 from DSDP Site 535, Leg 77 in the southeastern Gulf of Mexico, including from an interval at the base of that hole which was dated as Berriasian in age, mainly on calpionellids (Premoli Silva and McNulty 1984) with some supporting evidence from calcareous nannofossils (Watkins and Bowdler 1984).

Dinogymnium aerlicum Londeix et al. 1996

Remarks: A characteristic pointed antapex, with a short, curved terminal spine, is characteristic of *Dinogymnium aerlicum* Londeix et al. 1996. In the present study two subspecies have been recognised, *D. aerlicum* subsp. *aerlicum* autonym and *D. aerlicum* subsp. *curvispinum* n. subsp. The latter is completely smooth, lacking the "strongly to faintly marked ridges" described for *D. aerlicum* by Londeix et al. (1996), as clearly shown in the holotype (Londeix et al. 1996, pl. I, fig. 11a-c, text-fig. 7F - not E, as stated in the text). Fenton (pers. comm.) has confirmed that in the type material, "All specimens had ridges on the epitest, with reduced development on the hypotest".

Dinogymnium aerlicum subsp. *aerlicum* Autonym
Plate 5, Figures 8, 9

Dinogymnium aerlicum LONDEIX et al. 1996, p. 380, pl. 1, figs. 10a–c, 11a–c; text-figs. 7E–F. Holotype: Londeix et al. 1996, pl. 1, figs. 11a–c; text-fig. 7F.

Remarks: Isolated specimens of *Dinogymnium aerlicum* subsp. *aerlicum* were recorded at Vergol from Beds B136M, V19M and V42m, the first being the oldest European onshore record to date (early Valanginian, *pertransiens* Zone, *premolicus* Sub-zone).

Although the size range quoted for *Dinogymnium aerlicum* sub-

sp. *aerlicum* by Londeix et al., as length 35 (38) 43 µm, breadth 22 (23.5) 25 µm suggests that it is significantly smaller than *Dinogymnium aerlicum* subsp. *curvispinum*, this contrasts with observations here. Specimens assigned to *D. aerlicum* subsp. *aerlicum* in the current study had the following dimensions: 58 (55) 51 × 41 (36) 30 µm, significantly larger than quoted in Londeix et al. (op. cit.).

Dinogymnium aerlicum subsp. *curvispinum* Duxbury n. subsp.
Plate 4, Figures 1–5

Holotype: Plate 4, Figures 1, 2

Type Locality: Vergol outcrop, late Valanginian, Bed V124M, *peregrinus* ammonite Zone, *peregrinus* Sub-zone. Holotype: Slide V124M(1), E.F. W35.3.

Derivation of Name: From the Latin *curvus*, bent and *spina*, thorn - in reference to the curved terminal spine.

Diagnosis: A small, completely smooth, spindle-shaped subspecies of *Dinogymnium aerlicum* with a sharply pointed antapex bearing a short, curved terminal spine. There is no clear cingulum although this is indicated by two surface folds at approximately the mid-point of the cyst. A small apical "lid" is sometimes observed, hinged close to the apex.

Dimensions: Holotype 51 × 35 µm.
Overall 51 (50) 48 µm × 35 (34) 30 µm.
Specimens measured - 4.

Remarks: *Dinogymnium aerlicum* subsp. *curvispinum* was recorded in Bed V91M (early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone) and in Beds V123M and V124M from the late Valanginian. The last two occurrences span the boundary between the *verrucosum* and *peregrinus* Zones. A single specimen was also recorded in La Charce sample LCH113M, top *verrucosum* Zone. All of these occurrences are significantly younger than the late Berriasian age quoted by Londeix et al. (op. cit.) for *D. aerlicum* subsp. *aerlicum*.

Dinogymnium circulos Duxbury n. sp.
Plate 4, Figures 17, 18, 22
Holotype: Plate 4, Figure 22

Type Locality: Vergol outcrop, early Valanginian, Bed V91M, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone. Holotype: Slide V91M(Schulze), E.F. P44.0.

Derivation of Name: From the Latin *circulos*, circle - in reference to the surface folds.

Diagnosis: A small, proximate, acavate species with an ovoidal to almost square ambitus. The epi- and hypocyst can be symmetrical or the epicyst may be longer than the hypocyst and narrow slightly towards the apex. The test wall is thin and smooth, without obvious trichocyst pores and bears a small number of sub-circular, unornamented ridges each with a small number of longitudinal ridges within them. The cingulum is broad and slightly indented. The "archeopyle" is apical.

Dimensions: Holotype 41 × 41 µm.
Overall 48 (44) 41 µm × 41 (37) 35 µm.
Specimens measured - 2.

Remarks: The sub-circular ridged areas displayed by *Dinogymnium circulos* n. sp. appear to be a unique feature within this genus. They are restricted to regions directly adjacent to the cingulum and may reflect pre- and post-cingular plate series.

Only two specimens of this species were recorded here, but it is considered sufficiently distinctive to include as a new species. Both of the specimens recovered were from the early Valanginian, *inostranzewi* ammonite Zone, Beds V91M (*inostranzewi* Sub-zone) and V97M (*platycostatus* Sub-zone).

Dinogymnium rotundum Duxbury n. sp.
Plate 4, Figures 20, 21, 23, 24

Holotype: Plate 4, Figure 21

Type Locality: Vergol outcrop, early Valanginian, Bed V94M, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone. Holotype: Slide V94M(schulze), E.F. D40.4.

Derivation of Name: From the Latin *rotundus*, round, spherical - in reference to the spherical shape.

Diagnosis: A small, proximate, acavate species with an approximately circular ambitus. The epi- and hypocyst are symmetrical with only minor narrowing towards the apices. The test wall is thin and smooth, without obvious trichocyst pores and lacks well-defined surface ridges, although very faint striations may be seen, restricted to the epicyst. The cingulum is broad and slightly indented and is expressed by clear transverse folds. The "archeopyle" is apical.

Dimensions: Holotype: 48 × 43 µm.
Overall: 51 (48) 46 µm × 46 (44) 43 µm.
Specimens measured - 3.

Remarks: The spheroidal shape and smooth surface of *Dinogymnium rotundum*, essentially lacking the clear surface ridges more typical of the genus, sets this species apart. The closest species, *Dinogymnium circulos* n. sp. can have a square ambitus (but not circular) and the striate, possibly penitabular "enclosures" of the latter species are unique.

Only three specimens of this species were recorded here, but it is considered sufficiently distinctive to include as a new species. These were from the early Valanginian, Beds V48M (*neocomiensiformis* Zone, *neocomiensiformis* Sub-zone) and V94M (*inostranzewi* Zone, *inostranzewi* Sub-zone), and late Valanginian, Bed V124M (base *peregrinus* Zone, *peregrinus* Sub-zone). The wide separation of these occurrences may reflect a significant age range but extreme rarity for this species.

Genus ***Discorsia*** Duxbury 1977

Type: Davey 1974, pl. 4, fig. 9, as *Oligosphaeridium nannus*.

Discorsia nannus (Davey 1974) Duxbury 1977 emend. Duxbury 1977 emend. Khowaja-Ateequzzaman et al. 1985
Plate 7, Figures 15, 18

Oligosphaeridium nannum DAVEY 1974, p. 59, pl. 4, figs. 9, 10. Holotype: Davey 1974, pl. 4, fig. 9. – FENSOME et al., 1995, p.1619, fig. 1. – FAUCONNIER and MASURE 2004, pl. 22, fig. 1.

Discorsia nannus (Davey 1974). – DUXBURY 1977, p. 31.

Remarks: The oldest occurrence of *Discorsia nannus* at Speeton, reported by Duxbury (2018, fig. 10) from Bed D3D, is towards the base of the Polyptychites Beds, early Valanginian. Its first occurrence in southeast France was shown by Monteil (1992b, Table 1) at the base of his *campylotoxum* Zone, again early Valanginian. Habib and Drugg (1983, fig. 3) had the FO of this species at the base of the late Valanginian, base *verrucosum* Zone but the reason for this discrepancy is unclear.

In the present study, *Discorsia nannus* was recorded at Vergol as deep as Bed V59M with an isolated occurrence in Bed V45M, both within the early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone, confirming Monteil's observations (n.b. Monteil's use of an earlier ammonite zonation scheme). This appears to suggest similar first occurrence datums in Boreal and Tethyan settings.

Genus ***Dissiliodinium*** Drugg 1978 emend. Bailey and Partington 1991 emend. Feist-Burkhardt and Monteil 2001

Type: Drugg, 1978, pl. 4, fig. 5, as *Dissiliodinium globulus*

Remarks: Feist-Burkhardt and Monteil (2001, fig. 8 and Table 2) illustrated this genus mainly from the Middle Jurassic, with only a single species, *Dissiliodinium curiosum* Burger and Sarjeant 1995 recorded from the Early Cretaceous; it was also observed in the current study.

Dissiliodinium curiosum Burger and Sarjeant 1995
Plate 15, Figures 12, 13, 15, 16

Dissiliodinium curiosum BURGER and SARJEANT 1995, p. 120–122, 124, figs. 3, 4a–c, 5a–b, 6a–b, 7a–b, 8a–b, 9a–b, 10a–b, 11a–c, 12a–b, 13a–b, 14a–b. Holotype: Burger and Sarjeant 1995, figs. 4a–c.

Dissiliodinium globulum Drugg 1978. – LEEREVELD 1997a, fig. 9i. – LEEREVELD 1997b, fig. 7b.

Remarks: The surface ornament of *Dissiliodinium curiosum* sets this species apart from all others of the genus. A comparable species, *Dissiliodinium globulum* was described (Drugg 1978, p. 68) as "granulate to vaguely spinose. At times there is an approach to the development of a microreticulate pattern but this is neither distinct nor always present".

Where present, the irregular, relatively coarse reticulum of *D. globulum* (compared with *D. curiosum*) was shown by Feist-Burkhardt and Monteil (2001) to be significantly coarser than specimens illustrated as *D. globulum* in Leereveld 1997a, fig. 9I and 1997b, fig. 7b. Leereveld's, specimens have therefore been included in *Dissiliodinium curiosum* here and Leereveld's (1997a, p. 413) suggestion that *D. curiosum* is a junior synonym of *D. globulus* is rejected.

Feist-Burkhardt (pers. comm.) considers that, compared to *Dissiliodinium globulum*, "in *D. curiosum* ornamentation is much finer and more regular" She also stresses the importance of, "the different shape of the 1st and 4th apical plates. They are very long and slender, especially the 1st apical. In the Jurassic specimens of *Dissiliodinium* they are more equally sized and are closer in shape to the standard paratabulation scheme".

Dissiliodinium curiosum is a long-ranging species, shown by Feist-Burkhardt and Monteil (2001, fig. 8) to range at least between the late Berriasian and the Albien and the present author has

also recorded it (pers. obs.) as old as the late Berriasian, Bed D6E, at Speeton. It was recorded from Spain by Leereveld (1997a, b, as *Dissilodinium globulum*) from the early Valanginian, *pertransiens* Zone to near the top of the late Barremian. In the current study sporadic, rare occurrences were recorded at Vergol, as old as sample B138M, early Valanginian, *pertransiens* Zone, *pre-molicus* Sub-zone, similar to the FO observed by Leereveld.

At La Charce, *Dissilodinium curiosum* occurred between sample LCH173M, late Valanginian, *furcillata* Zone, *furcillata* Sub-zone and the top of the studied section. It was relatively rare in the late Valanginian, except for an isolated abundant occurrence in sample LCH176M (*furcillata* Zone, *furcillata* Sub-zone) but it was particularly common within the early Hauterivian, *radiatus* Zone, peaking in sample LCH216M, where it was very abundant.

Genus ***Downiesphaeridium*** Islam 1993 emend. Masure in Fauconnier and Masure 2004

Type: Islam 1983, pl.2, fig.1, as *Cleistosphaeridium spinulastrum*.

Remarks: This genus was described by Islam (1993) to accommodate cysts possessing nontabular, tapering, hollow and distally closed processes and it was emended by Masure (in Fauconnier and Masure 2004), stating in the emended diagnosis, "Les processus non paratabulaires sont nombreux, coniques à aciculaires, parfois tronconiques, creux et fermés distalement". The latter statement more or less repeats part of Islam's diagnosis.

Several taxa with hollow, distally closed processes observed in the present study have been included in *Downiesphaeridium*, although in overall morphology some were very similar to *Dapsilidinium warrenii* (Habib 1976) Lentin and Williams 1981. The separation of species with closed distal process terminations (e.g. *Downiesphaeridium flexuosum*) from very similar forms with distally open processes (e.g. *Dapsilidinium warrenii*) is entirely valid but may be an over-emphasis on this one difference at the expense of many similarities.

This is a similar situation to that described by Eaton et al. (2001, p. 172): "In our view, the synonymy of *Cleistosphaeridium* with *Systematophora* on the basis of the presence of process complexes over-emphasizes this one morphological feature at the expense of other features that may have more important phylogenetic implications". Of course, in a purely morphological classification system, consideration of phylogenetic factors is difficult.

A further feature seen in some specimens recorded here (e.g. *Downiesphaeridium obtusum* n. sp., below) is the presence of closed but distally bluntly-rounded processes. Such forms fit Islam's original diagnosis of the genus, but not necessarily Masure's emendation.

Downiesphaeridium chems (Below 1982c) Duxbury n. comb.
Plate 13, Figures 10, 13

Polysphaeridium chems BELOW 1982c, p. 27–28, pl. 2, figs. 8a–b; text-fig. 6b. Holotype: Below 1982c, pl. 2, figs. 8a–b. – FAUCCONNIER and MASURE 2004, pl. 19, figs. 12, 13.

Dapsilidinium chems (Below 1982c). – LENTIN and WILLIAMS 1985, p. 91.

Remarks: As described by Below (1982c, p. 27), this is a smooth, spheroidal species bearing numerous, distally-closed, hollow

processes which taper and may be bifid. It was recorded in the present study between Vergol Bed V68M (early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone) and the top of the studied La Charce section. It was particularly common in Vergol Bed 88 (Barrande layer B4), again within the early Valanginian. The Valanginian occurrences recorded here extend the range of this species below the Hauterivian as quoted by Below (op. cit., p. 28 and fig. 14).

In overall morphology, *Downiesphaeridium chems* resembles *D. flexuosum* but in the present study it tends to be smaller (see pl. 13, figs. 16, 17). As highlighted by Below (1982c, p. 28), the cyst wall is smooth, as opposed to the microgranular to microspinose ("chagrinat" in Below op. cit., p. 29) main body ornament observed in *D. flexuosum*.

Downiesphaeridium flexuosum (Davey et al. 1966) Islam 1993 emend Sarkar and Singh 1988
Plate 13, Figures 2, 3

Cleistosphaeridium? flexuosum DAVEY et al. 1966, p. 169, pl. 2, fig. 5.

Holotype Davey et al. 1966, pl. 2, fig. 5.

Polysphaeridium? flexuosum (Davey et al. 1966). – BELOW 1982c, p.28
Cleistosphaeridium flexuosum (Davey et al. 1966). – SARKAR and SINGH 1988, p. 39

Downiesphaeridium flexuosum (Davey et al. 1966). – ISLAM 1993

Remarks: In their description of this species, Davey et al. (1966, p. 169) stated that, "The most distinctive feature of ?*C. flexuosum* is the flexuous nature of the broad fibrous processes". In the present study, chorate cysts with a subspherical central body and a microgranular to microspinose ornament have been included in this species, although the processes appear to be smooth; they are however typically hollow, tapering, distally closed and acuminate. The archeopyle is confirmed as apical with a simple type tA operculum which often remains attached. Other than the archeopyle margin there is no indication of tabulation.

As interpreted here, *Downiesphaeridium flexuosum* is essentially similar to *D. warrenii* and *D. obtusum* n. sp. but with significant tapering of the processes, terminating in acuminate tips. In extreme cases the processes are proximally wide and flattened, reminiscent of *Dapsilidinium pastielsii* (Davey and Williams 1966b) Bujak et al. 1980, although the last species has open-ended processes.

Downiesphaeridium flexuosum was long-ranging in the present study, occurring between Vergol sample B113M and La Charce sample LCH216M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone to early Hauterivian, *radiatus* Zone).

Downiesphaeridium obtusum Duxbury n. sp.
Plate 13, Figures 6, 9

Holotype: Plate 13, Figure 6

Type Locality: Vergol outcrop, early Valanginian, Bed V88, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone. Holotype: Slide V88(Schulze), E.F. F41.0.

Derivation of Name: From the Latin obtusus, blunt - in reference to the distally closed and rounded processes.

Diagnosis: Chorate dinoflagellate cysts with a subspherical cen-

tral body and microgranular to microspinose ornament. Sixty or more long, thin, smooth-walled processes extend outward perpendicularly. These are hollow, cylindrical to slightly tapering, distally closed and bluntly rounded. The archeopyle is apical with a simple type tA operculum which often remains attached. Other than the archeopyle margin there is no indication of tabulation.

Dimensions: Holotype Central body $35 \times 38 \mu\text{m}$.
Overall $61 \times 61 \mu\text{m}$.

Size range: Central body $46 (36) 33 \times 46 (36) 29 \mu\text{m}$.
Overall $68 (57) 51 \times 66 (59) 48 \mu\text{m}$.
Specimens measured - 7.

Remarks: *Downiesphaeridium obtusum* n. sp. is essentially similar to *Dapsilidinium warrenii* and *Downiesphaeridium flexuosum* but with closed, bluntly rounded process terminations as opposed to the distally open processes of *D. warrenii* and the acuminate, closed processes of *D. flexuosum*.

Occurrences of this species were largely restricted to the interval between Vergol Beds B110M and B118M (late Berriasian, *alpillensis* Zone, *alpillensis* to *otopeta* Sub-zones) but with sporadic occurrences in the early Valanginian, Vergol Beds V59M, V72M and V88, and in the late Valanginian of La Charce, Bed LCH118M.

Genus ***Druggidium*** Habib 1973 emend. Harding 1986b

Type: Habib 1973, Plate 1, fig. 3; Text-figure 3, as *Druggidium apicopaucicum*.

Remarks: Comments on several species of this genus have been included in Duxbury 2019 and 2023, and further, brief notes are included below on the two species observed here.

Druggidium apicopaucicum Habib 1973

Plate 8, Figures 1-4, 6

Druggidium apicopaucicum HABIB 1973, p. 51–52, pl. 1, figs. 1–3; pl. 3, figs. 1–3; text-fig. 3. Holotype: Habib, 1973, pl. 1, fig. 3; text-fig. 3.

Remarks: Specimens referred to this species *sensu stricto* have clear tabulation, similar to that illustrated by Habib (1973, text-fig. 3) and low crests that are either entire or proximally perforate, similar to crestal structure on the holotype (Habib, op. cit., pl. 1, fig. 3a in particular). Because of the absence of surface ornament, the tabulation of this species tends to be well-marked, although the very small size of some plates, particularly the anterior intercalaries and apicals makes interpretation difficult in transmitted light (see fig. 4 and pl. 3, figs. 1–3 in Habib and Drugg 1983 and Pl. 8, Figs. 1, 2 here).

Druggidium apicopaucicum sensu stricto was recorded consistently between Beds V45M and V59M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone, where it was very common. Some variation in size and in the degree of surface ornamentation was noted, however, with younger specimens, as high as Bed V124M (late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone) tending to be microgranular to scabrate and/or to be smaller than the smoother, larger specimens observed below. These variants are included here as *Druggidium cf. apicopaucicum* and are illustrated in Plate 8, Figs. 5, 7, 10, 11, 14.

The observed range of *Druggidium apicopaucicum sensu stricto* plus *Druggidium cf. apicopaucicum* is very similar to that reported by Monteil (1992b, Table 1) for *D. apicopaucicum*.

Druggidium deflandrei (Millioud 1969) Habib 1973 *sensu* Habib 1973

Plate 8, Figs. 8, 9, 12

non *Microdinium deflandrei* MILLIOUD 1969, p. 429–430, pl. 2, figs. 5–7. Holotype: Millioud 1969, Plate 2, figs. 5, 6
Druggidium deflandrei (Millioud 1969). – HABIB 1973, p. 52

Remarks: *Druggidium deflandrei* was discussed and illustrated by Duxbury (2023, p. 139, pl. 16, figs 7, 8, 12, 13, 19, 20, 21) using specimens from the Barremian, like Millioud's type material. The surface varies from scabrate to very finely reticulate or finely vacuolar, the ornament tending to be penitabular. The specimens recorded in Duxbury 2023, whilst apparently very similar to Millioud's material, did not conform to Habib's interpretation of this species (Habib 1973, p. 52, pl. 1, figs. 4, 5, pl. 2, figs. 1, 2). Millioud (op. cit., p. 429) stated, "sutures low, probably perforate. Wall finely vacuolar and sometimes scabrate", but Habib (op. cit.) included clearly reticulate specimens in this species (Habib op cit., pl. 1, fig. 1, pl. 2, fig. 2), which is not accepted here, although that interpretation has been followed by other authors.

Reticulate specimens similar to Habib's were restricted to the late Valanginian in the present study, in Vergol sample V124M, late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone and between La Charce samples LCH128M and LCH176M, *peregrinus* Zone, *peregrinus* Sub-zone to *furcillata* Zone, *furcillata* Sub-zone. This taxon is referred informally to *D. deflandrei* (Millioud 1969) Habib 1973 *sensu* Habib 1973.

The FO of *D. deflandrei sensu* Habib 1973 in the present study is therefore similar to the base range of "*D. deflandrei*" quoted by Habib and Drugg (1983, fig. 3) and by Leereveld (1997, fig. 2), who illustrated its FO close to the base of the *trinodosum* Zone. Monteil (1992b, Table 1), in contrast, placed the FO of his "*D. deflandrei*" at the base of the *campylotoxum* Zone (i.e. within the early Valanginian).

Genus ***Elimatia*** Duxbury 2019

Type: Davey 1974, p. 63, pl. 7, figs. 2, 3 as *Trichodinium speetonense*.

Elimatia discus (Harding 1990 ex Harding in Williams et al. 1998) Duxbury 2019

Plate 12, Figures 12, 17

Trichodinium discus HARDING 1990, p. 38, pl. 18, figs. 7–13 ex Harding in Williams et al. 1998, p. 615. Holotype: Harding 1990, pl. 18, fig. 7.
Elimatia discus (Harding 1990 ex Harding in Williams et al. 1998). – DUXBURY 2019, p.190.

Remarks: This species was recorded in the present study as old as Vergol Bed V105M (late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone) and throughout the La Charce section.

Ellipsoidictyum Klement 1960

Ellipsoidictyum Klement 1960, p. 78

Dictyopyxis Cookson and Eisenack 1960, p.255 (an illegitimate name)

Dictyopyxidina Eisenack 1961, p. 316

Type: Klement 1960, pl. 6, figs. 15, 16, as *Ellipsoidictyum cinctum*.

Remarks: In his description of *Cassiculosphaeridia*, Davey (1969a, p. 141) noted the similarity of his genus to the type species of *Ellipsoidictyum*, *E. cinctum* Klement 1960, the first differing in lacking "all signs of a tabulation", whereas in *Ellipsoidictyum* "there is an obvious cingulum". Davey (op. cit.) also remarked that, "*Dictyopyxidina* Eisenack (1961) is also very similar but possesses a cingulum and sulcus" (suggesting that *Ellipsoidictyum* does not possess the latter feature). However, in his diagnosis of *Ellipsoidictyum*, Klement (1960, p. 78) described (translation), "indication of a long furrow region".

Further discussion of *Cassiculosphaeridia* and comparisons with Cretaceous species of *Ellipsoidictyum* were included by Duxbury (2019, p. 181, 182).

Ellipsoidictyum minusculum Duxbury n. sp.
Plate 7, Figures 4, 5, 9, 10-13

Holotype: Plate 7, Figures 12, 13

Paratype: Plate 7, Figures 4, 5, 9

Type Locality: Vergol outcrop, Valanginian. Holotype: early Valanginian, Bed V94M, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone, Slide V94M(schulze), E.F. C55.2. Paratype: late Valanginian, Bed V102M, *verrucosum* ammonite Zone, *verrucosum* Sub-zone, Slide V102M(schulze), E.F. F39.3.

Derivation of Name: From the Latin minusculus, rather small - in reference to the size of this species.

Diagnosis: A small, relatively thick-walled species with a spherical main body and with the epicyst approximately equal in length to the hypocyst. The epicyst is rounded triangular in outline and typically extends into a low apical prominence. The hypocyst is semicircular. A vestigial reticulum of variable mesh size covers the cyst, and some lineation of crests marks a broad cingulum. The archeopyle is apical, with the operculum attached.

Dimensions: Holotype 35 × 35 µm
Paratype 41 × 41 µm
Overall 43 (38) 33 µm × 43 (38) 33 µm.
Specimens measured – 8.

Remarks: The presence of a cingulum associated with a surface reticulum allows this species to be placed in *Ellipsoidictyum*; its small size and the characteristic presence of an apical prominence are particularly notable features.

The consistent occurrence of this species at Vergol spans the early/late Valanginian boundary, ranging from Bed V88, *inostranzewi* Zone, *inostranzewi* Sub-zone to Bed V102M, *verrucosum* Zone, *verrucosum* Sub-zone. A single, isolated specimen was also recorded from Bed V42M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone.

Genus ***Exiguisphaera*** Duxbury 1979 emend. Duxbury 2023

Type: Duxbury 1979a, pl. 2, figs. 2, 3; text-figs. 1A, B, as *Exigu-*

isphaera phragma

Remarks: Three species of *Exiguisphaera* were recorded in the present study and are illustrated here; *Exiguisphaera phragma* Duxbury 1979 (pl. 7, figs. 22, 23), *E. asketa* Duxbury 2018 (pl. 7, fig. 21) and *E. lita* Duxbury 2023 (pl. 7, fig. 24).

The first is a long-ranging species, recorded at Speeton (the type locality - pers. obs.) as old as Bed D7E (late Berriasian) and at Vergol as old as Bed B115M, late Berriasian, *alpillensis* Zone, base *otopeta* Sub-zone.

In contrast, the common occurrence of *Exiguisphaera asketa* is restricted to a short interval across the Berriasian/Valanginian boundary at Speeton (Duxbury 2018, p. 181), occurring rarely as old as the upper part of Bed D6I (late Berriasian, *albidum* Zone). At Vergol, *E. asketa* was observed (but never common) between Beds B97M (oldest sample analysed) and B142M (early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone).

The "catch-all" species *E. lita* ranged through much of the studied interval here, from Vergol Bed B110M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) to La Charce Bed LCH208M (early Hauterivian, *radiatus* Zone).

Genus ***Exochosphaeridium*** Davey et al. 1966 emend. Helenes 2000

Type: Davey et al. 1966, pl. 2, figs. 9, 10, as *Exochosphaeridium phragmites*.

Exochosphaeridium robustum Backhouse 1988
Plate 14, Figures 3, 18

Exochosphaeridium robustum BACKHOUSE 1988, p. 85, pl. 26, figs. 9a–b, 10a–b; pl. 28, fig. 7; pl. 48, fig. 1. Holotype: Backhouse 1988, pl. 26, figs. 10a–b. – FENSOME et al. 1996, p. 2331, figs. 3, 4.

Remarks: The proven geographic range of this species is considerable - it was described from Australia by Backhouse (1988), was recorded at Speeton by Duxbury (2018) and is also present at Vergol and La Charce. It is a long-ranging species, first recorded in Vergol Bed B113M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) and ranging to the top of the studied section at La Charce.

Backhouse (op. cit.) reported that in Australia, the FO of *Exochosphaeridium robustum* was within his *Kaiwaradinium scrutilinum* Zone, which Helby et al. (1987, fig. 11) correlated into their *Senoniasphaera tabulata* Zone, assigning a middle to late Valanginian age (Helby et al. op. cit., p. 43). At Speeton, the FO of this species is in Bed D4C, early Valanginian, *Paratollia* Zone (Duxbury 2018, fig. 2). The apparently slightly older FO of *E. robustum* at Vergol may be due to some discrepancy between Speeton and Vergol around the Berriasian/Valanginian boundary (see Fig. 14 and comments under "Boundaries", below).

Genus ***Fibradinium*** Morgenroth 1968

Type: Morgenroth 1968, pl. 42, fig. 4, as *Fibradinium annetorpense*.

Fibradinium variculum Stover and Helby 1987c
Plate 6, Figures 13, 16, 18, 21

Fibradinium variculum STOVER and HELBY 1987c, p. 267, figs. 7A–K

Remarks: As stated in Duxbury 2019 (p. 192), "it is unclear whether or not *Fibradinium variculum* should remain within this genus as, although it is a small, fibrous species with some similarity to the Danian type species *Fibradinium annetorpense*, it displays no clear tabulation (a consistent characteristic of *F. annetorpense*) other than indicated by the cingulum and sulcus. Also, the archeopyle type described by Stover and Helby (1987c, p. 267) for *F. variculum* is apical, type [tA], whereas Slimani (1994) describes the loss of apical and intercalary plates, 9 in total".

Specimens assigned to *F. variculum* here were rare and occurred between Vergol Bed V94M (early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone) and La Charce Bed LCH203M (early Hauterivian, *radiatus* Zone). They varied in their wall thickness, with the older specimens thinner-walled than younger ones (see pl. 6, figs. 13, 16, 18, 21). All specimens had the characteristic rounded-triangular hypocyst and prominent, notched cingulum however.

The type material for *Fibradinium variculum* is of a Barremian to early Aptian age, and Duxbury (2019) recorded it from similar-aged material from the Heselton No. 2 borehole, northern England. Its occurrence at Vergol confirms its very wide geographic spread and is its oldest published record to date.

Genus ***Foucheria*** Monteil 1992a

Type: Monteil 1992a, pl. 3, figs. 1–4, as *Foucheria modesta*

Foucheria modesta Monteil 1992a
Plate 13, Figures 5, 11

Foucheria modesta MONTEIL 1992a, p. 278, pl. 3, figs. 1–7; pl. 4, figs. 1–7. Holotype: Monteil 1992a, pl. 3, figs. 1–4. – FAUCONNIER and MASURE 2004, pl. 27, figs. 9, 10.

Remarks: *Foucheria modesta* was present consistently at Vergol from Bed B111M to Bed V87, late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone to early Valanginian, base *inostranzewi* Zone. An isolated, slightly younger, late Valanginian influx was also observed, in samples V104M and V105M, *verrucosum* Zone, *verrucosum* Sub-zone. A marked up-section increase in numbers of *F. modesta* was recorded between Beds V14M and V19M (early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone) and the peak occurrence of this species was in the early Valanginian, Bed V54M, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone; there was a major reduction in numbers above that level. This species was not recorded at la Charce.

The consistent range of *F. modesta* at Vergol is very similar to that quoted (also in southeast France) by Monteil (1992b, Table 1); Monteil did not record *F. modesta* in the late Valanginian.

Leereveld (1997a, p. 387) stated that in Spain, "Because the nominative species has not yet been found in the Rio Argos succession, the base of the *S. verrucosum* ammonite Zone cannot be defined". However, using indirect evidence, Hoedemaeker and Leereveld (1995) considered that the *B. campylotoxus*-*S. verrucosum* zonal boundary coincides with Rio Argos Bed M323. Leereveld (op. cit., fig. 2) recorded *F. modesta* in Rio Argos as old as Bed M329/330, thereby suggesting a possible *verrucosum* Zone LO, similar to that recorded in the present study at Vergol.

Duxbury (2018, p. 201) stated, "For the purpose of the current study, the Valanginian/Hauterivian boundary has been placed at the LAD of *Foucheria modesta*/FAD of *H. furcatum*, although the precise relationship of this level to macrofossil data still needs to be established". The oldest occurrence of *H. furcatum* at Vergol was in Bed V101M, below but close to the LO of *F. modesta*, as in Duxbury (op. cit.), but clearly within the *verrucosum* Zone. Leereveld recorded a single occurrence of *H. furcatum* in his Rio Argos sample M326/327, immediately below the LO of *F. modesta* and immediately above Hoedemaeker and Leereveld's (1995) pick for the base of the *verrucosum* Zone.

Evidence from Vergol in the present study, from other southeast France sections in Monteil 1992b and from Spain therefore suggests a significant mis-match between this evidence and the use of *F. modesta* as a top Valanginian marker in Duxbury 2018 (see also the section "Boundaries", below).

Genus ***Gochteodinia*** Norris 1978 emend. Below 1990

Type: Vozzhennikova 1967, Plate 12, figs. 3a–b, Plate 15, fig. 1, as *Imbatodinium villosum*.

Gochteodinia brevispina Duxbury n. sp.
Plate 8, Figures 13, 18

Gochteodinia sp. D3E. – DUXBURY 2019, p. 195, pl. 20, fig. 8

Holotype: Plate 8, Figure 13.

Paratype: Plate 8 Figure 18.

Type Locality: Speeton Clay Formation, early Valanginian.

Holotype: Speeton Outcrop, Slide D3E(K-2), early Valanginian, *Polyptychites* ammonite Zone. E.F. K48.2. **Paratype:** Vergol Outcrop, Slide V124M, late Valanginian, *peregrinus* ammonite Zone. E.F. V38.0.

Derivation of Name: From the Latin *brevis*, short and *spina*, thorn – in reference to the much reduced ornament of this species.

Diagnosis: A small, rotund species with a short, bluntly rounded apical horn. The entire cyst surface is finely and evenly granular and bears short, solid, distally-tapering, flat-ended processes, occasionally with a small number of very short terminal spines. Tabulation is expressed only by the archeopyle margin, which involves the displacement of two intercalary plates.

Dimensions: Holotype: Body length - 40 µm. Width - 34 µm.
Paratype Length - 35 µm. Width - 33 µm.
Overall 43 (39) 35 µm × 35 (34) 33 µm
Specimens measured - 4.

Remarks: A single specimen of this species was recorded from the early Valanginian of the Speeton coastal outcrop and was included as informal species *Gochteodinia* sp. D3E in Duxbury 2019. Further, rare specimens have been recorded in the current study including from the late Valanginian (sediments of this age are absent at Speeton). Their preservation was not as good as for the Speeton specimen, which was therefore chosen as the holotype.

Specimens of *G. brevispina* were observed at Vergol between Beds V97M and V124M, early Valanginian, *inostranzewi* Zone,

platycostatus Sub-zone to late Valanginian, basal *peregrinus* Zone, *peregrinus* Sub-zone.

This small, rounded taxon displays several features similar to those observed in *Gochteodinia minuta* Duxbury 2023, including a low, bluntly-rounded apical termination and a finely and evenly granular surface. The horn is relatively broad and short so that the large two-plate intercalary archeopyle is "high" on the cyst of both species. *Gochteodinia brevispina* differs, however, in having much shorter spines. Only a single specimen of *G. minuta* was recorded here, from La Charce Bed 160 (late Valanginian, top *peregrinus* Zone), slightly older than the early Hauterivian type material from Speeton. This specimen is illustrated in pl. 8, fig. 19 for comparison.

Gochteodinia? variabilis Duxbury n. sp.
Plate 3, Figures 5, 9, 10, 14

Holotype: Plate 3, Figures 5, 9.

Type Locality: La Charce outcrop, late Valanginian.

Holotype: La Charce outcrop, Slide LCH164/2, early Valanginian, base *furcellata* Zone, *furcellata* Sub-zone, E.F. B46.3.

Derivation of Name: From the Latin *variabilis*, changeable - in reference to the variable ornament of this species.

Diagnosis: A spheroidal to rounded ellipsoidal species with a short, bluntly rounded apical horn. The surface is covered with ornament ranging from granular to coarsely verrucate on individual specimens and which varies between specimens; there is no discernible organisation of the ornament, although it can reduce significantly towards the apex. Tabulation is not expressed and the archeopyle is uncertain.

Dimensions: Holotype Body length - 63 µm. Width - 43 µm.
Overall 71 (64) 56 µm × 48 (44) 41 µm
Specimens measured - 5.

Remarks: This species is tentatively assigned to *Gochteodinia* because of its pareodinioid shape and its cover of sometimes coarse ornament. The variability of the surface ornament between specimens and on individuals and its general coarseness distinguishes this species from other pareodinioids. Its rounded outline separates it from most others. Unfortunately, the archeopyle could not be determined from the small number of specimens recorded here. Occurrences of this species were restricted to La Charce Bed LCH164 (base *furcellata* Zone, *furcellata* Sub-zone).

Genus ***Hapsocysta*** Davey 1979a emend. Heilmann-Clausen and Van Simaëys 2005

Type: Eisenack and Cookson 1960; pl.3, fig. 6, as *Cannosphaeropsis peridictya*

Hapsocysta minuta Duxbury n. sp.
Plate 8, Figures 21, 25. Plate 15, Figures 8, 9

Holotype: Plate 8, Figure 25

Paratype: Plate 8, Figure 21

Type Locality: Vergol outcrop. *Holotype*: early Valanginian,

Bed V88, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone, slide V88(Schulze), E.F. W49.0. Paratype: late Valanginian, Bed V101M, base *verrucosum* ammonite Zone, *verrucosum* Sub-zone, slide V101/1, E.F. G43.2

Derivation of Name: From the Latin *minutus*, little, small - in reference to the small size of this species.

Diagnosis: A small, spheroidal dinocyst species consisting of a clearly-defined, smooth, elongate endocyst with a small, distally rounded apical projection. A spheroidal, open trabecular (sutural) network supports a delicate, fine-meshed reticulum. Individual sutures are V-shaped in cross-section, composed of a thickened, linear base and two smooth, ribbon-like flanges.

Dimensions: Holotype 41 × 33 µm.
Paratype 30 × 28 µm.
Overall 41 (34) 30 µm × 33 (31) 28 µm.
Specimens measured - 4.

Remarks: This species has been placed in *Hapsocysta* Davey 1979a because it is essentially an open meshwork, composed of narrow strands, outlining a so-far unresolved tabulation and surrounding an endocyst. The small size, delicate fine-meshed reticulum infilling the trabecular network and elongate endocyst with a rounded apical projection set this species apart from others of this genus. The archeopyle type could not be determined.

Hapsocysta minuta was restricted to the early/late Valanginian boundary section at Vergol, Samples V87 to V102M, *inostranzewi* Zone, *inostranzewi* Sub-zone to *verrucosum* Zone, *verrucosum* Sub-zone.

Hapsocysta peridictya (Eisenack and Cookson 1960) Davey 1979a
Plate 20, Figures 5, 7, 8, 9-12

Cannosphaeropsis fenestrata COOKSON and EISENACK 1958, p. 46, pl. 7, figs. 1-3.
Cannosphaeropsis peridictya EISENACK and COOKSON 1960, p. 8, pl. 3, figs. 5, 6. *Holotype*: pl. 3 fig. 6.
Hapsocysta peridictya DAVEY 1979a, p. 556, pl. 4, figs. 1-5.
non *Hapsocysta peridictya* (Eisenack and Cookson 1960) Davey 1979. – JAN DU CHÊNE et al. 2016, pl. 8, fig. 9.

Remarks: In the present study, *Hapsocysta peridictya* was recorded in La Charce samples LCH208M to LCH220M, no older than the early Hauterivian, mid *radiatus* Zone. Much-reduced trabecular height was a feature of specimens towards the base of its range (Pl. 20, Figs. 5, 7, 8, 11).

Duxbury 2001 (p. 107, 108) described *Impagidinium diversum* as having, "fairly low, distally finely denticulate, often sinuous crests with many, small fenestrations to high, trabeculate structures", and this is a very similar morphological range to the early representatives of *H. peridictya* seen here. Common to abundant occurrences of informal species *Impagidinium* LC1 (Pl. 20, Figs. 1-4, 6) were recorded between beds LCH203M and LCH213M; other than lacking trabeculae, that form is also very similar to some older specimens of *H. peridictya* and might suggest that it could be a precursor.

Londeix (1990, vol. 2, p. 115, Chart B) recorded this species as old as the early Hauterivian, *radiatus* Zone at Vergons and he list-

ed two other early Hauterivian records – Fauconnier 1982 (from the original Hauterivian stratotype at Hauterive, Neuchâtel) and Pourtoy 1989 (Veveyse de Chatel-St.-Denis), both in Switzerland. *Hapsocysta peridictya* has been recorded by Leereveld (1997b), restricted to the early Hauterivian of the Rio Argos section in southern Spain and it was reported from Speeton in Duxbury 2023 - Bed C11B, early Hauterivian, towards the base of the *regale* ammonite Zone, the most northerly Hauterivian record to date.

A specimen assigned by Jan du Chêne et al. (2016) to *Hapsocysta peridictya* and illustrated in their pl. 8, fig. 9, shows complex, irregular periphragm fenestration. The single occurrence that they recorded was from the top of the Vions Formation, sample 255.0 m, latest Berriasian (Jan du Chêne et al. op. cit., p. 159). However, in view of evidence in the present study and in other Tethyan studies (Fauconnier 1982; Leereveld 1997b; Londeix 1990 and Pourtoy 1989) for a FO no older than the early Hauterivian for *H. peridictya*, Jan du Chêne et al.'s assignment is not accepted here.

Genus ***Heslertonia*** Sarjeant 1966b emend. Duxbury 1980 emend.

Heslertonia Sarjeant 1966b, p. 133

Dimidium Pearce 2010, p. 56

Type: Neale and Sarjeant 1962, pl. 19, fig. 5; text-fig. 1, as *Gonyaulax heslertonensis*

Emended Diagnosis: Spheroidal to ovoidal dinoflagellate cysts of moderate size bearing sutural crests outlining a typically gonyaulacacean tabulation pattern; the crests may vary in height between species and on individual specimens. There is no apical projection. The main body surface is smooth, finely granular, rugulate or reticulate and the archeopyle is epicystal.

Remarks: The original diagnosis of this genus (Sarjeant 1966b, p. 133) was emended by Duxbury (1980, p. 123) essentially to emphasise the epicystal archeopyle. It is further emended here in light of more recent studies to encompass the rugulate *H. senecta* Harding 1990 ex Harding in Williams et al. 1998 and the reticulate *Heslertonia reticulata* Duxbury 2023. Crestal height has now been shown as very variable between species, being reduced in *Heslertonia inferior* n. sp. and *H. reticulata*, certainly lower than, "¼ the main body diameter", as specified by Sarjeant 1966b and Duxbury 1980.

In discussing his genus *Dimidium*, Pearce (2010, p. 57) stated that, "*Dimidium* most closely resembles *Heslertonia* Sarjeant, 1966 but differs in possessing parasutural crests that are much lower than ¼ body width". The very low crest height of his material is atypical when compared to Clarke and Verdier's type material for their *Gonyaulacysta striata*. Pearce recognised this in stating (op. cit., p. 60), "it is clear the crest heights of *Dimidium striatum* from the Trunch borehole are lower than those from the type material of Clarke and Verdier".

Pearce (op. cit., p. 57, 60) combined Yun's (1981) species *Heslertonia regula* and *Gonyaulacysta striata* Clarke and Verdier 1967 into *Dimidium striatum* (Clarke and Verdier 1967) Pearce 2010. He recognised, however, that for *H. regula* "The average maximum crest height...is less than ¼ the average shortest body dimension...(although only just exceeds that in the holotype)" and that the maximum crest height of Yun's *P. striatum* specimens exceeded ¼ of the largest body dimension. Pearce thus contradicted his stipulation that sutural crest height should be "much lower than ¼ body width" in *Dimidium*.

Dimidium Pearce 2010 is included in *Heslertonia* here, honouring the diagnosis of *Heslertonia* as emended above to include such low-crested species as *Heslertonia inferior* n. sp. and *H. reticulata* Duxbury 2023. This is in agreement with Pearce's own assertion (op. cit., p. 57), "Ornamentation height (i.e. processes or crests) is probably an unsuitable generic level discriminator" and follows Yun's lead in his assignment of *Heslertonia regula* to that genus. The last species is considered a synonym of *Heslertonia striata* (Eisenack and Cookson 1960) n. comb.

Sarjeant (1966b, p. 133) compared the type species, *Heslertonia heslertonensis* (Neale and Sarjeant 1962) Sarjeant 1966b to *Cymatiosphaera striata* Eisenack and Cookson 1960 (transferred to *Heslertonia* in Norvick 1975), stating that "both forms have in common high, striate crests" and suggesting that if these taxa were congeneric or conspecific, "the earlier name *striata* would have priority". Despite this, Norvick (1975, p.47), in re-assigning *Cymatiosphaera striata* to *Heslertonia*, stated that *H. heslertonensis*, "differs slightly from the Australian species in having branched and non-striate lists".

Norvik (op. cit.) also stated that in *H. striata*, "A precingular, haplotabular archeopyle is sometimes developed", and the specimen figured in Norvik 1975, pl. 10, fig. 10 does appear to show a single-plate precingular archeopyle, which is a key criterion excluding "*Cymatiosphaera striata*" from *Heslertonia*.

Neale and Sarjeant (1962, p. 441) and Norvik (1975, p. 47) both assumed *H. heslertonense* to have a precingular archeopyle. Neale and Sarjeant (op. cit.) stated, "A resemblance exists to the genus *Pterodinium* Eisenack 1958, which also has high crests" and Norvik (1975, p. 47) transferred *Cymatiosphaera striata* to *Heslertonia* because of, "The presence of tabulation, the high sutural lists and the precingular archeopyle". Although Norvik recognised that some forms of *Pterodinium* bear high sutural lists, he felt that, "these were never as well-developed as in *Heslertonia striata*". However, in his emendation of *Pterodinium*, Sarjeant (1975, p. 71) specified crestal height as, "in the range 20-30% of the central body breadth", and the specimen of "*Heslertonia striata*" illustrated by Norvik (op. cit., pl.10, fig. 10) falls within that range. *Cymatiosphaera striata* is re-assigned to *Pterodinium* below.

Heslertonia inferior Duxbury n. sp.

Plate 11, Figures 1-3, 5, 7

Holotype: Plate 11, Figure 3, 7.

Paratype: Plate 11, Figure 2.

Type Locality: Vergol outcrop. Holotype: early Valanginian, Bed V19M, *pertransiens* ammonite Zone, *salinarium* Sub-zone, slide V19M/2, E.F. E59.1. Paratype: late Valanginian, Bed V124M, base *peregrinus* ammonite Zone, *peregrinus* Sub-zone, slide V124M(Schulze)/1, E.F. K46.1

Derivation of Name: From the Latin inferior, lower - in reference to the reduced sutural crests of this species.

Diagnosis: A spheroidal cyst of moderate size with smooth, thin wall layers and no apical projection. Tabulation is apparently typically gonyaulacacean and is outlined by low, smooth sutural crests. Crests contact the main body along narrow sutures and distally bear narrow linear thickenings which may be entire or variably denticulate; crests of equal height, similar to those elsewhere

on the cyst, outline and sub-divide a narrow cingulum. The archeopyle is epicystal and the operculum usually remains attached ventrally.

Dimensions: Holotype: Length - 53 μ m. Width - 56 μ m.
Paratype 56 μ m. Width - 58 μ m.
Overall 63 (53) 46 \times 61 (57) 48 μ m.
Specimens measured - 6.

Remarks: This species is similar to *Heslertonia heslertonensis* (Neale and Sarjeant 1962) Sarjeant 1966b in being thin-walled and in having sutural crests which are of even height over the entire cyst. It differs in having particularly low crests and in lacking crestal striations. Low crests are features shared with *Heslertonia reticulata* Duxbury 2023 and *Heslertonia striata* (Eisenack and Cookson 1960) n. comb.

In his diagnosis of *Heslertonia senecta* Harding 1990 ex Harding in Williams et al. 1998, Harding (1990, p. 27) stated that the sutural crests of that species, "are two-layered and usually distally entire (if open the edges are denticulate)". This variability was also observed in *Heslertonia inferior*, where the distal crestal thickenings may bear very small to more conspicuous denticles (see pl. 11 fig. 2).

The moderate size and lack of any apical prominence are highlighted here to contrast *Heslertonia inferior* and *Cauca redacta* n. sp. The latter species has a rounded-triangular epicyst, and an apical protuberance typical of *Cauca* and it is significantly smaller than *H. inferior*:

Cauca redacta: 43 (41) 38 μ m \times 38 (35) 33 μ m.
Heslertonia inferior: 63 (53) 46 μ m \times 61 (57) 48 μ m.

Heslertonia inferior was a rare but long-ranging species in the current study, occurring between Beds B134M and V124M, top Berriasian, *alpillensis* Zone, *otopeta* Sub-zone to late Valanginian, base *peregrinus* Zone, *peregrinus* Sub-zone.

***Heslertonia reticulata* Duxbury 2023**
Plate 11, Figure 10

Heslertonia reticulata DUXBURY 2023, p. 143, pl. 27, figs. 3, 5, 7, 8.
Holotype: plate 27, figs. 3, 8.

Remarks: This species was described from the early Hauterivian in Duxbury 2023 (p. 143) but in the present study it was recorded only as high as La Charce Bed LCH180M, late Valanginian, *furcillata* Zone, *furcillata* Sub-zone and this may reflect some mismatch around the Valanginian/Hauterivian boundary at Speeton and La Charce (see Fig. 16 and comments under "Boundaries", below). The FO of *Heslertonia reticulata* was observed in the late Valanginian at Vergol, sample V111M, *verrucosum* Zone, top *verrucosum* Sub-zone.

Other species:

Pterodinium striatum (Eisenack and Cookson 1960) n. comb.
= *Cymatiosphaera striata* Eisenack and Cookson 1960, p. 9, pl. 3, figs. 10–11.

Heslertonia striata (Clarke and Verdier 1967) n. comb.
= *Gonyaulacysta striata* Clarke and Verdier 1967, p. 31, pl. 4, figs. 11–13; pl. 5, fig. 15; text-fig. 12.

Genus ***Hystrichodinium*** Deflandre 1935 emend. Sarjeant 1966b emend. Clarke and Verdier 1967 emend. Pestchevitskaya 2009

Type: Deflandre 1935, pl. 5, fig. 1; text-figs. 9–11, as *Hystrichodinium pulchrum*.

Remarks: This genus was represented throughout the studied sections, although only two species, *Hystrichodinium pulchrum* Deflandre 1935 (pl. 11, fig. 9) and *H. voigtii* (Alberti 1961) Davey 1974 (pl. 11, fig. 13) were prominent. The abundance of *Hystrichodinium pulchrum* varied widely, this species being particularly common at Vergol, in Bed V111M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) and between samples B131M and B151M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone to early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone). Sporadic increases in numbers were recorded as high as Vergol Bed V116M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone), but it was much less common above that level.

The distribution of *Hystrichodinium voigtii* was significantly different to that of *H. pulchrum*, being rare as high as Vergol Bed V116M and then common to abundant from Vergol Bed 120M to La Charce Bed LCH183M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone to *furcillata* Zone, *callidiscus* Sub-zone). It was most prominent in the *peregrinus* Zone.

Hystrichodinium furcatum Alberti 1961 and *H. ramoides* Alberti 1961 were also recorded here, although they were invariably rare. The oldest occurrence (of *H. furcatum* - pl. 11, fig. 14) was in Vergol Bed V101M, base late Valanginian, base *verrucosum* Zone. Leereveld recorded a single occurrence of *H. furcatum* in his Rio Argos sample M326/327, immediately above Hoedemaeker and Leereveld's (1995) pick for the base of the *verrucosum* Zone. However, Monteil (1997b, Table 1) recorded it only as old as the mid *trinodosum* Zone, a significantly younger late Valanginian level.

Genus ***Hystrichosphaeridium*** (Deflandre 1937) Davey and Williams 1966b

Type: Ehrenberg 1837, pl. 1, fig. 16, as *Xanthidium tubiferum*.

***Hystrichosphaeridium diversum* Duxbury 2018**
Plate 19, Figures 20–22

Hystrichosphaeridium diversum DUXBURY 2018, p. 182, 183, pl. 2, figs. 12, 15–17. Holotype: Duxbury 2018, pl. 2, fig. 12.

Remarks: Specimens assigned to this species were recorded in the present study, having processes ranging from entire, broadly-striate tubes with relatively simple distal margins to more flamboyant examples, although more extreme forms such as that illustrated by Duxbury (2018, pl. 2, fig. 16) were not observed.

The Vergol examples were also slightly smaller overall than those recorded at Speeton, with relatively shorter processes, thus:

Speeton (from Duxbury 2018)	Vergol
Main body: 43 (37) 30 μ m \times 43 (38) 33 μ m.	Main body: 41 (35) 28 μ m \times 43 (40) 38 μ m.
Overall: 66 (57) 46 μ m \times 71 (62) 53 μ m.	Overall: 63 (51) 41 μ m \times 61 (56) 51 μ m.
Specimens measured: 22.	Specimens measured: 7.

Occurrences of *H. diversum* at Vergol were restricted to the Berriasian/Valanginian boundary section, between Beds B131M and B138M, *alpillensis* Zone, upper *otopeta* Sub-zone to *pertransiens* Zone, lower *premollicus* Sub-zone. At Speeton, this species was restricted to the early Valanginian, with its inception in Bed D4B (*paratollia* Zone).

Genus ***Hystrichosphaerina*** Alberti, 1961 emend. Stancliffe and Sarjeant 1990

Hystrichosphaerina Alberti 1961, p. 38.
Polystephanephorus Sarjeant 1961, p. 1096.

Type: Alberti 1961, pl. 10, figs. 2, 3, as *Hystrichosphaerina schindewolfii*.

Remarks: Duxbury (1980, p. 125, 126) considered *Polystephanephorus* Sarjeant 1961 to be a junior synonym of *Hystrichosphaerina* Alberti 1961 and this is further maintained here, although rejected by Lentin and Williams (1981, p. 232). The generic diagnoses of *Hystrichosphaerina* and *Polystephanephorus* were emended by Stancliffe and Sarjeant (1990) but they did not refer to Duxbury's combination of these genera.

Stancliffe and Sarjeant (op. cit., p. 204) stated, "*Hystrichosphaerina* differs from *Polystephanephorus* in that the latter has a different paratabulation formula with fewer process clusters and with the bifurcation of one process per cluster to form a ring trabecula" and they gave the following plate formulae:

Hystrichosphaerina: ?4', 6", 4-6c, 5-6"', 1p, 1'''.
Polystephanephorus: ?4', 5", × or 5c, 6"', 1''', × or 4s.

The formula for *Hystrichosphaerina* was quoted by Stancliffe and Sarjeant directly from Stover and Evitt (1978, p. 57, 58) and they stated (op. cit., p. 204), "A re-examination of the type material is needed to properly define the genus, but its present whereabouts in the German Democratic Republic is unknown to the authors".

For *Polystephanephorus*, they stated (op. cit., p. 205), "The genus differs from *Systematophora* in that *Polystephanephorus* has ring trabeculae and inter-process cluster trabeculae". Also (p. 206), for "the type species of *Polystephanephorus*, only a holotype and one paratype were originally designated. The holotype suffered damage when made into a single mount during the 70's, and the paratype has not been located. The epittract of the holotype was folded, some of the trabeculae being broken and some processes folded... on the accompanying line drawing (text-fig. 1), the area around clusters 2" and 2"' remains difficult to resolve and the detail should be considered as tentative".

In view of the obvious uncertainty involved here, the somewhat minor cited differences in tabulation formulae are difficult to accept as either critical or definitive. Also, the line drawing referred to by Stancliffe and Sarjeant is of the holotype of the type species *Polystephanephorus calathus*, and shows no "inter-process cluster trabeculae" - reference to this feature in their emended generic diagnosis appears to refer to *Polystephanephorus paracalathus* (Sarjeant 1960) Sarjeant 1961 which does possess such trabeculae.

Duxbury (1980, p. 126) transferred *P. paracalathus* to *Hystrichosphaerina*, but the presence of trabeculae connecting process clusters might suggest that *Rigaudella* would be a better placement; *P. paracalathus* might be considered a junior synonym of *Rigaudella*

filamentosa (Cookson and Eisenack 1958) Below 1982b.

Hystrichosphaerina schindewolfii Alberti 1961
Plate 19, Figures 17-19

Hystrichosphaerina schindewolfii ALBERTI 1961, p. 38, 39, pl. 10, figs. 1-3, 6, 7.

Systematophora schindewolfii (Alberti). – DOWNIE and SARJEANT 1965, p. 146.

Perisseiasphaeridium eisenacki DAVEY and WILLIAMS 1969, p. 6.

Remarks: Although this species has been reported from much of the Early Cretaceous, in the current study it was recorded only between Vergol Beds B147M and V105M (early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone to late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone). It was absent from La Charce. A similar range was reported by Leereveld (1997a) from Rio Argos, between his samples M253 and M317 (*pertransiens* Zone to an unresolved interval between proven *campylotoxus* and *verrucosum* Zones). The restricted range at Vergol, supported by Leereveld's evidence, is considered potentially useful locally.

Genus ***Impletosphaeridium*** Morgenroth 1966 emend. Islam 1993

Type: Morgenroth 1966, pl. 10, fig. 5, as *Impletosphaeridium transfodum*.

Remarks: See comments on this genus under "Notes on some chorate genera", above.

Impletosphaeridium multifurcillatum (Prössl 1990 ex Prössl 1992) Williams et al. 1998
Plate 19, Figure 4

Cleistosphaeridium multifurcillatum PRÖSSL 1990, p. 100, 101, pl. 9, figs. 2, 8, 11 (not validly published). Holotype: Prössl 1990, pl. 9, figs. 8, 11. – FAUCONNIER and MASURE 2004, pl. 49, figs. 9, 10.

Cleistosphaeridium multifurcillatum PRÖSSL 1992, p. 113, 114 nomen nudum

Impletosphaeridium multifurcillatum (Prössl 1990 ex Prössl 1992). – WILLIAMS et al. 1998, p. 333.

Remarks: In the present study, *Impletosphaeridium multifurcillatum* has been restricted to specimens with numerous, solid processes with distal filaments which tend to furcate. This contrasts with the simple, unbranched distal spines of *Impletosphaeridium tribuliferum*. In the present study, specimens of *I. multifurcillatum* also tended to be significantly larger than *I. tribuliferum* (see pl. 19, figs. 4, 6, 8).

Prössl (op. cit.) recorded *Impletosphaeridium multifurcillatum* between the early Hauterivian and the late Barremian. The FO in the current study was in Vergol Bed V101M (i.e., the base of the upper Valanginian). It therefore appears to be a useful marker for late Valanginian and younger intervals.

Impletosphaeridium tribuliferum (Sarjeant 1962) Islam 1993
Plate 19, Figures 6, 8

Baltisphaeridium tribuliferum SARJEANT 1962, p. 487, pl. 70, fig. 4; text-figs. 6c, 7. Holotype: Sarjeant, 1962, pl. 70, fig. 4. – FAUCONNIER and MASURE 2004, pl. 23, fig. 11.

Cleistosphaeridium? tribuliferum (Sarjeant 1962). – DAVEY et al. 1969, p. 16.

Hystriospheraeidium petilum GITMEZ 1970, p. 289, 290, pl. 9, figs. 1, 6; text-fig. 24.

Impletosphaeridium tribuliferum (Sarjeant 1962). – ISLAM 1993, p. 87.
Downiesphaeridium (?) *tribuliferum* (Sarjeant 1962) Masure in FAUCONNIER and MASURE 2004, p. 196, 197.

Remarks: This species was described by Sarjeant (1962, p. 488) as having hollow processes numbering "between about forty-five and sixty", although his illustrations of the holotype (op. cit. fig. 6c, pl. 70, fig. 4) suggest fewer than that. Gitmez (1970, p. 287, 288) described the processes of *I. tribuliferum* (as *Cleistosphaeridium*) as "conical, hollow, distally closed...between 28-60 in number" and confirmed an apical archeopyle, as implied by Davey et al. (1966, p. 270) in their transfer of this species to their new genus *Cleistosphaeridium*.

Masure (in Fauconnier and Masure 2004, p. 196, 197) tentatively transferred this species to *Downiesphaeridium* Islam 1993 because hollow processes were described by Sarjeant, although the archeopyle type was not specified in the original description. This transfer is rejected here, and Islam's transfer to *Impletosphaeridium* is accepted - the processes of this species (pers. obs.) do appear to be solid, as stated by Islam (1993, p. 87); i.e., not hollow, as stated by Sarjeant and Gitmez and as accepted by Fauconnier and Masure.

The similarity between published illustrations of *Impletosphaeridium tribuliferum* and *Hystriospheraeidium petilum* Gitmez 1970 is striking. Although Gitmez (op. cit.) included both they were not directly compared. Both are relatively small, smooth-walled, chorate taxa bearing slender processes which bear a small number of distal spines. Again, although Gitmez (op. cit., p. 289, 290) described hollow processes in *H. petilum*, personal observations, both of basal Kimmeridgian, *baylei* Zone material from Dorset (close to the type material) and of specimens in the present and other studies suggest that they are solid.

The plate formula given by Gitmez (op. cit., p. 289) for "*H. petilum*" was 4', 6", 6c, 0-1s, 6", 1p, 1"', totalling 25, although fig. 24 also included a process labelled 1a, for a total of 26 (including the 4 detached apicals). Other than the numbers of processes quoted, *I. tribuliferum* and *H. petilum* appear to be identical, and they are synonymised here; *H. petilum* is interpreted as an end member of *I. tribuliferum*, with particularly low process numbers.

Occurrences of *Impletosphaeridium tribuliferum* were recorded in the current study between Vergol Beds B113M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) and V5M (early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone). A peak in this species was recorded at the lower level, with a further, minor peak in Bed B125M, within the *otopeta* Sub-zone. The present author has recorded *I. tribuliferum* at least to the base of the lower Oxfordian at outcrop, consistent with the records of Sarjeant and Gitmez.

Genus *Isthmocystis* Duxbury 1979

Type: Duxbury, 1979, pl. 1, figs. 1, 2; text-fig. 4, as *Isthmocystis distincta*.

Isthmocystis distincta Duxbury 1979
Plate 17, Figures 2, 3, 5, 6

Isthmocystis distincta DUXBURY 1979, p. 201, pl. 1, figs. 1-6; pl. 2, fig. 8; text-figs. 3A-B, 4. Holotype: Duxbury 1979, pl. 1, figs. 1, 2; text-fig.

4. – Fensome et al. 1993, p. 1133, figs. 1, 2, 7.

Remarks: This is a very long-ranging species in Boreal settings with a proven age-range of late Berriasian, *albidum* Zone to latest early Hauterivian, mid *inversum* Zone, Speeton beds D7E to C7E (pers. obs.). A similar but smaller form, with a less-elaborate circular crest has been recorded in the UKCS Central North Sea by the present author (termed *Isthmocystis* cf. *distincta* in Duxbury et al. 1999), and this ranges as old as the middle Volgian (late Tithonian), palynofloral zone UJP13.1 (Duxbury et al. 1999, fig. 2).

Although the Tethyan range of *I. distincta* is not clear, the "Kim-méridgien inférieur" record from Morocco proposed by Hssaida et al. (2014 p. 13) is considered here a doubtful attribution. Their illustration (op. cit., fig. 11I) appears to be of a broken specimen of another, indeterminate taxon.

Isthmocystis distincta was recorded by Jan du Chêne et al. (2016) from the early Valanginian (Marnes d'Arzier) of the of the Morand borehole, at the foot of the Vaud Jura Mountains, Switzerland. Subsequently, Strasser et al. (2019, p. 231) recorded common *I. distincta* from the late Valanginian/earliest Hauterivian, *furcillata* to lower *radiatus* Zones of the Grand Essert Formation, French-Swiss Jura Mountains; in discussing this species they concluded (translation):

- *Isthmocystis distincta* has been only rarely mentioned from the Franco-Swiss Jura and southeastern France
- Fauconnier (1989) recorded this species from none of the four studied sections included in his palynological study of the Hauterivian stratotype
- Monteil (1985) recorded specimens in the upper Valanginian (*verrucosum* to *callidiscus* Zones) and basal Hauterivian (*radiatus* Zone) of Ardèche, southeast France in a hemipelagic setting. However, only a single, late Valanginian *I. distincta* was noted by Monteil (1986) in the middle of the basin, at Angles
- *Isthmocystis distincta* was not reported by Pourtoy (1989) or Londeix (1990) from Châtel-St-Denis (Ultra-Helvetic, Canton of Fribourg), Buissières (Ardèche) or Haut Vergons (Alpes de Haute-Provence)
- The presence or absence of *I. distincta* appears closely related to environmental conditions, occurring mainly in the hemipelagic domain.

In the present study, *Isthmocystis distincta* was rare with a relatively restricted range, entirely within the upper Valanginian. It was recorded between Vergol beds V105M and V127M, *verrucosum* Zone, *verrucosum* Sub-zone to *peregrinus* Zone, *peregrinus* Sub-zone and at La Charce as young as Bed LCH149M, *peregrinus* Zone, *nicklesi* Sub-zone. The only common occurrence of this species was in La Charce sample LCH107M, late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone.

This species was not reported by Leereveld (1997 a, b), and its apparent absence from the pelagic sediments at Rio Argos (Spain) may also be due to the type of palaeoenvironmental control suggested by Strasser et al. (op. cit.).

Genus *Kleithriasphaeridium* Davey 1974

Type: Davey 1974, pl. 5, figs. 1, 2; text-fig. 3, as *Kleithriasphaeridium corrugatum*.

Remarks: According to Stover and Evitt (1978, p.167, 168),

Diversispina Benson 1976 is a taxonomic junior synonym of *Kleithriasphaeridium*, but they stated (op. cit., p. 168) that, "*Kleithriasphaeridium* differs from *Cordosphaeridium* in having hollow, nonfibrous processes". In discussing his type species *Diversispina truncata*, Benson (1976, p. 185) stated, "In view of the fibrous nature of the processes (even though the fibrous character is obscure) *Diversispina truncata* is most likely related to the genus *Cordosphaeridium*". Benson's 1976, pl. 2, fig. 9 shows this fibrous nature particularly well.

In their remarks on *Kleithriasphaeridium*, Fensome and Williams (2019, p. 117), stated that, "*Kleithriasphaeridium* is similar to *Cordosphaeridium* in being chorate with one process per paraplate, and bearing a precingular archeopyle. However, in *Cordosphaeridium* the processes are fibrous".

It seems more appropriate for the above reasons, therefore, to include *Diversispina truncata* in *Cordosphaeridium*, consistent with Slimani's (2001, p. 193) contention that *Cordosphaeridium digitatum* Wilson in Slimani 2001 (name not validly published) is a taxonomic junior synonym of *D. truncata*.

See also the discussion in Duxbury 2019 (p. 192) concerning Fensome et al.'s (2016) treatment of *Kleithriasphaeridium vis-avis Florentinia* Davey and Verdier 1973 and remarks below on *Kleithriasphaeridium porosispinum* Davey 1982.

***Kleithriasphaeridium corrugatum* Davey 1974**
Plate 14, Figure 2

Kleithriasphaeridium corrugatum DAVEY 1974, p. 56–57, pl. 5, figs. 1–5; text-fig. 3. Holotype: Davey 1974, pl. 5, figs. 1, 2; text-fig. 3.

Remarks: The FO of this species was observed in Bed V68M (early Valanginian, *neocomiensiformis* Zone, top *neocomiensiformis* Sub-zone). Although this extends its range in southeast France significantly below the late Valanginian, *trinodosum* Zone level illustrated by Monteil (1992b, Table 1), this is still much younger than its known range in Boreal settings where it ranges at least as old as the late Berriasian, palyzone LKP5 (Duxbury 2001).

***Kleithriasphaeridium fasciatum* (Davey and Williams 1966b) Davey 1974**
Plate 14, Figures 4, 5

?*Cordosphaeridium fasciatum* DAVEY and WILLIAMS 1966b, p. 90, pl. 7, figs. 5, 6. Holotype: Davey and Williams 1966b, pl. 7, fig. 5.

Kleithriasphaeridium fasciatum (Davey and Williams 1966b). – DAVEY 1974, p. 58.

Remarks: Although this species was transferred to his new genus *Kleithriasphaeridium* by Davey (1974, p. 58), he did not compare it with the type species *Kleithriasphaeridium corrugatum* Davey 1974, although they are essentially very similar. The only significant difference between *K. fasciatum* and *K. corrugatum* is that the processes of *K. fasciatum* are much shorter.

Kleithriasphaeridium telaspinosum (Fisher and Riley 1980) Lentin and Williams 1981 is a remarkably similar species to *K. fasciatum* although it has a stratigraphic range in the UKCS Central North Sea restricted to the Late Jurassic (early and middle Volgian, palynofloral Sub-zones UJP 9.2 to UJP10.2 of Duxbury et al. 1999). *Kleithriasphaeridium telaspinosum* is similar in size to *K. fasciatum* and has striate tubular processes of a similar length,

differing only in having significantly more irregular/ragged distal process margins.

The FO of *Kleithriasphaeridium fasciatum* was noted by Monteil (1992b, 1993) within Sub-zone A of his *Muderongia macwhaei* Zone. He stated, "The first occurrence of *K. fasciatum* coincides with the base of the Valanginian", at the base of the *otopeta* Sub-zone. A similar base *otopeta* position was noted for this event here, within Bed B115M. The *otopeta* Sub-zone was not seen by Leereveld, who therefore recorded *K. fasciatum* only to the base of the *pertransiens* Zone, recognising the FO of *K. fasciatum* high in his *P. pelliiferum* Zone.

At Vergol, *Kleithriasphaeridium fasciatum* was particularly common across the Berriasian/Valanginian boundary, between Beds B129M and V19M, peaking in Bed V14M (*pertransiens* Zone, *salinarium* Sub-zone), where it was abundant.

***Kleithriasphaeridium porosispinum* Davey 1982**
Plate 2, Figure 13, 17

Kleithriasphaeridium porosispinum DAVEY 1982, p. 29, 30, pl. 10, figs. 8–12. Holotype: Davey 1982, pl. 10, figs. 10–12.

Remarks: As noted by Duxbury (2019, p. 232), "*Kleithriasphaeridium porosispinum* is listed per se in Williams et al. (2017, p. 477), although it has many characteristics distinctly similar to those of *Cordosphaeridium*, including one fibrous process per plate and a precingular archeopyle. Its retention in *Kleithriasphaeridium* by various authors is presumably because of its much older range (early Volgian to late Ryazanian - Duxbury et al. 1999) than "accepted" *Cordosphaeridium* spp.". Although Davey's (1969b, p. 35) emended diagnosis for *Cordosphaeridium* could also accommodate *K. porosispinum*, Davey (1982, p. 29, 30) did not discuss this possibility when describing this "extremely fibrous" species. *Kleithriasphaeridium porosispinum* is also listed per se in Fensome et al. 2019.

Duxbury (2018, p. 206), also noted that "In the Golden Eagle Field wells, where common reworked Kimmeridge Clay Formation material is often present, the resolution of the "true" tops of long-ranging taxa, including *Dingodinium spinosum* and *Kleithriasphaeridium porosispinum* can be difficult". Duxbury et al. (1999) defined the top of Zone LKP5 (= top Berriasian) on the LAD's of *Dingodinium spinosum*, *Dichadogonyaulax culmula* and *Kleithriasphaeridium porosispinum*.

Reworking was generally very rare in the present study - single occurrences of *Polygonifera staffinensis* and *Prolixosphaeridium mixtispinosum* in Vergol sample V123M and single *Tubotuberella apatela* in La Charce samples LCH154 and LCH183. In addition, however, *Kleithriasphaeridium porosispinum* was common between La Charce samples LCH128M and LCH141M and fairly common in sample LCH160M; this species was otherwise rare but persistent between Vergol sample V111 and La Charce sample LCH187M (i.e., it was present and sometimes common throughout much of the upper Valanginian but absent from older samples).

It would be unusual for a single reworked taxon to occur commonly (or even persistently) without an associated reworked assemblage, so the unusual presence of *K. porosispinum* here is anomalous. No conclusions have been reached and the presence of this species in the upper Valanginian at Vergol and La Charce remains unexplained.

Kleithriasphaeridium simplicispinum (Davey and Williams 1966b) Davey 1974
Plate 14, Figure 1

Kleithriasphaeridium simplicispinum (Davey and Williams 1966b, p. 59, 60, pl. 9, fig. 3). –DAVEY 1974, p. 57. Holotype: Davey and Williams 1966b, pl. 9, fig. 3.

Remarks: This species was considered to be a taxonomic junior synonym of *Kleithriasphaeridium eoinodes* (Eisenack 1958) Davey 1974 by Below (1982c, p. 17), but although Below stated (op. cit., p. 18) (translation), "In my opinion, there is no difference between *Kleithriasphaeridium simplicispinum* ... and *Kleithriasphaeridium eoinodes*" he didn't elaborate.

This was something specifically excluded by Davey and Williams (1966b, p. 60), who stated, "In general appearance *H. simplicispinum* strongly resembles *Cordosphaeridium eoinodes* but the fibrous periphragm is absent and the number of processes is greater". Although they specified *Cordosphaeridium eoinodes* in this statement, in Davey and Williams (op. cit., p. 91), those authors only questionably assigned it to that genus.

Similarly, Davey (1974, p. 58) stated, "*K. simplicispinum* comb. nov. appears to be similar to "*Cordosphaeridium*" *eoinodes* (Eisenack 1958) from the Aptian of Germany but differs in being larger and having non-fibrous processes".

Sarjeant (1985) re-examined Eisenack's type material and emended the diagnosis of *K. eoinodes*, claiming that (op. cit., p. 75), "the original diagnosis was vague". Although he referred to Below 1982c elsewhere, Sarjeant (1985), did not refer to Below's inclusion of *K. simplicispinum* in *K. eoinodes*.

Sarjeant's emended diagnosis concluded, "Sulcal processes solid, other processes hollow, with walls that are non-fibrous but often (consistently?) very finely perforate. Paratabulation 4', 6", 6c, 5--?6", lp, 1"', ?4s. Surface of phragma laevigate to granulate".

Neither Eisenack's original diagnosis for *Kleithriasphaeridium eoinodes* (for English translation see Sarjeant 1985, p. 74) nor Sarjeant's emendation described fibrous processes and Sarjeant specifically stated "non-fibrous". It is unclear therefore why Davey and Williams 1966b and Davey 1974 assumed that this was a characteristic feature of *K. eoinodes*.

A feature which seems to be typical of *K. simplicispinum* is the presence of granular/microreticulate patches on the endocyst at process bases. This feature was described by Davey and Williams (1966b, p. 60) as, "At the base of each process there is a characteristic thickening of the endophragm, which is here reticulate" and by Davey (1974, p. 57) as, "The cyst wall beneath these processes is noticeably thickened and coarsely granular". This feature may be seen on the holotype (Davey and Williams 1966b, pl. 9, fig. 3) and was also illustrated by Harding (1990, pl. 22, fig. 15) and Duxbury (2023, pl. 16, figs. 1, 2).

How "characteristic" these ornate patches are of *K. simplicispinum* is debatable, but no such features were noted for *K. eoinodes* by Eisenack, Sarjeant or Below. These two taxa are clearly very similar, although further re-examination of the type material might be necessary to resolve the true morphology of *K. eoinodes*. Pending this, both species are maintained in the present study, but with reservations. *Kleithriasphaeridium simplicispinum*

ranged throughout the studied interval.

Genus ***Mendicodinium*** Morgenroth 1970 emend. Bucefalo Palliani et al. 1997

Type: Morgenroth 1970, pl.9, figs. 5, 6, as *Mendicodinium reticulatum*

Remarks: There is some difficulty in separating the various species of this very long-ranging genus, with differentiation relying to a large degree on the nature, configuration and density of surface ornament. No attempt has been made in the current study to formally subdivide this genus, and taxa have been placed into two informal groupings, *Mendicodinium* "granular" and *Mendicodinium* "reticulate". These are briefly discussed below.

***Mendicodinium* "granular"**

Plate 15, Figures 1, 2, 10

Remarks: Specimens included in this grouping include individuals whose surface ornament ranges from microgranules to conical but with no obvious resolution into a reticulum. No clearly spinose individuals were observed. The cyst wall of these individuals is fairly thick and the operculum is usually retained.

Occurrences of this group were observed throughout the studied sections at Vergol and La Charce, but they were usually rare. Common occurrences were restricted to Vergol samples B131M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone) and V116M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone). They were also common within the lower Hauterivian, *radiatus* Zone of La Charce, however, between samples LCH198M and LCH208M.

***Mendicodinium* "reticulate"**

Plate 15, Figures 3, 5-7

Remarks: A wide variety of forms are included here, ranging from microreticulate to more coarsely reticulate, some with a clear reticulum and others with a degraded, partly vermiculate ornament. Thin-walled to significantly thicker-walled forms occur and the operculum is usually retained.

Occurrences of this group were observed throughout much of the studied sections at Vergol, although no older than Bed B142M (early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone). At La Charce, occurrences were restricted to the interval between Bed LCH183M (latest Valanginian, *furcellata* Zone, *callidiscus* Sub-zone) and the top of the studied section.

Common occurrences of *Mendicodinium* "reticulate" were restricted to Vergol Bed V120M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone) and La Charce Beds LCH189 and LCH191 (base Hauterivian, *radiatus* Zone).

Genus ***Muderongia*** Cookson and Eisenack 1958

Type: Cookson and Eisenack 1958, pl. 6, fig. 2, as *Muderongia mcwhaei*.

Muderongia dedecosa (Gocht 1957) Duxbury 2023

Plate 16, Figure 3

Wetzelietta ? neocomica forma *dedecosa* GOCHT 1957, p. 177; text-fig. 11. Holotype: Gocht, 1957, text-fig. 11.

Wetzeliiella ? neocomica forma *circulata* GOCHT 1957, p. 178; text-fig. 14. *Phoberocysta neocomica* subsp. *dedecosa* (Gocht 1957). – LENTIN and WILLIAMS 1973, p. 112.

Phoberocysta neocomica subsp. *circulata* (Gocht, 1957, p. 178; text-fig. 14). – LENTIN and WILLIAMS 1973, p. 112.

Muderongia dedecosa (Gocht 1957). – DUXBURY 2023, p. 147, pl. 34, figs. 4, 5.

Remarks: The presence of this species in Tethyan material was confirmed in the present study. Although rare, it was recorded as old as Vergol Bed V19M, early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone.

Muderongia extensiva Duxbury 1977

Muderongia extensiva DUXBURY 1977, p. 54, 55, pl. 15, fig. 10. Holotype: Duxbury 1977, pl. 15, fig. 10. – MONTEIL 1991, pl. 4, fig. 5.

Remarks: The morphological variability displayed by this species in the present study has allowed its division into two subspecies below. The synonymisation by Monteil (1991) of *Muderongia extensiva* into *Muderongia mcwhaei* Cookson and Eisenack 1958 is rejected here, as by Poulsen (1996, p. 57). In the present study, specimens assigned to *M. mcwhaei* bear short lateral horns similar to the holotype (Cookson and Eisenack 1958, pl. 6, fig. 2), and therefore include only the shorter-horned specimens of "*Muderongia mcwhaei* (sic) forma A" of Monteil 1991.

Muderongia extensiva Duxbury 1977 subsp. *extensiva* Autonym Plate 16, Figure 12

Muderongia extensiva DUXBURY 1977, p. 54, 55, pl. 15, fig. 10. Holotype: Duxbury 1977, pl. 15, fig. 10. – MONTEIL 1991, pl. 4, fig. 5.

Muderongia mcwhaei (sic) Cookson and Eisenack 1958 forma B. – MONTEIL 1991, pl. 3, figs. 7, 8, pl. 4, fig. 5.

Remarks: This subspecies of *M. extensiva* is distinguished by its lack of surface ornament.

In the present study, the FO of *M. extensiva* subsp. *extensiva* at Vergol was in Bed V5 (*pertransiens* Zone, *salinarium* Sub-zone), a similar level to the base range of this species illustrated by Monteil (1992b, Table 1 as *M. mcwhaei* forma B) and Habib and Drugg (1983, fig. 3) and its oldest common occurrence was in Bed V42M (base *neocomiensiformis* Zone).

Occurrences of common to abundant *Muderongia extensiva* subsp. *extensiva* appear either to suggest some regional age variation or that the macrofossil data might be questioned. At Speeton, the lower Valanginian is sub-divided into two zones, an older *Paratollia* Zone (= *Platylenticeras*) and a younger *Polyptychites* Zone (see Rawson et al. 1978, p. 11, 12 and Duxbury 2018, fig. 2). The top of the *Polyptychites* Zone, upper Bed D2E is unique in yielding abundant *M. extensiva* subsp. *extensiva*, which is otherwise absent from Speeton except for rare occurrences in overlying Bed D2D, immediately above a major early Valanginian/Hauterivian hiatus.

In contributing to Jeremiah et al. 2010, the present author analysed well and outcrop samples from the Saxony Basin, including the Suddendorf I quarry and many Dutch and German drill cores in its vicinity (some with *Platylenticeras* ammonites). The *Polyptychites* ammonite-dated Bentheim Sands from the Romberg Quarry and a number of core chips within the Bentheim

shales were also analysed. Four samples were analysed from the Suddendorf I quarry, at 10 cm, 40 cm, 1.2 m and 9 m below the base of the Bentheim Sandstone. A significantly richer dinocyst assemblage was recorded from the 9 m sample than above including very common *Muderongia extensiva* and fairly common *Bourkidinium granulatum*. These pre-Bentheim Sands sediments in the Saxony Basin are unambiguously from the *Paratollia* Zone (ammonite dated).

Because of the evidence from the Saxony Basin, the oldest occurrence of common to abundant *M. extensiva* was plotted in Jeremiah et al. 2010, fig. 2 at an upper *Paratollia* Zone level, but this conflicts with the evidence from Speeton. There is an obvious mis-match between the Speeton and Saxony Basin sections either because the base of common to abundant *M. extensiva* differs significantly even between eastern England and Germany, at similar latitudes (Suddendorf: 51° 00', Speeton: 54° 9'), or because the ammonite dating needs to be reviewed.

Muderongia extensiva Duxbury 1977 subsp. *spinosa* n. subsp. Plate 16, Figures 7, 8, 10

Muderongia mcwhaei (sic) Cookson and Eisenack 1958 forma C. – MONTEIL 1991, pl. 4, fig. 2 only

Holotype: Plate 16, Figure 8.

Paratype: Plate 16, Figures 7, 10.

Type Locality: Vergol outcrop, late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone. Holotype - Bed V107M, Slide V107M(1), E.F. K49.0. Paratype - Bed V107M, Slide V107M(schulze), E.F. E47.2.

Derivation of Name: From the Latin spinosus, thorny - in reference to the spiny ornament.

Diagnosis: A subspecies of *Muderongia extensiva* with spiny ornament on the horns which is often restricted to their distal parts.

Dimensions: Holotype: 210 × 122 µm (complete). Paratype 101 × 122 µm (operculum detached).

Overall Complete specimens - 220 (192) 159 µm × 159 (134) 114 µm.
Specimens measured – 6.
Operculum detached - 114 (102) 89 µm × 149 (130) 109 µm.
Specimens measured – 10.

Remarks: The spiny covering demonstrated by this subspecies can cover all of the horns but can be restricted to their distal parts or in extreme cases to only the left antapical horn. In his description of his *Muderongia mcwhaei* (sic) forma C, Monteil (1991, p. 474) stated, "Periphragm often spinous", and his pl. 4, fig. 2 was clearly so.

This subspecies ranged between Beds V5M and V107M at Vergol, early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone to late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone. It was common only from Bed V76M (*neocomiensiformis* Zone, *campylotoxus* Sub-zone) to the top of its range.

Muderongia perforata Alberti 1961 emend. Monteil 1991 emend Riding et al. 2001
Plate 16, Figure 6

Muderongia perforata ALBERTI 1961, p. 13, pl. 2, figs. 8, 9 (non pl. 2., fig. 7). Holotype: Alberti 1961, pl. 2, fig. 8 (the holotype of this species is lost). Neotype: Alberti 1961 pl. 2, fig. 9 and Riding et al. 2001, pl. 1, fig. 3.

Remarks: Specimens assigned to this species in the current study were very similar to those described and illustrated in Duxbury 2018 and 2023. They are again included in this species with reservations, pending further data, for reasons fully explained by Duxbury (2023, p. 147, 148).

Muderongia perforata was present in the current study between Vergol Beds V51M and V124M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to late Valanginian, *peregrinus* Zone, base *peregrinus* Sub-zone; a minor peak occurrence was recorded in Bed V120M, where it was common. A very similar LO was proved at La Charce where single occurrences were recorded in samples LCH107M and LCH113M (i.e., to the top of the *verrucosum* Zone, *pronecostatum* Sub-zone). The range of *M. simplex* proved here for southeast France is therefore somewhat different to that assigned in the Central North Sea and onshore at Speeton, into the base of the Hauterivian, *amblygonium* ammonite Zone, palynofloral Subzone LKP10.3 (Duxbury 2018, p. 204, text-fig. 10).

Although a specimen of *M. perforata* from the upper Valanginian (*verrucosum* Zone) of southeast France was illustrated by Monteil (1991, pl. 2, fig. 11, pl. 7, fig. 2 and pl. 11, fig. 2), that author did not provide a stratigraphic range for this species.

***Muderongia simplex* Alberti 1961**
Plate 16, Figures 9, 11

Muderongia simplex ALBERTI 1961, p. 12, pl. 2, figs. 1-6, pl. 12, figs. 1, 2. Holotype: Alberti 1961, p. 12, pl. 2, fig. 4.

Muderongia cf. *mcwhaei* Cookson and Eisenack 1958. – ALBERTI 1961, p. 14, pl. 2, fig. 3.

?*Muderongia tomaszowensis* ALBERTI 1961, pp. 12, 13, pl. 2, figs. 12, 13.

?*Muderongia tabulata* (Raynaud 1978). – MONTEIL 1991, p. 476, pl. 2, figs. 4, 5; and pl. 8, fig. 1 only.

Muderongia tomaszowensis Alberti 1961. – MONTEIL 1991, pl. 3, figs. 1, 2 only.

Muderongia australis Helby 1987. – MONTEIL 1991, pl. 5, fig. 1; and pl. 9, fig. 6 only.

Muderongia endovata RIDING et al. 2001, pl. 1, figs. 1, 2; text-figure 3.

Remarks: Duxbury (2018, p. 183-187) discussed this species in some detail and included various forms separated-out by other authors as part of a wide morphological range. A similar range was recorded in the current study and again these are considered part of a continuum.

It was observed in the Central North Sea (Duxbury (2018, p. 186) that, "there was development within the lower Valanginian from smaller examples of *M. simplex* near the base of its range to larger examples having longer, narrower horns". Also (op. cit., p. 184) that, "Monteil's (1991) large morphotypes were reported to be from the *pertransiens* Zone (basal Valanginian) of the Swiss Jura. According to Hoedemaeker and Herngreen (2003), the *pertransiens* ammonite zone is equivalent at Speeton to the Paratollia Beds (Beds D4C to D4A), but in the present study, none of the very large *M. simplex* variants were observed within that interval".

As in Duxbury 2018, specimens of *Muderongia simplex* in the lower part of its range at Vergol were smaller with shorter lateral horns than above. However, unlike the evidence from the Central North Sea, larger forms similar to Alberti's type material first appeared towards the base of the Valanginian, in Bed B136M (*pertransiens* Zone, *premollicus* Sub-zone), thus confirming Monteil's observations.

A further dissimilarity between the distribution of *M. simplex* in the present study and in the Central North Sea is that in the latter, a major influx of *Muderongia simplex* was recorded over a short interval, restricted to the late Valanginian. At Vergol, however, although there were some fluctuations in numbers, *M. simplex* was a prominent species, often very common to abundant, between the base of the studied section and Bed V112M (late Valanginian, *verrucosum* Zone, base *pronecostatum* Sub-zone); above Bed V112M it was rare. The highest very common occurrence of *M. simplex* was further confirmed at La Charce, where it was abundant only in Bed LCH107M (also within the *pronecostatum* Sub-zone), and rare above.

The LO of common *M. simplex* in the current study contrasts with that in the Central North Sea, where it occurs towards the top of the Valanginian, Subzone LKP10.2 (Duxbury 2018, p. 186).

Genus ***Nelchinopsis*** Wiggins 1972 emend. Harding 1996

Nelchinopsis Wiggins 1972, p. 299-302, Plate IA-F, fig. 2.

Alaskadinium Duxbury 1977, p. 37.

Type: Vozzhennikova 1967, pl. 26, figs. 1-6, as *Gonyaulax kostromiensis*.

Nelchinopsis kostromiensis (Vozzhennikova 1967) Wiggins 1972 emend. Harding 1996
Plate 5, Figure 5

Nelchinopsis kostromiensis (Vozzhennikova 1967, p. 85, 86, pl. 26, figs. 1-6; pl. 27, figs. 1, 2). – WIGGINS 1972, p. 301, 302. Holotype: Vozzhennikova 1967, pl. 26, figs. 1-6. – JAN DU CHÊNE et al. 1986a, pl. 44, figs. 7, 8. – LENTIN and VOZZHENNIKOVA 1990, text-fig. 64; lost according to Lentin and Vozzhennikova (1990, p. 109). Lectotype: Lentin and Vozzhennikova 1990, pl. 15, figs. 5, 6, designated by Lentin and Vozzhennikova (1990, p. 109). – HARDING 1996, pl. 1, fig. 1.

non *Nelchinopsis kostromiensis* (Vozzhennikova 1967) Wiggins 1972. – CHAROLLAIS et al. 2023, pl. 11, fig. 6, pl. 12, fig. 6.

Remarks: The FO of *Nelchinopsis kostromiensis* was shown by Monteil (1992b, Table 1) to be within the early Valanginian, at the base of the *campylotoxus* Zone. However, Habib and Drugg (1983, fig. 3) showed its FO close to the top of the late Valanginian, within their *callidiscus* Sub-zone and in the present study it was recorded no older than Vergol Bed V112M, late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone. All of these studies referred to sections in southeast France. Specimens illustrated as *N. kostromiensis* in Charollais et al. 2023 have been included in *Dingodinium? globosum* Duxbury n. sp. here and the similarity between *N. kostromiensis* and *D.? globosum* is discussed under the latter species. If *D.? globosum* has been included in *N. kostromiensis* by some authors then this might explain some of the older southeast France FO's.

An isolated, very common occurrence of *Nelchinopsis kostromiensis* was noted in La Charce Bed 183M (latest Valanginian, *furcillata* Zone, *callidiscus* Sub-zone) and peak occurrences have been recorded towards the top of the Valanginian in several Central North Sea proprietary studies. In addition, however, consistently very common occurrences have been observed at Speeton between Beds D2B and C11B (early Hauterivian, *amblygonium* to base *regale* Zones), suggesting that high numbers of *N. kostromiensis* may be typical across the Valanginian/Hauterivian boundary.

Genus *Nematosphaeropsis* Deflandre and Cookson 1955

Type: Deflandre and Cookson 1955 pl. 8, fig. 5, as *Nematosphaeropsis balcombiana*.

Nematosphaeropsis scala Duxbury 1977
Plate 2, Figures 2, 3

Nematosphaeropsis scala DUXBURY 1977, p. 43, pl. 9, fig. 2. Holotype: Duxbury 1977, pl. 9, fig. 2.

Remarks: The FO of this species was reported in Duxbury 2018 within the late Valanginian, palynofloral Sub-zone LKP9.2 and it was illustrated at that level by Duxbury (2018, fig. 10). However, Duxbury (1977, fig. 21) also illustrated the presence of this species in Speeton Bed D2E, which lies immediately below a major hiatus at Speeton, separating the lower Hauterivian from the lower Valanginian; this oldest record may be open to question, considering subsequent data.

In the present study, *Nematosphaeropsis scala* was recorded between Vergol Bed V111M (late Valanginian, *verrucosum* Zone, upper *verrucosum* Sub-zone) to La Charce Bed LCH194 (early Hauterivian, *radiatus* Zone); previous work (Duxbury 1977; 2023) has also shown its LO towards the base of the upper Hauterivian.

Genus *Occisucysta* Gitmez, 1970 emend. Jan du Chêne et al. 1986b

Type: Gitmez 1970, pl.5, figs.1–2; text-fig.16, as *Occisucysta balios*.

Remarks: Jan du Chêne et al. (1986b, p. 17) listed several characteristics to distinguish *Occisucysta duxburyi* Jan du Chêne et al. 1986b from *Occisucysta tentorium* Duxbury 1977. Duxbury (2023, p. 150) noted that despite the considerable morphological variation displayed by *O. duxburyi*, a very fine vermiculate/reticulate surface ornament appeared to be a consistent feature. The distinctive nature of this surface ornament was contrasted with the, "irregularly granular, sometimes aligned" ornament of the holotype of *O. tentorium*, as noted by Dr. G. L. Eaton (pers. comm.).

However, a photograph of the holotype of *O. tentorium* taken from the Natural History Museum, London "Duxbury Collection" (<https://data.nhm.ac.uk/dataset/collection-specimens/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/2159561>) and reproduced here as Pl. 18, Fig. 1 also appears to show a reticulate surface ornament. This therefore appears to be an invalid means of distinguishing these two species, and unless the other defining characteristics listed for *O. duxburyi* by Jan du Chêne et al. (1986b, p. 17) are proved to be valid, it must bring into doubt the validity of *O. duxburyi*.

Genus *Oligosphaeridium* Davey and Williams 1966b emend. Davey 1982

Original type: White 1842, pl. 4, fig. 11, as *Xanthidium tubiferum* var. *complex*.

Neotype: Davey and Williams 1966b pl. 7, fig. 1, designated by Davey and Williams (1966b, p.71).

Oligosphaeridium complex (White 1842) Davey and Williams 1966b

Plate 18, Figure 19

Oligosphaeridium complex WHITE 1842, pl. 4, fig. 11, lost according to Davey and Williams (1966b, p. 74). Neotype: Davey and Williams 1966b, pl. 7, fig. 1, designated by Davey and Williams (1966b, p. 71).

Remarks: *Oligosphaeridium complex* is consistently one of the most common species in the Boreal Early Cretaceous and the base of its range at Speeton is within the early Valanginian, *Paratollia* Zone (Duxbury 2018). In the present study, however, it was rare and ranged only as old as the late Valanginian, Vergol Bed V105M, *verrucosum* Zone, *verrucosum* Sub-zone, supporting the *verrucosum* Zone base range quoted by Monteil (1992b, Table 1).

An older FO was indicated in Spain by Leereveld (1997a, figs. 2, 3), however, who recorded it as old as the early Valanginian; consistently through much of the *campylotoxus* Zone with an isolated occurrence towards the base of the *pertransiens* Zone. This record cannot be fully assessed, however, as Leereveld (op. cit.) did not illustrate this species.

The late Berriasian FO illustrated by Habib and Drugg (1983, fig. 3) is anomalously old for either Boreal or Tethyan settings.

Oligosphaeridium distinctum Duxbury 2018

Oligosphaeridium distinctum DUXBURY 2018, p. 188, pl. 7, figs. 1,3–5,8. Holotype: Duxbury 2018, pl. 1, figs. 1, 4, 8.

Remarks: This species was shown to range across the early/late Valanginian boundary in the Central North Sea (Duxbury 2018, fig. 10), whereas in the current study it was restricted to just three contiguous samples at La Charce, LCH 164M, LCH166M and LCH170M, all within the late Valanginian, *furcillata* Zone, lower *furcillata* Sub-zone. Because of mis-placement of the early/late Valanginian boundary in Duxbury 2018 (probably at a position equivalent to La Charce Bed LCH141 - i.e., at a mid late Valanginian level - see comments on "Boundaries", below), the range of *O. distinctum* in the Central North Sea may be entirely within the late Valanginian, although still ranging older than seen at La Charce.

Genus *Ovoidinium* Davey 1970 emend Lentin and Williams 1976 emend Duxbury 1983

Type: Cookson and Hughes, 1964, pl. 5, fig. 4, as *Ascodinium verrucosum*

Ovoidinium? glebulentum Duxbury n. sp.
Plate 13, Figs. 8, 12, 16

Holotype: Plate 13, Figures 12, 16

Type Locality: Vergol outcrop, early Valanginian, Bed V10M, *per-*

transiens ammonite Zone, *salinarium* Sub-zone. Holotype: Slide V10M/3, E.F. P41.2.

Derivation of Name: From the Latin *glebulentus*, lumpy- in reference to the mesotabular thickenings.

Diagnosis: A sub-spherical cyst with a thick, multi-layered endophragm and a delicate periphragm. The latter is usually broken and represented by fragments. Solid, domed, circular mesotabular thickenings occur over the surface of the endophragm, one per plate. A combination archeopyle is always developed and the operculum usually remains attached. No sutural or cingular features.

Dimensions: Holotype Length - 56 µm. Width - 63 µm. Overall - 56 (49) 43 µm × 63 (50) 41 µm. Specimens measured - 7.

Remarks: *Ovoidinium? glebulentum* is most similar to *Ovoidinium diversum* Davey 1979a, particularly in its thick endophragm which has "a spongy appearance" (Davey, op cit. p. 558). *Ovoidinium diversum* does not have the mesotabular thickenings characteristic of *O.? glebulentum*, however.

Ovoidinium? glebulentum is only questionably assigned to the genus *Ovoidinium* Davey 1970 because it has not been possible here to determine the exact composition of the operculum. Davey (1979a, p. 558) stated that the archeopyle of *O. diversum*, "could be mistaken for a simple apical archeopyle", although the most distinctive characteristic is, "the straight paraplate boundary parallel to the paracingulum on the dorsal surface". Davey (op. cit.) interpreted this as the boundary between intercalary plate 2a and plate 4". The true archeopyle type was described by Davey as compound 4A3I and this was clearly demonstrated in some of his illustrations (Davey op. cit., pl. 6, figs. 6-8, 11 and 16).

The observed range of *Ovoidinium? glebulentum* was between Vergol Beds B111M and V76M, late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone to early Valanginian, *neocomiensis* Zone, *campylotoxus* Sub-zone. This is significantly older than most other records of *Ovoidinium* spp., which are mainly of a mid-Cretaceous age. However, Leereveld (1997a) recorded "*Ovoidinium diversum*" throughout the Valanginian (i.e., post-*otopeta* Sub-zone) interval at Rio Argos; the specimen he illustrated (op. cit., fig. 8k) does not show the mesotabular thickenings characteristic of *O.? glebulentum*.

Genus ***Palaecysta*** Chen 2013

Type: Chen 2013, pl. 1, fig. 1, as *Palaecysta integra*.

Remarks: Chen (2013) considered the presence of arcuate basal process ridges to be sufficient reason to separate his genus *Palaecysta* from *Systematophora*, citing 3 points of divergence by which *Palaecysta* differs from *Systematophora* (Chen, op. cit., p. 285). He considered these, "essential, fundamental and quite distinct":

- [*Palaecysta*] possesses arcuate, whereas [*Systematophora*] possesses annulate process clusters for their pre- and postcingular paraplates
- the former lacks while the latter possesses a linked basal ridge for their paracingular process pairs
- the distal end of the process clusters in the former group bends outward (flares) whereas that in the latter remains straight and columnar

Although Davey's concept of *Systematophora* included adcingular reduction or complete absence of basal annular ridges, *Palaecysta* is accepted in principle here, as there are no universally accepted criteria of what constitutes a "key characteristic" for generic separation of dinocysts, so that separation of *Palaecysta* from *Systematophora* based on Chen's criteria is perfectly valid. As with any similar taxonomic sub-division, however, the main question is whether it is reasonable, sustainable and consistently applicable.

Palaecysta palmula (Davey 1982) Williams and Fensome 2016 Plate 1, Figure 16

Systematophora palmula DAVEY 1982, p. 11, 12, pl. 1, figs. 1-4. Holotype: Davey 1982, pl. 1, figs. 1-3. – FAUCONNIER and MASURE 2004, pl. 76, figs. 11-13.

Palaecysta palmula (Davey 1982). – WILLIAMS and FENSOME 2016, p. 140.

Remarks: Transfer of this species to *Palaecysta* Chen 2013 is accepted here, although despite the second of Chen's "essential, fundamental and quite distinct" criteria separating *Palaecysta* from *Systematophora* (see above), Davey (1982, p. 12) stated that in *Systematophora palmula*, "The paracingular processes occur in pairs, two per paraplate, and each pair may be linked proximally by a ridge".

The Boreal range of this species was reported by Davey (1982, p. 12) as Ryazanian to Valanginian in the Haldager No. 1 borehole (Denmark) and between the *albidum* (late Ryazanian) and *Paratollia* (early Valanginian) zones of the Speeton Clay. Chen (2013, p. 293) reported *P. palmula* consistently in all six of his zones, early Tithonian to Hauterivian, in the Ankamotra-1 well (Madagascar), although his fig. 3 illustrated it no younger than the Valanginian, up to the top of his Zone 2.

In the present study, *P. palmula* ranged from the deepest sample analysed at Vergol, B97M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) to sample V104M (late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone).

Genus ***Palleodinium*** Duxbury n. gen.

Type species: *Palleodinium digitatum* n. sp.

Derivation of Name: From the Latin *palleo*, to be pale – in reference to its characteristic delicate, thin-walled nature.

Diagnosis: Small, pear-shaped to elongate ovoidal dinocysts bearing a small number of long, solid spines restricted to circum-polar areas. The surface is smooth to very finely granular and the spines are produced into fine, complexly-ramifying distal terminations. No clear archeopyle but common breakage suggests that it is apical. Minor concavity might suggest the position of an otherwise undefined cingulum. No tabulation is expressed.

Remarks: This genus is so far represented by a single, essentially featureless species which is distinguished by its pear-shaped body and circum-polar distribution of the small number of solid spines. Some breakage at the apex is assumed to represent the archeopyle, but because of the tapering epicyst of most specimens of this very small form, this has proved impossible to fully interpret in transmitted light.

Nohr-Hansen (1993, p. 47-50) emended the description of the prolate genus *Bourkidinium* Morgan 1985, citing, "long, hollow, tubular processes which are restricted to the apex (reflecting apical, or apical and precingular plate-series) and antapex (reflecting antapical, or maybe antapical, postcingular and sulcal plate-series). The equatorial zone is wide and devoid of processes". This differs from *Palleodinium* since the latter has primary spines only on what are assumed to be the precingular and postcingular series. Also, the spines of *Palleodinium* are solid and distally ramify into a complex network whereas the processes of *Bourkidinium* are hollow and distally flared with entire margins.

Palleodinium digitatum Duxbury n. sp.
Plate 14, Figures 9, 10. Plate 17, Figure 13

Rhombodella spp. TORRICELLI 2001, pl. 8, fig. 20.

Holotype: Plate 14, Figure 10

Paratype: Plate 17, Figure 13

Type Locality: Vergol outcrop, early Valanginian, *inostranzewi* Zone. *Holotype*: Bed V91M, *inostranzewi* Sub-zone, Slide V91M(schulze), E.F. R48.2. *Paratype*: Bed V97M, *platycostatus* Sub-zone, Slide V97M(A), E.F. C47.3.

Derivation of Name: From the Latin *digitatus*, having fingers – in reference to the distal complexity of the spines.

Diagnosis: As for the genus.

Dimensions: *Holotype* 46 × 46 µm. *Paratype* 35 × 35 µm.
Overall 46 (38) 33 µm × 46 (41) 30 µm.
Specimens measured – 9.

Remarks: The number of primary spines observed in this species varies with up to six at each circum-polar area and these are presumed to reflect the precingular and postcingular series. The finely-ramifying spine terminations are similar to those of *Cauca perplexa* Duxbury 2023, another small species, although the latter is significantly younger, the primary spines are flattened (those in *P. digitatum* are not) and the archeopyle is epicystal.

Palleodinium digitatum n. gen. n. sp. was observed from the base of Bed V87 (sample included in Appendix 3), immediately below Barrande layer B1 to Bed V124M at Vergol, early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone to late Valanginian, *peregrinus* Zone, *peregrinus* Sub-zone. A slightly longer Tethyan range is suggested however, as this species has also been recorded towards the base of the Valanginian, *pertransiens* Zone, *premolicus* Sub-zone in Spain (pers. obs.) and a single specimen was illustrated in Torricelli 2001 (pl. 8, fig. 20 as *Rhombodella* spp.), from the lower Hauterivian of the Vallone Rosmarino section, Sicily.

The specimen illustrated by Helby et al. (1988, fig. 18, A, B) and referred to *Oligosphaeridium*? sp. nov. A appears to be very similar to *P. digitatum* but Helby et al. provided no description. Also, their Australian species is restricted to the "lower Tithonian" Puti Siltstone.

Genus ***Perisseiasphaeridium*** Davey and Williams 1966b

Type: Davey and Williams 1966b, pl.11, fig.8, as *Perisseiasphaeridium pannosum*.

Perisseiasphaeridium cretaceum Duxbury 2018
Plate 18, Figure 9

Perisseiasphaeridium cretaceum DUXBURY 2018, p. 181, pl. 7, figs. 7, 9, 10. *Holotype*: Duxbury 2018, pl. 7, fig. 7.

Remarks: A very short stratigraphic range was noted for *Perisseiasphaeridium cretaceum* by Duxbury (2018, p. 190, fig. 10), "within the lower Valanginian, Palyzone LKP6, immediately below the FAD of *Oligosphaeridium complex*". In the present study, this species was recorded between Vergol Beds B121M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone) and V54 (early Valanginian, *neocomiensis* Zone, *neocomiensis* Sub-zone). Its peak occurrence was in Bed B151 (early Valanginian, *pertransiens* Zone, *premolicus* Sub-zone), where it was common.

Genus ***Phoberocysta*** Millioud 1969 emend. Helby 1987

Type: Gocht 1957, pl. 19, fig. 1; text-fig. 7, as *Wetzelilla? neocomica*.

Remarks: Similarities between this genus and *Muderongia* Cookson and Eisenack 1958 have been noted widely, and Monteil (1991, p. 470) considered *Phoberocysta* to be a taxonomic junior synonym of *Muderongia*. Both *Muderongia* and *Phoberocysta* are recognised here, following Helby (1987) and Riding et al. (2001, p. 24).

There is a great deal of morphological variation within this genus and for the most part specimens appear to be part of a continuum; this has led to *Phoberocysta neocomica* (Gocht 1957) Millioud 1969 becoming something of a "bucket taxon"; the various "formas" of *P. neocomica* described by Gocht (1957) and formalised into subspecies in Lentini and Williams 1973 are difficult to separate consistently. This was the case in the present study, although one extreme form appears to be distinguishable, and it is described below as *Phoberocysta latissima* Duxbury n. sp.

Considerable size variation is a further feature of *P. neocomica*, and such variation was seen in the present study. Rare, particularly small but otherwise "typical" specimens of *P. neocomica* were recorded in two upper Valanginian samples, V107M and V111 (pl. 17, fig. 8), *verrucosum* Zone, *verrucosum* Sub-zone, but the reason for this reduction from its more normal size is unknown. Specimens of the "usual" size are illustrated in pl. 16, fig. 4 and pl. 17, fig. 11.

Phoberocysta latissima Duxbury n. sp.
Plate 16, Figures 1, 2, 5

?*Phoberocysta neocomica* Alberti 1961. – MILLIOUD 1969, pl. 2, fig. 4, pl. 3, fig. 4.

?*Muderongia tomaszowensis* Alberti 1961. – MONTEIL 1991, pl. 9, fig. 4 only.

Holotype: Plate 16, Figure 2.

Paratype: Plate 16, Figure 1.

Type Locality: Vergol outcrop, early Valanginian, Bed V31M, *pertransiens* ammonite Zone, *salinarium* Sub-zone. *Holotype*: Slide V31M/3, E.F. H47.0. *Paratype*: Slide V31M/3, E.F. M46.1.

Derivation of Name: From the Latin *latissima*, very wide.

Diagnosis: A large, smooth, proximochoate cyst with two wall layers clearly represented. Four long, slender horns of approximately equal length are present, including an apical, two equal laterals and a left antapical. The laterals are distally notched with short postcingular projections. A rudimentary right antapical horn may also be present. Tabulation is marked only by the zig-zag apical archeopyle margin. The endocyst is diamond-shaped and clearly defined, with rounded apices. Acuminate, capitate or briefly furcate spines of moderate length cover the cyst surface. The operculum is usually retained.

Dimensions: Holotype: Length - 144 μm . Width - 119 μm . Paratype: Length - 144 μm . Width - 114 μm . Both are complete specimens

Overall - Complete specimens: 144 (142) 132 μm \times 127 (115) 101 μm (5 specimens).

Operculum detached: 104 (88) 81 μm \times 122 (116) 104 μm (6 specimens).

Remarks: This species possesses significantly longer, more slender horns than other members of this genus. The very wide morphological range currently included in *Phoberocysta neocomica* does include some morphotypes with fairly long horns, but the essentially cruciform nature of *P. latissima* falls outside the range.

Gocht (1957) described several "forma" of *Wetzelietta ? neocomica* - now *Phoberocysta neocomica* (Gocht 1957) Millioud 1969, including *Wetzelietta ? neocomica* forma *cruciformis*, and this appears to be the closest morphologically to *P. latissima*. All of Gocht's "formae" were incorporated into *Phoberocysta neocomica* by Millioud (1969, p. 432), and this was further formalised by Lentin and Williams (1973) who listed them as subspecies of *P. neocomica*. Subsequently, by implication in Monteil (1991, p. 477), *Wetzelietta ? neocomica* forma *cruciformis* was listed as a taxonomic junior synonym of *Phoberocysta neocomica*.

In his treatment of "*Wetzelietta ? neocomica* forma *cruciformis*", Gocht (1957, p. 176) described a diamond-shaped test with well-developed horns at the poles, features in common with *P. latissima*. However, he also described, "somewhat squat" lateral horns, with, "one of them often inclined forward" and an inner body, "somewhat hinted at". This contrasts with the long lateral horns and clearly-defined endocyst of *P. latissima*. In addition, Gocht (op. cit.) described, "a weak transverse structure" (Gocht op. cit., fig. 10), again not observed in *P. latissima*.

In the present study, *Phoberocysta latissima* was largely restricted to the early Valanginian, ranging consistently between Beds V10M (*pertransiens* Zone, *salinarium* Sub-zone) and V82M (*neocomiensis* Zone, *campylotoxus* Sub-zone). A major increase in this species was recorded between Beds V26M and V36M, peaking at the higher level where it was abundant. It is therefore particularly characteristic of the upper part of the *salinarium* Sub-zone.

Further occurrences of *Phoberocysta latissima* were noted as isolated occurrences in La Charce Beds LCH206M and LCH220M, both in the early Hauterivian, *radiatus* ammonite zone. The apparently damaged specimen figured as *Muderongia tomaszowensis* Alberti 1961 by Monteil (1991, pl. 9, fig. 4), from the *pertransiens* Zone of southeastern France might also be assignable to *P. latissima*, as might that specimen from the upper Hauterivian at Angles (SE France) figured as *Phoberocysta neocomica* in Millioud 1969, pl. II, fig. 4, pl. III, fig. 4.

Genus ***Prolixosphaeridium*** Davey et al. 1966 emend. Davey 1969a

Type: Davey et al. 1966, pl.3, fig.2; text-fig.45, as *Prolixosphaeridium deirense*.

Remarks: The nature of *Prolixosphaeridium* and its relationship to *Tanyosphaeridium* Davey and Williams 1966b has been variously discussed. For *Tanyosphaeridium*, Davey and Williams (op. cit., p. 98) considered that, "The marked feature of this genus is the elongate nature of the central body", but they also described, "Processes cylindrical, open distally"; they did not discuss *Prolixosphaeridium*. In the same volume, Davey et al. (1966, p. 171) described *Prolixosphaeridium*, as having "an elongate central body" stating, "Processes closed proximally, closed or open distally: their distal terminations simple; flaring in varied fashion; or briefly furcate"; they did not discuss *Tanyosphaeridium*.

The possibility of distally open processes in *Prolixosphaeridium* was repeated by Davey (1969a, p. 160) in his emendation of that genus, stating, "processes closed proximally, typically but not constantly closed distally". However, in his remarks he then stated, "The processes of *Prolixosphaeridium* usually taper distally and are closed. Specimens with open tubular processes belong to *Tanyosphaeridium*". He again maintained that processes could be "briefly furcate".

Harding (1990, p. 47) considered the surface sculpture of *Prolixosphaeridium deirense* Davey et al. 1966 to be very similar to that of *Tanyosphaeridium*, and that, "these genera appear closely related, being distinguished only by the solid processes of the former and the hollow ones of the latter". Harding's stipulation of solid processes in *Prolixosphaeridium* appears to be a novel concept, not recognised by Davey and Williams (1966b) or Davey (1969a). The last author (op. cit., p. 161), in describing *Prolixosphaeridium conulum*, stated, "The processes...are approximately half the shell width in length, hollow and typically rigid".

Harding (1990) included in *P. deirense* both Boreal and Tethyan examples, the former similar to the type material and the latter from the Tethyan at Angles. Both were described (Harding op. cit., p. 46, 47), "with solid processes formed from fusion of extended papillae", and were well-illustrated in Harding (op. cit., pl. 29, figs. 6-8). This formation of processes through fusion of extended papillae is particularly well-illustrated in *Prolixosphaeridium basifurcatum* Dodekova 1969 (see Fauconnier and Masure 2004, p. 465 fig. 3 and Monteil 1993, pl. 1, fig. 7). The elongate Tethyan form included in *P. deirense* by Harding is described as *Prolixosphaeridium prolatum* Duxbury n. sp. here.

Fauconnier and Masure (2004, p. 461) were unequivocal, however, stating (translation), "The processes are non-tabular, tubular, unconnected distally and proximally, and distally simple and closed". On p. 465, fig. 1, however, they illustrated *P. deirense* with a single "briefly furcate" process, reflecting Davey et al.'s 1966, fig. 45 illustration of that species.

Taken together, this suggests that *Tanyosphaeridium* and *Prolixosphaeridium* are essentially similar but, whereas *Tanyosphaeridium* possesses tubular processes which are always open distally, *Prolixosphaeridium* has solid processes or hollow ones which are usually distally closed but occasionally open and rarely "briefly furcate".

Elongate morphotypes of varying lengths but with similarly ornamented central bodies were recorded in the present study. These included *Tanyosphaeridium* cf. *variecalamum* and *Bourkidinium granulatum*, and these are briefly discussed elsewhere in the present text. They also included taxa referred here to *Prolixosphaeridium prolatum* Duxbury n. sp. and *Tanyosphaeridium hirsutum* Duxbury n. sp., which are undoubtedly very similar; there may be good reason to invoke development of the latter from the former by tubularisation of processes.

***Prolixosphaeridium prolatum* Duxbury n. sp.**
Plate 12, Figures 14-16

Prolixosphaeridium sp. A. MONTEIL 1993, pl. 1, fig. 6. – LEEREVELD 1997a, fig. 7g.

Prolixosphaeridium deirense Davey et al. 1966. – HARDING 1990, pl. 29, figs. 5, 6 only.

Holotype: Plate 12, Figure 16.

Type Locality: Vergol outcrop, late Berriasian, Bed B131M, *alpillensis* ammonite Zone, *otopeta* Sub-zone. Holotype: Slide B131(R1), E.F. Q42.2.

Derivation of Name: From the Latin *prolatus*, extended, elongated - in reference to the unusual length of this species.

Diagnosis: A fairly large, elongate-ellipsoidal species with the main body between 2 and 3 times as long as broad. The poles are rounded with the apical pole notably broader than the antapical. A fine, granular ornament covers the cyst surface and numerous (>60) slender, acuminate processes are present, typically approximating to half the main body width or less. Process length is usually consistent on individual specimens. The presumed tetratabular apical archeopyle is relatively small and the operculum often remains attached.

Dimensions: Holotype Main body $89 \times 35 \mu\text{m}$. Overall - $99 \times 58 \mu\text{m}$.
All specimens - Main body 104 (90) $78 \mu\text{m} \times 43$ (38) $35 \mu\text{m}$.
Overall 111 (99) $86 \mu\text{m} \times 71$ (59) $51 \mu\text{m}$.

Specimens measured: 8 (3 complete and 5 with the operculum detached).

Remarks: This is a large species compared to others of the genus, very elongate with numerous slender processes and it is restricted here to individuals with distally acuminate terminations; the process length is typically half of the body width or less. On this basis, the specimen illustrated by Monteil (1993, pl. 1, fig. 6) is somewhat atypical but is nevertheless assigned to *P. prolatum* here.

Prolixosphaeridium prolatum n. sp. resembles *P. deirense* Davey et al. 1966 emend Harding 1990 but is more elongate with shorter processes. Harding (op. cit., pl. 29, fig included in *P. deirense* a Tethyan specimen from Angles, "more elongate and with shorter processes" (Harding op. cit., pl. 29, figs. 5, 6); this is included in *Prolixosphaeridium prolatum* here.

Prolixosphaeridium prolatum is also superficially similar to *Prolixosphaeridium? foratum* Dodekova 1994 but differs in being significantly longer (the main body length of *P.? foratum* ranges only between $60 \mu\text{m}$ and $79 \mu\text{m}$ as opposed to the $78 \mu\text{m}$ to $104 \mu\text{m}$ range of *P. prolatum*). Also, Dodekova (1994, p. 27) suggests that the surface of the autophragm in *P.? foratum*, "is rather scabrate

than granulate", again contrasting with the finely granular surface of *P. prolatum*.

Very common to abundant *Prolixosphaeridium prolatum* were recorded between Beds B97M and B138M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone to early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone), so that this appears to be a characteristic species as high as the basal Valanginian. The FO of *P. prolatum* is uncertain. Monteil's (1992b, Table 1) range for "*Prolixosphaeridium* sp. A" suggests a possible range at least as old as the Tithonian.

At Vergol, a major reduction in numbers of *P. prolatum* was observed above Bed B138M although consistent but relatively rare occurrences were recorded between Beds B142M and V42M (*pertransiens* to basal *neocomiensiformis* Zones). Monteil (1992b, Table 1) recorded this species to the top of the *pertransiens* Zone in southeast France and Leereveld (1997a, figs. 2, 3) recorded it up to a similar level in Spain.

The FO of a form similar to *P. prolatum*, *Tanyosphaeridium hirsutum* Duxbury n. sp., was in Bed B121M. Although similar, *T. hirsutum* tends to be somewhat smaller than *P. prolatum* and the processes, still numerous and still slender, are longer and distally open. *Tanyosphaeridium hirsutum* was common as old as Bed B151M (*pertransiens* Zone, *premollicus* Sub-zone) and ranged up to Bed V111 (late Valanginian, *verrucosum* Zone, base *verrucosum* Sub-zone).

The possible transition from *P. prolatum* to *Tanyosphaeridium hirsutum* close to the Berriasian/Valanginian boundary supports Harding's (1990, p. 47) suggestion that "these genera appear closely related".

Genus ***Protobatioladinium*** Nøhr-Hansen 1986

Protobatioladinium Nøhr-Hansen 1986, p. 36, 37.

Type: Nøhr-Hansen 1986, pl. 3, fig. 5; text-fig. 7, as *Protobatioladinium westburiense*.

Remarks: Nøhr-Hansen (1986, p. 37) compared this genus to genera of Davey's (1982) "*Broomea* complex", and this is not further discussed here. He (op. cit.) stated that, "*Protobatioladinium* gen. nov. is very similar to *Batioladinium* Brideaux (1975) in general outline and with respect to the presence of a distinct sulcal notch, but differs in the possession of a compound tA2I archeopyle in contrast to a tA type".

***Protobatioladinium modestum* Duxbury n. sp.**
Plate 3, Figures 6-8, 11-13, 15-17

Holotype: Plate 3, Figure 8

Paratype: Plate 3, Figure 17

Type Locality: La Charce outcrop, late Valanginian, Bed LCH164M, base *furcellata* Zone, *furcellata* Sub-zone. Holotype: Slide LCH164(2), E.F. S43.2. Paratype: Slide LCH164(1), E.F. G26.0.

Derivation of Name: From the Latin *modestus*, moderate, unassuming - in reference to the inconspicuous nature of this species.

Diagnosis: A broadly ovoidal species of *Protobatioladinium*, autophragm only, with a microgranular ornament and a short, distally-rounded apical horn. A broad-based but vestigial left antapical horn may also be present. The archeopyle is compound type tA2I.

Dimensions: Holotype Length - 78 µm. Width - 63 µm. Paratype (operculum detached): Length - 61 µm. Width - 56 µm. Complete specimens - 78 (70) 66 µm × 63 (53) 46 µm. Specimens measured - 6. Operculum detached - length: 61 (61) 61 µm, width: 56 (56) 56 µm. Specimens measured - 3.

Remarks: In his illustration of the type species, *Protobatioladinium westburiensis*, Nøhr-Hansen (1986, p. 37) showed it to have antapical bulges offset laterally with the left antapical better-developed and forming a distinct horn; this lateral offset appears to be the case with *Protobatioladinium modestum*.

Schrank (2005, p. 72) described *Protobatioladinium lindiense* from the Tithonian of Tanzania and, like *P. modestum*, this is broadly ovoidal, covered in "minute granules or bacula" (Schrank, op. cit.) and possesses a short apical horn. It contrasts with *P. modestum*, however, in possessing a prominent antapical horn that is offset ventrally, not laterally.

In *P. modestum*, as described for *P. lindiense* by Schrank (op. cit.), "The archeopyle may be...incompletely demarcated by sutures. In dorso-ventral orientation it may appear apical. In lateral orientation, a few specimens show rudimentary sutures indicating inclusion of intercalary plates". Sometimes in *P. modestum* the operculum is completely lost (as in the paratype), resulting in a zig-zag archeopyle margin. Very rarely the intercalary plates may be lost separately, resulting in a cyst very similar to the genus *Pareodinia* (see pl. 3, fig. 7).

Protobatioladinium modestum is significantly larger than the size quoted by Schrank for *P. lindiense*: Holotype 58 × 40 µm. Length range: 67 (59.6) 53 µm.

Occurrences of *Protobatioladinium modestum* were restricted to the La Charce section, ranging between Beds LCH164M and LCH220M (late Valanginian, *furcillata* Zone to early Hauterivian, *loryi* Zone).

Genus ***Protoellipsodinium*** Davey and Verdier 1971

Type: Davey and Verdier 1971, pl. 5, fig. 2, as *Protoellipsodinium spinocristatum*.

Remarks: Duxbury (2018, p. 190) described *Protoellipsodinium vacuolatum* from Speeton Beds D4A and D3E as, "the oldest representative of this genus reported to date". Beds D4A and D3E are of an early Valanginian age and bracket the *Paratollia*/*Polyptychites* ammonite zonal boundary. The LO of this species was noted in Duxbury 2023 (p. 155) in Speeton Bed C10 (early Hauterivian, *regale* ammonite Zone), and it was particularly common in Bed C11.

Similarly short-spined taxa *Protoellipsodinium seghire* subsp. *medaure* Below 1981 (pl. 10, figs. 1, 2, 5, 6) and *P. touile muga-taë* Below 1981 (pl. 10, figs. 3, 9, 10, 17 and 22) were recorded in the present study and their FO's were in Beds V26M and V31M respectively. These are adjacent samples within the upper

part of the *pertransiens* Zone, *salinarium* Sub-zone and therefore at a similar level to the FO of *Protoellipsodinium vacuolatum* Duxbury 2018 at Speeton.

Protoellipsodinium vacuolatum sensu stricto was not recorded here, but rare, very similar specimens have been referred to *Protoellipsodinium* cf. *vacuolatum* (pl. 10, figs. 7, 11). These were restricted to La Charce Bed LCH183M, late Valanginian, *furcillata* Zone, *callidiscus* Sub-zone. They have broad-based spines along surface ridges but no vacuoles.

Genus ***Pseudoceratium*** Gocht 1957 emend. Dörhöfer and Davies 1980 emend. Bint 1986 emend. Helby 1987 emend. Fensome et al. 2019

Pseudoceratium Gocht 1957, p. 166.

Eopseudoceratium Neale and Sarjeant 1962, p. 446.

Type: Gocht 1957, pl. 18, fig. 1, as *Pseudoceratium pelliferum*.

Remarks: Although there was some variation in cyst outline, none of the specimens assigned to *Pseudoceratium* here possessed an "ectophragmal trabecular reticulum", as described for *Pseudoceratium aulaeum* Harding 1990 ex Harding in Williams et al. 1998 (see Harding 1990, p. 18), a feature also demonstrated by Australian species *Pseudoceratium iehiense* Helby 1987 and *P. weymouthense* Helby 1987.

Pseudoceratium pelliferum Gocht 1957 subsp. *pelliferum* autonym.

Plate 20, Figures 13, 14, 16

Pseudoceratium pelliferum GOCHT 1957, p. 166-168, pl. 18, figs. 1a-c, 2; text-figs. 1-3. Holotype: Gocht 1957, pl. 18, figs. 1a-c. – FENSOME et al. 2019, figs. 19I-K.

Remarks: *Pseudoceratium pelliferum* was recorded throughout much of the studied section, and a particularly noteworthy and age-restricted form, *Pseudoceratium pelliferum* Gocht 1957 subsp. *radiculatum* n. subsp. is described below. Otherwise, all specimens of *Pseudoceratium* recorded in the present study were assigned to *Pseudoceratium pelliferum* Gocht 1957 subsp. *pelliferum* autonym.

The FO of *P. pelliferum* Gocht 1957 subsp. *pelliferum* in the present study was in Bed B113M, late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone. However, its FO was illustrated in Monteil 1993 (figs. 2 and 5 and Tables II and III) below his *Systematophora* sp. A influx at Angles and above it at Berrias. In both cases, both the FO of *P. pelliferum* and the *Systematophora* sp. A influx were consistently below the FO of *Muderongia mcwhaei*. At Vergol the FO of *M. mcwhaei* was in Bed B110M, suggesting that the FO of *P. pelliferum*, in Bed B113M is "too high", its absence below being possibly due to extreme rarity towards the base of its range at Vergol.

Leereveld (1997a, p. 394) stated, "the FO of *P. pelliferum* in the Rio Argos succession corresponds to that in the Berriasian stratotype...in the upper part of the Picteti ammonite Subzone". This is older than anything analysed from Vergol in the present study, suggesting that Vergol Bed B97M is no older than Leereveld's *Pseudoceratium pelliferum* Zone, again indicating that the FO of *P. pelliferum* as seen here is high.

Pseudoceratium pelliferum Gocht 1957 subsp. ***radiculatum*** Duxbury n. subsp.
Plate 20, Figures 17, 18

Holotype: Plate 20, Figures 18.

Type Locality: Vergol outcrop, early Valanginian, Bed B136M, *pertransiens* ammonite Zone, *premolicus* Sub-zone. Holotype: Slide B136/R1, E.F. T56.0.

Derivation of Name: From the Latin radix, root - in reference to the long antapical horn.

Diagnosis: A large subspecies of *Pseudoceratium pelliferum* with a particularly long antapical horn and a reduced right lateral. The operculum is invariably detached.

Dimensions: Holotype Length - 129 µm. Width - 104 µm.
Overall - 149 (129) 113 µm × 104 (84) 78 µm.
Specimens measured - 8 (all with the operculum detached).

Remarks: This subspecies has a very restricted range at Vergol, being confined to Beds B136M to B147M, *pertransiens* ammonite Zone, *premolicus* Sub-zone and it therefore appears to be characteristic of the basal Valanginian.

Genus ***Reticulasphaera*** Harding 1990 ex Harding in Williams et al. 1998

Type: Harding 1990, pl. 27, fig. 1, as *Reticulasphaera medusae*.

Reticulasphaera fasciculata Duxbury n. sp.
Plate 10, Figures 14-16, 19, 20

Holotype: Plate 10, Figures 15, 16.

Paratype: Plate 10, Figure 19.

Type Locality: Vergol outcrop, early Valanginian, Bed V97M, *inostranzewi* ammonite Zone, *platycostatus* Sub-zone. Holotype: Slide V97M(A), E.F. H46.4. Paratype: Vergol Bed B131M, late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone, Slide B131(R1 extra schulze), E.F. U49.3.

Derivation of Name: From the Latin fasciculus, a small bundle - in reference to the penitabular clustering of processes.

Diagnosis: A small, ellipsoidal to ovoidal species with a smooth surface and bearing acuminate processes in the form of long, solid, hair-like fibres. These fibres vary in number and length on individual specimens and are typically linked on the body surface into penitabular clusters. The archeopyle is epicystal and usually remains attached ventrally.

Dimensions: Holotype Length - 38 µm. Width - 33 µm.
Paratype Length - 35 µm. Width - 33 µm.
Overall - 41 (38) 35 µm × 35 (32) 30 µm.
Specimens measured - 5 (all with the operculum attached).

Remarks: This small species is similar in some respects to *Reticulasphaera medusae* Harding 1990 ex Harding in Williams et al. 1998, particularly the small size, possession of hair-like fibres and an epicystal archeopyle. It differs, however, in having a smooth surface as opposed to the, "sculpture of fine interwoven, matted

fibres" (Harding 1990, p. 44) and in its clear penitabular clustering of the hair-like fibres. In contrast, these are, "apparently partially non-tabular and partially sutural" (Harding, op. cit.) in *R. medusae*.

In addition, the tendency in *Reticulasphaera fasciculata* is for the operculum to remain attached, whereas this only rarely occurs in *R. medusae*. In the latter species the, "Anterior edge of paracingulum becomes rolled over towards the antapex after archaeopyle formation" (Harding, op. cit.) but this tendency has not been observed in *R. fasciculata*.

Reticulasphaera fasciculata was observed throughout much of the studied section. It was very common as deep as Vergol sample B121M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone) and common between Vergol beds V97M and V107M (i.e. across the early/late Valanginian boundary). These constitute by far the oldest records of this genus to date. The youngest record in the current study was from La Charce Bed LCH216M (early Hauterivian, top *radiatus* Zone).

Genus ***Scriniodinium*** Klement 1957

Type: Deflandre 1939, pl. 5, figs. 1, 2, as *Gymnodinium crystallinum*.

Scriniodinium elimatum Duxbury 2018
Plate 17, Figures 9, 10, 12, 14

Scriniodinium dictyotum Cookson and Eisenack 1960. – HABIB 1974, pl. 1, figs. 3, 4, pl. 2, fig. 1, text-fig. 2, c, d.

Remarks: *Scriniodinium elimatum* Duxbury 2018 was observed here between Vergol Bed V88, early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone (where it was common) and La Charce Bed LCH 149M, late Valanginian, *peregrinus* Zone, *nicklesi* Sub-zone, entirely within the Valanginian to early Hauterivian Boreal range quoted for this species by Duxbury (2018, p. 192, 193).

Genus ***Spiculodinium*** Duxbury 2018

Type: Eisenack 1958, pl. 26, fig. 7, as *Baltisphaeridium neptuni*.

Remarks: This genus includes cysts typically bearing a moderate number of processes each with sharply pointed distal terminations and often joined proximally by ridges or crests. The archeopyle is mid-dorsal, single-plate precingular (3") with the operculum bearing a mesotabular, hollow process similar in length to the others. The large size and micro-reticulate to fibrous body texture are also characteristic of *Spiculodinium*.

In the present study, the type species *Spiculodinium neptuni* (Eisenack 1958) Duxbury 2018 was typically long-ranging, occurring between Bed B113M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) and the top of the studied interval at La Charce. Its apparent absence from the 4 oldest samples analysed is possibly due to extreme rarity, as it was shown to range significantly older within the Berriasian of southeast France by Monteil (1992b) and of Spain by Leereveld (1997a).

Spiculodinium? inordinatum Duxbury n. sp.
Plate 18, Figures 2, 3, 6, 12, 13

Holotype: Plate 18, Figure 3

Type Locality: Vergol outcrop, early Valanginian, Bed V26M, *pertransiens* Zone, *salinarium* Sub-zone. Holotype: Slide V26M/1, E.F. O38.0.

Derivation of Name: From the Latin *inordinatus*, disorderly, irregular - in reference to the irregular nature of this species.

Diagnosis: A moderately large, fairly thick-walled species with an ovoidal main body and a single-plate precingular archeopyle (3"). The test surface is produced into irregular, fibro-perforate extensions, ranging from simple spines to broad structures with or without distal spines. A broad, arcuate structure is at the antapex and ridges or surface folds can connect individual extensions, possibly marking sutures.

Dimensions: Holotype $89 \times 76 \mu\text{m}$.
Overall - 119 (94) $73 \mu\text{m} \times 101$ (80) $63 \mu\text{m}$.
Specimens measured - 7.

Remarks: *Spiculodinium?* *inordinatum* n. sp. is only tentatively assigned to this genus because it does not possess clear gonol and sutural processes with terminal spikes typical of *Spiculodinium neptuni* (Eisenack 1958) Duxbury 2018, *Spiculodinium alatum* (Duxbury 1977) Duxbury 2018 and *Spiculodinium verdieri* (Below 1982c) Duxbury 2018. The fibro-perforate nature of this species and the single-plate precingular archeopyle are characteristic, however, suggesting that this species could be a particularly "degenerate" *Spiculodinium*.

This species has a very restricted stratigraphic range at Vergol, entirely within the early Valanginian, between Beds V26M and V59M, *pertransiens* Zone, *salinarium* Sub-zone to *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone.

Genus *Spiniferites* Mantell 1850 emend Sarjeant 1970

Spiniferites Mantell 1850, p. 191
Hystrichosphaera Wetzel 1933 ex Deflandre 1937, p. 61
Hystrichokibotium Klumpp 1953, p. 387
Achomosphaera Evitt 1963, p. 163
Hystrichostrogylon Agelopoulos 1964, p. 674
Spiniferites Mantell 1850 in Sarjeant 1970, p. 75

Type: Ehrenberg 1837, pl. 1, fig. 15, as *Xanthidium ramosum* - lectotype designated by Davey and Williams (1966a, p. 32)

Remarks: The large majority of *Spiniferites* recorded in the present study were assigned to *Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990. This species was common to very common as old as Vergol Bed V59M and it was consistent as old as Bed V54M (both of these beds are within the early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone). A single, isolated occurrence of *S. twistringiensis* was also recorded in Bed V42M, towards the base of the *neocomiensiformis* Sub-zone.

Duxbury stated (2018, p. 193), "The FAD of *Spiniferites* spp., including ...*S. twistringiensis* (Maier 1959) Fensome et al. 1990, is within the lower Valanginian at Speeton, Bed D4B, *paratollia* Zone", which is similar to its FO at Vergol. However, previous authors have reported older inceptions for *Spiniferites* spp., as old as the early Berriasian, *jacobi-grandis* Zone (Monteil 1992b, Ta-

ble 1) and to the base of the Valanginian, base *pertransiens* Zone (Leereveld 1997a, figs. 2, 3). These discrepancies are presumably due to differences in interpreting the morphological boundaries of this genus.

***Spiniferites modestus* Duxbury 2023**

Plate 2, Figures 4, 8

Spiniferites modestus DUXBURY 2023, p. 161, pl. 25, figs. 3, 4, 8, 11.
Holotype: pl. 25 figs. 3, 4

Remarks: Duxbury (2023) recorded this species throughout much of the early Hauterivian, between Speeton Beds D2D and C7E (*amblygonium* to *inversum* Zones). Occurrences in the current study have shown that, although rare, this species also ranges into the late Valanginian (a part of the section missing at Speeton). The FO of *S. modestus* in the current study was in La Charce Bed LCH164M, late Valanginian, base *furcillata* Zone; it was not observed at Vergol.

***Spiniferites primaevus* (Duxbury 1977) Monteil 1992b**

Plate 2, Figures 10, 11

Spiniferites ramosus (Ehrenberg 1837) Mantell 1854 subsp. *primaevus* DUXBURY 1977, p. 50, pl. 4, figs. 2, 3. Holotype: Duxbury, 1977, pl. 4, figs. 2, 3.
Spiniferites primaevus (Duxbury 1977). – MONTEIL 1992b, p. 304.

Remarks: *Spiniferites primaevus* is a fairly long-ranging species in Boreal settings. At Speeton, its FO of is in Bed D4B, early Valanginian, upper *Paratollia* Zone (Duxbury 2018, figs. 2, 10) and its LO is in Bed D2B towards the base of the Hauterivian, *amblygonium* Zone (Duxbury 2023, p. 161, fig. 4 - n.b. the late Valanginian LO in Duxbury 2023, fig. 6 is wrongly drawn).

Its range appears to be shorter in southeast France, however, although there are very few records. Occurrences in the current study were rare, ranging between Vergol Beds V104M and V132M (late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone to *peregrinus* Zone, *peregrinus* Sub-zone). It was not observed at La Charce. Monteil (1992b, Table 1) illustrated the range of *S. primaevus* no older than the latest Valanginian, upper *callidiscus* Zone, significantly younger than the Vergol evidence.

Apparent differences in the stratigraphic range of *S. primaevus* between Boreal and Tethyan sections might be due more to the rarity of this form in the latter sections but this needs to be tested through further studies.

Genus *Stephanelytron* Sarjeant 1961 emend. Stover et al. 1977 emend. Courtinat 1999

Type: Sarjeant 1961a, pl. 15, fig. 11; text-fig. 10, as *Stephanelytron redcliffense*.

***Stephanelytron cretaceum* Duxbury 1983**

Plate 5, Figures 18, 19

Stephanelytron cretaceum DUXBURY 1983, p. 56, pl. 7, figs. 5, 6. Holotype: Duxbury 1983, pl. 7, figs. 5, 6. – FAUCONNIER and MASURE 2004, pl. 73, figs. 1, 2.

Remarks: This very long-ranging species was recorded throughout the Vergol and La Charce sections, although it was rare and

sporadic as high as Vergol Bed V116M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone). Between Vergol Bed V120M (*pronecostatum* Sub-zone) and the top of the La Charce section it was common to very common. This variation in numbers is presumably due to palaeoenvironmental factors but its geographic extent remains to be tested.

Genus *Subtilisphaera* Jain and Millepied 1973 emend. Lentin and Williams 1976

Type: Jain and Millepied 1973, pl. 3, fig. 31, as *Subtilisphaera senegalensis*.

Subtilisphaera terrula (Davey 1974) Lentin and Williams 1976 emend. Harding 1986a
Plate 4, Figures 6, 10, 14, 19

Deflandrea terrula DAVEY 1974, p. 65, pl. 8, figs. 4, 5. Holotype: Davey 1974, pl. 8, fig. 4.

Subtilisphaera? terrula (Davey 1974). – LENTIN and WILLIAMS 1976, p. 119.

Subtilisphaera terrula (Davey 1974). – HARDING 1986a, p. 101.

Remarks: Duxbury (2023) discussed the occurrence of this species at Speeton and showed its consistent occurrence from Speeton Bed C4C (late Hauterivian, *gottschei* Zone) to the top of the early Barremian. A single specimen was recorded by Duxbury (op. cit.) in Speeton Bed C7B, proving that it may occur rarely as old as the latest early Hauterivian, top *inversum* Zone in Boreal settings. In the present study, significantly older specimens assigned to *S. terrula* were recorded as old as the late Valanginian, Vergol Bed V120M (*verrucosum* Zone, *pronecostatum* Sub-zone), and this species was common in Bed V132M (*peregrinus* Zone, *peregrinus* Sub-zone) at the top of the Vergol section.

These late Valanginian occurrences concur with Monteil's (1992b, Table 1) and Leereveld's (1997a, figs. 2 and 3) records of what they assigned to *Subtilisphaera perlucida* (Alberti 1959) Jain and Millepied 1973. Monteil recorded it as old as the upper part of the *verrucosum* Zone, also in southeast France and Leereveld recorded it as old as the *trinodosum* Zone in southern Spain.

Genus *Systematophora* Klement 1960 emend. Brenner 1988 emend. Stancliffe and Sarjeant 1990 emend. Riding and Helby 2001a.

Type: Klement 1960, pl. 9, figs. 1-3, as *Systematophora areolata*.

Remarks: This genus was regarded by Davey (1982) as the "root stock" of all of the other genera in his *Systematophora-Oligosphaeridium-Surculosphaeridium* complex and this opinion is largely supported here. Although Davey (1982) did not formally emend *Systematophora*, he provided a detailed description (op. cit., p. 11).

See also comments under *Amphorulacysta* Chen 2013, *Palaecysta* Chen 2013, *Systematophora cf. areolata sensu* Davey 1982 and *Systematophora daveyi* Riding and Thomas 1988.

Systematophora cf. areolata Klement 1960 in Davey 1982
Plate 1, Figures 11, 12, 15

Remarks: Davey (1992, p. 12) compared his *Systematophora cf. areolata* with *Systematophora areolata* Klement 1960, stating,

"the proximate ridges of the annulate complexes that are sub-polygonal in *S. areolata* are reduced to either circular or arcuate ridges, or are apparently absent altogether in *S. cf. areolata*". This range from complete proximate ridges through arcuate features to total absence within a single species again might bring into question the consistent separability of *Palaecysta* Chen 2013.

Chen (2013, p. 266) stated that, "The specimens determined... as *S. cf. areolata* by Davey (1982, 1987; pl. 1, figs. 5 and 6, and pl. 11, fig. 14, respectively), also possess arcuate process clusters and should be assigned to *Palaecysta* (now *P. pectita* sp. nov.)". This does not appear to be entirely the case, as Davey 1982, pl. 1, fig. 5 has particularly clear annular process bases. Further, specimens of *S. cf. areolata sensu* Davey 1982 were recorded in Duxbury 2018 (pl. 11, fig. 16) and in the present study (pl. 1, fig. 15) and again these clearly display annular process bases. However, specimens of *S. cf. areolata sensu* Davey were also observed in the present study with arcuate surface ridges (pl. 1, fig. 11), confirming that both types can occur within this taxon, as stated by Davey (1982, p. 12).

Specimens of *S. cf. areolata sensu* Davey 1982 with annular proximal ridges, as illustrated in Davey 1982, pl. 1, fig. 5, Duxbury 2018, pl. 11, fig. 16 and in the present work, pl. 1, fig. 15 are very similar to those illustrated as *Systematophora areolata* by Chen (op. cit. pl. 9, figs. 99, 102, 103 and 106). Chen (op. cit., p. 263) also stated that, "Two populations of species and occurrences, Jurassic and Cretaceous, have been separated out", and he included *Systematophora areolata* Klement 1960, "Amongst the Jurassic occurrences". He also stated (op. cit., p. 266) that, "The Jurassic occurrences of *Systematophora areolata*, perhaps not coincidentally, all originated from one region (Europe) and one age (Kimmeridgian), nowhere else, suggesting that the type species most likely was geographically and geologically restricted".

However, some specimens assigned by Chen's to *Systematophora areolata* (pl. 9, figs. 99, 102, 103 and 106) are from between 1316 m and 1250 m in well Ankamotra-1; his fig. 3 (p. 262) shows these to be of a mid Tithonian to Berriasian age. For Chen to separate-out specimens with arcuate ridges (as *Palaecysta pectita*) from otherwise apparently identical taxa with annular process bases (as *Systematophora areolata*), within a single population, as in well Ankamotra-1 and as seen in the present study, is questionable. From his own designation therefore, it is clear that there is no clear Jurassic/Cretaceous separation of "populations of species and occurrences". It is arguable rather that the species *pectita* should be included in the genus *Systematophora*. In the present study, Davey's *Systematophora cf. areolata* is retained, as originally described, pending further assessment, including fuller understanding of any morphological variations in undisputed Oxfordian/Kimmeridgian *Systematophora areolata* Klement 1960 (i.e. can that species also have both annular and arcuate basal ridges?).

Systematophora cf. areolata occurred throughout the studied interval at Vergol, although it was generally rare above Bed B147 (early Valanginian, *pertransiens* Zone, *premolicus* Sub-zone). Its LO was in La Charce Bed LCH160M, late Valanginian, *peregrinus* Zone, *nicklesi* Sub-zone. This range is significantly longer than that cited by Monteil (1992b, Table 1) where it ranged no younger than the late Berriasian, basal *otopeta* Zone.

In Boreal settings, *Systematophora cf. areolata* ranges no younger than the early Valanginian. Davey (1992, p. 12) quoted a range no

younger than Speeton Bed D4 (*Paratollia* Zone) and a Bed D4C LO was confirmed by Duxbury (2018, text-fig. 2).

***Systematophora complicata* Neale and Sarjeant 1962**
Plate 1, Figures 5, 6

Systematophora complicata NEALE and SARJEANT 1962, p. 455, 456, pl. 19, figs. 6, 7. Holotype: Neale and Sarjeant 1962, pl. 19, figs. 6, 7. – FAUCONNIER and MASURE 2004, pl. 75, figs. 7, 8.

Remarks: The transfer of this species to *Palaecysta* by Chen 2013 (not validly published), and formalised by Fensome et al. 2019 is rejected here as it does not appear to meet the defining criteria for that genus, particularly Chen's description of arcuate process clusters and isolated circular projections. In his proposed transfer of this species, Chen (op. cit., p. 290) listed the records of Neale and Sarjeant 1962, Duxbury 1980 and Feist-Burkhardt et al. 2012 and he stated, "All the specimens illustrated in the articles cited above show arcuate process clusters in the pre- and postcingular series, together with many characteristics common to *Palaecysta*", but this is not the case.

Although Chen (op. cit., p. 271) stated, "The specimen of *S. complicata* Neale and Sarjeant 1962 by Duxbury (1980; pl. 5, fig. 8) shows arcuate process clusters and should also be transferred to *Palaecysta* (now *P. complicata* (Neale and Sarjeant 1962) comb. nov.)", the proximal process arrangement is unclear from the illustration in Duxbury 1980 (pl. 5, fig. 8), but illustrations of the holotype (Neale and Sarjeant 1962, fig. 9 and pl. 19, figs. 6, 7) show annular ridges and linked circular processes (both atypical of *Palaecysta*).

Chen also remarked, "The specimens illustrated as *Systematophora complicata* by Feist-Burkhardt et al. (2012, website citation) possess arcuate process clusters and should be re-assigned to *Palaecysta* (now *P. complicata* [Neale and Sarjeant 1962])". This refers to a single specimen from the "Duxbury Collection" of the Natural History Museum (NHM), London, first illustrated as pl. 7, fig. 1 in Duxbury 1983. The NHM illustration is reproduced here as pl. 1, fig. 6 and again clearly shows annular proximal connections, contrary to Chen's statement as well as linked circular processes. A similar specimen from Vergol is also illustrated (pl. 1, fig. 5), again confirming the annular proximal features.

The possession of annular proximal connections and linked circular processes suggests that this species might be better retained within the genus *Systematophora*.

***Systematophora? daveyi* Riding and Thomas 1988**
Plate 1, Figures 4, 8

Systematophora sp. I DAVEY 1982, p. 12, 13, pl. 1, figs. 7-9.
Systematophora daveyi RIDING and THOMAS 1988, p. 82-86, pl. 3, figs. 8-10; text-figs. 10a, b. Holotype: Riding and Thomas 1988, pl. 3, figs. 8, 9. – FAUCONNIER and MASURE 2004, pl. 77, fig. 5.
Systematophora? daveyi Riding and Thomas 1988. – STANCLIFFE and SARJEANT 1990 p. 208.

Remarks: This species was described as *Systematophora* sp. I by Davey (1982), stating that, "The annulate complexes are variably developed and proximally usually have a circular ridge from which arise the solid processes". In their formalisation of the species as *Systematophora daveyi*, however, Riding and Thomas (1988, p. 82) described, "process complexes arising from arcuate

ridges which are open towards the paracingulum", and they figured arcuate ridges in their text-fig. 1.

If it proves to be a consistent feature, the presence of arcuate proximal ridges might suggest that *Palaecysta* Chen 2013 could be a more appropriate genus for this species, although because of some uncertainty about whether or not the arcuate nature of the surface ridges is a constant or variable feature, it is not transferred here. Stancliffe and Sarjeant (1990) considered that, "The assignment of this species to *Systematophora* is questionable, owing to its incomplete development of circular process clusters", in this case referring to the arcuate nature of the process complexes (i.e. not specifically the surface ridges).

In his remarks on this species, Davey (1982, p. 13) stated, "The most similar species to *Systematophora* sp. I appears to be *Adnatosphaeridium caulleryi* (Deflandre) Williams and Downie 1969 which has finer processes and more extensive trabeculae... *Systematophora* sp. I may fall within the range of variation acceptable for this species". Stancliffe and Sarjeant (1990, p. 208) emended and discussed *Adnatosphaeridium caulleryi*, but they did not directly compare it with *Systematophora? daveyi*.

The LO of *Systematophora* sp. I Davey in the Haldager borehole (Davey 1982, fig. 3) was within the early Ryazanian (at the same level as the LO of *Rotosphaeropsis thula*). In the present study, significantly younger occurrences were recorded; *Systematophora? daveyi* occurred between Vergol Beds B111M and V88, late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone to early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone. It was most common between Beds V48M and V72M, early Valanginian, *neocomiensiformis* Zone.

***Systematophora? scoriacea* (Raynaud 1978) Monteil 1992b**
Plate 19, Figures 1, 5

Hystrichosphaeridium scoriaceum RAYNAUD 1978, p. 393, pl. 1, figs. 4, 5. Holotype: Raynaud 1978, pl. 1, fig. 4. – FAUCONNIER and MASURE 2004, pl. 77, figs. 1, 2.
Systematophora sp. II DAVEY 1982, p. 13, pl. 1, fig. 10, 11.
Systematophora scoriacea (Raynaud 1978). – MONTEIL 1992b, p. 304.

Remarks: This species is clearly different from typical members of Davey's *Systematophora-Oligosphaeridium-Surculosphaeridium* complex, being significantly smaller and having a strong surface ornament, originally described as "scoriacé" by Raynaud (op. cit.) and "slightly to heavily granular" by Davey (1982, p. 13 - as *Systematophora* sp. II). Focusing on process complexes as the main defining feature may over-emphasise that feature at the expense of others. In its overall morphology, *Systematophora scoriacea* is very similar to *Hystrichosphaeridium arborispinum* Davey and Williams 1966b and *H. diversum* Duxbury 2018 and might represent a forerunner of those species – i.e., not a member of Davey's *Systematophora-Oligosphaeridium-Surculosphaeridium* complex at all.

Chen (2013, p. 269) stated that, "The specimens identified as *Hystrichosphaeridium scoriaceum* by Raynaud (1978; pl. 1, figs. 4 and 5) appear to possess arcuate process clusters; however, the relatively low quality of the photomicrographs makes the re-assignment uncertain (now possibly *P. pectita* sp. nov.)". The holotype of this species was illustrated in Raynaud 1978, pl. 1, fig. 4 and Fauconnier and Masure 2004, pl. 77, figs. 1, 2, and it shows some annular proximal connection. Re-examination of the holo-

type by Monteil (1992b, p. 304) resulted in his conclusion (translation), "annular complexes, present but often poorly-defined". Similarly, specimens illustrated in Duxbury 2018, pl. 11 figs. 8, 9 from the late Berriasian show similar annular ridges (fig. 8), or these are absent (fig. 9). This species is questionably retained in *Systematophora* here with reservations, pending further study.

Systematophora? scoriacea is typical of the late Berriasian and earliest Valanginian at Vergol, common at the base of the studied section (Bed B97M) then gradually reducing in numbers uphole but still common as high as Bed B147M (early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone). It occurred consistently as high as Bed V10M and single, isolated specimens were recorded from Beds V31M (*pertransiens* Zone, *salinarium* Sub-zone) and V94M (*inostranzewi* Zone, *inostranzewi* Sub-zone).

The early Valanginian LO of this species supports a similar LO reported by Monteil (1992b, Table 1). However, Leereveld (1997a, p. 389) reported isolated late Valanginian occurrences of this species in the Rio Argos section and, "considered [them] to be in place since Monteil (pers. comm., 1995) observed the species to range throughout the Valanginian in the Angles section". Leereveld (op. cit.) recognised that this extends the range of this species, "upwards compared to that reported in Monteil (1992)", although Monteil's 1992b, Table 1 is a synthesis of data from three south-east France sections, including Angles.

Although *Systematophora? scoriacea* had a limited range in the present study, specimens essentially similar to it were prominent and sometimes abundant throughout the sections at Vergol and La Charce. They shared the generally small size, prominent "scoriacé" ornament and process clusters either connected by proximal annular ridges or free-standing, but their processes were longer and they ranged widely in complexity (see pl. 19, figs. 7, 11-16). Like *S.? scoriacea* these are atypical of Davey's *Systematophora-Oligosphaeridium-Surculosphaeridium* complex. No attempt has been made to sub-divide them here, as this wide range of forms appears throughout. For the present study, all have been included in the informal grouping *Systematophora? cf. scoriacea*.

***Systematophora* sp. A Monteil 1993**

Plate 19, Figure 2

Systematophora sp. A MONTEIL 1993, pl. 4, fig. 2.

Amphorula delicata van Helden 1986. – LEEREVELD 1997a, fig. 8a.

Remarks: This species is retained informally here. Although the delicate, proximally fenestrate and distally divided processes are very similar to those of *Palaecysta foveoreticulata* Chen 2013, attribution to that species has not been possible because of poor preservation, so that the nature of the processes, particularly their proximal connections, was unclear. This is despite it being very abundant in Vergol Beds B97M and B104M (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone), to which it was restricted. *Palaecysta foveoreticulata* was "extremely abundant" in Chen's Madagascan Zone 2 (Late Berriasian to earliest Valanginian - see Chen 2013, fig. 3).

Leereveld (1997a, fig. 8a) illustrated a specimen which he placed in *Amphorula delicata* van Helden 1986, although in another context he invoked (op. cit., p. 411), "the strict concept of Monteil (1990)". This refers to Monteil's restriction of *A. delicata* to forms with, "high and wide arch-shaped perforations. The latter start at the base of the septa but do not reach the distal end of the septa, thereby leaving an entire margin" (Monteil 1990, p.

603). Leereveld's "*Amphorula delicata*" was also restricted to the *alpillensis* Zone and is included in *Systematophora* sp. A Monteil here.

Monteil (1993) recorded, "a massive and sudden appearance of *Systematophora* sp. A" within his *Foucheria modesta* dinocyst Zone (late Berriasian, *boissieri* ammonite Zone), although because of a slight discrepancy between palynofloral and sequence stratigraphic interpretations between the Angles and Berrias sections, its precise position is unclear. Vergol Beds B97M and B104M also fall within Monteil's *F. modesta* Zone.

The FO of *Pseudoceratium pelliiferum* was illustrated by Monteil (1993, figs. 2 and 5 and Tables II and III) below the *Systematophora* sp. A influx at Angles and above it at Berrias. In both cases, however, both the FO of *P. pelliiferum* and the *Systematophora* sp. A influx were consistently below the FO of *Muderongia mcwhaei*. At Vergol the FO of *M. mcwhaei* was in Bed B110M, above the *Systematophora* sp. A influx, again suggesting that the FO of *P. pelliiferum*, in Bed B113M is too high, its absence below being possibly due to extreme rarity.

Genus *Tanyosphaeridium* Davey and Williams 1966b

Type: Davey and Williams 1966b, pl.6, fig.7; text-fig.20, as *Tanyosphaeridium variecalamum*

Remarks: Specimens assigned to this genus were broadly similar to *Tanyosphaeridium variecalamum* Davey and Williams 1966b, although significant variation was observed, largely in flaring or not of process terminations and in process numbers. The high degree of variation and the apparent intergradation of forms suggests that any attempt at detailed sub-division into the various published species would be pointless in the present context. The large majority of specimens have been assigned informally to the "bucket taxon" *Tanyosphaeridium* cf. *variecalamum*.

Exceptions, however, included *Bourkidinium granulatum* Morgan 1975 emend. Nøhr-Hansen 1993 and the fairly large, elongate species *Tanyosphaeridium hirsutum* Duxbury n. sp., which is described below.

Tanyosphaeridium cf. *variecalamum* includes specimens recorded consistently as old as the base of the middle Volgian in Boreal settings (Duxbury et al. 1999, fig. 2) and similar forms occur at least as young as the Palaeocene (pers. obs.); the Tethyan range is unknown. At Vergol and La Charce, this group ranged throughout the studied interval and, although occasionally common below, it showed a marked up-section increase in numbers in Vergol Bed V94M and samples above (i.e., mainly within the late Valanginian). Similarly, *T. cf. variecalamum* was particularly common at La Charce in the late Valanginian and as high as Bed LCH 191M (early Hauterivian, base *radiatus* Zone).

In his brief comments on this genus, Harding (1990, p. 47) referred to its similarity to *Prolixosphaeridium* (see remarks under that genus above).

***Tanyosphaeridium hirsutum* Duxbury n. sp.**

Plate 12, Figures 7-9, 13

Holotype: Plate 12, Figure 13

Paratype: Plate 12, Figure 7

Type Locality: Vergol outcrop, late Valanginian, Bed B101M, *verrucosum* ammonite Zone, *verrucosum* Sub-zone.

Holotype: Vergol Bed B131M, late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone, Slide B131M(R1), E.F. W42.1. *Paratype:* Vergol Bed V101M, Slide V101M(schulze), E.F. R51.3.

Derivation of Name: From the Latin *hirsutus*, hairy - in reference to the numerous processes of this species.

Diagnosis: A fairly large, elongate ellipsoidal species with the main body approximately twice as long as broad. The poles are rounded with the apical pole notably broader than the antapical. A finely granular ornament covers the cyst surface and numerous (often >100) slender, tubular processes are present which are distally open; processes typically approximate to half the main body width or more. Process length is largely consistent on individual specimens but can be shorter at the poles. The presumed tetratabular apical archeopyle is relatively small and the operculum often remains attached.

Dimensions: Holotype Main body $86 \times 38 \mu\text{m}$. Overall - $101 \times 63 \mu\text{m}$.
Paratype Main body $71 \times 30 \mu\text{m}$. Overall - $76 \times 46 \mu\text{m}$.
All specimens - Main body 86 (61) $53 \mu\text{m} \times 38$ (34) $28 \mu\text{m}$.
Overall 101 (76) $63 \mu\text{m} \times 63$ (53) $43 \mu\text{m}$.
Specimens measured – 10 (5 complete and 5 with the operculum detached).

Remarks: This relatively large, elongate form with very numerous, slender processes is restricted here to individuals bearing tubular processes with open terminations. Processes are slender and tend either not to flare distally or to flare slightly. The cyst outline is elongate ellipsoidal and in particularly elongated specimens the central part of the cyst can be parallel-sided. *Tanyosphaeridium hirsutum* is similar in many features to *Prolixosphaeridium prolatum* Duxbury n. sp., although somewhat smaller, and this is further discussed under that species, above.

This species was common as old as Bed B151M (early Valanginian, *pertransiens* Zone, *premolicus* Sub-zone) and ranged up to Bed V111 (late Valanginian, *verrucosum* Zone, base *verrucosum* Sub-zone).

Genus *Tenua* Eisenack 1958 emend. Sarjeant 1968 emend. Pocock 1972 emend. Sarjeant 1985 emend. Fensome et al. 2019

Tenua Eisenack 1958, p. 410.

Doidyx Sarjeant 1966c, p. 205–206.

Tenua Eisenack; emend. Sarjeant 1968, p. 230–231.

Tenua Eisenack; emend. Pocock 1972, p. 94.

non *Tenua* Davey 1978, p. 894.

Tenua Eisenack; emend. Sarjeant 1985, p. 94.

Tenua Eisenack; emend. Fensome et al. 2019, p. 45.

Type: Eisenack 1958, pl. 23, fig. 1, as *Tenua hystrix*

Remarks: A discussion of this genus was included in Duxbury 2023, and no further elaboration is offered here. At Vergol and La Charce, there are several forms which may be included within *Tenua*, but no attempt has been made here to differentiate most of them in what is necessarily a preliminary study; further work might yield some local stratigraphic value.

Tenua sp. cf. *Tenua colliveri* (Cookson and Eisenack 1960) Fensome et al. 2019
Plate 18, Figures 14, 15

Remarks: This taxon was recorded in Duxbury 2023 (p. 165), restricted to Speeton Bed C11B, early Hauterivian, base *regale* ammonite Zone. In the present study, it was recorded at Vergol as old as Bed V107M (late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone) and it ranged as high as La Charce Bed LC191M (early Hauterivian, base *radiatus* Zone).

Genus *Thalassiphora* Eisenack and Gocht 1960 emend. Williams and Downie 1966 emend. Gocht 1968 emend. Benedek and Gocht 1981

Type: Eisenack 1954b, pl.12, fig.17, as *Pterospermopsis pelagica*.

Thalassiphora? charollaisii Monteil (in press)
Plate 18, Figures 7, 10, 16

?*Hapsocysta peridictya* (Eisenack and Cookson 1960) Davey 1979. – JAN DU CHÊNE et al. 2016, pl. 8, fig. 9.

?*Thalassiphora* sp. D (= Dino D). – CHAROLLAIS et al. 2023, pl. 11, fig. 3, pl. 12, fig. 2.

Thalassiphora charollaisii MONTEIL (in press)

Remarks: This moderately large species possesses a delicate ovoidal endocyst enclosed within an irregularly fenestrate periphragm network. Both wall layers are smooth and unornamented. Individual fenestrations vary in size and are significantly smaller at the poles.

Assignment of this species to *Thalassiphora* is questioned here, as that is essentially a Tertiary genus. The presence of a clearly-defined endocyst surrounded by a "trabecular" network may suggest that *Hapsocysta* might be a better choice although as shown in the current study, the type species of that genus, *H. peridictya* (Eisenack and Cookson 1960) Davey 1979, occurs only as old as the early Hauterivian, *radiatus* Zone. *Thalassiphora? charollaisii* was restricted to a single sample at Vergol, Bed B142M, towards the base of the Valanginian, *pertransiens* Zone (Fig. 6A), a level exactly as described by Monteil.

A specimen assigned by Jan du Chêne et al. (2016, pl. 8, fig. 9) to *Hapsocysta peridictya* (Eisenack and Cookson 1960) Davey 1979a shows complex, irregular periphragm fenestration. The single occurrence that they recorded was from the top of the Vions Formation, sample 255.0 m, latest Berriasian (Jan du Chêne et al. op. cit., p. 159). A latest Berriasian occurrence of *Hapsocysta peridictya* would be most unlikely, and their "*Hapsocysta peridictya*" has been tentatively included in *Thalassiphora? charollaisii* here.

Similarly, specimens referred to ?*Thalassiphora* sp. D (= Dino D) by Charollais et al. (2023, pl. 11, fig. 3, pl. 12, fig. 2) have also been included in *Thalassiphora charollaisii*. Charollais et al. (op. cit., p. 39) stated that ?*Thalassiphora* sp. D (= "Dino D") Monteil in Martini and Zaninetti 1995) is only known from the early Valanginian (*pertransiens* Zone), consistent with its very restricted occurrence at Vergol, where it was observed only in Bed B142M (*pertransiens* Zone, *premolicus* Sub-zone).

Further, comparable cysts of a similar age have been allocated

informally in Jan du Chêne et al. 2016 to *Thalassiphora* sp. 246 ("Dino D" Monteil in Charollais and Wernli 1995); see Jan du Chêne et al. 2016, pl. 8, figs. 2, 3 and pl. 9, figs. 1-4. However, that cavate species does not show the complex, irregular periphragm fenestration of *Thalassiphora? charollaisii*, although it was also restricted to the base of the Valanginian.

Genus *Valensiella* Eisenack 1963 emend. Courtinat 1989

Type: Deflandre 1947, text-fig. 22, as *Membranilarnax ovulum*.

Valensiella sp. cf. *Valensiella ovula* (Deflandre 1947) Eisenack 1963

Plate 7, Figures 1-3, 6-8

Remarks: In the present study, specimens similar to that illustrated in Duxbury 2018, pl. 2, fig. 5, as part of a broad "*Valensiella/Egmontodinium*" group, have been included as *Valensiella* cf. *ovula* (Deflandre 1947) Eisenack 1963. This taxon was recorded at Vergol between Beds V54M and V116M, early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone.

Valensiella prenannus Duxbury 2023

Plate 14, Figures 11, 16

"*Valensiella prenannus*" (informal) DUXBURY 2018, pl. 6, fig. 1

Valensiella prenannus DUXBURY 2023, p. 165, pl. 17, figs. 3, 12-14.

Holotype: Duxbury 2023, pl. 17, fig. 3.

Remarks: Previous (Boreal) records of this species (Duxbury 2018, 2023) ranged between the late Berriasian, *albidum* Zone and the early Hauterivian, *regale* Zone. A similar range was observed here, from Vergol sample B131M (*alpillensis* Zone, *otopeta* Sub-zone) to La Charce sample LCH216M, early Hauterivian, *radiatus* Zone, although it was rare throughout.

Intermediates between *Valensiella prenannus* and *Discorsia nannus* (Davey 1974) Duxbury 1977 show a gradual transition from high sutural crests to mesotabular tubular processes, maintaining faint longitudinal striations throughout (see Duxbury 2018). Such intermediates were first noted in Duxbury (2018, p. 198, 210, pl. 6, figs. 2-4). An example of such an intermediate was observed in sample B88, well within the range of *Discorsia nannus*; this specimen (pl. 14, fig. 19) is very similar to that illustrated in Duxbury 2018 (pl. 6, fig. 4).

Genus *Vexillocysta* Harding 1990 ex Harding in Williams et al. 1998 emend. Duxbury 2018

Type: Harding 1990, pl. 24, fig. 8, as *Vexillocysta retis*.

Vexillocysta colligata (Morgan 1980) Duxbury 2018

Plate 8, Figure 20

Systematophora sp. A BJAERKE 1978, pl. 1, figs. 14, 15, 17, 18.

Tenua colligata MORGAN 1980, pl. 29, figs. 6-11. Holotype: Morgan 1980, pl. 29, figs. 6-8 as *Tenua colligata*.

Cleistosphaeridium sp. KE MCINTYRE and BRIDEAUX 1980, pp. 20, 21, pl. 8, figs. 1-5.

Sentusidinium cuculiformis DAVIES 1983, p. 29, pl. 10, figs. 1-4, text-fig. 26.

Cyclonephelium cuculiforme (Davies 1983). – ÅRHUS 1992, p. 312, figs. 5 G, J-L.

Epelidosphaeridia colligata (Morgan 1980). – LENTIN and WILLIAMS 1985, p. 127.

Vexillocysta retis HARDING 1990, p. 45, pl. 24, figs. 8-14 ex Harding. – WILLIAMS et al. 1998, p. 628.

Remarks: This is usually a common to very common species in Boreal settings, as noted by Århus (1992, p. 312), McIntyre and Brideaux (1980, p. 20) and Harding (1990, p. 45). Duxbury (2018, p. 196, fig. 10) recorded the acme occurrence of *V. colligata* in the Central North Sea within the Valanginian, where it was abundant. It is also a very long ranging species, recorded from the late Berriasian (Duxbury 2018), as young as the late Barremian in Harding 1990 and from the Aptian to early Albian of Australia (Morgan 1980, p. 32).

Despite again demonstrating its longevity by occurring throughout the studied sections at Vergol and La Charce, *V. colligata* was mainly a rare component in the present study. However, it was uniquely very common to abundant between La Charce Beds LCH203M and LCH220M, early Hauterivian, upper *radiatus* to *loryi* Zones.

Vexillocysta spinosa Duxbury 2018

Plate 13, Figure 14

Vexillocysta spinosa DUXBURY 2018, p. 196, 197, pl. 3, figs. 9, 13-15.

Holotype: Duxbury 2018, pl. 3, fig. 9.

Remarks: *Vexillocysta spinosa* ranges from the Berriasian to the early Valanginian (base *Paratollia* Zone) at Speeton, peaking close to the Berriasian/Valanginian boundary (Duxbury 2018, fig. 10). The peak occurrence of this generally common species is a useful top Berriasian marker in the Central North Sea.

In contrast, *Vexillocysta spinosa* was rare in the present study, although its range, between Vergol Beds B118M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone) and V10M (early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone) appears to be similar to that at Speeton. A slight increase in numbers (but only 4 specimens - peak occurrence) was noted in Bed B138M, towards the base of the early Valanginian but this would be very poor evidence for any comparison with the Boreal peak of this species.

Genus *Wallodinium* Loeblich Jr. and Loeblich III 1968 emend. Riding 1994

Type: Cookson and Eisenack 1960, pl. 39, fig. 4, as *Diplotesta glaessneri*.

Remarks: This is an unusual genus, which Duxbury (1983, p. 68) and Fensome et al. (1990, p. 535) considered to represent acritarchs. Although Fensome et al. (2019, p. 871) stated that, "Riding (1994, p. 17-18) confirmed its dinoflagellate affinity", its status is still not entirely clear.

The exact nature of this "dinoflagellate affinity" remains debatable, although Riding (op. cit.) noted its "apparent gonyaulacacean paratabulation", further study will be necessary to prove this convincingly - see also comments under *Wallodinium cylindricum* (Habib 1970) Duxbury 1983 below.

Three species of *Wallodinium* were recorded in the present study, *W. cylindricum* (Habib 1970) Duxbury 1983, *W. krutzschii* (Alberti 1961) Habib 1972 and *W. luna* (Cookson and Eisenack

1960) Lentin and Williams 1973. Only *Wallodinium krutzschii* ranged throughout the studied intervals at Vergol and La Charce but despite much longer published ranges, *W. cylindricum* and *W. luna* were not recorded above the Valanginian. In addition, *W. luna* ranged no older than Vergol Bed B151 (early Valanginian, *pertransiens* Zone, *premollicus* Sub-zone), a similar FO to that recorded (pers. obs.) in the Central North Sea.

Wallodinium cylindricum (Habib 1970) Duxbury 1983 emend. Prauss 1989 emend. Riding 1994 emend. Feist-Burkhardt and Monteil 1994

Prismatocystis cylindrica HABIB 1970, p. 374, pl. 10, fig. 2.

Hexagonifera cylindrica (Habib). – HABIB 1972, p. 378, pl. 10, fig. 5.

Wallodinium cylindricum (Habib). – DUXBURY 1983, p. 68.

Remarks: Habib (1972, p. 378) stated, "Examination of numerous well-preserved specimens recovered during Leg 11, and consequently re-examination of the holotype, have revealed that the "truncated apex" of Habib (1970) is an apical archeopyle with a six-sided margin". However, although his pl. 10, fig. 5 caption to the single specimen illustrated stated, "Note occurrence of six-sided apical archeopyle" there was no clear evidence.

The similarity of this species to *Phallocysta elongata* (Beju 1971) Riding 1994 was commented on by Riding (op. cit., p. 19), stating, "The latter [*P. elongata*] differs in having an anterior intercalary, type 3I, periarcheopyle and a characteristically elongate triangular ambitus". Specimens of *Wallodinium cylindricum* photographically illustrated by Riding (op. cit., pl. 1, figs. 16-20) all possessed archeopyle margins which were essentially flat and at right angles to the cyst axis, and the sulcal notch drawn in his fig. 1B was unclear except, perhaps in his pl. 1, fig. 16.

A sulcal notch was also interpreted by Feist-Burkhardt and Monteil (1994), as well as a complete precingular plate series; they emended the diagnosis of *Wallodinium cylindricum* to include the, "Partial paratabulation formula: 4', 6" + as". This was interpreted by Riding (1994, p. 18) as, "apparent gonyaulacacean paratabulation". In his generic emendation, Riding (op. cit., p. 17) suggested that *Wallodinium*, may possess, "four apical paraplates, six precingular paraplates and a single anterior parasulcal paraplate in a gonyaulacacean configuration", extrapolating from very limited evidence in a single species to the whole genus.

In the present study, no clear tabulation was apparent in the specimens recorded and, despite the detailed work of others, further study will be necessary to elucidate it. In some specimens, rather than the archeopyle margin being at right angles to the cyst axis, a clear slope was observed. The significance of this angularity is unclear, but it does bring the morphology of these specimens even closer to the "elongate triangular ambitus" of *Phallocysta elongata* (see pl. 2, figs. 9, 12 here and pl. 1, figs. 1, 8 in Riding 1994).

Wallodinium cylindricum ranged through much of the studied interval, as old as Vergol Bed B97 (late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone) but only as young as La Charce Bed LCH176 (late Valanginian, *furcillata* Zone, *furcillata* Sub-zone). Its absence from the Hauterivian is unexpected, as Habib (1970) described this species from the Albian/Cenomanian and Duxbury (1983) confirmed an age at least as young as the early Albian.

A restricted range was presented by Habib and Drugg (1983, fig.

3) between the base of the Valanginian and the early Hauterivian but it was absent through much of the late Valanginian. In contrast, Monteil (1992b, Table 1) illustrated an intra-early Berriasian FO and a positive range only as young as the top of the Berriasian (*otopeta* Zone). The reason for these discrepancies is unclear.

A much longer range was quoted by Feist-Burkhardt and Monteil (1994), as old as the early and late Kimmeridgian (Riding and Thomas, 1988) and the late Kimmeridgian (Ioannides, et al. 1988).

Wallodinium cylindricum (Habib 1970) Duxbury 1983 subsp. ***ornatum*** n. subsp.

Plate 2, Figures 9, 12, 16

Holotype: Plate 2, Figure 12.

Type Locality: Vergol outcrop, early Valanginian, Bed V88, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone. Holotype: Slide V88(1), E.F. B49.0.

Derivation of Name: From the Latin *ornatus*, ornate - in reference to the surface ornament.

Diagnosis: A subspecies of *Wallodinium cylindricum* bearing clear surface ornament which varies from fine granules to short, slender spines, often on an individual specimen. The ornament is restricted to the epicyst.

Dimensions: Holotype (complete): 56 × 35 µm.

Overall - 56 (52) 51 µm × 38 (35) 33 µm.

Specimens measured - 3.

Remarks: This is a rare form, ranging between Vergol Beds V87 (immediately above Barrande layer B3 - sample included in Appendix 3) and V124M, early Valanginian, *inostranzewi* ammonite Zone, *inostranzewi* Sub-zone to late Valanginian, base *peregrinus* Zone. It was not recorded at La Charce.

Genus ***Wrevittia*** Helenes and Lucas-Clark 1997

Type: Eisenack and Cookson 1960, pl. 1, fig. 4, as *Gonyaulax helicoidea*.

Remarks: Occurrences of this genus were observed throughout the studied section, and taxa have been recorded to species or subspecies level where possible. In some cases, however, a more broad-brush approach has been taken, with some taxa assigned more generally to a "*Wrevittia helicoidea* grp.". There was a marked increase in this *Wrevittia helicoidea* grp. in the lower part of the studied section at Vergol, and it was very common to abundant only as high as sample B125M (late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone).

Wrevittia* sp. cf. *Wrevittia cassidata (Eisenack and Cookson 1960) Helenes and Lucas-Clark 1997

Plate 18, Figures 8, 11

Remarks: In his comments on *Wrevittia teichos* (as *Gonyaulax teicha*), Harding (1990, p. 34) stated, "The possession of a strongly inflated apical pericoel indicates a close relationship with ... the *G. cassidata* lineage". Duxbury (2019, p. 204) felt that, "The roots of this "lineage" appear to be in the lower Barre-

mian, well before the FAD of *Wrevittia cassidata* (Aptian of Australia - Eisenack and Cookson 1960, p. 3 and Morgan 1980, fig. 8 and England - Duxbury 1983, text-fig. 3)". *Wrevittia* cf. *cassidata sensu* Duxbury 2019 was restricted to the late Barremian and was again considered to be part of the "*Gonyaulacysta cassidata* lineage".

Further specimens, again referred to informally as *Wrevittia* cf. *cassidata*, were noted in Duxbury 2023 (p. 166) and restricted to the lower Hauterivian (Speeton Beds D2D to C7F, *amblygonium* to *inversum* Zones).

A similar, apically cavate taxon was recorded in the current study, in this case single specimens restricted to adjacent La Charce samples LCH170M and LCH173M (late Valanginian, *furcellata* Zone, *furcellata* Sub-zone). These occurrences extend the range of Harding's "*Gonyaulacysta cassidata* lineage" well below the Barremian base assumed by Duxbury (2019). However, as noted by Duxbury (2023, p. 166), "the concept of a single *G. cassidata* lineage may be a false one".

Wrevittia diutina (Duxbury 1977) Duxbury 2023

Gonyaulacysta diutina DUXBURY 1977, p. 34, 35, pl. 1, figs. 3, 4; text-fig. 9. Holotype: Duxbury 1977, pl. 1, fig. 3; text-fig. 9. – JAN DU CHÊNE et al. 1986a, pl. 41, figs. 3, 4.

Millioudodinium? diutinum (Duxbury 1977). – SARJEANT 1982, p. 39.

Wrevittia? diutina (Duxbury 1977). – HELENES and LUCAS-CLARK 1997, p. 190.

Wrevittia diutina (Duxbury 1977). – DUXBURY 2023, p. 167.

Remarks: This species was formally placed in *Wrevittia* by Duxbury (2023, p. 167) on confirmation of an anterior ventral arrangement typical of that genus.

As in Duxbury (op. cit.), specimens of *Wrevittia diutina* recorded in the present study displayed several morphological variations; these included pterocavation and variations in the distribution and height of surface ornament. Two of the four subspecies recorded in Duxbury 2023 are included below.

Wrevittia diutina (Duxbury 1977) Helenes and Lucas-Clark 1997 subsp. *patula* Duxbury 2023 Plate 6, Figures 1-4, 5, 6, 9

Remarks: This subspecies is distinguished from others by its pterocavation. In Duxbury (2023), occurrences of *W. diutina* subsp. *patula* were restricted to the oldest early Hauterivian, Speeton Beds D2D to D1, *amblygonium* to *norium* ammonite Zones. In the present study, *W. diutina* subsp. *patula* was recorded as old as Vergol Bed V112M (late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone) and through much of the studied section at La Charce, as high as Bed LCH191, early Hauterivian, *radiatus* Zone.

Wrevittia diutina (Duxbury 1977) Helenes and Lucas-Clark 1997 subsp. *tabulacornuta* (Prössl 1990 ex Prössl 1992) Williams et al. 1998 Plate 14, Figures 6, 7; Plate 20, Figure 15

Gonyaulacysta diutina subsp. *tabulacornuta* PRÖSSL 1990, p. 102, 103, pl. 8, figs. 1, 2, 4, 5 ex PRÖSSL 1992b, p. 113, 115. Holotype: Prössl 1990, pl. 8, figs. 1, 2, 4, 5.

Wrevittia? diutina subsp. *tabulacornuta* (Prössl 1990 ex Prössl 1992). –

WILLIAMS et al. 1998, p. 642.

Remarks: Prössl (1990, p. 102, 103) suggested the possibility that *Wrevittia diutina* subsp. *tabulacornuta* may represent a facies adjustment as it only occurred associated with the "Hauptblättertön". In his Table 5, Prössl shows this subspecies occurring only at a level close to the FAD of *Tenua anaphrissa*.

However, this subspecies was recorded in Duxbury 2023 as old as Speeton Bed C11B (early Hauterivian, *regale* ammonite Zone) and in the current study, although rare, it occurred in La Charce Beds LCH187M, LCH208M and LCH213M, proving a latest Valanginian FO, *furcellata* Zone, *callidiscus* Sub-zone.

Wrevittia? perforobtus (Duxbury 1977) Helenes and Lucas - Clark 1997 Plate 6, Figures 7, 11

Gonyaulacysta perforobtus DUXBURY 1977, p. 39, pl. 1, fig. 1; text-fig. 13. Holotype: Duxbury 1977, pl. 1, fig. 1; text-fig. 13.

Gonyaulacysta? perforobtus Duxbury 1977. – SARJEANT 1982, p. 28.

Wrevittia? perforobtus (Duxbury 1977). – HELENES and LUCAS-CLARK 1997, p. 192.

Remarks: Duxbury (2023, p. 169) showed that the stratigraphic range at Speeton of this species was between Beds D2D and C2B (early Hauterivian, *amblygonium* Zone to earliest Barremian, *variabilis* Zone). In the current study, two isolated occurrences of this species were recorded, in La Charce Beds LCH149M and LCH208M (late Valanginian, *peregrinus* Zone, *nicklesi* Sub-zone and early Hauterivian, *radiatus* Zone), extending its range into the late Valanginian, albeit through very rare occurrences.

Wrevittia speciosa (Harding 1990) Duxbury 2019

Gonyaulacysta speciosa HARDING 1990, p. 33, pl. 14, figs. 1-15; pl. 15, figs. 12-14; text-fig. 14 ex Harding in WILLIAMS et al. 1998, p. 257.

Holotype: Harding, 1990, pl. 14, fig. 1

Wrevittia speciosa (Harding 1990). – DUXBURY 2019, p. 204

Remarks: The main stable characteristic of this species appears to be "the striking sculpture of the exposed endophragm" (Harding 1990, p. 33). The approach of Duxbury (2023, p. 169) is again followed here: "Towards the base of its range, the apical pericoel of *W. speciosa* is present but is no better developed than in other taxa, including *Wrevittia diutina*. In view of this, all specimens with this striking sculpture have been included in *W. speciosa*". Specimens with poorly-developed apical pericoels but "striking sculpture" were recorded at La Charce as old as Bed LCH173M, therefore extending the known range of this species into the late Valanginian, *furcellata* Zone, *furcellata* Sub-zone.

Acritarchs

Genus *Halophoridia* Cookson and Eisenack 1962a emend.

Halophoridia Cookson and Eisenack 1962a, p. 271

Cithariplana Srivastava 1984, p. 64

Type: Cookson and Eisenack 1962a, pl. 37, fig. 6, as *Halophoridia xena*.

Emended diagnosis: A two-layered cyst with a roughly hour-glass-shaped capsule enclosed in a more delicate pericyst. The

pericyst may be circular in outline or may be quadrate, trapezoidal or quadrilobate, and follow the shape of the endocyst to varying degrees. Wall separation may be very clear or much reduced.

Remarks: The genera *Halophoridia* Cookson and Eisenack 1962a and *Cithariplana* Srivastava 1984 are here combined, the former having seniority. The generic diagnosis has been emended to allow for the large variations in pericyst outline exhibited by this genus.

Halophoridia caperata (Srivastava 1984) Duxbury n. comb.
Plate 14, Figures 12-15

Cithariplana caperata SRIVASTAVA 1984, p. 64, pl. 35, figs. 5-8. Holotype: Srivastava 1984, pl. 35, fig. 5. – TORRICELLI 2001, pl. 12, figs. 12-14.

Halophoridia cf. *xena* RILEY and FENTON 1984, pl. 3, fig. 6.

Remarks: *Halophoridia caperata* is most similar to *Halophoridia xena* Cookson and Eisenack 1962a but differs in being quadrate to trapezoidal rather than circular to subcircular, and the degree of separation of the two layers is significantly greater in *H. xena*. Prominent folding between opposite apices of the outer layer of *H. caperata* appears to be characteristic of that species, and not of *H. xena*.

The specimen figured as *Halophoridia* cf. *xena* in Riley and Fenton (1984, pl. 3, fig. 6) is here included in *H. caperata*, its regular polygonal outline being very similar to Srivastava's holotype (Srivastava 1984, pl. 35, fig. 5).

Halophoridia caperata was very rare at Vergol, being recorded from the late Valanginian, Beds V101M (*verrucosum* Zone, *verrucosum* Sub-zone) and V124M (base *peregrinus* Zone, *peregrinus* Sub-zone) and from the latest Berriasian, Bed B131M (*alpilensis* Zone, *otopeta* Sub-zone). These are the oldest records of this genus to date, with previous records apparently typical of the late Albian and Cenomanian, although Srivastava's material was from the Barremian of southeast France.

Other species

Halophoridia merraba (Srivastava 1984) n. comb.

Cithariplana merraba SRIVASTAVA 1984, p. 64, pl. 35, figs. 9, 10. Holotype: Srivastava 1984, p. 64, pl. 35, figs. 9, 10.

Genus ***Rhombodella*** Cookson and Eisenack 1962b

Type: Cookson and Eisenack, 1962b, pl. 7, fig. 13, as *Rhombodella natans*

Rhombodella vesca Duxbury 1980
Plate 15, Figures 11, 14

Rhombodella vesca DUXBURY 1980, p. 135-136, pl. 5, figs. 7,10; text-fig. 16. Holotype: Duxbury 1980, pl. 5, figs. 7, 10.

Remarks: The main distinguishing characteristics of this species, as described in Duxbury (1980, p. 135) are its small size and that, "Each "corner" bears long (approximately ¼ main body diameter), slightly flexuous processes which number up to 10 per "corner" and which divide distally into numerous fine hairs which may be recurved towards the body". In the present study,

all specimens with these main characteristics have been assigned to *R. vesca*.

The most comparable species, *Rhombodella natans* Cookson and Eisenack 1962 is generally larger, more robust and bears processes which are shorter with respect to the main body size than those of *R. vesca*. The sizes of the type material for these two species (from their original descriptions) are:

<i>Rhombodella natans</i>	<i>Rhombodella vesca</i>
Holotype: Overall 60 × 55µm	Holotype: - 49 × 41 µm
Paratype: Overall 73 × 62µm	Overall - 59 (43) 35 × 41 (37) 35µm
Another example: Overall 68 × 53µm	Specimens measured - 5

In addition to forms having distally spinose processes and assigned to *R. vesca*, other small but similar specimens were observed in the current study which have simple, acuminate process terminations. These have been assigned to *Rhombodella* cf. *vesca* - although they may be part of a wider morphological range for *R. vesca* itself.

Tethyan occurrences of *Rhombodella vesca* in published and unpublished work range significantly older than further north; at Speeton (Duxbury 1980) and in the UKCS Central North Sea it is typical of sediments no older than the middle Barremian. In contrast, Torricelli (2001, fig. 4) recorded it from the early Hauterivian of the Vallone Rosmarino section, Sicily and Londeix (1990 - unpublished PhD) noted its occurrence in the late Hauterivian of southeast France.

In the present study, *Rhombodella vesca* was recorded between Beds V88 and V123M, early Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone to late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone, the oldest records of this species *sensu stricto* to date. Rare, older occurrences of *Rhombodella* cf. *vesca* were noted as old as Bed B121M, however, late Berriasian, *alpilensis* Zone, *otopeta* Sub-zone.

DINOCYST ZONATION

Numerous palynofloral zonation schemes have been proposed for the Early Cretaceous and most were well-summarised in Williams and Bujak (1985) and Stover et al. (1996); reference should be made to those works for further detail. Unfortunately the large majority of schemes have little or no relevance here.

The zonation schemes most appropriate to the present study are those of Habib (1976; 1977; 1978), Habib and Drugg (1983), Monteil (1985; 1990; 1992b; 1993) and Leereveld (1997a, b). Brief notes on each are included below and assemblages recorded in the current study are interpreted as far as possible using those schemes.

Habib (1976; 1977; 1978), Habib and Drugg (1983).

Biorbifera johnnewingii Zone (Berriasian to early Valanginian). Interval from the FO of *B. johnnewingii* to the FO of *D. apicopaucicum*.

Druggidium apicopaucicum Zone (Valanginian). Interval from the FO of *D. apicopaucicum* to the FO of *Druggidium deflandrei*.

Druggidium deflandrei Zone (late Valanginian to Hauterivian). Interval from the FO of *D. deflandrei* to the FO of *Druggidium rhabdoreticulatum*.

Remarks: Habib's (1976, 1977) zonation was applied by Habib and Drugg (1983) to "sediments deposited in the European Tethyan during the Neocomian" and the ranges of various species were illustrated against that scheme for the "Neocomian stratotype and parastratotype sections" in their Figure 3.

The part of Habib's zonation most relevant here was largely defined on species of *Druggidium* but these are small and in the current study tend to be sporadic and often rare; its small size probably leads to variable recovery between studies during processing because of variously-sized sieve mesh.

Although not particularly relevant locally, there is some evidence that species of *Druggidium* may be unreliable between regions. Ogg (1994, p. 259) stated, "*Druggidium apicopaucicum*, *Druggidium deflandrei* and *Druggidium rhabdoreticulatum* occur in the eastern Central Atlantic in slightly younger strata, with respect to nannofossils and benthic foraminifers, than in the western Central Atlantic. These results indicate that either the dinoflagellate assemblages, or else the nannofossil and benthic foraminifer assemblages are time transgressive between the opposing sides of the Atlantic".

There is also some evidence of differences in interpretation in southeast France. The FO's of *D. apicopaucicum* and *D. deflandrei* were illustrated in Habib and Drugg (1983, fig. 3) at the base of the *pertransiens* Zone and of the former *trinodosum* zones respectively, whereas Monteil (1992, table 1) placed them at base of the *pertransiens* Zone and the base of the former *B. campylotoxum* Zone (this discrepancy was also recognised in Ogg (op. cit., fig. 5).

Despite these reservations, some interpretation of Habib's essentially broad-brush zones has been possible here, using both primary and secondary markers described by Habib and Drugg (op. cit.).

Vergol/La Charce Bed	Habib Zone
V101M - LCH220M	<i>Druggidium deflandrei</i>
V5M - V97M	<i>Druggidium apicopaucicum</i>
B97M - B151M	<i>Biorbifera johnewingii</i>

Leereveld 1997a, b.

Pseudoceratium pelliferum Zone (late Berriasian). Interval from the FO of *P. pelliferum* to the FO of *Spiniferites* spp. (excluding *Spiniferites* sp. A).

Prolixosphaeridium sp. A Sub-zone (late Berriasian). Interval from the FO of *P. pelliferum* to the FO of *Amphorula delicata*. *Diacanthum hollisteri* Sub-zone (late Berriasian). Interval from the FO of *A. delicata* to the FO of *Spiniferites* spp. (excluding *Spiniferites* sp. A).

Spiniferites spp. Zone (early-late Valanginian). Interval from the FO of *Spiniferites* spp. (excluding *Spiniferites* sp. A) to the FO of *Cymosphaeridium validum*.

Circulodinium vermiculatum Sub-zone (early Valanginian). Interval from the FO of *Spiniferites* spp. (excluding *Spiniferites* sp. A) to the FO of *Pareodinia* sp. 1 of Davey (1982). *Pareodinia* sp. 1 Sub-zone (early Valanginian). Interval from the FO of *Pareodinia* sp. 1 of Davey (1982) to the FO of *Endoscrinium bessebae*.

Tanyosphaeridium magneticum Sub-zone (early Valanginian-earliest late Valanginian). Interval from the FO of *Endoscrinium bessebae* to the FO of *C. validum*.

Cymosphaeridium validum Zone (late Valanginian- earliest Hauterivian). Interval from the FO of *Cymosphaeridium validum* to the FO of *Muderongia staurota*.

Lagenadinium? membranoideum Sub-zone (late Valanginian). Interval from the FO of *Cymosphaeridium validum* to the FO of *Sentusidinium* sp. A.

Sentusidinium sp. A Sub-zone (late Valanginian-earliest Hauterivian). Interval from the FO of *Sentusidinium* sp. A to the FO of *Muderongia staurota*.

Remarks: Leereveld extrapolated his zones from Spain regionally into Morocco, Libya, southern France, Switzerland, Romania and the North Atlantic but his claim that, "Despite profound regional and local differences in the distribution pattern of diagnostic taxa the zonation has potential application on a global scale" is perhaps ambitious. Although he used Monteil's (1993) data from the Broyon quarry to define and calibrate the base of his oldest zone, Leereveld concluded that, "based on the selected dinocyst events the suite of zones cannot be recognised in southeast Spain. In the Rio Argos succession, the position of the French middle Berriasian-Valanginian dinocyst zones can only be approximated, because of distinct differences in ranges of the diagnostic taxa".

The difficulty in matching French and Spanish dinocyst zonation schemes led Bulot et al. (1996) to state, "after comparison between the ranges proposed by Monteil (1992) and Leereveld in Hoedemaeker and Leereveld (1995), it is difficult to see how far the dinoflagellates can help in defining the Berriasian/Valanginian boundary". Leereveld (1997a, p. 385-386) stated that, "Although various regional dinocyst zonations for the lowermost Cretaceous in the Alpine-Mediterranean region exist (e.g., Habib and Drugg, 1983; Jardiné et al. 1984; Monteil 1992; 1993, in France/Switzerland; Gübeli et al. 1984, in Morocco; Thusu et al. 1988, in Libya; Antonescu and Avram 1980, in Romania; Leereveld 1989, in southeast Spain) their value for interregional correlation is limited". He listed several reasons for discrepancies between workers and these are fully endorsed here:

- emphasis is put on local changes in the compositional development rather than on similarities and synchronism on a regional scale.
- the selected taxa have a strongly palaeoenvironmentally controlled distribution pattern.
- the stratigraphic resolution is low.
- the dinocyst data are not well calibrated.
- the applied taxonomical and nomenclatural concepts are unclear (because of lack of figured specimens, discrepancy of depicted specimens and identification concerned, etc.).

Several further possibilities which also contribute to inconsistencies between workers might also be added to Leereveld's list, including:

- variable and often poor sample processing leading to reduced diversity and truncated ranges.
- low specimen counts and almost total lack of quantitative data.
- mis-identification of taxa.
- author bias for species they consider particularly useful.
- often extreme differences in species represented - Australasian

assemblages are particularly "unusual".

- restriction of sometimes numerous, potentially valuable bioevents to a relatively few interpreted zones and sub-zones, thereby reducing resolution.

Several of the events noted at Vergol and La Charce were similar to those used by Leereveld although there are sometimes differences in species identification between the present work and Leereveld's and in some of the ranges quoted. Although exhaustive comparisons of events has not been possible, by applying Leereveld's scheme to the present study, the following broad zonal/sub-zonal sub-division is possible.

Vergol/La Charce Bed Leereveld Zone/Sub-zone

V120M - LCH220M	<i>Cymosphaeridium validum</i> / <i>Sentusidinium</i> sp. A
V101M - LCH220M	<i>Spiniferites</i> spp. - <i>Cymosphaeridium validum</i>
V5M - V97M	<i>P. pelliferum</i> - <i>Spiniferites</i> spp.
B97M - B151M	<i>P. pelliferum</i>

Monteil (1985; 1990; 1992b; 1993)

Dichadogonyaulax bensonii Zone (early to late Berriasian). Interval from the FO of *D. bensonii* to the FO of *Foucheria modesta*.

Foucheria modesta Zone (late Berriasian). Interval from the FO of *F. modesta* to the FO of *Muderongia macwhaei*.

Muderongia macwhaei Zone (late Berriasian to early Valanginian). Interval from the FO of *M. macwhaei* to the FO of *Muderongia australis*.

Muderongia macwhaei forma A Sub-zone (late Berriasian). Interval from the FO of *M. macwhaei* forma A to the FO of *M. macwhaei* forma B.

Muderongia macwhaei forma B Sub-zone (early Valanginian). Interval from the FO of *M. macwhaei* forma B to the FO of *M. australis*.

Muderongia australis Zone (early to late Valanginian). Interval from the FO of *M. australis* to the FO of *Cassiculosphaeridia magna*.

Cassiculosphaeridia magna Zone (late Valanginian). Interval from the FO of *Cassiculosphaeridia magna* to the FO of *Kleithriasphaeridium corrugatum*.

Kleithriasphaeridium corrugatum Zone (late Valanginian to basal Hauterivian). Interval from the FO of *Kleithriasphaeridium corrugatum* to the FO of *Muderongia staurola*.

Remarks: The Berriasian/Valanginian boundary at Vergol is at the base of Bed B136 (Kenjo et al. 2021), well within Monteil's *M. macwhaei* forma A Sub-zone. However, Monteil placed that sub-zone entirely within the *callisto* Sub-zone to *otopeta* Zone (see Monteil 1992b, Table 2), all of which is accepted as latest Berriasian here. This might suggest that the base of the overlying *M. macwhaei* forma B Sub-zone "should" be close to the base of the Valanginian, base *pertransiens* Zone (i.e., close to Bed B136M).

Also, the FO of *Kleithriasphaeridium fasciatum* is in Vergol Bed B115M, towards the base of the *otopeta* Zone, exactly as described by Monteil (1992b). Although this is an event considered

by Monteil to occur in the middle part of his *M. macwhaei* forma A Sub-zone, in the current study it is towards its base.

This might imply that Monteil's *M. macwhaei* forma A Sub-zone extends below Vergol Bed B110M. Only two older levels were analysed here, however, Beds B97M and B104M, and both yielded very abundant *Systematophora* sp. A *sensu* Monteil, an event which Monteil (1993) placed firmly within his *F. modesta* Zone.

Some discrepancies are apparent between the ranges of some species as illustrated by Monteil (1992b, Table 1) and as observed in the current study, including taxa associated with his zonal definitions. The FO's of *Cassiculosphaeridia magna* and *Kleithriasphaeridium corrugatum* were shown by Monteil towards the base of the *verrucosum* Zone and at a mid *trinodosum* Zone respectively. At Vergol the first event is also near the base of the *verrucosum* Zone (Bed V104M) but the FO of *K. corrugatum* was in Bed V68M (*neocomiensiformis* Zone), the reverse order of Monteil's observations.

The FO's of *Batioladinium longicornutum* and *Hystriochodinium furcatum/ramoides* were cited as secondary markers for the base of Monteil's *K. corrugatum* Zone (i.e., at a mid *trinodosum* Zone level). In the current study, positive *B. longicornutum* and consistent *H. furcatum/ramoides* were recorded as old as Beds V124M and V123M respectively (i.e., across the *verrucosum/peregrinus* boundary). This is slightly older than indicated by Monteil. However, isolated *H. furcatum* and a possible *B. longicornutum* were also observed at still older levels, in Beds V101M and V112M respectively; the first is older than the base of *Cassiculosphaeridia magna*.

Discrepancies in quoted ranges for particular species may be due to several factors (see comments above), but in this case the rarity of some species towards the base of their range may be a factor. Applying Monteil's scheme to the present study, the following zonal sub-division is possible:

Vergol Bed	Monteil Zone/Sub-zone
V123M - LCH 220M	<i>K. corrugatum</i>
V104M - V120M	<i>C. magna</i>
V45 - V102M	<i>M. australis</i>
V5M - V42M	<i>M. macwhaei</i> forma B
B110 - B151M	<i>M. macwhaei</i> forma A
B97M - B104M	<i>F. modesta</i>

A new zonation scheme for the Vergol/La Charce section

Because of difficulties reconciling published schemes and the necessarily broad-brush approach to applying them in the current study, often by using secondary markers, a new but preliminary zonation scheme for the Vergol/La Charce section is proposed. This new scheme is entirely based on observations during the present study and will need to be tested and refined in further work on the Vocontian Basin and elsewhere.

A comparative sub-division of the entire studied section is illustrated in text-fig. 8, set against other criteria which are further discussed in later sections. In addition, text-figs. 12 and 13 illustrate some of the more common taxa throughout the studied interval in order to demonstrate the constant and significant fluctuations in dinocyst assemblages.

Pseudoceratium pelliferum pelliferum Zone.

Definition: Interval from the FO of *Pseudoceratium pelliferum pelliferum* to the FO of *Kleithriasphaeridium fasciatum*.

Age: Late Berriasian, *picteti* Zone to *alpillensis* Zone, *alpillensis* Sub-zone

Remarks: Monteil (1993) recorded, "a massive and sudden appearance of *Systematophora* sp. A" within his *Foucheria modesta* Zone and a similar influx was noted here in the two oldest samples analysed, Vergol Beds B97M and B104M. Immediately above this influx there is a major up-section increase in *Systematophora*? cf. *scoriacea* and the FO's of *Muderongia mcwhaei* and *Systematophora*? *daveyi*.

Kleithriasphaeridium fasciatum Zone

Definition: Interval from the FO of *Kleithriasphaeridium fasciatum* to the FO of *Pseudoceratium pelliferum radiculatum*.

Age: Late Berriasian to earliest Valanginian, *alpillensis* Zone, *alpillensis* Sub-zone to *pertransiens* Zone, *premollicus* Sub-zone

Remarks: This zone is very largely restricted to the late Berriasian *otopeta* Sub-zone. The lower part of the zone is characterised by the FO's of *Aprobolocysta humilis*, *Cymosphaeridium validum*, *Perisseiasphaeridium cretaceum* and *Tanyosphaeridium hirsutum*. Common to abundant *Kleithriasphaeridium fasciatum* are restricted to the upper part of the zone, associated with the FO of *Hystriochosphaeridium diversum*, very rare occurrences of *Cauca redacta* and a significant up-section reduction in the *Wrevittia helicoidea* grp.

Pseudoceratium pelliferum radiculatum Zone

Definition: Interval from the FO of *Pseudoceratium pelliferum radiculatum* to the FO of *Muderongia extensiva*.

Age: Early Valanginian, *pertransiens* Zone, *premollicus* to *salinarium* Sub-zones.

Remarks: The base of this zone approximates the base of the Valanginian. In addition to the nominate taxon, which is restricted to the lower part of the zone, its base is characterised by the FO's of *Aprobolocysta extrema* and *Bourkidinium granulum*, although the latter tends to be very rare towards the base of its range. The LO of *Aprobolocysta humilis* and the peak occurrence of *Ctenodinium elegantulum* are also at this level.

Immediately above the base of this zone is the peak occurrence of *Vexilloecysta spinosa* followed by a major up-section reduction in *Prolixosphaeridium prolatum* and the FO of *Chlamydochorella caminus*.

A very distinctive though rare form, *Thalassiphora*? *charollaisii* occurs only in the lower part of this zone, restricted to Bed B142M at Vergol. This was previously informally assigned to *Dino D* (Monteil in Charollais and Wernli 1995) and *Thalassiphora* sp. 246 (Jan du Chêne et al. 2016), and was reported in all cases from the *pertransiens* Zone.

Further taxa first recorded in this zone include *Aprobolocysta pustulosa* and *Hystriochosphaerina schindewolfii*, and the oldest com-

mon occurrence of *T. hirsutum* is in the upper part. The LO's of *P. pelliferum radiculatum* and common *Systematophora*? *scoreacea* are also within this zone and *Bicornus obscurus* is restricted to it.

Muderongia extensiva Zone.

Definition: Interval from the FO of *Muderongia extensiva* to the FO of *Protoellipsodinium seghire*.

Age: Early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone.

Remarks: The FO's of *Phoberocysta latissima* and consistent *Hystriochodinium voigtii* occur in the lower part of this zone at approximately the same level as the LO's of *Vexilloecysta spinosa* and consistent *Systematophora*? *scoriacea*.

The peak occurrence of *Kleithriasphaeridium fasciatum* is a prominent feature in the middle of this zone, followed by a marked up-section increase in *Foucheria modesta* and the LO's of *Aprobolocysta pustulosa* and common/abundant *K. fasciatum*.

Protoellipsodinium seghire Zone.

Definition: Interval from the FO of *Protoellipsodinium seghire* to the FO of *Discorsia nannus*.

Age: Early Valanginian, *pertransiens* Zone, *salinarium* Sub-zone to *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone.

Remarks: The base of this zone is characterised by the appearance of small *Protoellipsodinium* spp. with simple, short spines, firstly *Protoellipsodinium seghiris medaure*, closely followed by *Protoellipsodinium touile mugataë*. *Spiculodinium*? *inordinatum* is restricted to the lower part of the zone associated with a major increase then sharp decrease in *Phoberocysta latissima*.

The FO of *Batioladinium varigranosum* is towards the base of this zone and the LO's of *Aprobolocysta extrema* and consistent *P. latissima* are significantly higher (both above the peak of *P. latissima* in Bed V36M at Vergol).

Discorsia nannus Zone

Definition: Interval from the FO of *Discorsia nannus* to the FO of *Cassiculosphaeridia magna*.

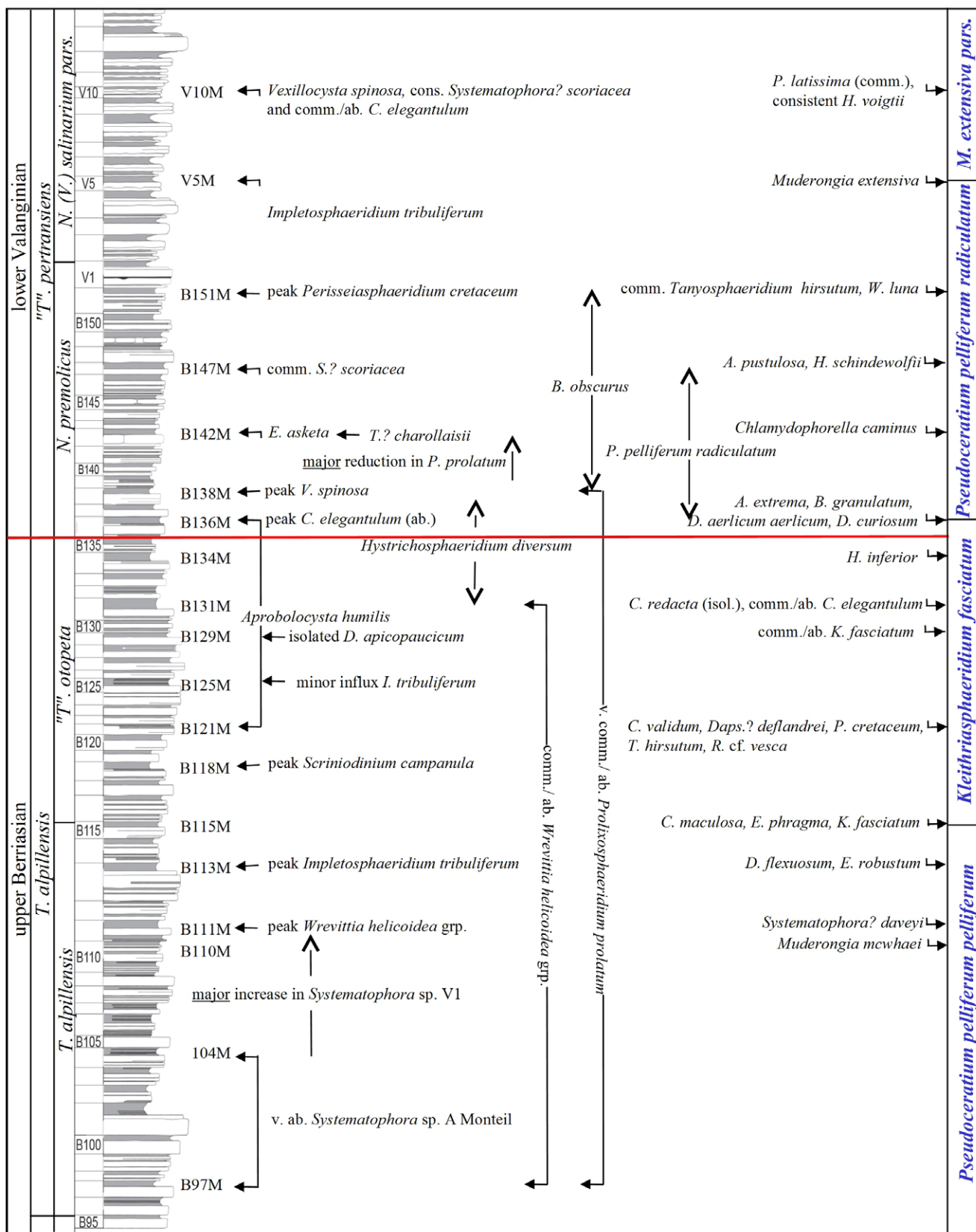
Age: Early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to late Valanginian, *verrucosum* Zone, *verrucosum* Sub-zone.

Remarks: In the current study the FO of *D. nannus* coincides with the FO's of *Aprobolocysta reticulata imparilis* and *Dingodinium*? *globosum* in Vergol Bed V45M. However, there is a large sampling gap between Beds V43M and V45M, which lie either side of the "V44 slump" (Fig. 6B). Although this is entirely within the *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone, further work on undisturbed sections will be necessary to separate these events.

The *Discorsia nannus* Zone is divided into two sub-zones:

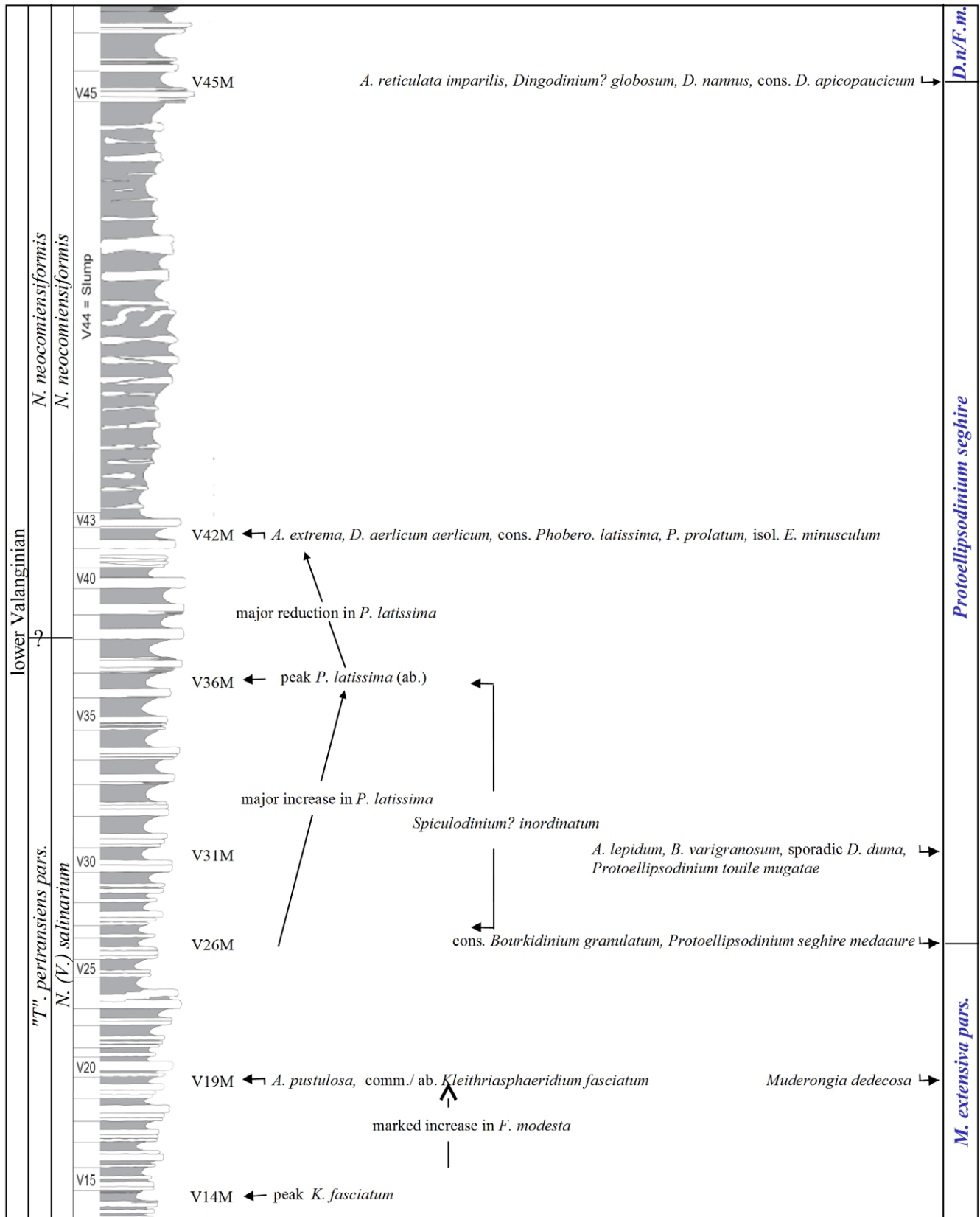
Foucheria modesta Sub-zone.

Definition: Interval from the FO of *Discorsia nannus* to the FO of *Codoniella prisca*.

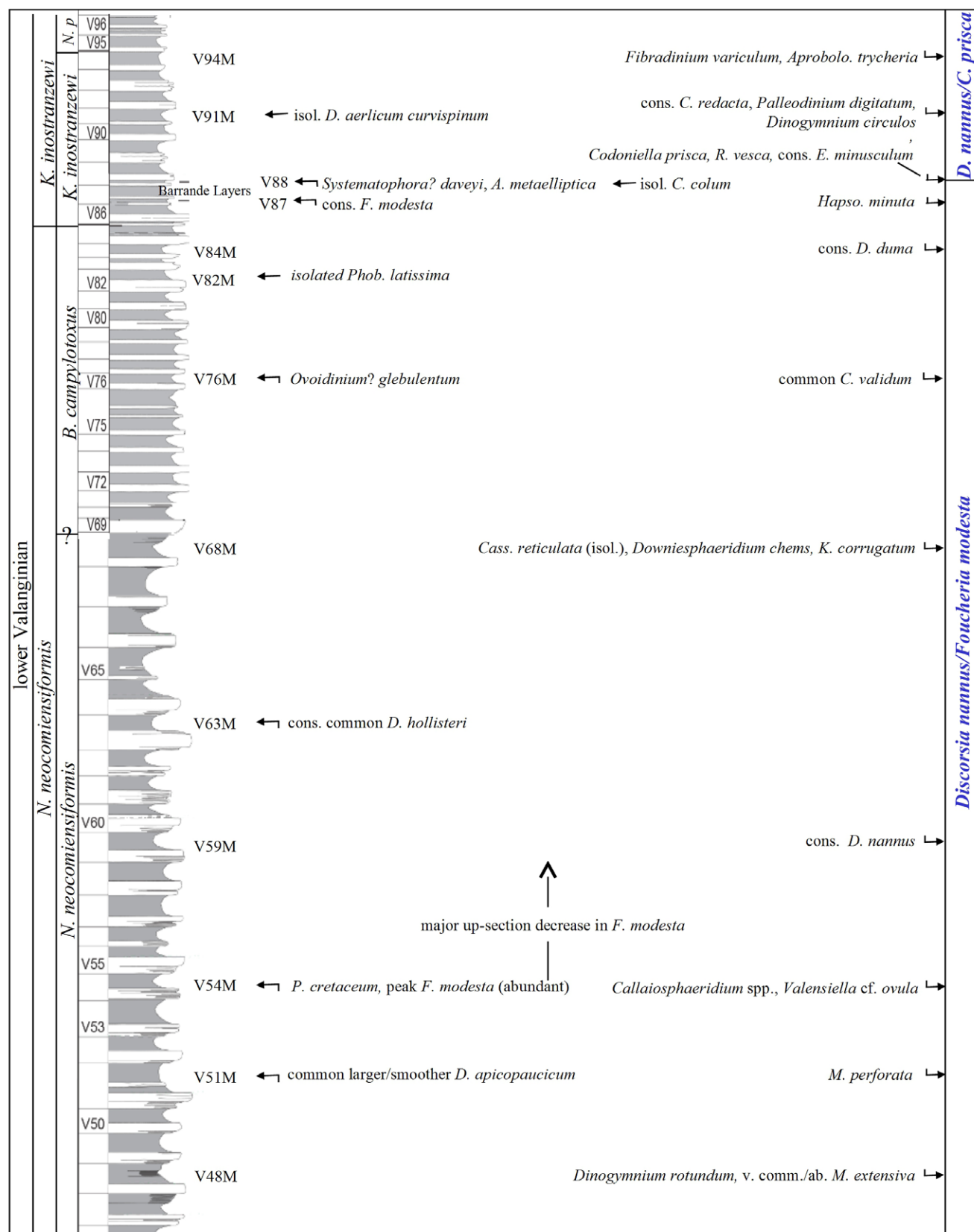


TEXT-FIGURE 6A

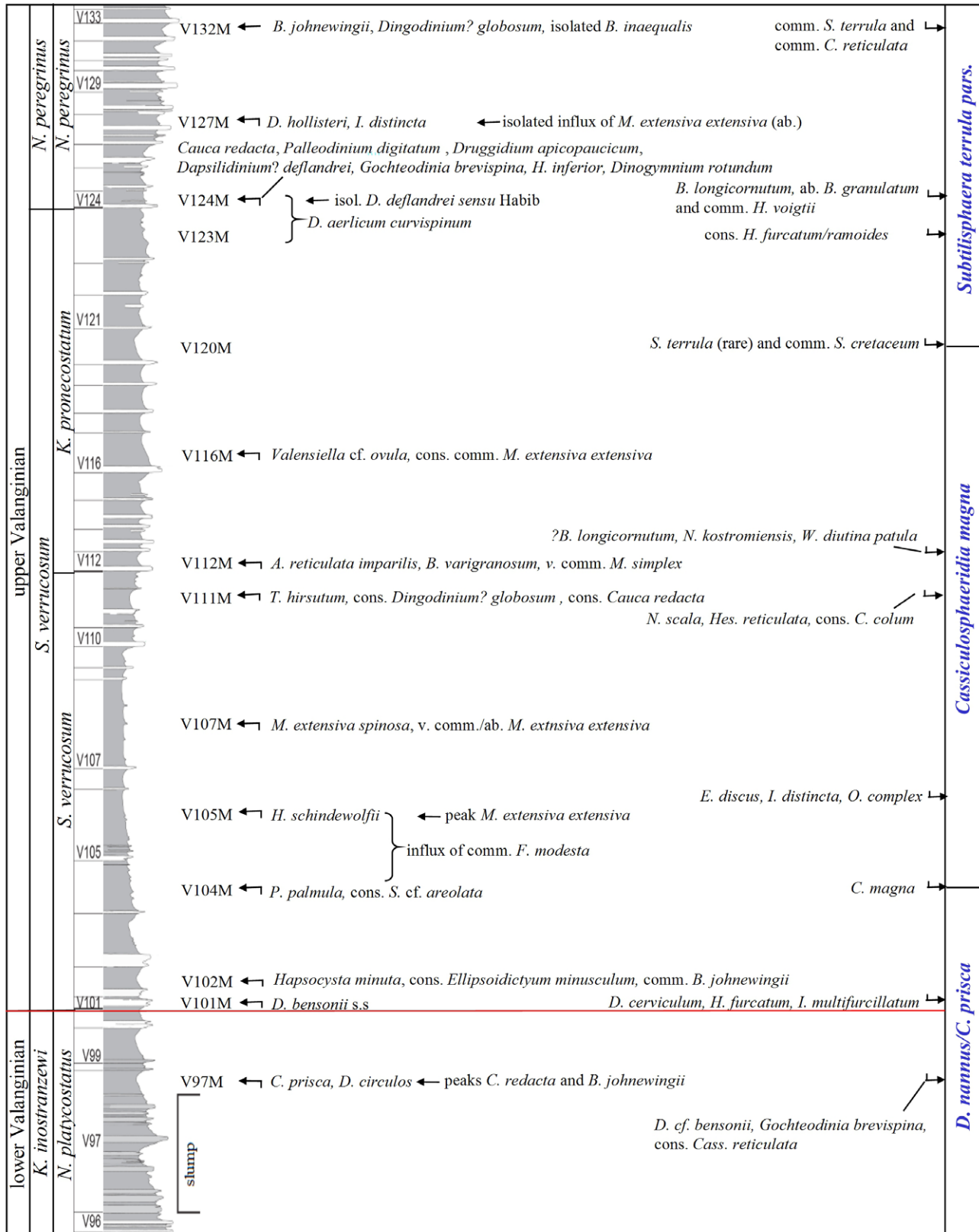
Palynofloral events at Vergol. The Berriasian/Valanginian boundary is in red and events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.



TEXT-FIGURE 6B
 Palynofloral events at Vergol. Events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.



TEXT-FIGURE 6C
Palynofloral events at Vergol. Events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.



TEXT-FIGURE 6D

Palynofloral events at Vergol. The lower/upper Valanginian boundary is in red and events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.

Age: Early Valanginian, *neocomiensiformis* Zone, *neocomiensiformis* Sub-zone to *inostranzewi* Zone, *inostranzewi* Sub-zone.

Remarks: This sub-zone is characterised by the nominate species which peaks within the *neocomiensiformis* Sub-zone (Bed V54M at Vergol) and declines markedly above that level. The youngest consistent occurrence of *F. modesta* and the FO of *Hapsocysta minuta* are close to the top of this sub-zone.

Events within this sub-zone include the FO's (in ascending sequence) of *Muderongia perforata*, *Callaiosphaeridium* spp. and *Kleithriasphaeridium corrugatum*, and the LO's of *Perisaisphaeridium cretaceum* and consistently common *Diacanthum hollisteri*. Very common to abundant *Muderongia extensiva* occur throughout.

Codoniella prisca Sub-zone.

Definition: Interval from the FO of *Codoniella prisca* to the FO of *Cassiculosphaeridia magna*.

Age: Early to late Valanginian, *inostranzewi* Zone, *inostranzewi* Sub-zone to *verrucosum* Zone, *verrucosum* Sub-zone.

Remarks: In addition to the FO of the nominate taxon, the base of this sub-zone is characterised by the LO's of *Systematophora? daveyi* and *Amphorulacysta metaelliptica*. *Codoniella prisca* and *Dinogymnium circulos* are restricted to this sub-zone. Further events within this sub-zone include (in ascending order) the FO of *Palleodinium digitatum*, the FO of consistent *Cassiculosphaeridia reticulata* and the peak occurrence of *Biorbifera johnewingii*. These are succeeded by the FO's of *Dingodinium cerviculum* and *Hystrichodinium furcatum*, the LO of *Dichadogonyaulax bensonii sensu stricto* and the LO's of *Hapsocysta minuta* and common *B. johnewingii*.

Cassiculosphaeridia magna Zone

Definition: Interval from the FO of *Cassiculosphaeridia magna* to the FO of *Subtilisphaera terrula*.

Age: Late Valanginian, *verrucosum* Zone, *verrucosum* to *pronecostatum* Sub-zones.

Remarks: The FO's of several taxa are recorded within this zone, including (in ascending order) *Isthmocystis distincta* and *Oligosphaeridium complex*, *Heslertonina reticulata* and *Nematosphaeropsis scala*, *Nelchinopsis kostromiensis* and *Wrevittia diutina patula*. In addition, questionable *Batioladinium longicornutum* occurs in the upper part.

The LO of *Palaecysta palmula* is at the base of the zone, followed closely by the LO of *Hystrichosphaerina schindewolfi* and the peak occurrence of *Muderongia extensiva extensiva*. The LO's of *Muderongia extensiva spinosa* and of very common/abundant *M. extensiva extensiva* are slightly higher in the zone.

The *C. magna* Zone is further characterised by the LO's of *Tanysphaeridium hirsutum*, *Aprobolocysta reticulata imparilis*, *Batioladinium varigranosum* and consistent *Dingodinium? globosum*. *Muderongia extensiva extensiva* was consistently common no higher than this zone.

Subtilisphaera terrula Zone

Definition: Interval from the FO of *Subtilisphaera terrula* to the FO of *Cribroperidinium sepimentum*.

Age: Late Valanginian, *verrucosum* Zone, *pronecostatum* Sub-zone to *peregrinus* Zone *nicklesi* Sub-zone.

Remarks: Several events characterise the lower part of this zone, including the FO's of *Druggidium deflandrei sensu* Habib, positive *Batioladinium longicornutum*, consistent *Hystrichodinium furcatum/ramoides*, common *Hystrichodinium voigtii* and very common *Cymososphaeridium validum*.

An influx of *Dinogymnium aerlicum curvispinum* characterises the *verrucosum/peregrinus* zonal boundary (associated with the base of the Faisceau Médian in both Vergol and La Charce), immediately followed by the LO's of *Diacanthum hollisteri* and an isolated influx of abundant *Muderongia extensiva extensiva* (both events again recorded in Vergol and La Charce).

The LO of *Biorbifera johnewingii* is in the middle of this zone, followed by the LO of consistent *Muderongia extensiva extensiva*.

Cribroperidinium sepimentum Zone

Definition: Interval from the FO of *Cribroperidinium sepimentum* to the FO of *Chlamydophorella ordinalis*.

Age: Late Valanginian, *peregrinus* Zone *nicklesi* Sub-zone to possibly base *furcillata* Zone, *furcillata* Sub-zone.

Remarks: The base of the overlying *Chlamydophorella ordinalis* Zone was placed at Bed LCH164M at La Charce, very close to the base of the *furcillata* ammonite Zone. Because of a sampling gap between that bed and Bed LCH160M, there is a possibility that the base of the *C. ordinalis* Zone might extend down into the *peregrinus* ammonite Zone, *nicklesi* Sub-zone and that the whole of the *Cribroperidinium sepimentum* Zone is restricted to the latter ammonite Sub-zone.

Characteristic palynofloral events within the *C. sepimentum* Zone include an influx of *Scriniodinium elimatum* in the lower part of the zone, followed by a marked reduction in numbers of *Circulodinium hirtellum* and the FO's of common *Nelchinopsis kostromiensis* and very common *Cymososphaeridium validum* towards the top, associated with the LO of *Systematophora cf. areolata*.

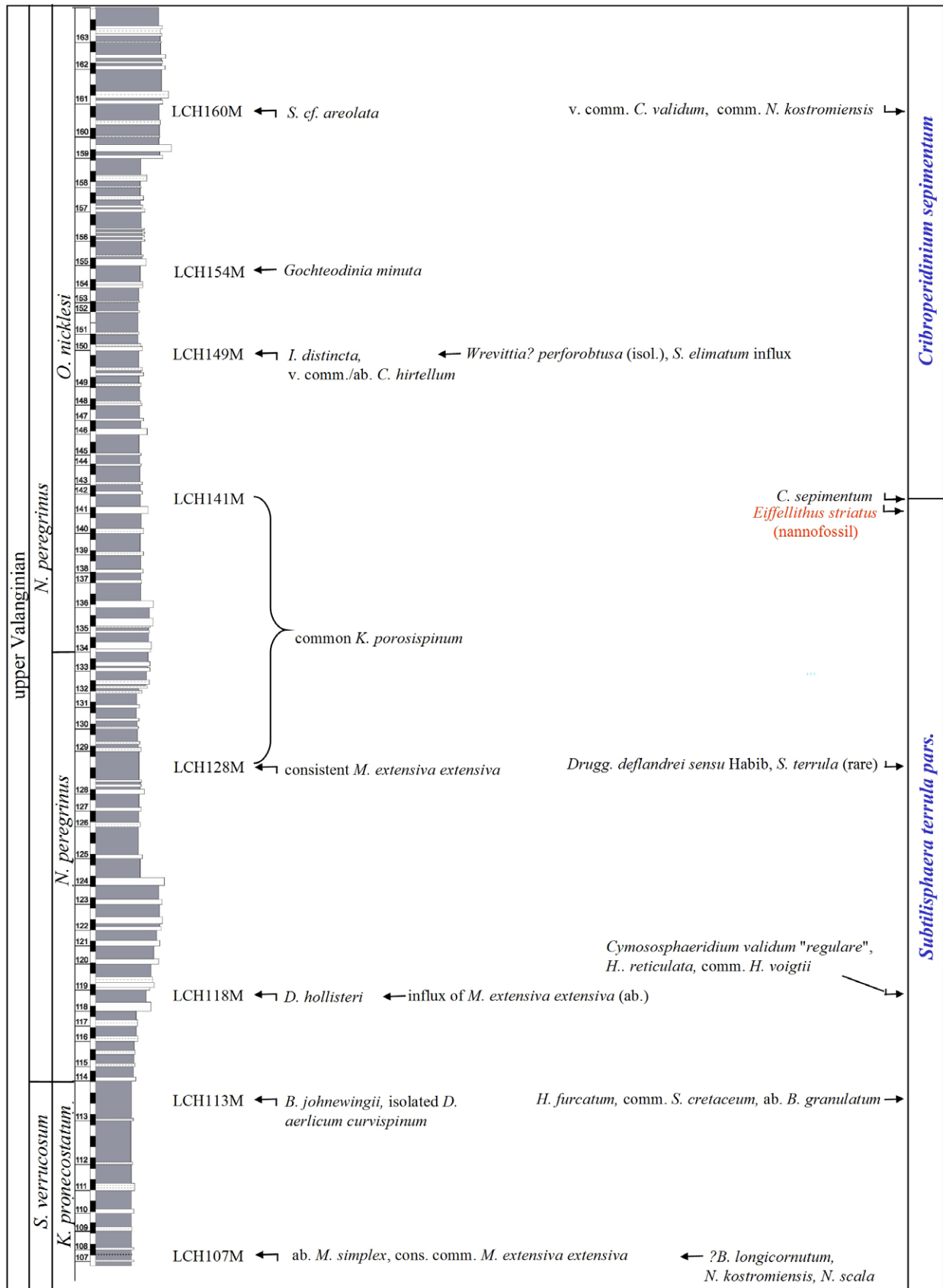
Chlamydophorella ordinalis Zone

Definition: Interval from the FO of *Chlamydophorella ordinalis* to the FO of *Bourkidinium elegans*.

Age: Late Valanginian, possibly base *furcillata* Zone, *furcillata* Sub-zone to base Hauterivian.

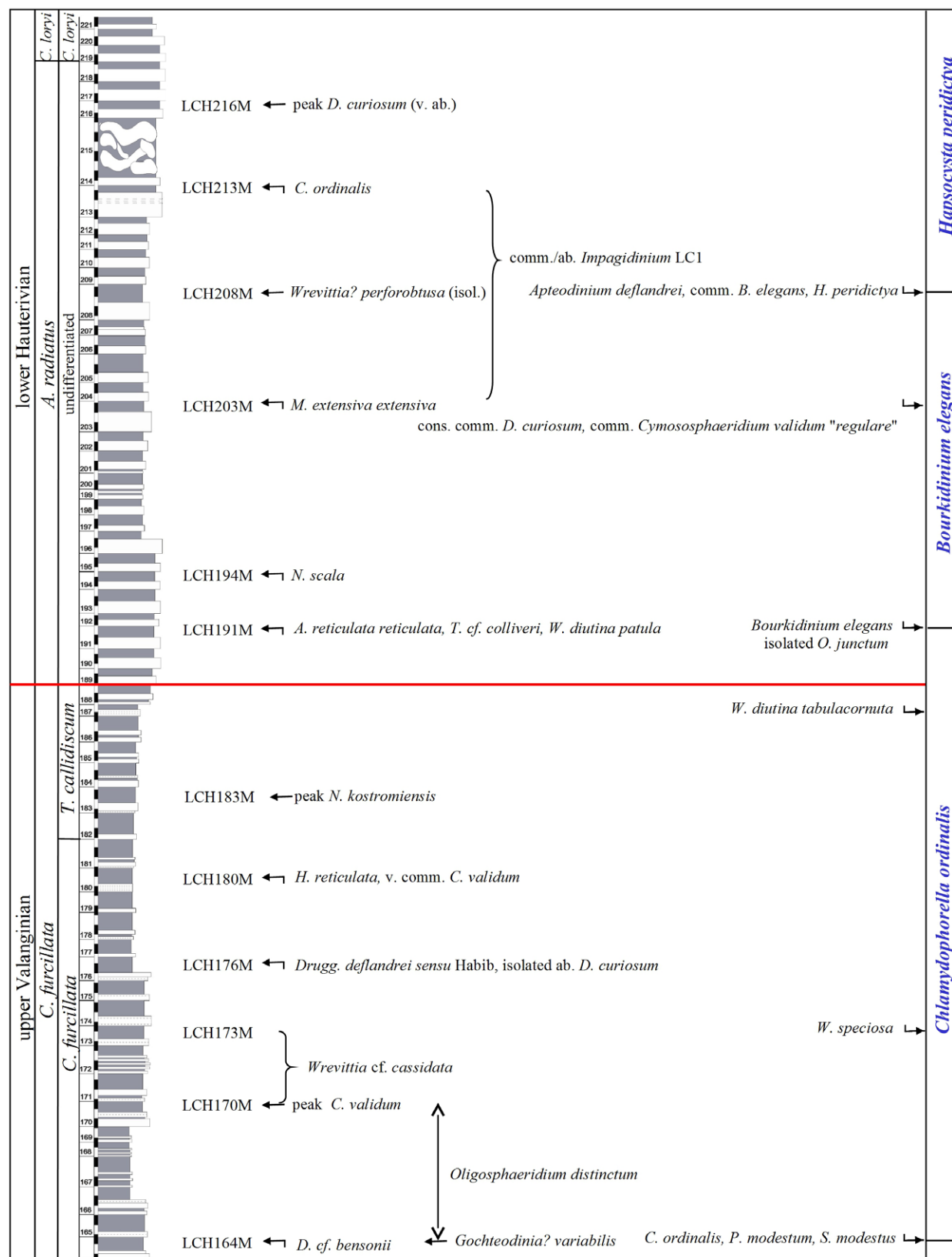
Remarks: The base of this zone is close to the *peregrinus/furcillata* ammonite zonal boundary, as discussed above.

In addition to the nominate taxon, the base of the *Chlamydophorella ordinalis* Zone is marked by the FO's of *Protobatioladinium modestum* and *Spiniferites modestus* and the LO of



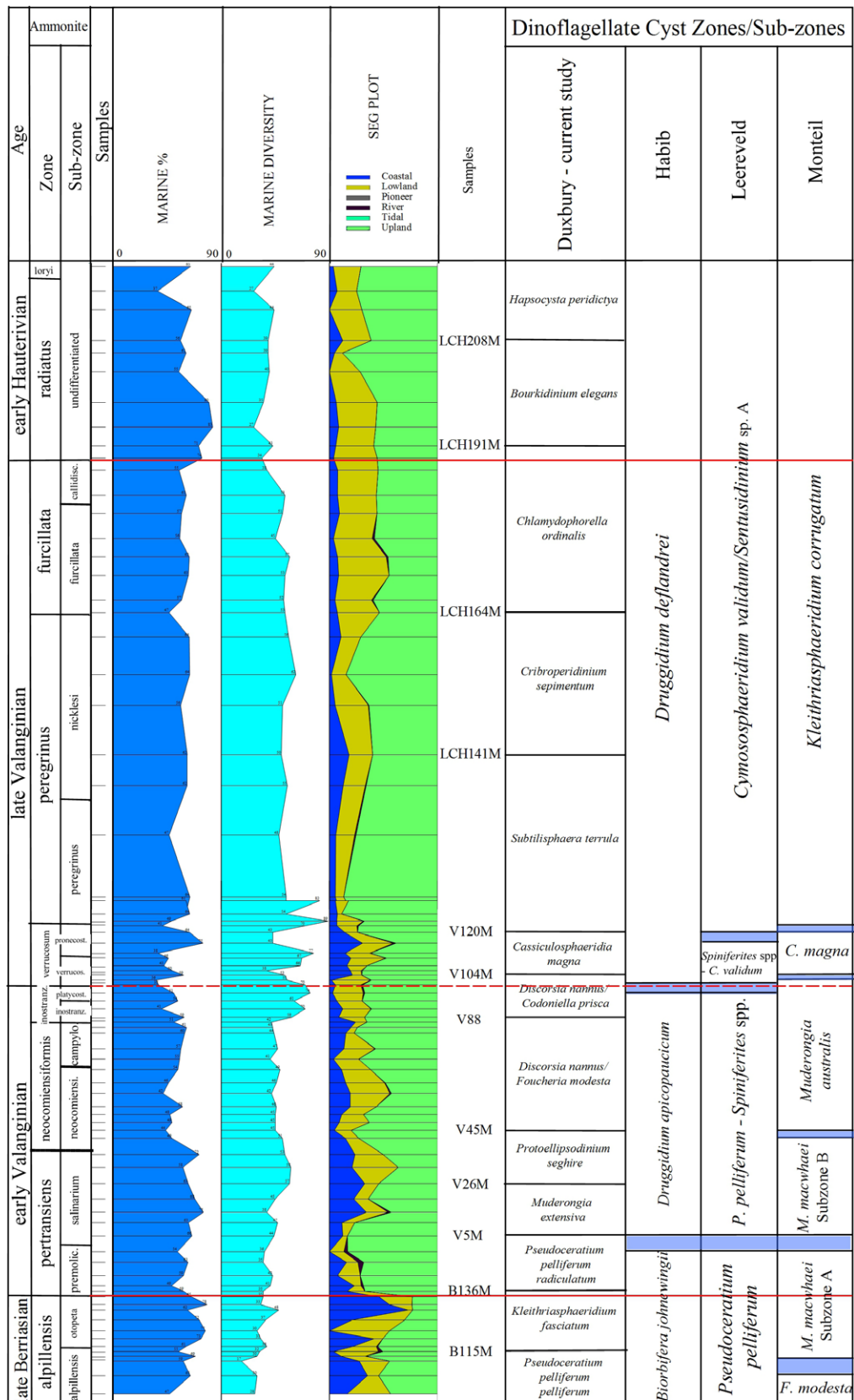
TEXT-FIGURE 7A

Palynofloral events at La Charce (the FO of the nannofossil *Eiffellithus striatus* is also marked for reference). Events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.



TEXT-FIGURE 7B

Palynofloral events at La Charce. The Valanginian/Hauterivian boundary (GSSP) is in red and events are set against a lithological column, ammonite zones/sub-zones and the newly-defined dinocyst zonation.



TEXT-FIGURE 8

The stratigraphy of the combined Vergol/La Charce section studied here. Standard ammonite divisions are set against marine percentage and diversity curves and a Sporomorph EcoGroup (SEG) plot. The new dinocyst zonation is included, set against previous schemes interpreted from current palynofloral observations.

Dichadogonyaulax cf. *bensonii*, followed closely by the LO of *Heslertonia reticulata*. *Oligosphaeridium distinctum* was restricted to the lower part of the zone.

Peak occurrences of *Cymosphaeridium validum* and *Nelchinosphaeridium kostromiensis* occur respectively in the lower part of the zone and towards its top.

Bourkidinium elegans Zone

Definition: Interval from the FO of *Bourkidinium elegans* to the FO of *Hapsocysta peridictya*.

Age: Early Hauterivian, *radiatus* Zone. The base of this dinocyst zone approximates the Valanginian/Hauterivian boundary.

Remarks: In addition to the nominate taxon, the base of this zone is marked by the LO's of *Aprobolocysta reticulata reticulata* and *Wrevittia diutina patula*. These are followed closely by the LO's of *Nematosphaeropsis scala* and *Muderongia extensiva*.

The upper part of this zone is characterised by common to abundant *Impagidinium* LC1 at La Charce.

Hapsocysta peridictya Zone.

Definition: Interval from the FO of *Hapsocysta peridictya* to the top of the studied interval.

Age: Early Hauterivian, from *radiatus* Zone

Remarks: In addition to the nominate taxon, the base of this zone is marked by the FO's of *Apteodinium deflandrei* and common *Bourkidinium elegans*.

The lower part of this zone is characterised by common to abundant *Impagidinium* LC1 at La Charce.

MICROFORAMINIFERA

Following Stancliffe (1989), the term "microforaminifera" is here restricted to, "the organic remains of microforaminifera found on palynological slides made using the standard palynological preparation procedure". These vary significantly in morphology but no attempt has been made to separate individual morphotypes in the present study, although they were common to very abundant throughout the studied section (an exception being Barrande layer B4 - see below). There was significant variation in numbers, with relative frequency dropping at sea level maxima and increasing particularly in later regressive phases, presumably demonstrating a preference for shallower settings in this context.

As noted by Lister and Batten (1988), "Foraminiferal test linings are also useful environmental indicators, being common in marine coastal and shallow shelf environments (Scull et al. 1966, Batten 1979)". Further analysis to separate the various morphotypes and to better map their distribution might be beneficial in future palaeoenvironmental studies in the Vocontian Basin.

SCOLECODONTS

Much of the work done to date on scolecodonts describes Palaeozoic material and the record of Cretaceous scolecodonts is poor. They were recorded throughout the sections analysed in the present study, although they were rare and occurred consistently

only as old as sample V84M (early Valanginian, top *neocomiensiformis* Zone). The reason for their extreme rarity below this level is unclear. Although the components of the complex jaw apparatuses are usually found separated in the fossil record, entirely preserved apparatuses can be found, and some semi-articulated examples were recovered from Vergol. Examples of Vergol scolecodonts, both separated and semi-articulated are shown in Plate 21.

Courtinat (1998) stated, "Mesozoic scolecodonts in black shales argue for suboxic deposits", and their presence in sample V88 (Barrande layer B4) might support this - most of the specimens in Plate 21 are from this layer. However, Eriksson (pers. comm.) suggests that it is not possible to tell if these taxa would be indicative of bottom dwellers in suboxic conditions, as they have been reported from very diverse settings in modern-day oceans, and are known to inhabit all kinds of substrates, including heavily polluted ones.

Although scolecodonts were present in Barrande layer B4, they were absent from Barrande layers B1-B3, contrary to the absence of microforaminifera from layer B4 and their abundance in layer B1; the reason for this reversal is unclear (see Appendix 3 for further discussion of microforaminifera).

MIOSPORES

Miospores formed consistently below 20% of the initial count of 500 specimens in the present study, and often below 10%; numbers of each species recorded are shown in text-figs. 9-11. Although the large majority of species were very long-ranging, fluctuations in their relative numbers can offer some insights into the effects of changing palaeoenvironmental conditions on terrestrial settings. The main focus of the present study was on the dinocysts but, as suggested by the following discussions, closer sample spacing and larger miospore counts might provide more detailed palaeoenvironmental interpretations than were attempted here.

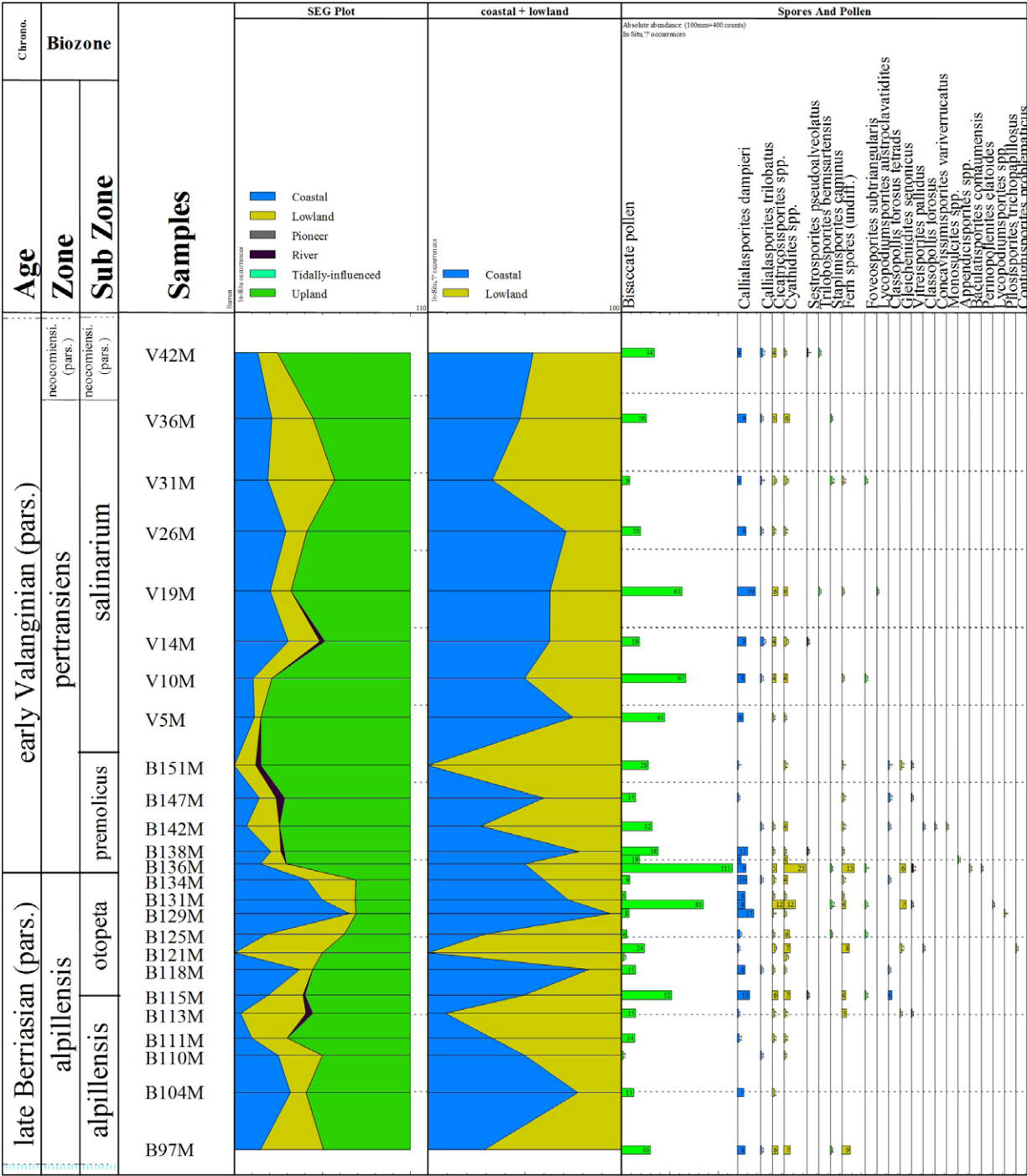
Previous work on the Vergol and La Charce sections was undertaken by Kujau et al. (2013) and reference to that work and to Abbink (1998) provides background data on the interpretation of palaeoenvironmental preferences for individual genera and species. Some comments on Kujau et al.'s conclusions are made at the end of this section.

Abbink (1998) developed a model for miospore assemblages, where groups of miospore taxa were interpreted paleoecologically, rather than considering individual genera. He termed these Sporomorph EcoGroups (SEGs); his scheme was further summarised in Abbink et al. (2004). Abbink's work was not referred to in Kujau et al. (op. cit.). Abbink described 6 SEGs, with parent plants inhabiting particular settings:

Upland: on higher terrain well above groundwater level that is never submerged by water.

Lowland: on plains and/or in fresh-water swamps; the plains may (periodically) be submerged by fresh water, resulting in the possible presence of 'wetter' (marsh) and 'drier' taxa in this group; there is no marine influence, except under extreme circumstances.

River: on river banks which are (periodically) submerged and subject to erosion.



TEXT-FIGURE 9
Quantitative miospore data across the Berriasian/Valanginian boundary and interpreted SEG and Coastal/Lowland curves. A stepped decline in coastal taxa associated with a peak in upland miospores (peaking at Sample B151M) is clearly shown.

Pioneer: on recently developed ecospace (e.g., vegetation growing at places that had been submerged by the sea for a longer period).

Coastal: growing immediately along the coast, never submerged by the sea but under a constant influence of salt spray.

Tidally-influenced: daily influenced by tidal changes (regularly submerged at high tide).

Miospores recorded in the present study have been similarly grouped. Three SEG's, Coastal, Lowland and Upland were shown to be particularly prominent, and these are plotted against various criteria in text-figs. 8-13. Whilst using similar data, this approach is subtly different to that of Kujau et al. (op. cit.), who emphasised changing levels of humidity as the main influence on assemblages.

For reasons fully discussed in Abbink (1998), the relationship between the coastal and lowland SEGs can be taken as a broad proxy for sea level change. This is mainly because of the relative loss of lowland habitat during sea level rise and the opposite effect during regressions. There are, however, many factors that can affect the numbers and distribution of particular miospores, as noted by Kujau et al. (op. cit., p. 61) but it is not within the scope of the current study to explore this further. Discussions below are based largely on Abbink's Coastal/Lowland interpretation and might be re-assessed with further study.

A SEG plot is presented in text-fig. 8, which also includes marine diversity, marine percentage curves, dinocyst zones and chronostratigraphy, showing the considerable complexity recorded over the entire studied interval. Several prominent peaks in the Coastal SEG associated with marked reductions in the Lowland SEG (sea level highstands *sensu* Abbink) were seen and a Coastal/Lowland curve is included in text-figs. 9-11; the Weissert Event $\delta^{13}\text{C}$ curve (from Martinez et al. 2015) is also included in text-figs. 10 and 11.

A marked, stepped reduction in the Coastal SEG and an associated increase in Lowland taxa was recorded across the Berriasian/Valanginian boundary (text-figs. 8, 9), possibly suggesting a lowstand event towards the top of the *pertransiens* Zone, *premolicus* Sub-zone, peaking at sample B151M.

To some extent, the Coastal/Lowland curve here approximates the spore-pollen ratio curve presented for the Vocontian Basin in Kujau et al. (op. cit., fig. 7) and this is particularly the case for the section as high as the *verrucosum* Zone. The Kujau et al. curve is interpreted as following changes in humidity, but the Coastal/Lowland curve in the present study is interpreted to be related to relative sea level changes.

The Kujau et al. humidity curve does not match the Coastal/Lowland curve across the Valanginian/Hauterivian boundary however, even though an increase in fern spores similar to that described by Kujau et al. as their "Assemblage VB5" was recorded at La Charce, between samples LCH164M and LCH191M (*furcillata* to base *radiatus* Zones). The difference is because the Coastal/Lowland curve presents a ratio of those SEGs without direct palaeoenvironmental interpretation, other than possible relationship to sea level. On that basis, the entire section studied at La Charce appears to represent an overall regressive phase, with Kujau et al.'s "Assemblage VB5" perhaps representing a particularly hu-

mid period within it.

Comparison of the Coastal/Lowland curve with the Weissert Event $\delta^{13}\text{C}$ curve in text-figs. 10 and 11 shows remarkable correspondence with Coastal peaks in the late Valanginian, at sample V104M (*verrucosum* Zone, *verrucosum* Sub-zone) and sample V127M (*peregrinus* Zone, *peregrinus* Sub-zone). In addition, however, a prominent Coastal peak occurs within the early Valanginian between samples V82M and V87 (*neocomiensiformis/inostranzewi* zonal boundary), thereby including the oldest Barrande layer, B1. This is very similar to younger peaks within the main Weissert Event and it does correspond to a small "blip" in the $\delta^{13}\text{C}$ curve (text-fig. 10), a feature illustrated but not commented on by Gréselle et al. (2011), Kujau et al. (2012), Martinez et al. (2015) and Reboulet (2015). A marked reduction in the Coastal/Lowland ratio (regression?) was noted between Barrande layers B1 and B4 (samples V87 and V88). See also Appendix 3.

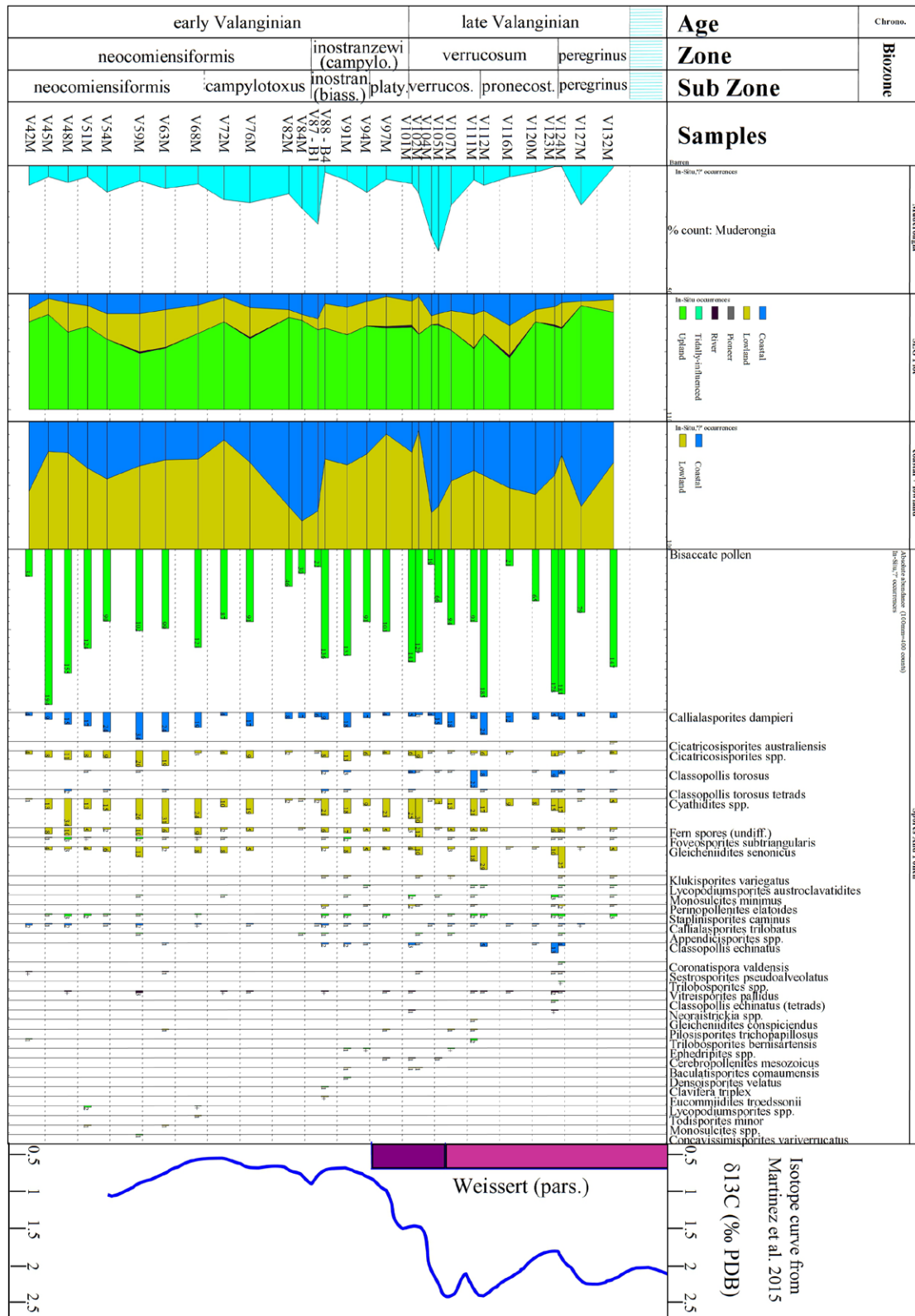
A further notable feature in text-fig. 10 is the correspondence of high numbers of the dinocyst genus *Muderongia* to peaks in the Coastal/Lowland curve and to peaks in the $\delta^{13}\text{C}$ curve, including the small "blip" noted above. Wilpshaar and Leereveld (1994) noted that high abundances of their *Muderongia* Group have been reported in sediments representing variable salinity conditions (also Lister and Batten 1988; Batten 1979). It may be the case therefore that high numbers of that genus may reflect reduced surface water salinity or derivation from such a setting.

From the palynological evidence, peaks in *Muderongia* correspond to peaks in the Coastal (versus Lowland) and $\delta^{13}\text{C}$ curves. One of the *Muderongia*/Coastal peaks is associated with a minor "blip" in the $\delta^{13}\text{C}$ curve which includes the oldest Barrande layer. This evidence might support some paleoenvironmental similarities between the Barrande layers (at least layer B1) and the main Weissert Event, although this is significantly below the main $\delta^{13}\text{C}$ excursion. The reasons for the co-occurrence of these seemingly disparate events are unclear, although the correspondence of Coastal/Upland and $\delta^{13}\text{C}$ curves presumably reflects floral response to base level, atmospheric and temperature/humidity changes, whatever the cause.

Peaks of potentially low-salinity dinocysts at levels interpreted here as highstands might be unexpected, although they might reflect increased runoff disproportionately affecting surface water chemistry. This might fit with the suggestion in Kujau et al. 2013 that, "Changes in moisture, identified as the key climatic factor determining trends and turnovers in vegetation, were probably controlled by a monsoonal circulation".

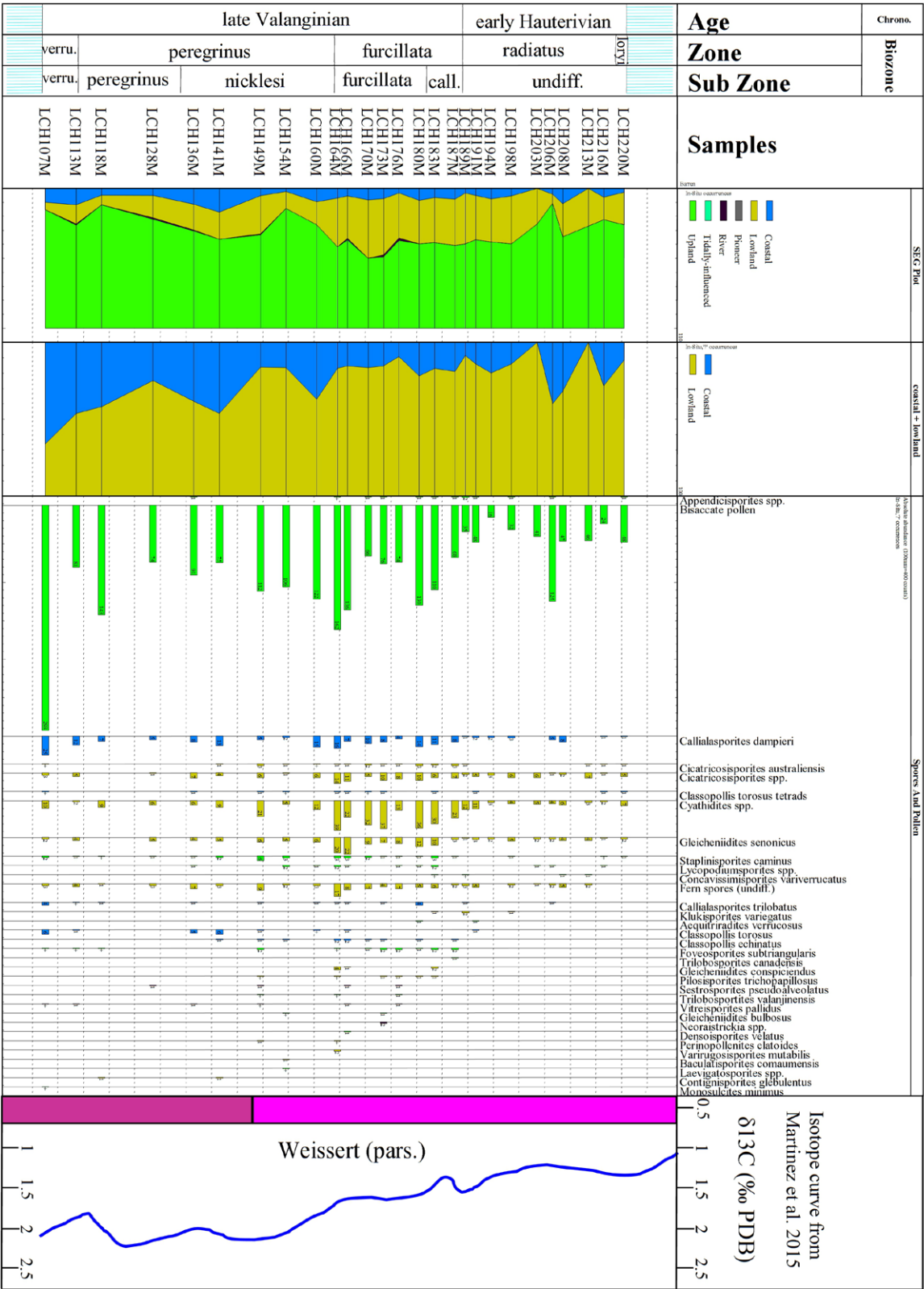
BOUNDARIES

Three key boundaries were included in the present study, Berriasian/Valanginian, early/late Valanginian and Valanginian/Hauterivian. The first (base Bed B136 at Vergol) is a candidate for the Global Boundary Stratotype Section and Point (GSSP) for the base of the Valanginian and the last (base Bed LCH189 at La Charce) has been selected as GSSP for the base of the Hauterivian (Mutterlose et al. 2021). Comments on the observed palynofloras at Vergol and La Charce are included throughout this paper. Because of the international importance of these sections, some discussion is also included below, relating where possible these Tethyan occurrences to more Boreal sections (Speeton, Central North Sea) published elsewhere (Duxbury 1977; 2001; 2018; 2023), focused on the three key boundary intervals.



TEXT-FIGURE 10

Quantitative miospore data across the early/late Valanginian boundary and interpreted SEG and Coastal/Lowland curves. A $\delta^{13}C$ isotope curve (from Martinez et al. 2015) and a *Muderongia* curve are included to show the co-occurrence of *Muderongia*, Coastal and $\delta^{13}C$ peaks within the Weissert carbon isotope excursion. Similar *Muderongia*/Coastal peaks also occur at a small $\delta^{13}C$ "blip" close to the base of the Barrande layers, Bed V87.



TEXT-FIGURE 11
Quantitative miospore data across the Valanginian/Hauterivian boundary and interpreted SEG and Coastal/Lowland curves. The latter shows an initial decline (?regression) mirroring the $\delta^{13}C$ curve before levelling through the *furcillata* Zone which is particularly rich in miospores (the "third spore maximum" of Kujau et al. 2013).

The Berriasian/Valanginian boundary

Many dinocyst events considered to be important in characterising the Berriasian/Valanginian boundary interval at Vergol are illustrated in text-fig. 6A. Several of the taxa are previously undescribed and some have not previously been recorded in southeast France (although some may have been attributed to other species).

There is little published on marine palynofloras covering the Berriasian/Valanginian interval in the Tethyan realm, other than work by Habib, Monteil and Leereveld (see above); difficulties in matching French and Spanish dinocyst zonation schemes were highlighted by Leereveld (1995; 1997a) and Bulot et al. (1996). Several of the events noted here were similar to those used by Habib, Monteil and Leereveld in defining their schemes although there are some differences both in species identification and consequently in some of the ranges quoted; exhaustive comparisons of events would serve little purpose here and the occurrences cited below refer only to first-hand observations by the present author.

Dinocyst events recorded across the Berriasian/Valanginian boundary at Speeton were listed in Duxbury 2018 (figs. 2, 10). Some of these were also recorded at Vergol, although despite the richness of assemblages at Speeton and Vergol, only a small number appear consistently in both provinces; some are illustrated in text-fig. 14. In view of the relatively small number of apparently equivalent occurrences, however, there must be some doubt regarding their value, as they may be coincidental; further work is necessary to test their potential and the potential of other ubiquitous taxa which currently appear to have differing ranges.

Some observations drawn from text-figure 14:

- the FO of *Kleithriasphaeridium simplicispinum* was within the upper part of Bed D5 at Speeton, and this species ranged down to the base of the studied interval (Sample B97M) at Vergol.
- the FO of *Exochosphaeridium robustum* was recorded in Bed D4C at Speeton, within the *Paratollia* Zone, early Valanginian. This event was recorded at Vergol in sample B113M, late Berriasian, *alpillensis* Zone, *alpillensis* Sub-zone.
- the FO of *Hystrichosphaeridium diversum* was recorded in Bed D4B at Speeton, within the *Paratollia* Zone, early Valanginian. This event was also recorded at Vergol but in sample B131M, late Berriasian, *alpillensis* Zone, *otopeta* Sub-zone.
- the FO of *Bourkidinium granulum* and a major influx of *Ctenidodinium elegantulum* were observed in Speeton Beds D4B and D4A respectively, and similar events occurred in Vergol Bed B136M, close to the base of the Valanginian (Bed B136).

The events illustrated in text-fig. 14 appear to show that by comparison with Vergol the Berriasian/Valanginian boundary at Speeton may be significantly higher in Unit D4 than at the base of that unit. This may reflect the current placement in the standard Tethyan scheme of the *alpillensis* Zone, *otopeta* Sub-zone at the top of the Berriasian, whereas in other schemes it was the oldest Valanginian unit.

Duxbury (2018, p. 207) suggested that there may be a hiatus between samples examined from Speeton Beds D4B and D4C, which "bunches" the FO's and LO's of several taxa, citing Rawson's pers. comm. that although Bed D4C appears to be a pale clay throughout, there is a band of corroded belemnites in the middle, and suggesting that this might represent this hiatus. From the evidence presented in text-fig. 14 here (albeit tentative), this intra-Bed D4C feature might be interpreted as (or at least be very close to) the

Berriasian/Valanginian boundary *sensu* Vergol. Should the Berriasian/Valanginian boundary at Speeton be raised, as suggested, then the lower part of palyzone LKP6 of Duxbury (2001, 2018) would represent the top of the Berriasian (see comments on Zone LKP6 in Duxbury 2018, p. 206).

The early/late Valanginian boundary

The early/late Valanginian boundary interval at Vergol is characterised by several palynofloral events (text-figs. 8, 9), although the current shortage of similar studies and often significant differences in ranges quoted precludes detailed comparison with other Tethyan and Boreal sections; events presented here therefore remain to be tested. It is also notable that although some taxa are present at Vergol which also occur in Boreal settings, the ranges of most of them appear to be somewhat different.

McArthur et al. (2007, p. 414) stated that, "Through the *S. verrucosum* Zone, Mg/Ca (and so temperature) decreases sharply by 30%.....It follows that the changes in Mg/Ca and $\delta_{18}O_c$ reflect a cooling of around 4 °C through the *S. verrucosum* Zone". They also stated (op. cit., p. 416) that, "The temperature decrease... through the *S. verrucosum* Zone, immediately precedes marked faunal changes in the *N. peregrinus* Zone, and supports the view that climate controlled, at least in part, the migration of Boreal ammonoid faunas observed in Western Europe (Kemper 1987; Rawson 1994; Reboulet and Atrops 1995; Reboulet 1996). The migration of Boreal ammonites to a southward limit at the southern margin of the European plate...occurred first at the Early-Late Valanginian boundary (Rawson, 1994), where Mg/Ca shows that temperature had started to decrease rapidly".

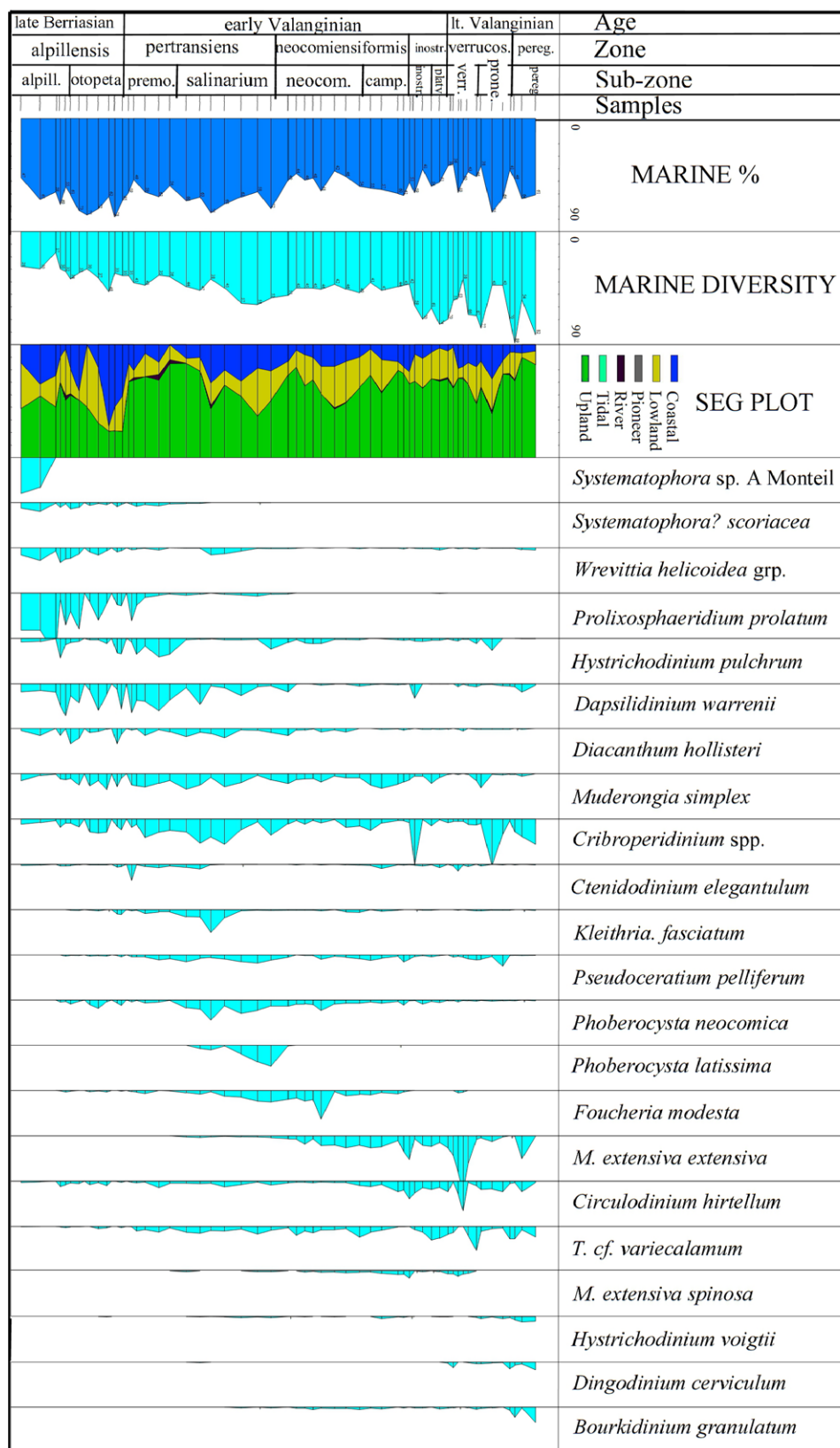
Similarly, Janssen (2021, p. 94) stated (referring to the base of the late Valanginian), "The species *H. aff. jaculoides* occurs suddenly and in abundance, first in basal, and later in more proximal facies. It originated most probably from the Boreal-Atlantic and would indicate that exchange was possible in that period".

Despite this evidence for macrofaunal migrations southwards during the earlier part of the late Valanginian, a similar migration of the microflora remains to be demonstrated.

Duxbury (2018, p. 199, 200) offered two alternatives for the position of this boundary offshore UK, calibrating the occurrence of a major influx of the dinocyst *Hystrichosphaeridium arborispinum* with the FO of the nannofossil *Eiffellithus striatus*. The first (Alternative A) was based on evidence from Rutledge 1994, Bown et al. 1999 and Jeremiah 2001, and placed the FAD of *E. striatus* at an intra-late Valanginian level.

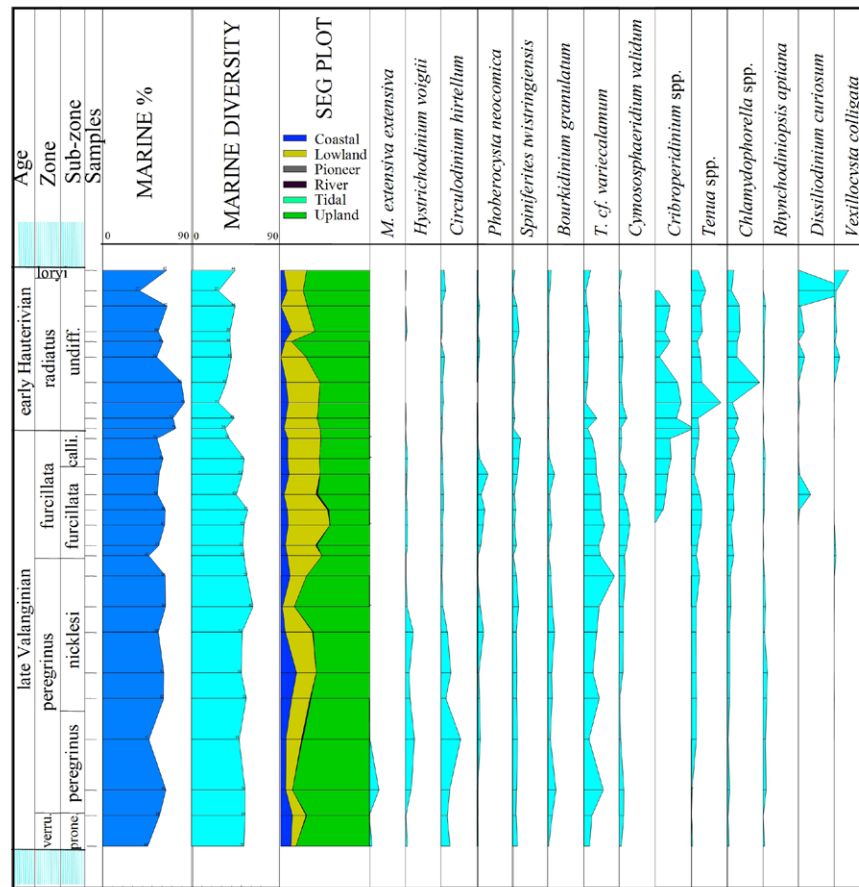
Duxbury's second alternative (Alternative B) was based on Mutterlose et al. (2000) and Dziadzio et al. 2004, the latter a multi-disciplinary study of Lower Cretaceous borehole material from central and southeastern Poland, including mixed Tethyan and Boreal macro- and microfaunas, allowing the recognition of ammonite and microfossil zones of both realms.

In their work on central and southeast Poland, Dziadzio et al. (op. cit.) referred to a modified Lower Saxony Basin scheme (Mutterlose 1991; 1992; Mutterlose et al. 2000) within which the co-occurrence of *E. striatus* with *hollwedensis* (Boreal) and *verrucosum* (Tethyan) ammonites allowed the placement of the FO of *E. striata* at the base of the late Valanginian. In addition to nannofloral evidence, key foraminiferal events within the late Valanginian in Dziadzio et al. (op. cit.) were consistent with those in Mutterlose



TEXT-FIGURE 12

Marine percentages and diversity, and a miospore SEG plot for all Vergol samples analysed here, illustrated with absolute abundance data for various dinocyst taxa. Constant variations are seen reflecting paleoenvironmental changes. The increase then decrease in marine diversity from the base of the studied interval to the top of the *neocomiensiformis* Zone (with a peak towards the top of the *pertransiens* Zone) is particularly striking.



TEXT-FIGURE 13

Marine percentages and diversity, and a miospore SEG plot for all La Charce samples analysed, illustrated with absolute abundance data for various dinocyst taxa. As in text-fig. 12, constant variations are seen reflecting paleoenvironmental changes. The marked peak in marine % associated with minimum marine diversity towards the base of the *radiatus* Zone corresponds to a level immediately above the "third spore maximum" of Kujau et al. 2013.

et al. (2000), and these again supported a base late Valanginian placement of the FAD of *E. striatus*.

Evidence from Dziadzio et al. (op. cit.) appeared to be the better-constrained, and Duxbury (op cit.) chose Alternative B for the base of the late Valanginian, placing the major influx of *H. arborispinum* at that level but with the caveat, "a higher base within the upper Valanginian might be possible if some regional diachroneity or taxonomic differences were proved".

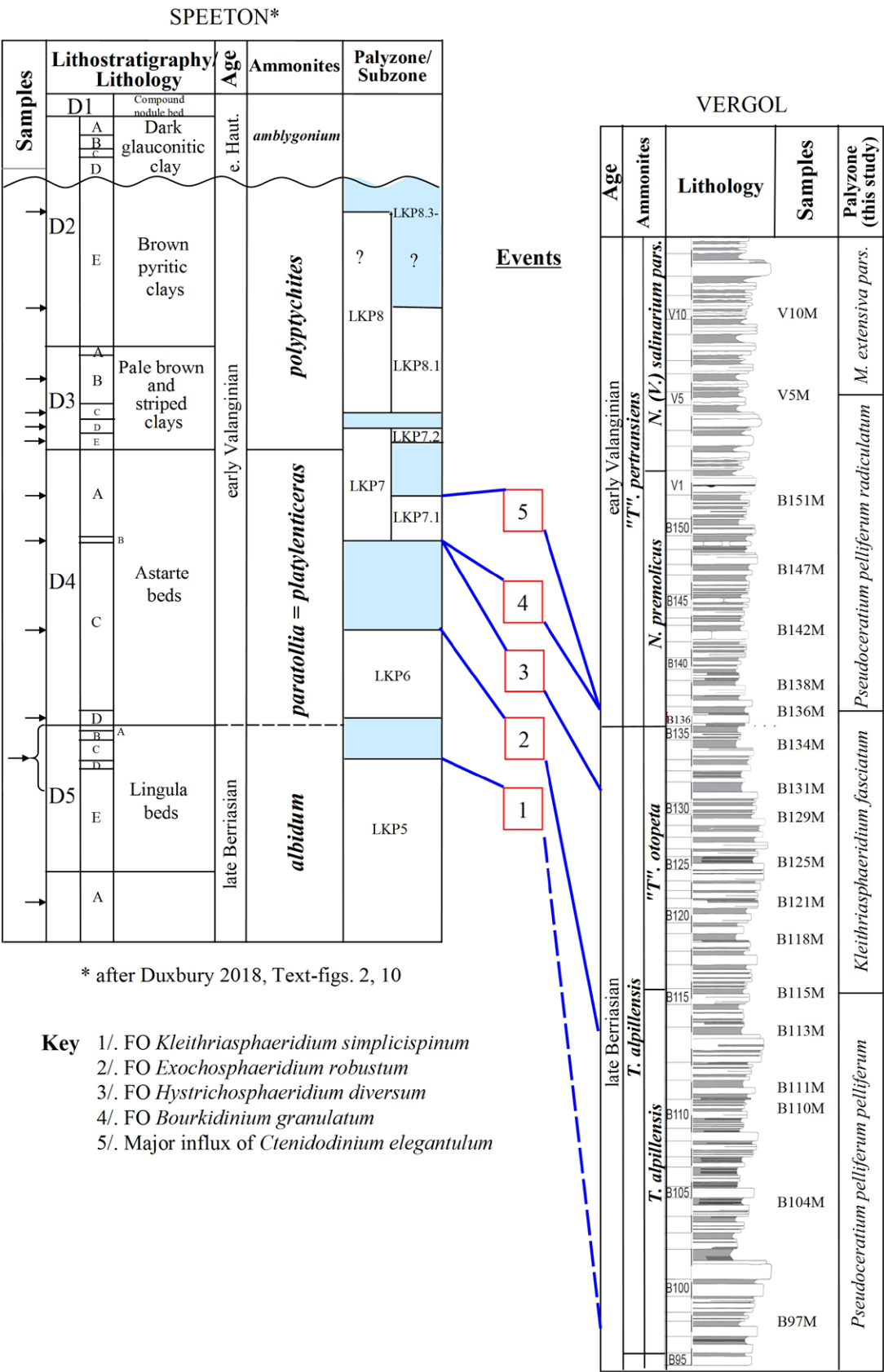
Kujau et al. (2013) compared climate-induced palynofloral (miospore) variations between the Mid Polish Trough and the Voconian Basin (including Vergol and La Charce), and they invoked a different nannofloral zonation to that of Dziadzio et al., in which, "The BC5 Zone ... spans the entire upper Valanginian and can be subdivided by the FO of *Eiffellithus striatus*". That is, they placed the FO of *E. striatus* within the late Valanginian; Kujau et al. did not refer to the alternative placement (also in mid-Poland) by Dziadzio et al.

Direct evidence from Vergol suggests that the Duxbury 2018 Alternative A should have been chosen. Gardin (pers. comm.) confirms that the FO of *E. striatus* occurs in La Charce Bed LCH 141, intra-late Valanginian, within the lower part of the *peregrius* Zone, *nicklesi* Sub-zone (text-fig. 7A). This further supports Rut-

ledge 1994, Bown et al. 1999 and Jeremiah 2001 and supports the *nicklesi* Sub-zone position for this event at Angles, in Duchamp-Alphonse et al. (2007).

This also suggests that his LKP8/LKP9 zonal boundary should have been placed in the upper part of the "Dichotomites" Zone by Duxbury (2018, fig. 10). Combined with the possibility of the Berriasian/Valanginian boundary at Speeton (and therefore in the Central North Sea dinocyst scheme - see Duxbury 2018, fig. 10) currently being too low (discussion above), then the number of Duxbury's palynofloral zones and sub-zones representing the "true" early Valanginian may need to be significantly reduced.

Unfortunately, *Hystrichosphaeridium arborispinum* is essentially absent from La Charce and no direct comparison may be made with the major Boreal influx discussed above. However, the FO of *Cribroperidinium sepimentum* is recorded consistently close to that influx in the Central North Sea and its FO was in Bed LCH141M at La Charce, immediately above the FO of *Eiffellithus striatus*. On this evidence, the FO of *C. sepimentum* may be a useful inter-regional marker at a mid late Valanginian level. It also suggests that the major influx of *H. arborispinum* placed (erroneously) at the base of the late Valanginian by Duxbury (2018) might also be of that age.



TEXT-FIGURE 14
Correlation of new data for the Berriasian/Valanginian boundary interval at Vergol and similar events at Speeton (from Duxbury 2018). If confirmed this may suggest that the boundary at Speeton is too low and may be raised higher in Unit D4.

The Valanginian/Hauterivian Boundary

The La Charce section has been accepted as the Global Boundary Stratotype Section and Point (GSSP) of the Hauterivian stage for reasons outlined in Mutterlose et al. 2021, and the base of the Hauterivian is placed at the base of Bed 189. This level coincides with the FO of the ammonite genus *Acanthodiscus*, marking the base of the *A. radiatus* Zone.

Although Mutterlose et al. (op. cit., p. 143) stated that at La Charce, "the nannofossil event that best approximates the Valanginian/Hauterivian boundary is the last occurrence (LO) of *Eiffellithus windii* (bed number 213)", they listed several other "valuable secondary markers" of "inter-regional correlation value", including the FO of the nannofossil *Stauroolithes mitcheneri* in Bed 190, much closer to the boundary.

The only dinocyst referred to by Mutterlose et al. (op. cit., p. 137) was *Muderongia staurota* Sarjeant 1966c which they argued was a possible alternative candidate for defining the Valanginian/Hauterivian boundary, being "an important event, allowing direct inter-regional correlation". Mutterlose et al. did not study La Charce dinocysts first-hand, however and, unfortunately, *M. staurota* was not recorded in the current study.

Dinocyst events around the Valanginian/Hauterivian boundary are illustrated here in text-fig. 7B. Although most have not been recorded previously in Tethyan settings they do offer some possible insights into the position of that boundary in the Boreal realm.

Ammonite zonal equivalence for the Tethyan and Boreal realms in this interval is shown in text-fig. 15. In Boreal settings, the *Endemoceras* Beds are taken as the base of the Hauterivian and the base of the *Endemoceras amblygonium* Zone is conventionally correlated with the base of the *A. radiatus* Zone (Thieuloy 1973; Rawson 1983, 1993; Mutterlose et al. 1996; Jacquin et al. 1998; Ogg et al. 2004). As noted by Reboulet (2015, p. 50), however, "The limited field data suggests that the genus *Acanthodiscus* appears in Germany around the middle of the *Amblygonium* zone and its stratigraphic extension continues into the *Noricum* zone (Kemper et al. 1981, p. 302), which could indicate that the base of the Hauterivian should be positioned within the *Amblygonium* zone". See McArthur et al. (2007, fig. 13). The alternatives are illustrated here in text-fig. 15.

The distribution of *Acanthodiscus* is apparently controlled by water depth and/or other proximal/distal factors; as noted by McArthur et al. (2007), in North Germany, it seems restricted to the *E. noricum* Zone (Thieuloy 1977; Quensel 1988) in sections of deep water palaeoenvironments but it is found in the upper part of the *E. amblygonium* Zone in sections with shallow palaeo-environments (Kemper et al., 1981; Mutterlose et al., 1996). It is noteworthy, however, that *Acanthodiscus* has not been recorded from the *E. amblygonium* Zone at Speeton, where Rawson (1971) recorded taxa he assigned to "*Acanthodiscus*" only between Speeton Beds C8A and C9C (upper *regale* Zone).

McArthur et al. (2007) proposed a revision of the Tethyan/Boreal ammonite correlation around the Valanginian/Hauterivian boundary, based on isotope data, and this is included in text-fig. 15 here. In their interpretation the *E. amblygonium* Zone crosses the boundary and all Boreal zones as high as the lower part of the *E. regale* Zone are included in the *Acanthodiscus radiatus* Zone. They stated that, "Sr isotopic data confirm that the *E. noricum* Zone is totally integrated in the *A. radiatus* Zone and that the base of the *E. regale*

Zone correlates to the middle part of the *A. radiatus* Zone".

Boreal dinocyst events were recorded in Duxbury (2018, fig. 10) and Duxbury (2023, fig. 4). Some of these were also recorded at La Charce and observed occurrences in the two provinces are illustrated in text-fig. 16. Conclusions drawn from text-fig. 16 may be summarised thus:

- *Oligosphaeridium distinctum* was not recorded at Speeton although it is present in the Central North Sea, suggesting that sediments above the Valanginian/Hauterivian hiatus at Speeton post-date its range. Occurrences of *O. distinctum* were recorded at La Charce as young as the late Valanginian, Bed LCH170M (lower *furcellata* Zone) and this appears to confirm a younger age for beds as old as Bed D2D at Speeton.
- an influx of very common *Nelchinopsis kostromiensis* was recorded at La Charce in sample LCH183M, close to the top of the Valanginian. At Speeton, this species is very common as old as Bed D2B (*E. amblygonium* Zone), suggesting a possible latest Valanginian age for much of that zone.
- several events were recorded in Speeton Bed C11B (base *regale* Zone) including the FO of *Oligosphaeridium junctum* and the LO's of *Aprobolocysta reticulata* and *Tenua* cf. *colliveri*. The last two events and an isolated occurrence of *O. junctum* were also observed in La Charce Bed LCH191M, close to the base of the Hauterivian.
- the FO's of *Hapsocysta peridictya* and *Apteodinium deflandrei* were in Bed LCH208M at La Charce. An influx of the first was observed as old as Bed C11B at Speeton, but the FO of *A. deflandrei* was higher, in Bed C9D. These events are in the lower *regale* Zone at Speeton and the mid *radiatus* Zone at La Charce.
- there was no clear correlation between anything above Bed C9D at Speeton and the La Charce section analysed here, suggesting that the La Charce section equivalent to the upper *regale* Zone and younger at Speeton lies above La Charce Bed LCH219.

From the above observations, palynofloral evidence gained from La Charce and from previous studies of the Speeton section appears to support the isotope-based correlations of McArthur et al. 2007 (summarised in text-fig. 15 column C here). This might suggest that the whole of the *amblygonium* Zone at Speeton could be of a youngest Valanginian age, which might explain the absence of *Acanthodiscus* (see comments above).

Further, the lower part of the *regale* Zone at Speeton appears to equate to the lower to mid part of the *radiatus* Zone at La Charce, again supporting McArthur et al., who stated (p. 424), "the base of the *E. regale* Zone correlates to the middle part of the *A. radiatus* Zone. This isotopic correlation supports the proposal of Thieuloy (1973), who correlated the base of the *E. regale* Zone with the upper part of the *A. radiatus* Zone".

STRATIGRAPHIC COMMENTS AND CONCLUSIONS

Upper Berriasian to lower Hauterivian sediments at Vergol/La Charce yield rich and diverse palynomorph assemblages, largely dinocysts, including several taxa previously undescribed and others recognised in Boreal settings but not previously reported from Tethyan material. Comparisons between Vergol/La Charce and Speeton/Central North Sea assemblages allow possible chronostratigraphic re-evaluation of the latter although some inter-regional similarities in species occurrences may be coincidental in view of the large number of taxa encountered; this needs to be tested further.

Significant fluctuations in dinocyst species diversity were observed (text-fig. 8), with a notable increase across the Berriasian/Valanginian boundary from 28 marine species in Bed B97M to 68 species in Bed V31M, towards the top of the *pertransiens* Zone. A steady decline in diversity then occurred up to Bed V87 (42 species) before a period of fluctuating but generally high diversity across the early/late Valanginian boundary. Except for minor peaks in samples LCH136M, LCH154M and LCH173M, species numbers throughout the *peregrinus* and *furcellata* zones were similar, averaging 56 marine species per sample. A significant drop in diversity was noted in Bed LCH187M, the youngest Valanginian sample analysed, a reduction which continued into the early Hauterivian. The average species count for the 9 samples analysed from the *radiatus* Zone was only 36 species per sample.

Many species are long-ranging, occurring throughout, but others have their first occurrences (FO's) and/or last occurrences (LO's) within the studied interval. As well as FO's and LO's, generation of quantitative data has allowed the recognition of acmes and top and/or base common occurrences. These have been summarised in text-figs. 6 to 9 to provide a palynostratigraphic framework throughout the entire Valanginian and across its boundaries. In addition, quantitative data for several dinocyst taxa have been plotted against the combined Vergol/La Charce stratigraphy in text-figs. 12 and 13 to demonstrate how the numbers of some of the more common taxa fluctuate through the studied interval.

Several zonation schemes, sometimes conflicting, have been proposed previously for southeast France and Spain, and these have allowed only broad application to the current study. A new dinocyst zonation scheme has been proposed here, consisting of twelve zones and two sub-zones, between the upper Berriasian and lower Hauterivian, eight of which define the Valanginian. These are based entirely on observations in the Vergol/La Charce area and remain to be tested regionally.

The effects of various palaeoenvironmental changes on dinocyst assemblages are only partially understood and, although assemblage fluctuations observed in the current study were often very marked, no detailed interpretation has been possible. Possible causes of assemblage change due to various palaeoenvironmental factors were discussed by Pross and Brinkhuis (2005), who stated, "it has been realized that organic-walled dinoflagellate cysts are sensitive to even the slightest of changes in the physio-chemical parameters of surface watermasses". The same could probably be applied to the Vocontian Basin once species' palaeoenvironmental preferences are better understood.

Miospore data have been interpreted in terms of Abbink's (1998) Sporomorph EcoGroup (SEG) sub-divisions. Abbink (op. cit.) grouped miospore taxa in terms of their ecological significance into Upland, Tidal, River, Pioneer, Lowland and Coastal SEGs, although in the present study the Upland, Lowland and Coastal groupings were overwhelmingly predominant. Variations in the relative percentages of these SEGs reflect the effects of palaeoenvironmental changes on land. Individual SEGs have been plotted in text-figs. 8-11, and together with percentages of marine taxa and marine taxa diversity in text-figs. 12 and 13.

The oldest section analysed in the current study was from the late Berriasian, *alpillensis* Zone (text-figs. 3, 6, 12, 13, 16, 18), with the oldest two samples, B97M and B104M, from the *alpillensis* Sub-zone, dominated by very abundant *Systematophora* sp. A

sensu Monteil, similar to the "massive and sudden appearance" of this species reported from the late Berriasian, *boissieri* Zone by Monteil (1993) at Angles and Berrias.

Sporomorph EcoGroup (SEG) plots for the *alpillensis* Zone, particularly the Coastal/Lowland curve, may suggest a stepped deepening trend, culminating in a peak transgression at sample B129M, close to the top of the Berriasian, *otopeta* Sub-zone (text-figs. 8, 9, 12). This is followed by a stepped reduction in the Coastal SEG and an associated increase in Lowland taxa across the Berriasian/Valanginian boundary (text-figs. 8, 9, 12), suggesting a lowstand event towards the top of the *pertransiens* Zone, *premollicus* Sub-zone, peaking at sample B151M.

A subsequent rise in the Coastal/Upland curve results in raised Coastal percentages throughout much of the *pertransiens* Zone, *salinarium* Sub-zone. Despite apparently significant sea level changes within the *pertransiens* Zone, the marine diversity curve rises fairly steadily, peaking at 58 species in sample V31M. Common to abundant occurrences of several dinocyst taxa, including *Dapsilidinium warrenii*, *Diacanthum hollisteri*, *Hystriochodinium pulchrum*, *Kleithriasphaeridium fasciatum* and *Prolioxosphaeridium prolatum* appear to be typical of the *pertransiens* Zone (text-fig. 12).

A significant change in dinocyst assemblages was observed as old as Bed V5M (*pertransiens* Zone, base *salinarium* Sub-zone), including an up-section increase in the ceratioid taxa *Phoberocysta neocomica* and *Pseudoceratium pelliferum*, although the last is common as old as Bed B147M (*pertransiens* Zone, *premollicus* Sub-zone). A further ceratioid, *Phoberocysta latissima* was essentially restricted to the early Valanginian, being prominent only between Beds V10M and V36M (*pertransiens* Zone, *salinarium* Sub-zone), peaking at the higher level where it was abundant. The last species is therefore particularly characteristic of the *salinarium* Sub-zone.

Wilpshaar and Leereveld (1994) noted that high abundances of their *Muderongia* Group (including *Phoberocysta*) have been reported in sediments representing variable salinity conditions (e.g., Lister and Batten 1988). It may be the case therefore that the *pertransiens* Zone, *salinarium* Sub-zone was deposited in conditions of relatively reduced surface water salinity. The *pertransiens/neocomiensiformis* transition (Beds V19M to V54M) yielded common to abundant *Foucheria modesta* which peaked in Bed V54M; above Bed V54M its numbers dropped markedly. The *neocomiensiformis* Zone and the basal part of the *inostranzewi* Zone were characterised by a steady reduction in marine diversity although accompanied by a rise in numbers of the genus *Muderongia* (text-figs. 10, 12), peaking at sample H87, Barrande layer B1. Miospores were abundant throughout but with marked reductions in samples V82M, V84M and V87. Significant changes in the Coastal to Lowland miospore ratio were observed, with a Coastal low at sample V72M and a peak at sample V84M, possibly suggesting a regressive/transgressive cycle through much of the *neocomiensiformis* Zone.

A top *neocomiensiformis* Zone Coastal peak coincides with a "blip" in the $\delta^{13}\text{C}$ curve and is immediately below the *Muderongia* peak in Barrande layer B1, similar to other Coastal and *Muderongia* peaks within the late Valanginian *verrucosum* and *peregrinus* Zones, which occur together with $\delta^{13}\text{C}$ peaks during the main Weissert Event (text-fig. 10). Although the coincident Coastal and *Muderongia* peaks and $\delta^{13}\text{C}$ "blip" at the

		A		B	C
AGE		ZONES	SUBZONES	ZONES	ZONES
HAUTERIVIAN	early	<i>L. nodosoplicatum</i>	<i>O. (O.) variegatus</i> Horizon	<i>S. inversum</i>	<i>S. inversum</i>
		<i>C. loryi</i>	<i>O. (J.) jeannoti</i>	<i>E. regale</i>	<i>E. regale</i>
			<i>C. loryi</i>		
VALANGINIAN	late	<i>C. furcillata</i>	<i>T. callidiscus</i>	<i>E. noricum</i>	<i>E. noricum</i>
			<i>C. furcillata</i>		
		<i>N. peregrinus</i>	<i>O. (O.) nicklesi</i>	<i>O. densicostatus</i>	<i>E. paucinodum</i>
				<i>S. tuberculata</i>	<i>S. tuberculata</i>
				<i>D. bidichotomoides</i>	<i>ivanovi</i> through <i>Polytomus</i> (5 zones)
		<i>D. tryptichoides</i>			
		<i>D. crassus</i>			
		<i>S. verrucosum</i>	<i>K. pronecostatum</i>	<i>P. polytomus</i>	
			<i>S. verrucosum</i>		

TEXT-FIGURE 15

Ammonite zone/sub-zone correlations between A/. the standard Tethyan zonation, B/. the northwestern European scheme according to Reboulet et al. 2014 and C/. the same scheme according to McArthur et al. 2007.

top of the *neocomiensiformis* Zone occur below the main Weissert Event (i.e., below CIE Segment II of Kujau et al. 2012), the close similarities between them and younger, similar co-occurrences might suggest causal linkage.

Occurrences of abundant miospores resumed in Bed V88, Barande layer B4 and the Coastal/Lowland curve then suggests a regressive phase throughout the *inostranzewi* Zone, although this is associated with an increase in marine diversity (text-figs. 8, 12).

Initiation of the main phase of the Weissert Event occurred towards the base of the late Valanginian, *verrucosum* Zone and peak $\delta^{13}\text{C}$ values were accompanied by a second major peak of *Muderongia* and a peak in the Coastal/Upland curve (text-fig. 10). A similar association of events was recorded within the *peregrinus* Zone. As noted above, high abundances of Wilpshaar and Leereveld's (1994) *Muderongia* Group appear to represent variable salinity conditions and it may be the case therefore that the three *Muderongia* influxes recorded here (peaking in Beds V87, V105 and V127) suggest reduced surface water salinity. As these coincide with relative peaks in Coastal miospores (implying high-stands *sensu* Abbink), some mechanism for reduced surface water salinity (or access to such a setting) is necessary, perhaps including increased runoff associated with the monsoonal conditions invoked by Kujau et al. (2013).

The significant differences between the Bed V87 and V88 (Barande layer B4) palynofloras mirror the macrofaunal findings of Reboulet et al. (2003), although other authors reached different conclusions - see "The Barande layers", above.

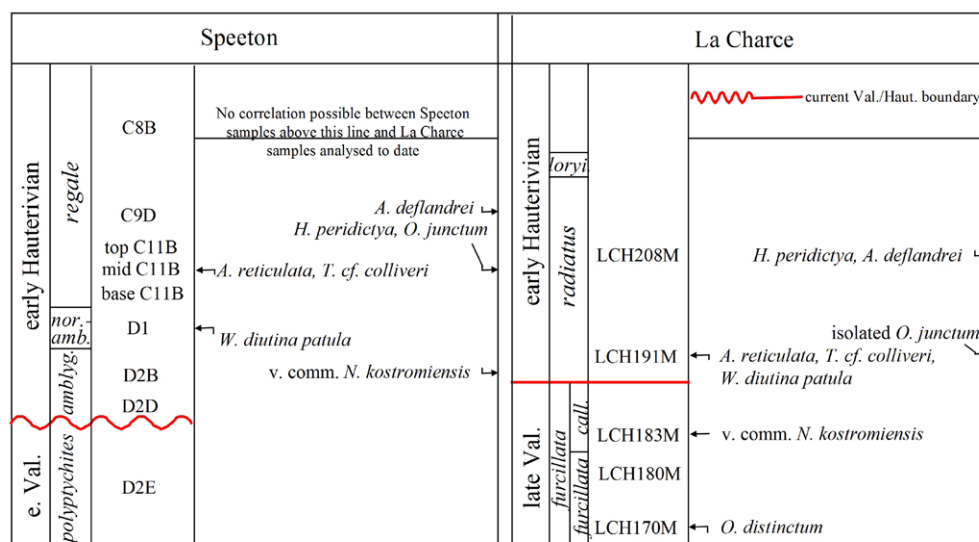
The base of the *peregrinus* Zone is marked by a major reduction in coastal and lowland miospores and relatively low numbers were maintained throughout that zone. In contrast, a marked increase

in coastal and lowland miospores was recorded in the *furcillata* Zone, tapering down to relatively low levels again into the base of the *radiatus* Zone. This is the "third spore maximum" of Kujau et al. (2013), recorded at La Charce within their Assemblage VB5, although in the current study it extends down to the base of the *furcillata* Zone, not the mid-point as in their fig. 7.

On miospore evidence, the lower part of the studied La Charce section appears to represent a regressive phase (up to the top of the *peregrinus* Zone), mirroring the declining $\delta^{13}\text{C}$ curve (text-fig. 11). However, Janssen (pers. comm.) points out that the nominate species for the *peregrinus* Zone also occurs abundantly in Varlheide (Germany), proving a major exchange between the Lower Saxony Basin and the Tethys; this diminished in the latest Valanginian.

Throughout the *furcillata* Zone and the lower part of the *radiatus* Zone (up to sample LCH194M) the coastal/lowland curve is steady, then it becomes more erratic. Kujau et al.'s "third spore maximum" falls entirely within this "steady" interval; it perhaps represents a particularly humid period within a period of peak regression. An up-section increase in *Phoberocysta neocomica* was also recorded within the *furcillata* Zone, peaking in sample LCH180. As discussed above, this genus (part of the "*Muderongia* group") may indicate reduced salinity, although in this case not associated with highstand deposits. Together with Kujau et al.'s interpretation of the increase in fern spores, this might also provide some evidence for increased runoff, whether monsoon-generated or otherwise.

The youngest prominent occurrences of *Circulodinium hirtellum* (peak in sample LCH128) and *Hystrichodinium voigtii* were within the *peregrinus* Zone and a marked up-section decrease in *Tan-yosphaeridium* cf. *variecalamum* was associated with an increase



TEXT-FIGURE 16

Correlation of new data for the Valanginian/Hauterivian boundary interval at La Charce and similar events at Speeton (from Duxbury 2023). If confirmed this may suggest that the boundary at Speeton is too low and that the *amblygonium* Zone at Speeton may be of a latest Valanginian (*furcillata* Zone) age.

in *Cribroperidinium* spp. within the *furcellata* Zone.

A reduction in miospores above Kujau et al.'s (2013) "third spore maximum" was associated with a major increase in the percentage of marine specimens (peaking at 82% in sample LCH194), although associated with a fall in marine diversity to a minimum of 27 taxa at the same level. Dominant dinocysts in the lower part of the *radiatus* Zone were *Cribroperidinium* spp., *Tenua* spp., and *Chlamydomphorella* spp. (peaking in samples LCH189, LCH194 and LCH198 respectively).

In their discussion of La Charce as the GSSP for the base Hauterivian, Mutterlose et al. (2021) referred only to one dinocyst, *Muderongia staurota* Sarjeant 1966c, which they argued was a possible alternative candidate for defining the Valanginian/Hauterivian boundary, and they quoted its FO as, "the upper part of the A. radiatus AZ". Mutterlose et al. did not study La Charce dinocysts first-hand, however. *Muderongia staurota* was not recorded in the present study but two dinocyst events, the FO's of *Bourkidinium elegans* and *Hapsocysta peridictya*, were recorded in Beds LCH191M and LCH208M, near-base and mid *radiatus* Zone respectively, and these are much closer to Bed 189, the base of the Hauterivian.

The top of the *radiatus* Zone, Bed LCH216M, was characterised at La Charce by very abundant *Dissiliodinium curiosum* and consistently common occurrences of this species were recorded as old as sample LCH203M. A further, isolated very common occurrence was noted in sample LCH176M (mid *furcillata* Zone). This genus is largely restricted to the Jurassic and most published comments relating to it refer to sections much older than La Charce. There is little palaeoenvironmental information for this genus although Feist-Burkhardt and Monteil (2001, p. 34) stated, "most of them occur in significant numbers and are useful for biostratigraphical and palaeoenvironmental interpretations", but they did not provide further detail.

The present author has recorded major influxes of *Dissiliodinium* in the Trigonia Clavellata Beds of Dorset and from the

cored Coal Marker Shale of Tartan Field, U.K. Central North Sea, both towards the base of the upper Oxfordian. The Trigonina Clavellata Beds were described by Brookfield (1978, p. 8) as, "typical tidal flat, lagoonal and shallow shelf carbonates" and the Coal Marker Shale is a laminated (without bioturbation) lagoonal shale indicative of brackish conditions. Assuming similar palaeoenvironmental preference, the more common *Dis-siliodinium curiosum* occurrences across the Valanginian/Hauterivian boundary at La Chazze may suggest access to similar settings, particularly for its very abundant occurrence at the top of the *radiatus* Zone, Bed LCH216M.

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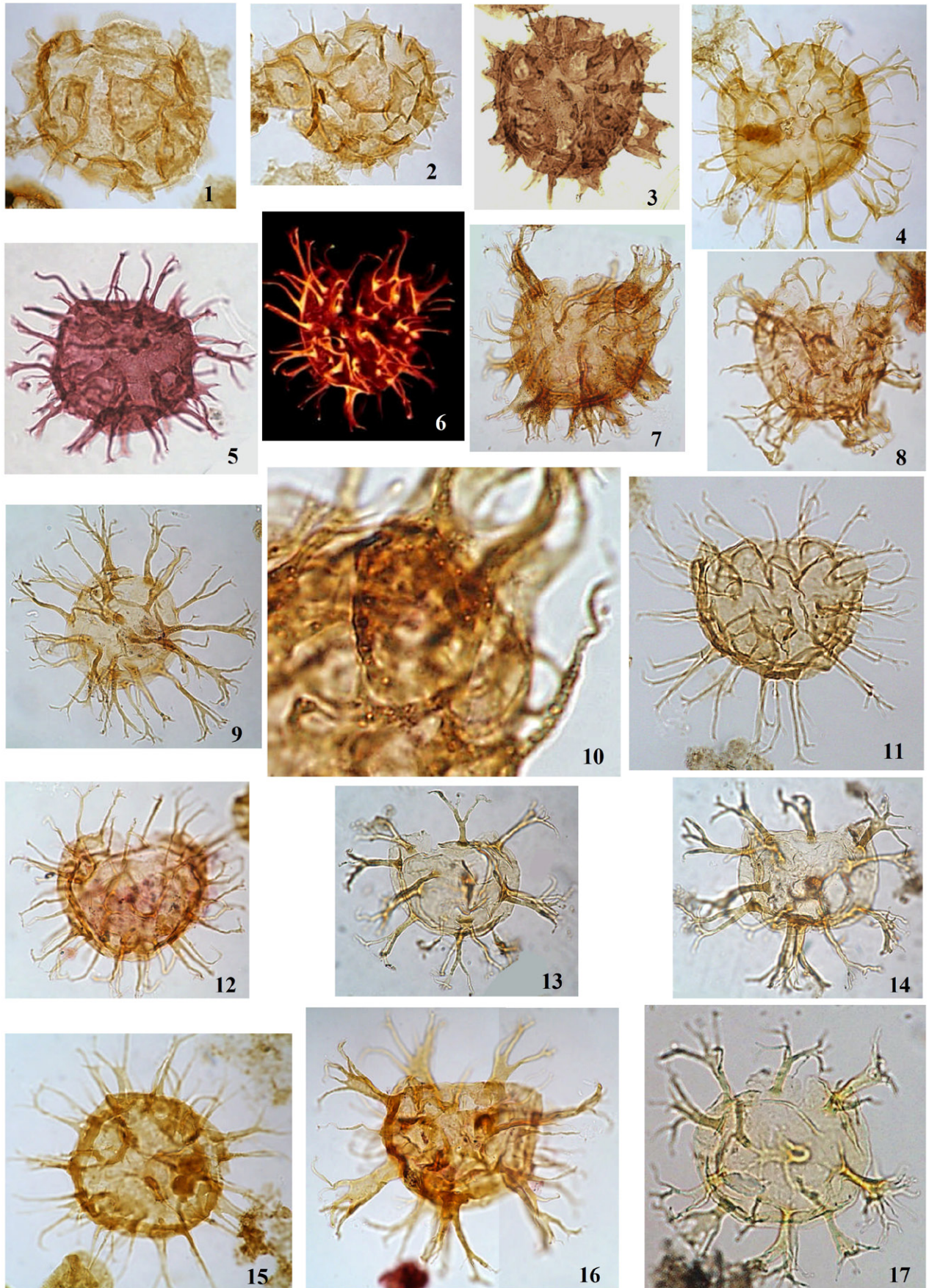
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Specimen magnification is indicated per plate. Slide details, England Finder (E.F.) references and Muséum d'histoire naturelle, Geneva catalogue numbers are given for all illustrated specimens in Appendix 2.

PLATE 1

All specimens are from Vergol except Figure 17, which is from La Charce. All photographs $\times 475$ except for Figures 5 and 6, which are $\times 700$ and Figure 10 which is $\times 1900$.

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| <p>1-3, 7, 10 <i>Amphorulacysta metaelliptica</i>. Specimens showing the wide range of process height. Figures 1-3 lower Valanginian, Bed V88 and Figures 7, 10 upper Berriasian, Bed B121M. Figure 10 enlarged to highlight an annular basal ridge.</p> <p>4, 8 <i>Systematophora? daveyi</i>. Figure 4 lower Valanginian, Bed 4V88 and Figure 8 upper Berriasian, Bed B121M.</p> <p>5, 6 <i>Systematophora complicata</i>. Figure 5 upper Berriasian, Bed B131M. Figure 6 lower Aptian of the Compton Bay Section, Isle of Wight, first illustrated as pl. 7, fig. 1 in Duxbury 1983 (photograph from the "Duxbury Collection" at the Natural History Museum, London). Both specimens show clear annular basal ridges and Fig. 6 shows linked cingular spines.</p> | <p>9, 13, 14 <i>Cymososphaeridium validum</i>. Specimens showing a range of process height and robustness, all upper Valanginian. Fig. 9 Bed V101M and figures 13, 14 Bed V120M.</p> <p>11, 12, 15 <i>Systematophora</i> cf. <i>areolata</i> sensu Davey 1982 showing variation from arcuate to annular basal ridges. Figures 11 and 15 lower Valanginian, Bed V88 and Figure 12 upper Valanginian, Bed V101M.</p> <p>16 <i>Palaecysta palmula</i> from the lower Valanginian, Bed V91M.</p> <p>17 <i>Cymososphaeridium validum</i> "regulare", lower Hauterivian, La Charce Bed LCH203M. A form similar to Figs. 13 and 14, but with no deeply furcate processes.</p> |
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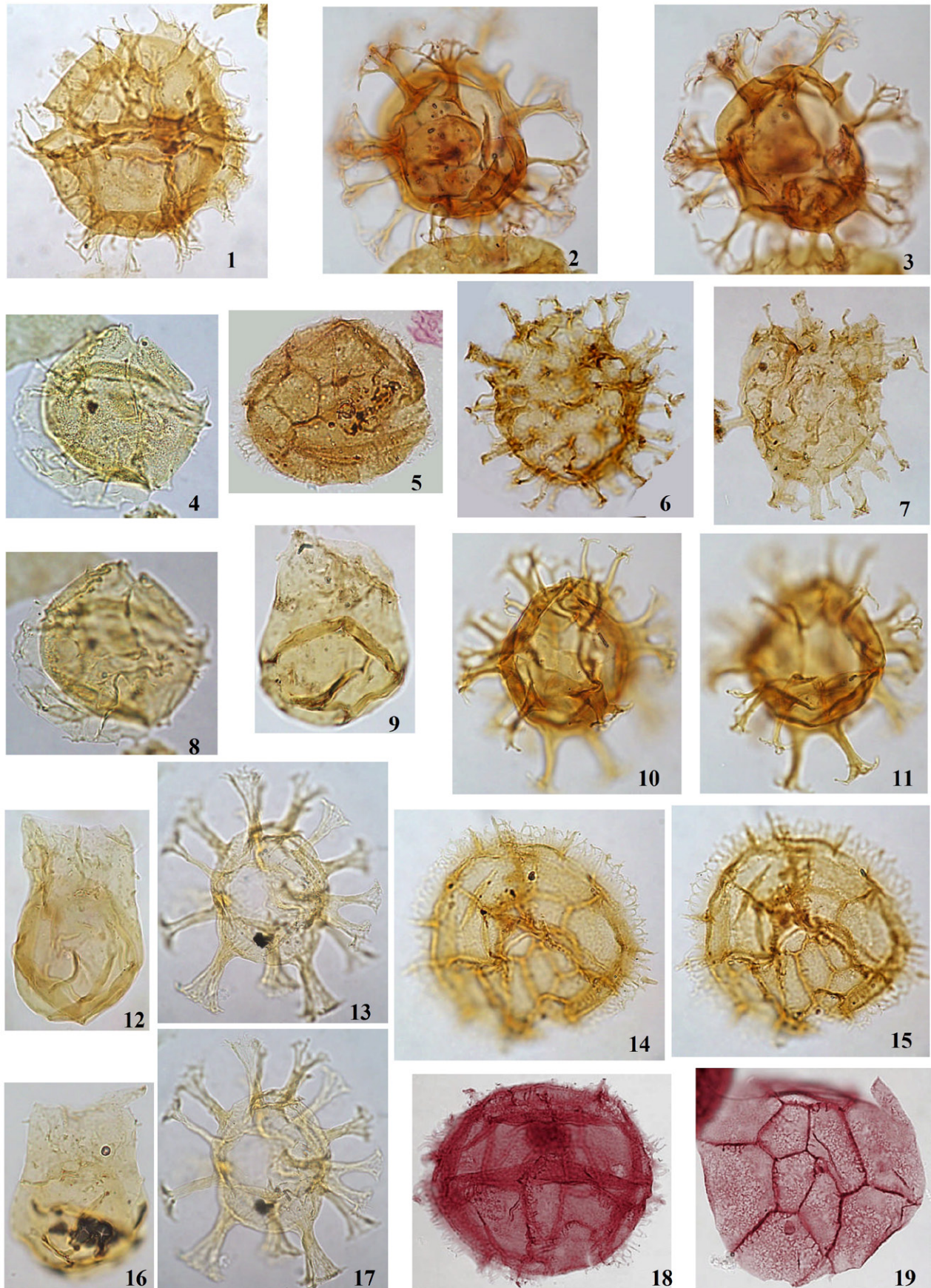


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PLATE 2

All specimens are from Vergol except Figures 4, 8, 13, 17 from La Charce. All photographs $\times 700$ except for Figs. 13 and 17 which are $\times 475$.

- 1 *Spiniferites twistringiensis*, right lateral view with operculum detached, lower Valanginian, Bed V88.
- 2, 3 *Nematosphaeropsis scala*, focused on the detached precingular (3") operculum and distal trabecular linkage respectively, upper Valanginian, Bed V123M.
- 4, 8 *Spiniferites modestus*. A specimen with a damaged apex, but showing well the characteristic dense, finely granular ornament and ventral pericoel, upper Valanginian, Bed LCH183M.
- 5 *Dichadogonyaulax* cf. *bensonii*, upper Valanginian, Bed V132.
- 6, 7 *Egmontodinium toryna* from the lower Valanginian, Beds V26M and V5M respectively.
- 9, 12, 16 *Wallodinium cylindricum* subsp. *ornatum* n. subsp. Figures 9 and 16 upper Valanginian, Beds V107M and V111M respectively. Figure 12 (holotype) from the lower Valanginian, Bed V88. The characteristic ornament is clear on all specimens, and the sloping archeopyle margin is well-illustrated in Figures 9 and 12.
- 10, 11 *Spiniferites primaevus*, upper Valanginian, Bed V132M. Focus of ventral and dorsal surfaces.
- 13, 17 *Kleithriasphaeridium porosispinum*, upper Valanginian, Bed LCH141M.
- 14, 15, 18 *Dichadogonyaulax bensonii* from the lower Valanginian.
- 19 Figures 14 and 15 from Bed V19M and Figures 18 and 19 from Bed V88. Figure 19 is a detached operculum.



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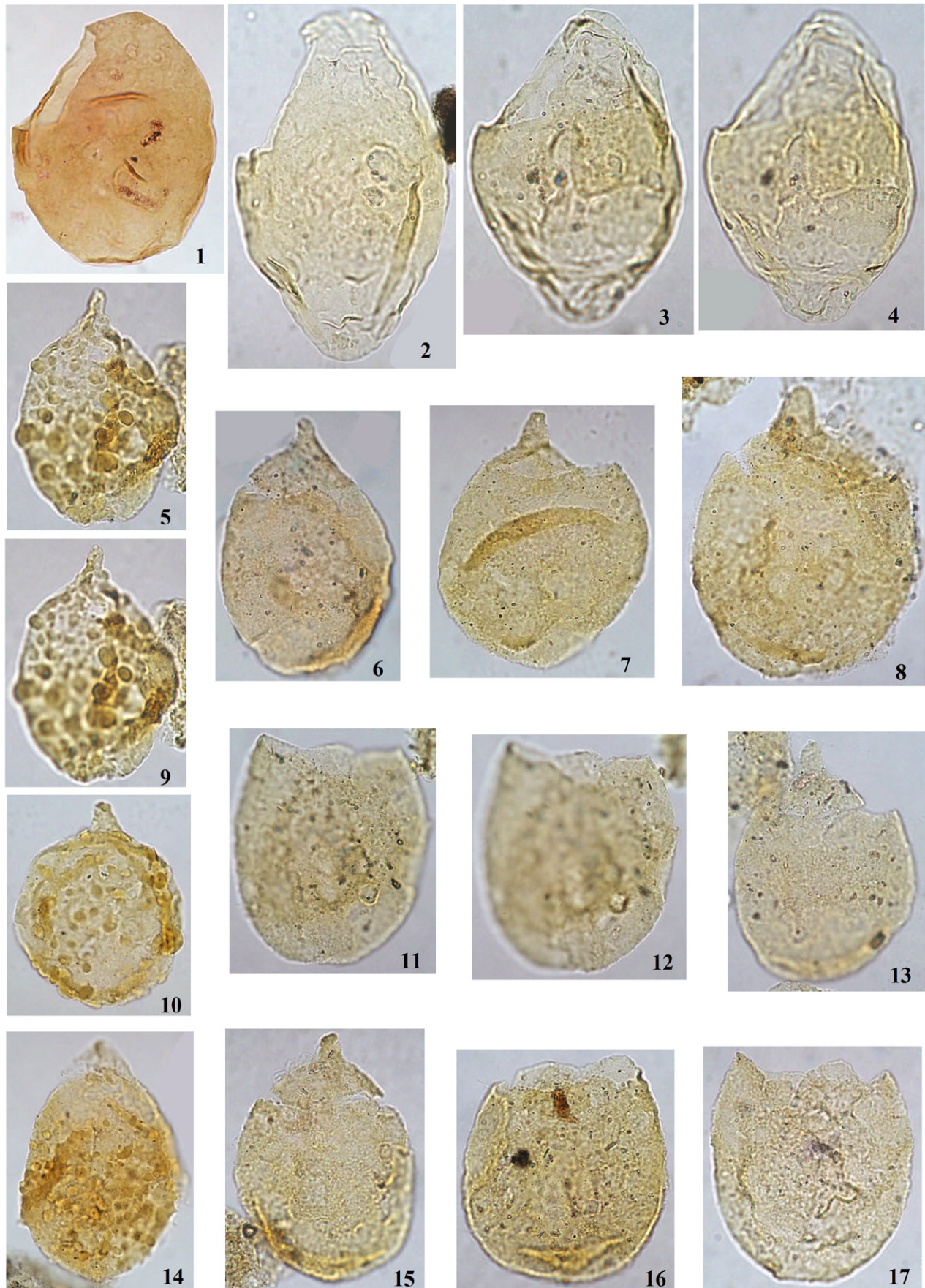
PLATE 3

All specimens are from La Charce except Figure 1 which is from Vergol. All photographs $\times 700$.

1-4 *Chytroesphaeridia conspicua* n. sp., all right lateral views. Fig. 1 (paratype) from the base Valanginian, Bed B136M, Figs. 2-4 from the upper Valanginian, Bed LCH164M - Fig. 2 is the holotype.

5, 9, 10, *Gochteodinia? variabilis* n. sp., all from the upper Valanginian, Bed LCH164M; Figs. 5 and 9 the holotype.

6-8, 11-13, *Protobatioladinium modestum* n. sp. from the upper Valanginian. Fig. 6 from Bed LCH 187M, Figs. 7, 11, 12, 13 from Bed LCH180M, Figs. 8 and 17 (holotype and paratype respectively) and 15 from Bed LCH164. Fig. 16 from Bed LCH173.

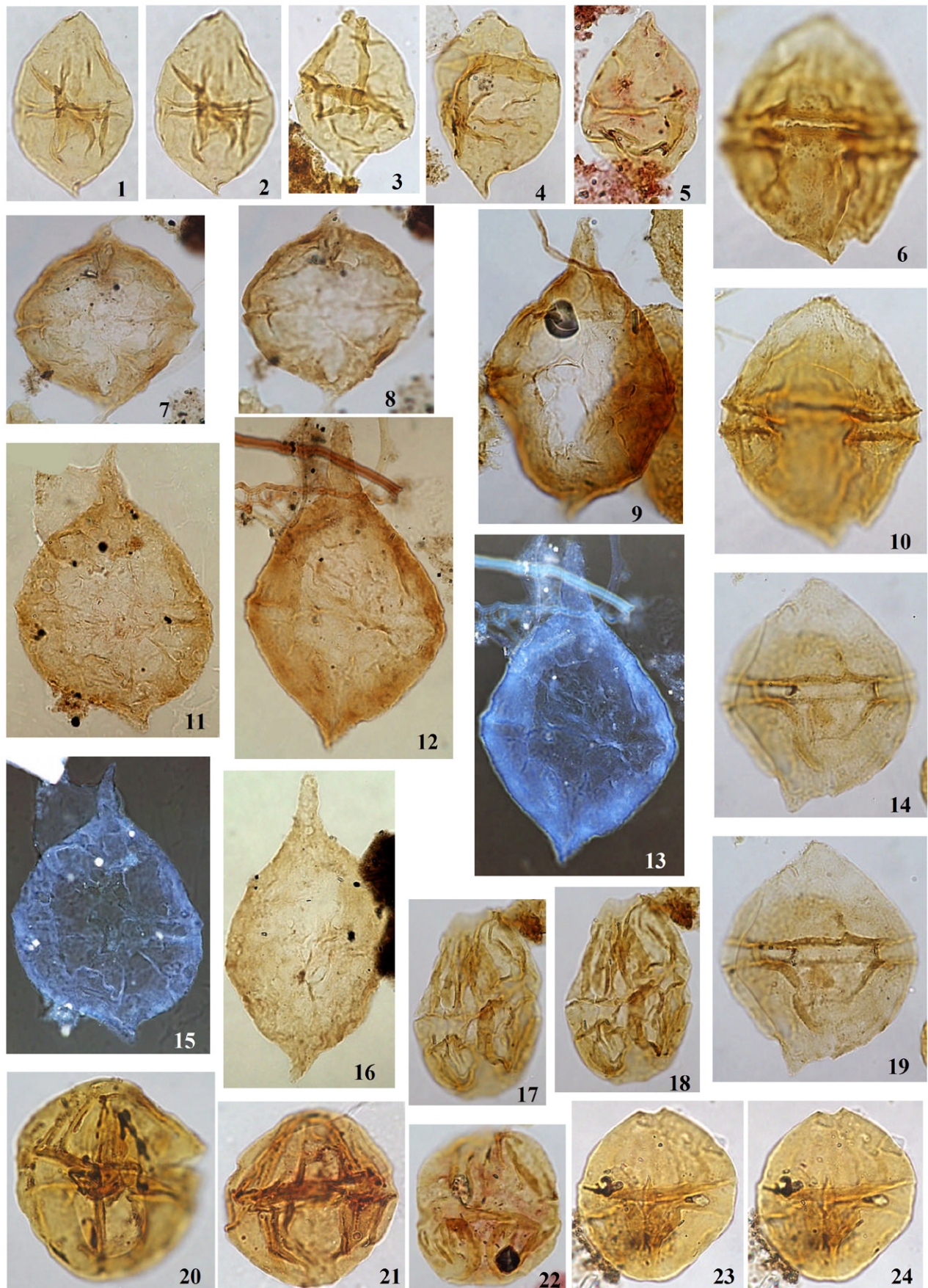


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PLATE 4

All specimens are from Vergol. All photographs ×700.

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| <p>1-5 <i>Dinogymnium aerlicum</i> subsp. <i>curvispinum</i> n. subsp. Figures 1, 2 (holotype) from Bed V124M, Figs. 3 and 4 from Bed V123M, all upper Valanginian. Figure 5 from Bed V91M, lower Valanginian.</p> <p>6, 10, <i>Subtilisphaera terrula</i>. Two specimens from the upper Valanginian, Bed V132M.</p> <p>7-9, 11- <i>Bicornus obscurus</i> n. gen. n. sp. All specimens from Bed 13, 15, B138M except for 11 and 15 (holotype) from Bed B151M, 16 all lower Valanginian. Paratype Figs. 12 and 13. Figures 13 and 15 are negative images of the paratype and holotype</p> | <p>respectively to better show the very faint tabulation and dorsal hole.</p> <p>17, 18, 22 <i>Dinogymnium circulos</i> n. sp. from the lower Valanginian. Figures 17, 18 from Bed V97M and Fig. 22 (holotype) from Bed V91M.</p> <p>20, 21, 23, <i>Dinogymnium rotundum</i> n. sp. Figure 20 from the upper Valanginian, Bed V124M. Figure 21 (holotype) and Figs. 23 and 24 from the lower Valanginian, Beds V94M and V48M respectively.</p> |
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PLATE 5

All specimens are from Vergol. All photographs ×700.

- 1–4, 6, 7 *Dingodinium? globosum* n. sp. Figures 1, 4, 6, and 7 from Bed V91M, lower Valanginian and Figs. 2 and 3 from Bed V107M, upper Valanginian. Figures 1, 6 holotype and Figure 7 paratype.
- 5 *Nelchinopsis kostromiensis* from the upper Valanginian, Bed V132M.
- 8, 9 *Dinogymnium aerlicum* subsp. *aerlicum*. Figure 8 from Bed B136M and Figure 9 from Bed V19M, both lower Valanginian.
- 10, 14, 22 *Dingodinium cerviculum*. Two specimens from Bed V132M, upper Valanginian.
- 11, 12, Two specimens of *Dingodinium jurassicum*, the type species, from the middle Oxfordian (Osmington Oolite Series) of Dorset, England, showing the broad, ovoidal endocyst, not laterally flattened (see text for discussion).
- 15, 16
- Figures 12 and 16 are negative images to better show the surface folding and "hinged" apical archeopyle.
- 13, 17 *Chlamydophorella caminus* n. sp. from the upper Valanginian. Figure 13 (holotype) from Bed V132M and Figure 17 from Bed V107M.
- 18, 19 *Stephanelytron cretaceum* from Bed V132M, upper Valanginian.
- 20, 21, 25 *Chlamydophorella* sp. A small morphotype typical of this genus throughout the studied sections. Figure 20 from the upper Valanginian, Bed V132M and Figures 21, 25 from the lower Valanginian, Bed V88.
- 23, 24, 26 *Chlamydophorella ambigua* subsp. *ambigua*. Figure 23 from Bed V94M and Figures 24, 26 from Bed V88, all lower Valanginian.

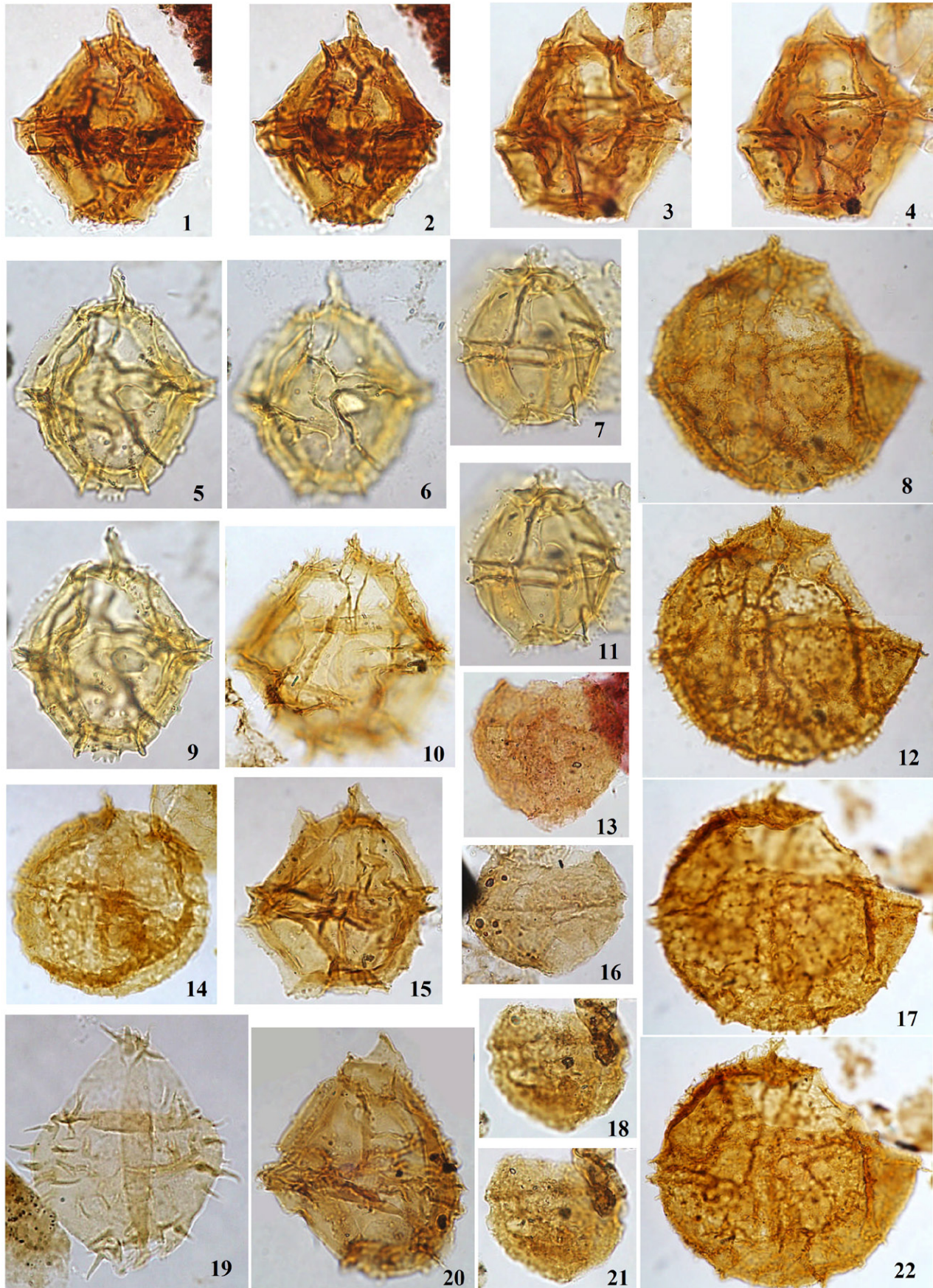


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PLATE 6

All specimens are from Vergol except for Figures 5, 6, 7, 9 and 11, which are from La Charce. Photographs $\times 700$ except for Figures 8, 12, 14, 17 and 22, which are $\times 475$ and Figure 20, which is $\times 950$.

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| 1–4, 5, <i>Wrevittia diutina</i> subsp. <i>patula</i> . Figures 1–4 from Bed 6, 9 V124M and Figures 5, 6, 9 from Bed LCH173M, all upper Valanginian. | 13, 16, 18, <i>Fibradinium variculum</i> . Figures 13, 18, 21 from the upper 21 Valanginian, Bed V124M and Figure 16 from the lower Valanginian, Bed V94M. |
| 7, 11 <i>Wrevittia?</i> <i>perforobtus</i> from the upper Valanginian, Bed LCH149M. | 14 <i>Cribroperidinium colum</i> from the lower Valanginian Bed V88. |
| 8, 12, 17, <i>Diacanthum hollisteri</i> . Two specimens from the lower Valanginian. Figures 8, 12 from Bed V97M and Figures 17, 22 from Bed V42M. | 15 <i>Wrevittia cretacea</i> from Bed V19M, lower Valanginian. |
| 10 <i>Stanfordella exsanguia</i> from Bed V112M, upper Valanginian. | 19 <i>Rhombodella</i> cf. <i>vesca</i> from the lower Valanginian, Bed V88. |
| | 20 <i>Wrevittia diutina</i> subsp. <i>diutina</i> from the upper Berriasian, Bed B125M |

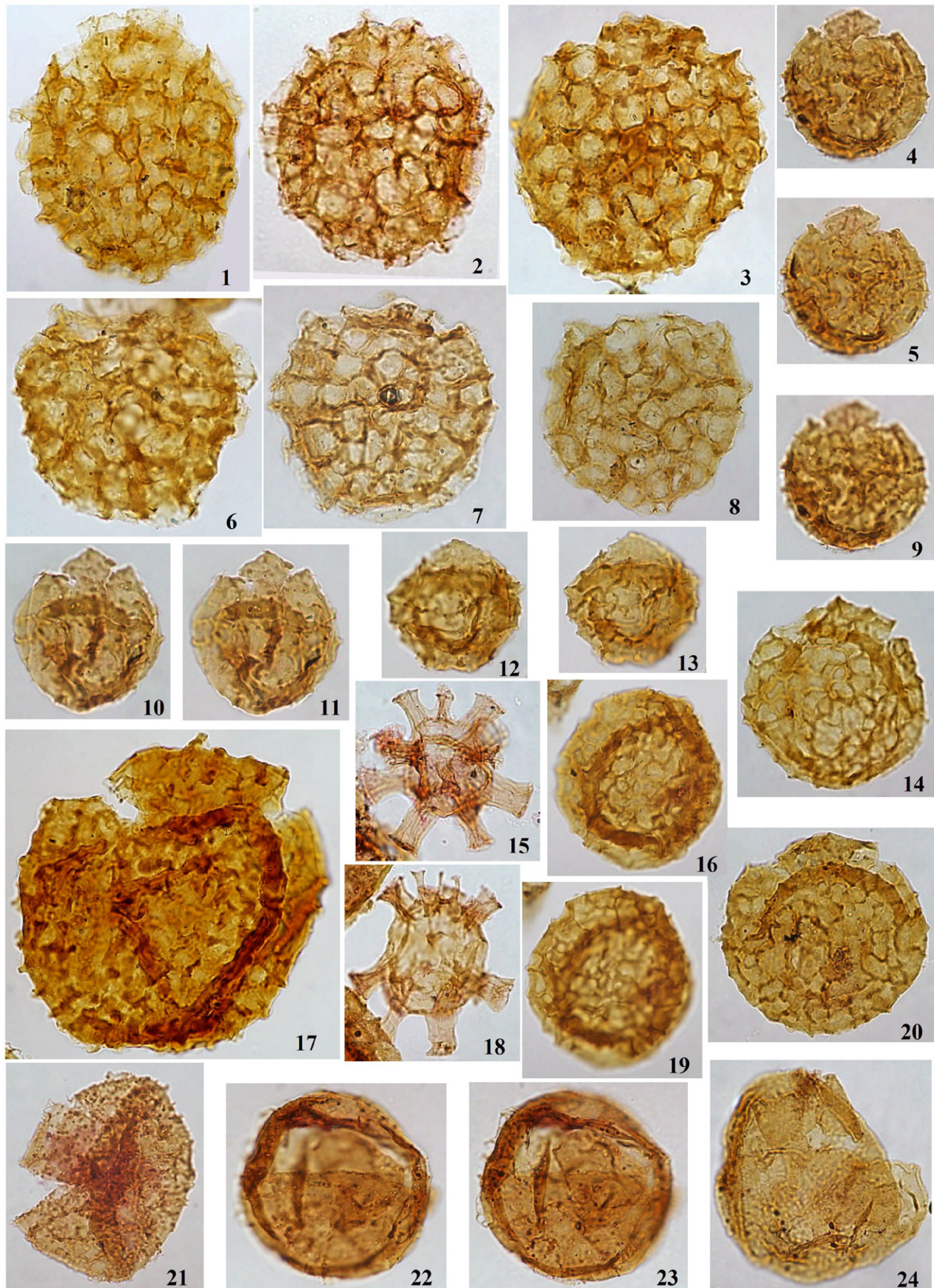


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PLATE 7

All specimens are from Vergol. Photographs $\times 700$.

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| <p>1-3, 6-8 <i>Valensiella</i> cf. <i>ovula</i>. Figures 1, 6 from Bed V91M and Figure 8 from Bed V94M, all lower Valanginian. Figures 2, 3 and 7 from Beds V107M, V102M and V101M, all upper-Valanginian.</p> <p>4, 5, 9, <i>Ellipsoidictyum minusculum</i> n. sp. Figures 4, 5, 9 (para-10-13 type) from Bed V102M, upper Valanginian. Figures 10, 11 and 12, 13 (holotype) from the lower Valanginian, Bed V94M.</p> <p>14, 16, <i>Cassiculosphaeridia reticulata</i> from the upper Valanginian.</p> <p>19, 20 Figures 14 and 20 from Bed V132M and Figures 16, 19 from Bed V107M.</p> | <p>15, 18 <i>Discorsia nannus</i> from the upper Valanginian, Beds V132M and V123M respectively.</p> <p>17 <i>Cassiculosphaeridia magna</i> from the upper Valanginian, Bed V132M.</p> <p>21 <i>Exiguosphaera asketa</i> from Bed B131M, upper Berriasian.</p> <p>22, 23 <i>Exiguosphaera phragma</i> from the upper Valanginian Bed V107M.</p> <p>24 <i>Exiguosphaera lita</i> from the lower Valanginian, Bed V5M.</p> |
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PLATE 8

All specimens are from Vergol except for Figure 13, which is from the Speeton Clay and Figures 19, 22 and 23, which are from La Charce. Photographs $\times 950$ except for Figures 20, 22–24, which are $\times 700$.

1–4, 6 *Druggidium apicopaucicum*. Figures 1–4 from Bed V45M and Figure 6 from Bed V48M, all lower Valanginian.

5, 7, 10, *Druggidium* cf. *apicopaucicum*. Figures 5, 7, 11, 14 from 11, 14 Bed V91M, lower Valanginian and Figure 10 from the base of the upper Valanginian, Bed V101M.

8, 9, 12 *Druggidium deflandrei* sensu Habib 1973, all from the upper Valanginian. Figures 8, 12 from Bed V124M and Figure 9 from Bed LCH128M.

13, 18 *Gochteodinia brevispina* n. sp. Figure 13 (holotype) from the Speeton Clay, Bed D3E, lower Valanginian, *Polyptychites ammonite* Zone. Specimen first illustrated as *Gochteodinia* sp. D3E in Duxbury 2019. Figure 18 (paratype) from Bed V124M, upper Valanginian.

15–17 *Codoniella prisca* n. sp. Figures 15 and 17 from Bed V97M and Figure 16 from Bed V88, all lower Valanginian.

Figures 16 and 17 are the paratype and holotype respectively.

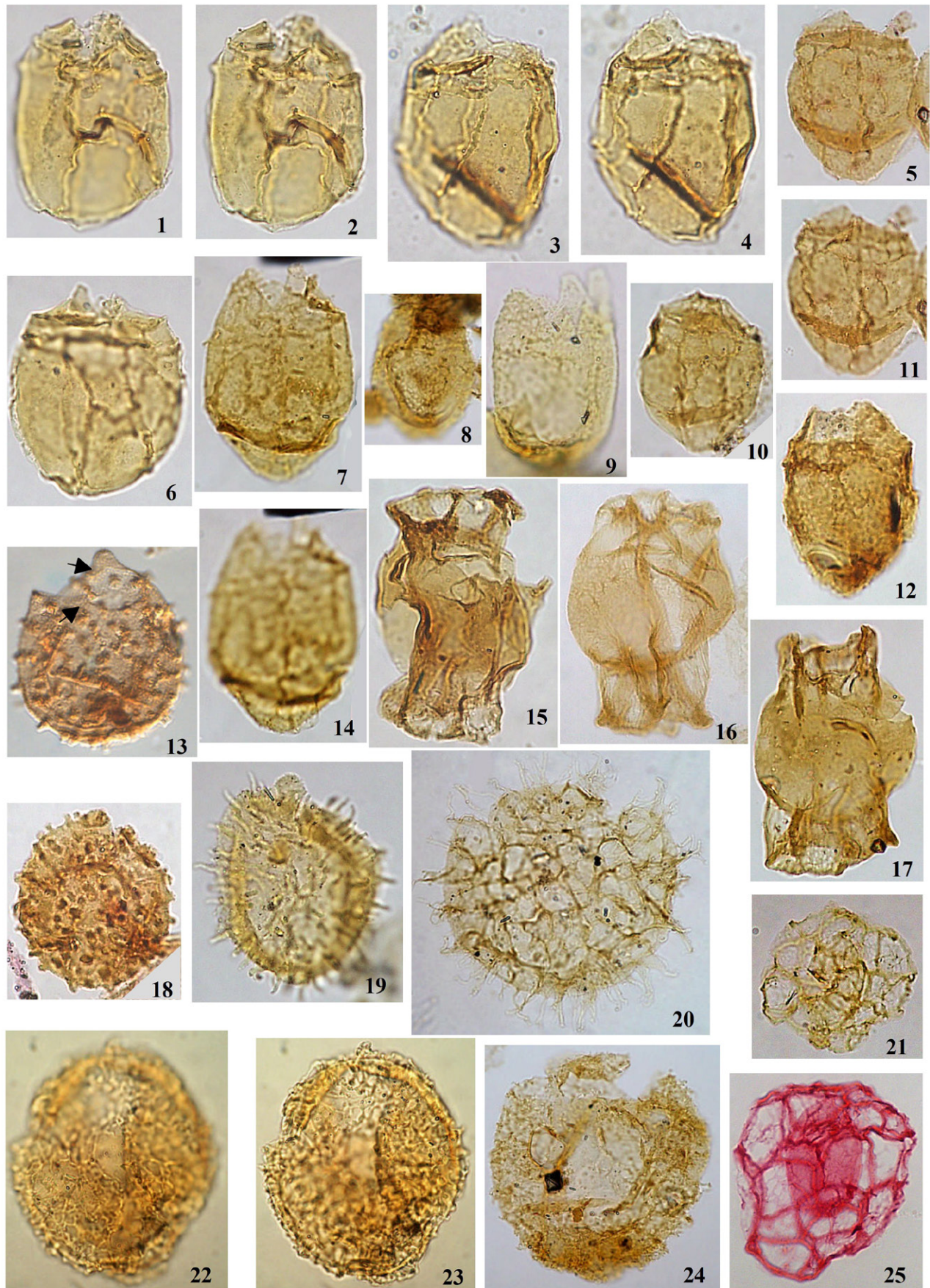
19 *Gochteodinia minuta* from the upper Valanginian, Bed LCH160M.

20 *Vexillocysta colligata* from the lower Valanginian, Bed V59M.

21, 25 *Hapsocysta minuta* n. sp. Figure 21 (paratype) from Bed V101M, base upper Valanginian and Figure 25 (holotype) from Bed V88, lower Valanginian.

22, 23 *Apteodinium deflandrei* from the lower Hauterivian, Bed LCH220M.

24 *Cyclonephelium maugaad* from the lower Valanginian, Bed V91M.

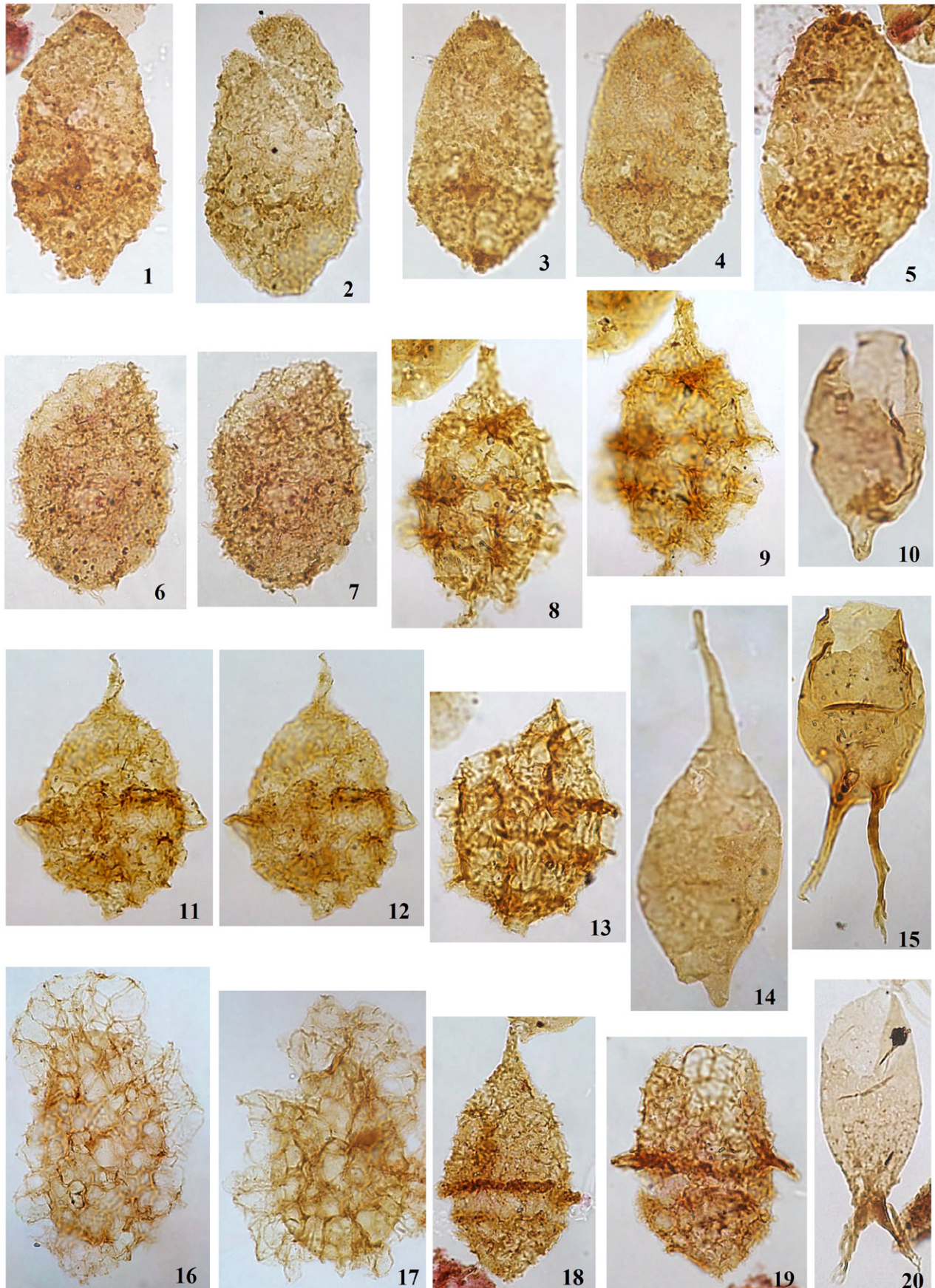


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PLATE 9

All specimens except Figure 20 are from Vergol. Photographs $\times 700$.

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| <p>1–5 <i>Batioladinium varigranulosum</i>. Figure 2 from Bed V97M, lower Valanginian and the rest from Bed V101M, base upper Valanginian.</p> <p>6, 7 <i>Aprobolocysta trycheria</i> from Bed V94M, lower Valanginian.</p> <p>8, 9, 13 <i>Aprobolocysta reticulata</i> subsp. <i>reticulata</i>. Figures 8, 9 from Bed V132M and Figure 13 from Bed V124M, all upper Valanginian.</p> <p>10, 14 <i>Batioladinium inaequalis</i>. Both specimens from Bed V132M.</p> | <p>11, 12, 18, <i>Aprobolocysta reticulata</i> subsp. <i>imparilis</i> n. subsp. Figures 11, 12 holotype and Figure 19 paratype. All specimens from Bed V112M, upper Valanginian.</p> <p>15 <i>Batioladinium longicornutum</i> from Bed V132M, upper Valanginian.</p> <p>16, 17 <i>Aprobolocysta extrema</i> from Beds V31M and V10M respectively, both lower Valanginian.</p> <p>20 <i>Batioladinium radiculatum</i> from the Central North Sea Kimmeridge Clay Formation, for comparison with Figure 15 (see text).</p> |
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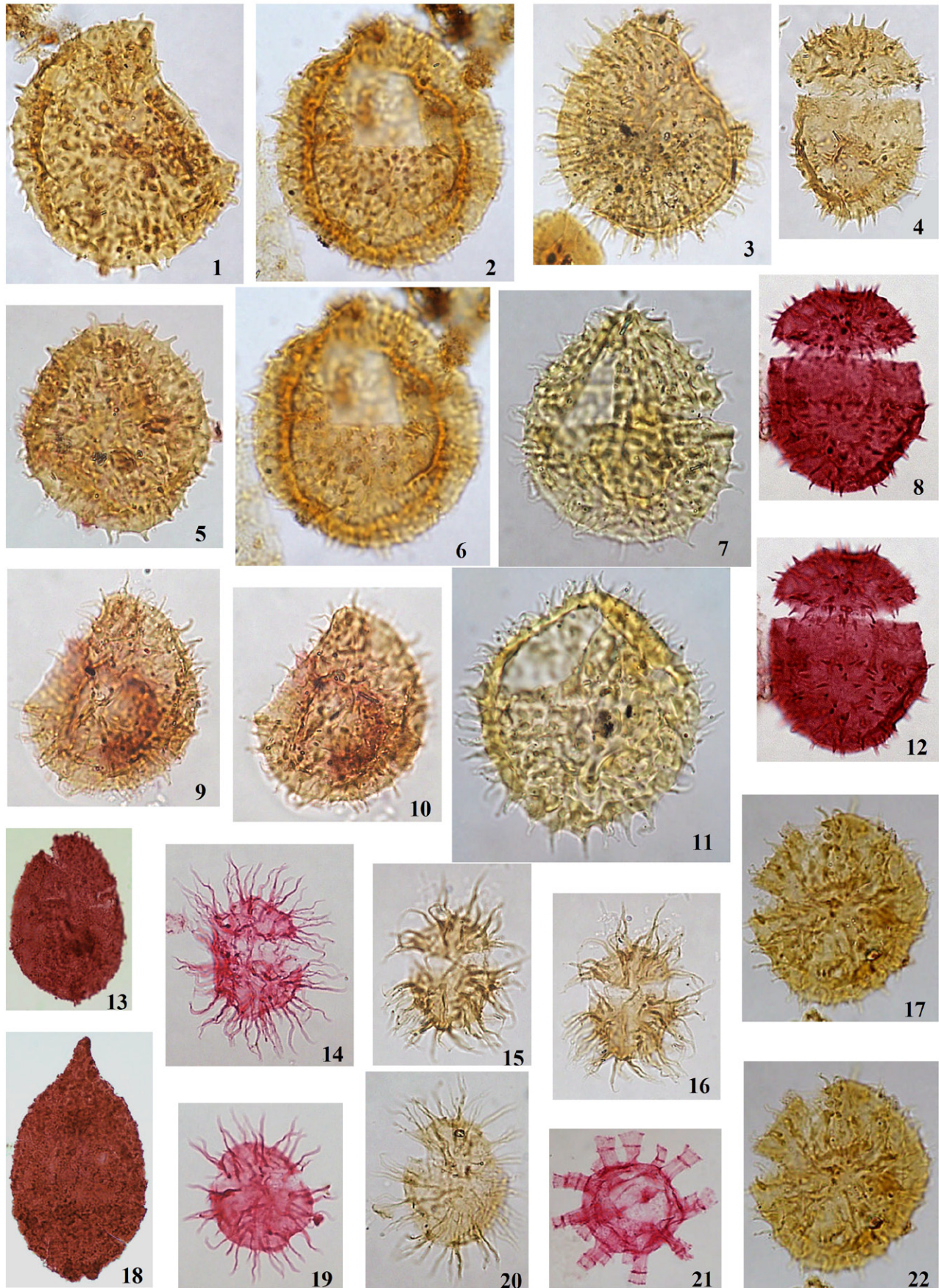


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PLATE 10

All specimens from Vergol except Figures 7, 11 which are from La Charce. Photographs $\times 950$ except for Figures 13 and 18 which are $\times 475$ and Figure 21 which is $\times 700$.

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| 1, 2, 5, 6 <i>Protoellipsodinium seghiris</i> subsp. <i>medaure</i> . Figure 1 from Bed V26M, Figures 2, 6 from Bed V36M, both lower Valanginian, and Figure 5 from Bed V102M, upper Valanginian. | 13 <i>Batioladinium</i> cf. <i>micropodum</i> from Bed V88, lower Valanginian. |
| 3, 9, 10, 17, 22 <i>Protoellipsodinium touile</i> subsp. <i>mugatae</i> . Figure 3 from Bed V132M, Figures 9, 10 from Bed V112M and Figures 17, 22 from Bed V102M, all upper Valanginian. | 14-16, 19, <i>Reticulasphaera fasciculata</i> n. sp. Figures 14 and 19 from Bed B131M, upper Berriasian, Figures 15 and 16 from Bed V97M, lower Valanginian and Figure 20 from Bed V124M, upper Valanginian. Figures 15, 16 holotype and Figure 19 paratype. |
| 4, 8, 12 <i>Biorbifera johnewingii</i> . Figure 4 from Bed V97M and Figures 8, 12 from Bed B136M, both specimens lower Valanginian. | 18 <i>Batioladinium micropodum</i> from Bed V88, lower Valanginian. |
| 7, 11 <i>Protoellipsodinium</i> cf. <i>vacuolatum</i> . Both specimens from Bed LCH183M, upper Valanginian. | 21 <i>Dapsilidinium?</i> <i>deflandrei</i> from Bed B136M, lower Valanginian. |

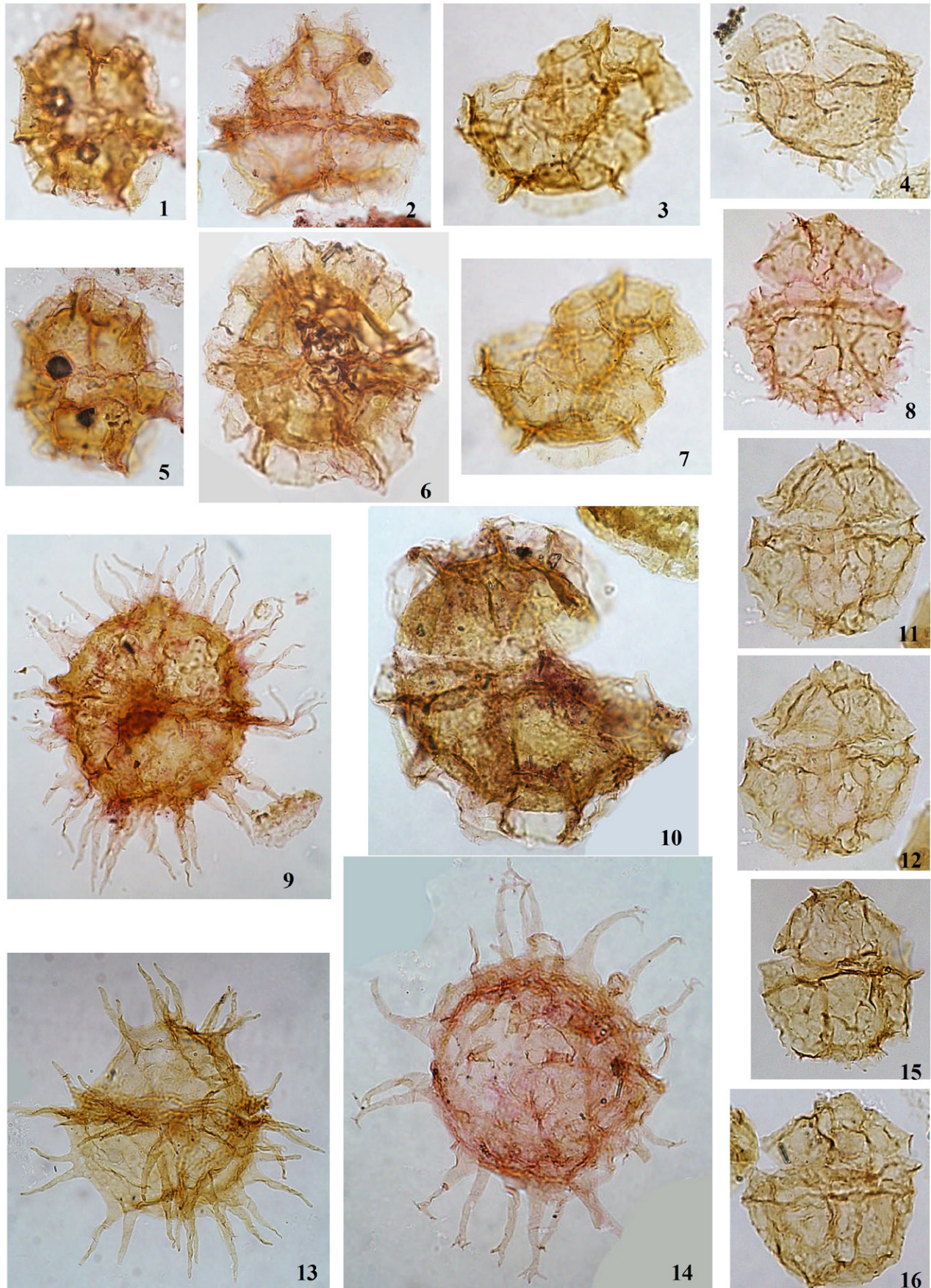


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PLATE 11

All specimens from Vergol. Photographs $\times 700$ except for Figures 4, 8, 11, 12, 15 and 16 which are $\times 950$.

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| 1-3, 5, 7 <i>Heslertonia inferior</i> n. sp. Figures 1, 5 from Bed V91M and Figures 3, 7 (holotype) from Bed V19M, both lower Valanginian. Figure 2 (paratype) from Bed V124M, upper Valanginian. | 9 <i>Hystrichodinium pulchrum</i> from Bed V102M, upper Valanginian. |
| 4 <i>Cauca maculosa</i> from Bed V97M, lower Valanginian. | 10 <i>Heslertonia reticulata</i> from Bed V132M, upper Valanginian. |
| 6 <i>Heslertonia heslertonensis</i> from Bed V91M, lower Valanginian. | 13 <i>Hystrichodinium voigtii</i> from Bed V97M, lower Valanginian. |
| 8, 11, 12, 15, 16 <i>Cauca redacta</i> . Figures 11, 12, 15 and 16 all from Bed V97M, lower Valanginian. Figure 8 from Bed V107M, upper Valanginian. Figures 11 and 12 holotype and Figure 16 paratype. | 14 <i>Hystrichodinium furcatum</i> from Bed V132M, upper Valanginian. |

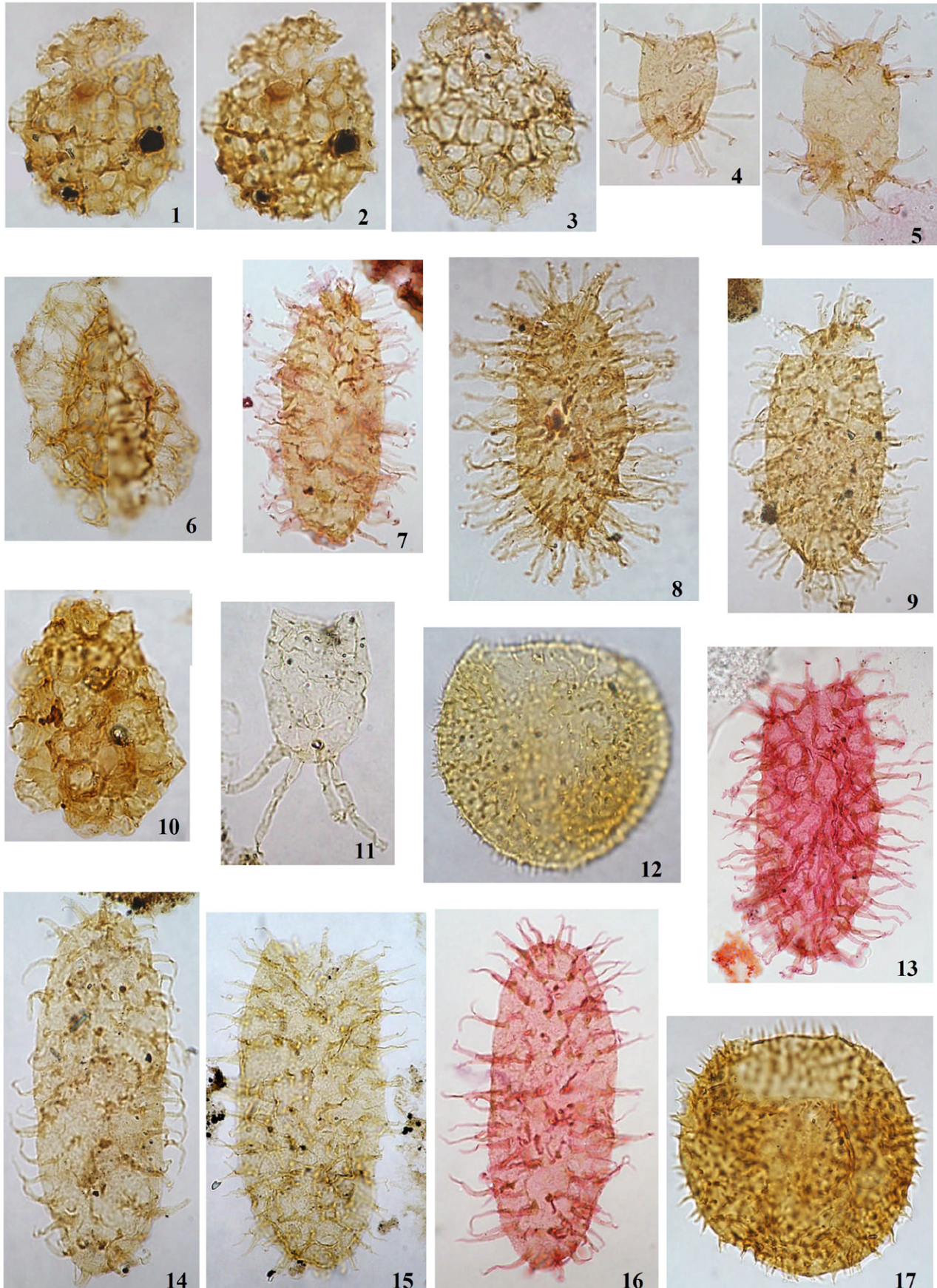


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PLATE 12

All specimens from Vergol except Figures 11 and 12 which are from La Charce. Photographs $\times 700$.

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| <p>1-3 <i>Aprobolocysta humilis</i> n. sp. Figures 1, 2 (holotype) from Bed B129M, upper Berriasian, and Figure 3 from Bed B136M, lower Valanginian.</p> <p>4, 5 <i>Bourkidinium granulatum</i> from Beds V132M and V101M respectively, both upper Valanginian.</p> <p>6 <i>Aprobolocysta extrema</i> from Bed V5M, lower Valanginian.</p> <p><i>Tanyosphaeridium hirsutum</i> n. sp. Figure 7 from Bed V101M, upper Valanginian and Figures 8, 9 and 13 from Beds V5M, V91M and B131M respectively, all lower Valanginian. Figure 13 holotype and Figure 7 paratype.</p> | <p>10 <i>Aprobolocysta pustulosa</i> from Bed V10M, lower Valanginian.</p> <p>11 <i>Bourkidinium elegans</i> from Bed LCH208M, lower Hauterivian.</p> <p>12, 17 <i>Elimatia discus</i> from Beds LCH141M and V132M respectively, both upper Valanginian.</p> <p>14-16 <i>Prolixosphaeridium prolatum</i> n. sp. . Figure 14 from Bed B138M, lower Valanginian and Figures 15 and 16 from Beds B129M and Bed B131M respectively, upper Berriasian. Figure 16 holotype.</p> |
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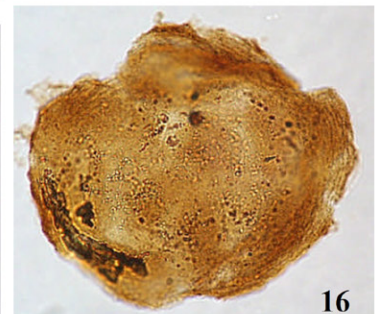
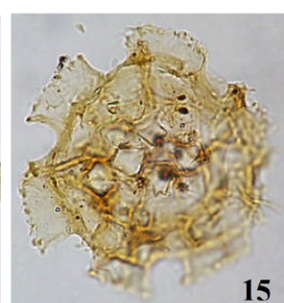
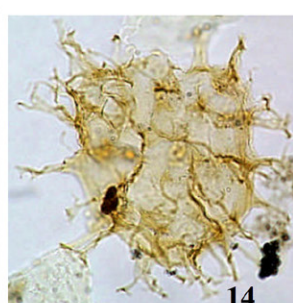
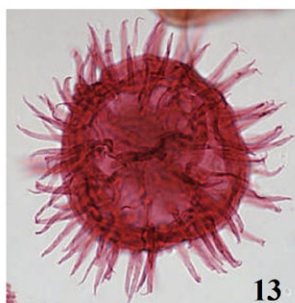
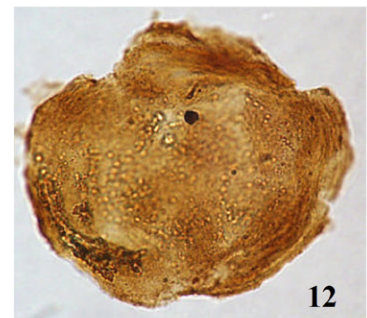
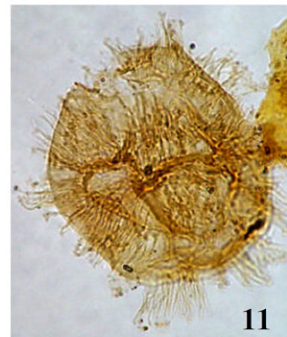
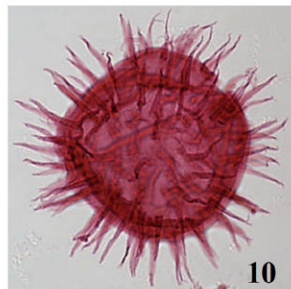
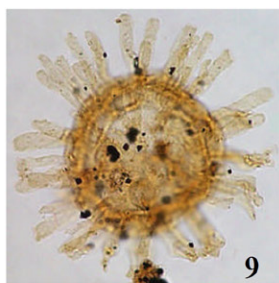
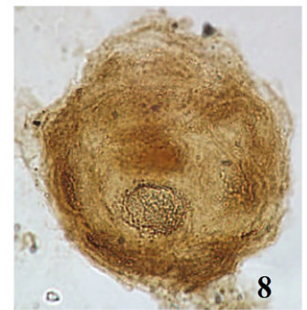
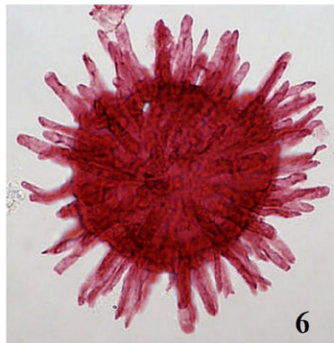
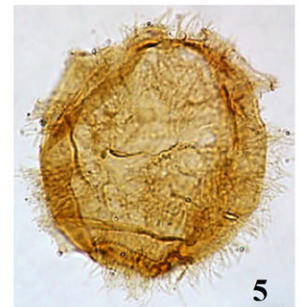
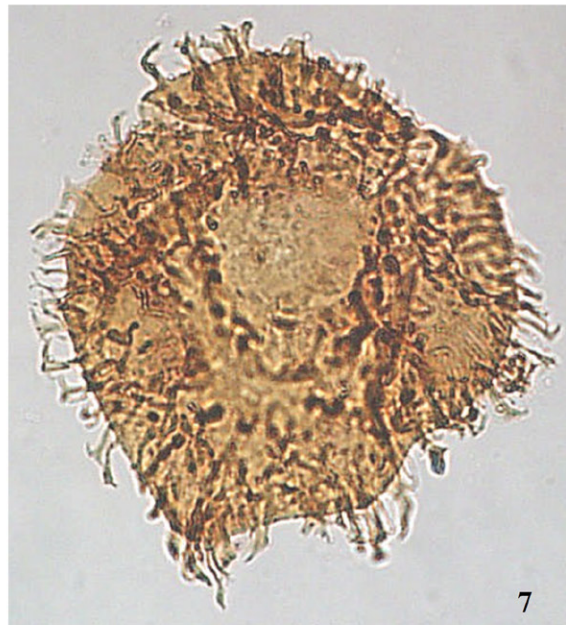
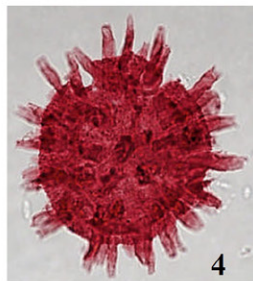
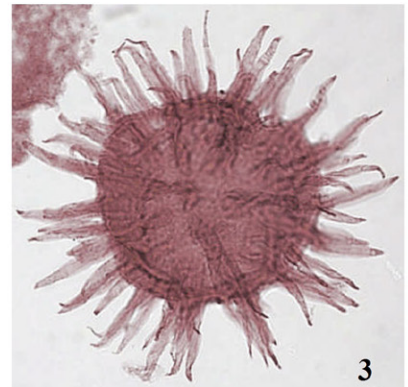
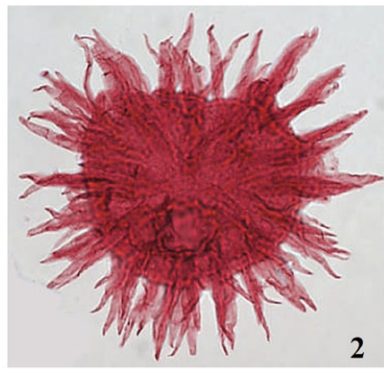
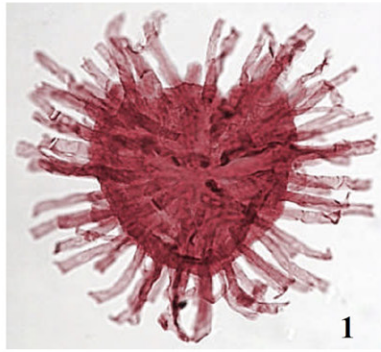


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PLATE 13

All specimens from Vergol. Photographs ×700.

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| 1-4 <i>Dapsilidinium warrenii</i> . Both specimens from the lower Valanginian, Bed V88. | Bed V94M. |
| 2, 3 <i>Downiesphaeridium flexuosum</i> from Bed V88, lower Valanginian. | 8, 12, 16 <i>Ovoidinium? glebulentum</i> n. sp. Figure 8 from Bed B138M and Figures 12, 16 (holotype) from Bed V10M. Both specimens from the lower Valanginian. |
| 5, 11 <i>Foucheria modesta</i> from the lower Valanginian, Beds V19M and V36M respectively. | 10, 13 <i>Downiesphaeridium chems</i> n. comb. from Bed V88, lower Valanginian. |
| 6, 9 <i>Downiesphaeridium obtusum</i> n. sp. Figure 6 (holotype) from Bed V88, lower Valanginian and Figure 9 from Bed B113M, upper Berriasian. | 14 <i>Vexillocysta spinosa</i> from Bed B129M, upper Berriasian. |
| 7 <i>Circulodinium hirtellum</i> from the lower Valanginian, | 15 <i>Callaiosphaeridium</i> sp. from Bed V101M, upper Valanginian. |

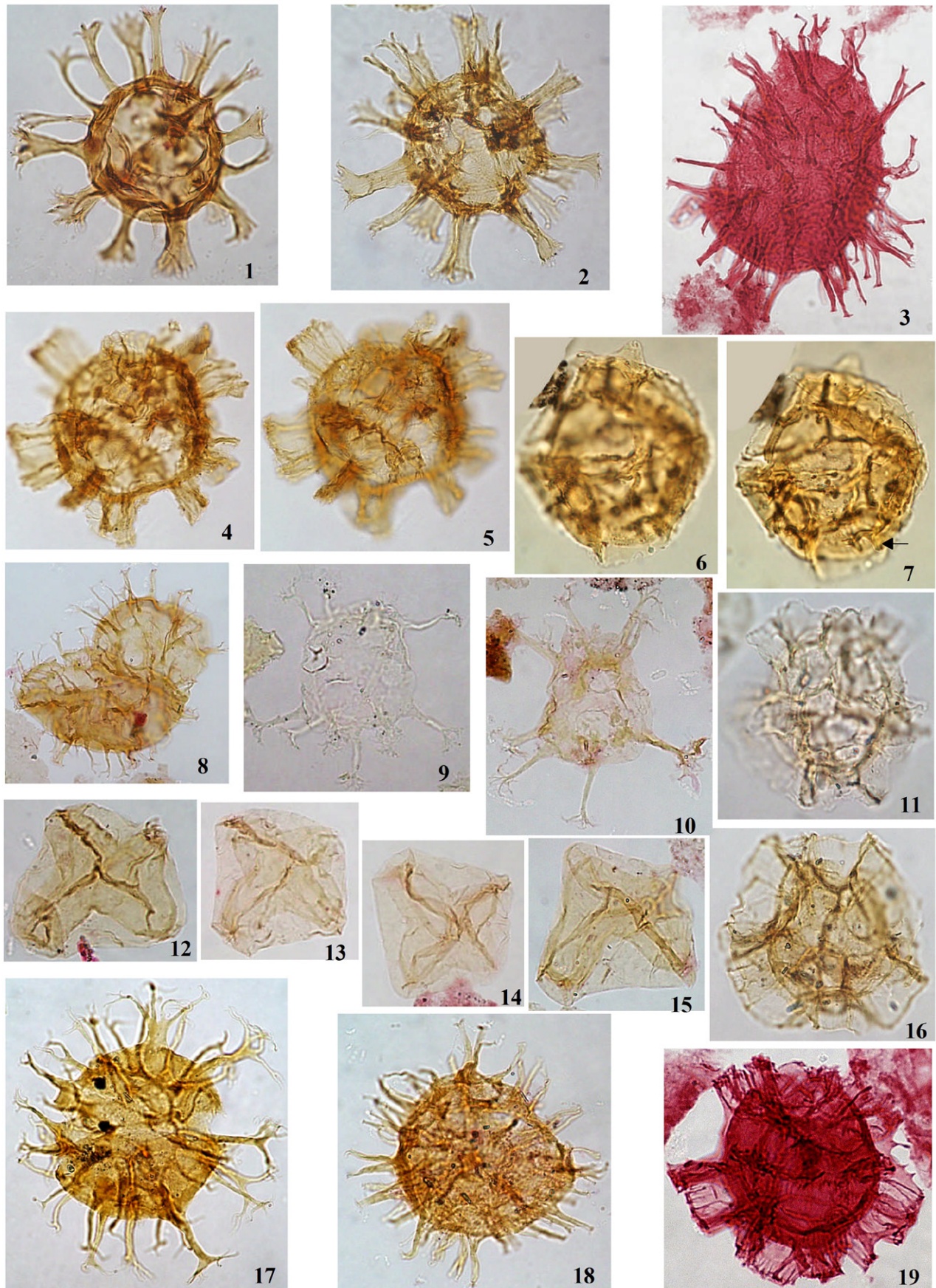


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PLATE 14

All specimens from Vergol except Figures 6, 7, 9 and 11 which are from La Charce. Photographs $\times 700$ except for Figures 9-16 and 18 which are $\times 950$.

- 1 *Kleithriasphaeridium simplicispinum* from the upper Valanginian, Bed V107M.
- 2 *Kleithriasphaeridium corrugatum* from Bed V97M, lower Valanginian.
- 3, 18 *Exochosphaeridium robustum* from the lower Valanginian, Beds V88 and V94M respectively.
- 4, 5 *Kleithriasphaeridium fasciatum* from Bed V14M, lower Valanginian.
- 6, 7 *Wrevittia diutina* subsp. *tabulacornuta* from the lower Hauterivian, Bed LCH208M. A characteristic spike on the antapical plate is arrowed on Figure 7.
- 8 *Avellodinium lepidum* from Bed V112M, upper Valanginian.
- 9, 10 *Palleodinium digitatum* n. gen, n. sp. Figure 9 from the upper Valanginian, Bed LCH180M and Figure 10 (holotype) from Bed V91M, lower Valanginian.
- 11, 16 *Valensiella prenannus* from Beds LCH216M, lower Hauterivian and V132M, upper Valanginian respectively.
- 12-15 *Halophoridia caperata* Figures 12, 15 from Bed V124M, upper Valanginian, and Figures 13, 14 from Bed B131M, upper Berriasian.
- 17 *Avellodinium falsificum* from Bed V132M, upper Valanginian.
- 19 A specimen intermediate between *Valensiella prenannus* and *Discorsia nannus* from Bed V88, lower Valanginian.

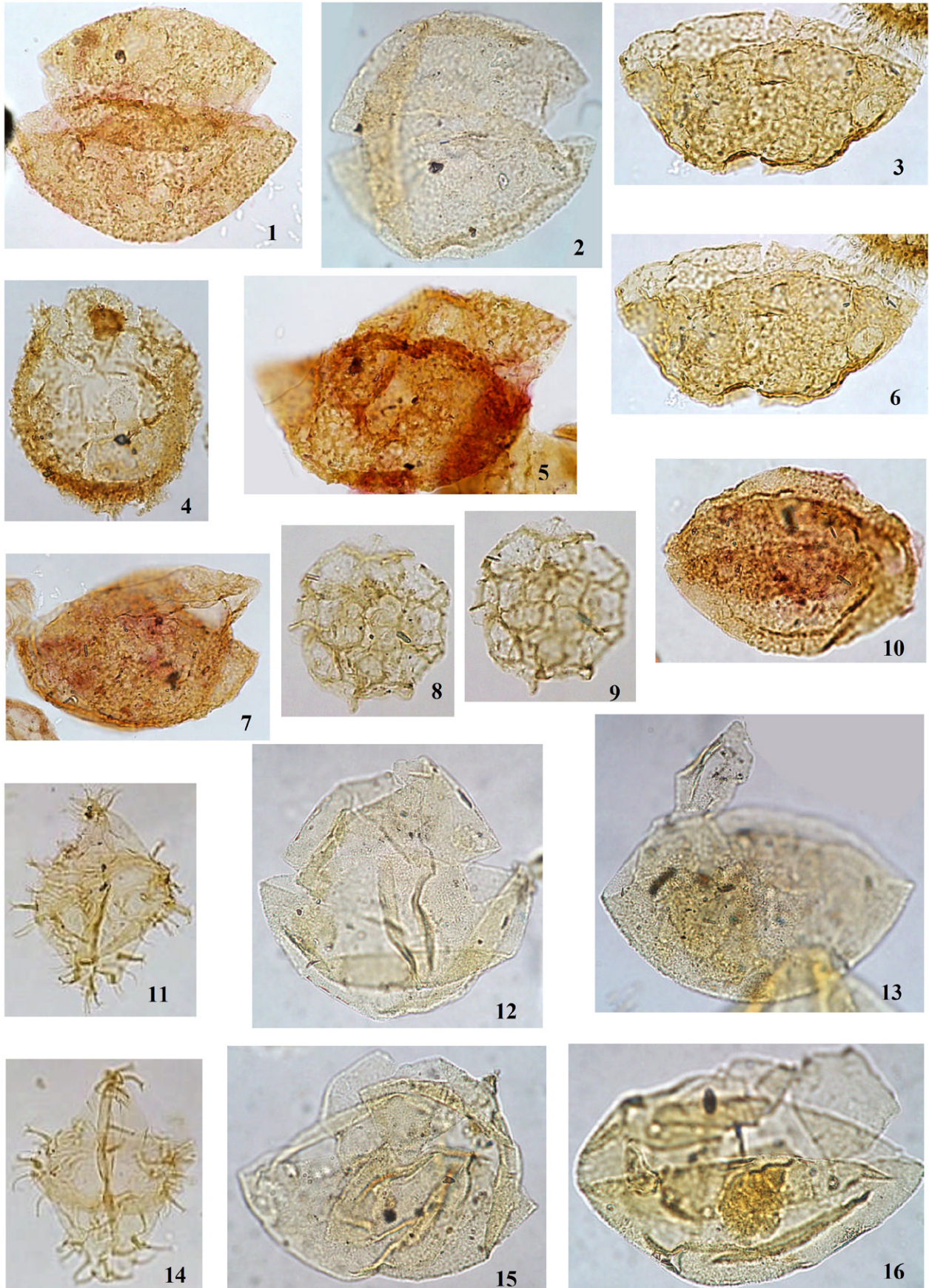


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PLATE 15

All specimens from Vergol except Figures 2, 12, 13, 15 and 16 which are from La Charce.
Photographs ×700 except for Figures 8, 9, 11 and 14 which are ×950.

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| <p>1, 2, 10 <i>Mendicodinium</i> "granular". Figure 1 from Bed V94M, lower Valanginian, Figure 2 from the lower Hauterivian, Bed LCH208M and Figure 10 from the upper Valanginian, Bed V132M.</p> | <p>8, 9 <i>Hapsocysta minuta</i> n. sp. from Bed V102M, upper Valanginian.</p> |
| <p>3, 5-7 <i>Mendicodinium</i> "reticulate", all from Bed V124M, upper Valanginian.</p> | <p>11, 14 <i>Rhombodella vesca</i> from the lower Valanginian, Beds V97M and V88M respectively.</p> |
| <p>4 <i>Cyclonephelium maugaad</i> from the upper Valanginian, Bed V101M.</p> | <p>12, 13, 15, <i>Dissiliodinium curiosum</i> all from Bed LCH216M, lower Hauterivian.</p> |

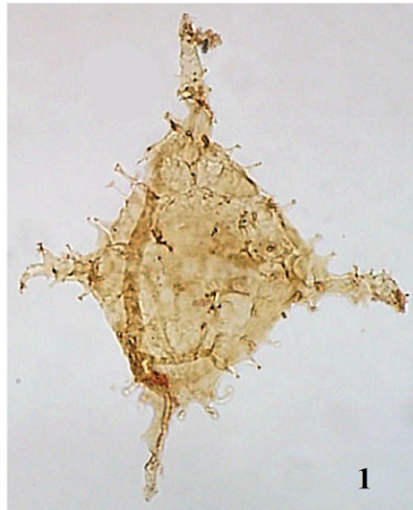


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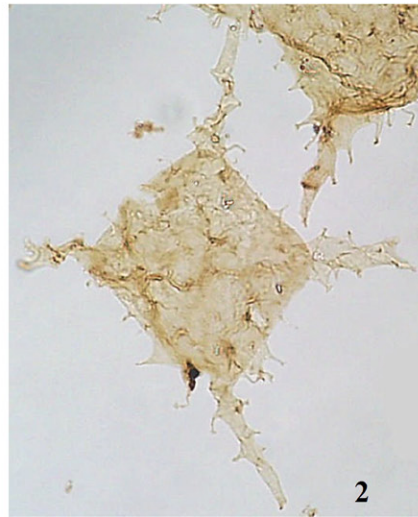
PLATE 16

All specimens from Vergol. Photographs $\times 475$ except for Figure 10 which is $\times 950$.

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| <p>1, 2, 5 <i>Phoberocysta latissima</i> n. sp., all from the lower Valanginian, Bed V31M. Figure 1 paratype and Figure 2 holotype.</p> | <p>7, 8, 10 <i>Muderongia extensiva</i> subsp. <i>spinosa</i> n. subsp., both specimens from the upper Valanginian, Bed V107M. Figures 7, paratype and Figure 8 holotype. Figure 10 magnifies the left antapical horn of the paratype to highlight the spiny ornament.</p> |
| <p>3 <i>Muderongia dedecosa</i>, showing the lateral splits typical of this species. Bed V97M, lower Valanginian.</p> | <p>9, 11 <i>Muderongia simplex</i>, from Beds B131M and V112M, upper Berriasian and upper Valanginian respectively.</p> |
| <p>4 <i>Phoberocysta neocomica</i> from the lower Valanginian, Bed V97M.</p> | <p>12 <i>Muderongia extensiva</i> subsp. <i>extensiva</i> from Bed V127M, upper Valanginian.</p> |
| <p>6 <i>Muderongia perforata</i> from Bed V123M, upper Valanginian.</p> | |



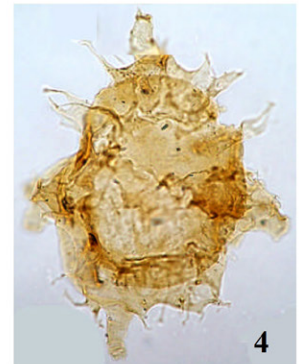
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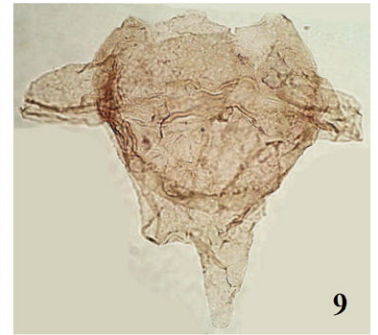
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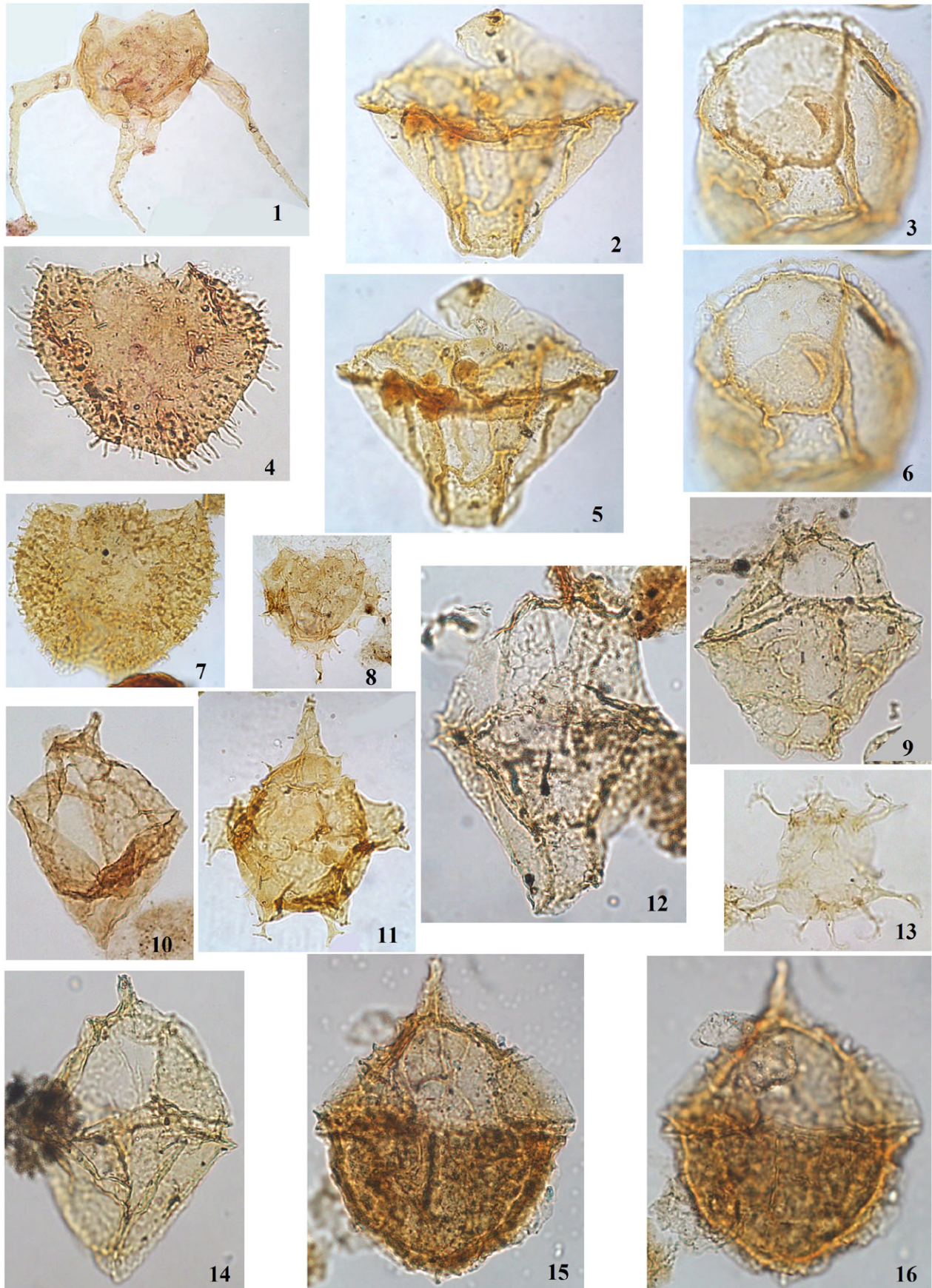
12

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PLATE 17

All specimens from Vergol. Photographs $\times 475$ except for Figure 10 which is $\times 950$.

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|---|---|
| 1 <i>Muderongia extensiva</i> subsp. <i>spinosa</i> n. subsp. from the upper Valanginian, Bed V102M. | V132M, both upper Valanginian. |
| 2, 3, 5, 6 <i>Isthmocystis distincta</i> from Bed LCH107M, upper Valanginian. | 9, 10, 12, <i>Scriniodinium elimatum</i> . Figures 9, 12 and 14 from Bed 14 LCH149M, upper Valanginian and Figure 10 from Bed V88, lower Valanginian. |
| 4, 7 <i>Circulodinium hirtellum</i> . Figure 4 from the lower Valanginian, Bed V94M and Figure 7 from the upper Valanginian, Bed V132M. | 13 <i>Palleodinium digitatum</i> n. gen, n. sp. (paratype) from Bed-V97M, lower Valanginian. |
| 8, 11 <i>Phoberocysta neocomica</i> . Figure 8 an unusually small specimen from Bed V107M and Figure 11 from, Bed | 15, 16 <i>Cribroperidinium sepimentum</i> from Bed LCH180M, upper Valanginian. |



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PLATE 18

All specimens from Vergol except Figure 1 which is from Speeton and Figures 8, 11, 17 and 18 which are from La Charce. Photographs $\times 475$ except for Figures 1, 4, 5, 8 and 11 which are $\times 700$.

- 1, 4, 5 *Occisucysta tentorium*. Figure 1 the holotype (Duxbury 1977), a photograph from the Natural History Museum, London "Duxbury Collection" (see text), showing some fine microreticulate ornament. Figures 4 and 5 a polar view from Bed V107M, upper Valanginian.
- 2, 3, 6, *Spiculodinium? inordinatum* n. sp. Figures 2, 3 (holotype), 12, 13 13 from Bed V26M, Figure 6 from Bed V36M and Figure 12 from Bed V59M, all lower Valanginian.
- 7, 10, 16 *Thalassiphora? charollaisii* from the lower Valanginian, Bed B142M.
- 8, 11 *Wrevittia* sp. cf. *Wrevittia cassidata* from Beds LCH170M and LCH173M, both upper Valanginian.
- 9 *Perisseiasphaeridium cretaceum* from Bed B136M, lower Valanginian.
- 14, 15 *Tenua* sp. cf. *Tenua colliveri* from Beds V132M and V107M, upper Valanginian.
- 17, 18 *Chlamydophorella ordinalis* from Bed LCH198M, lower Hauterivian.
- 19 *Oligosphaeridium complex* from Bed V132M, upper Valanginian.

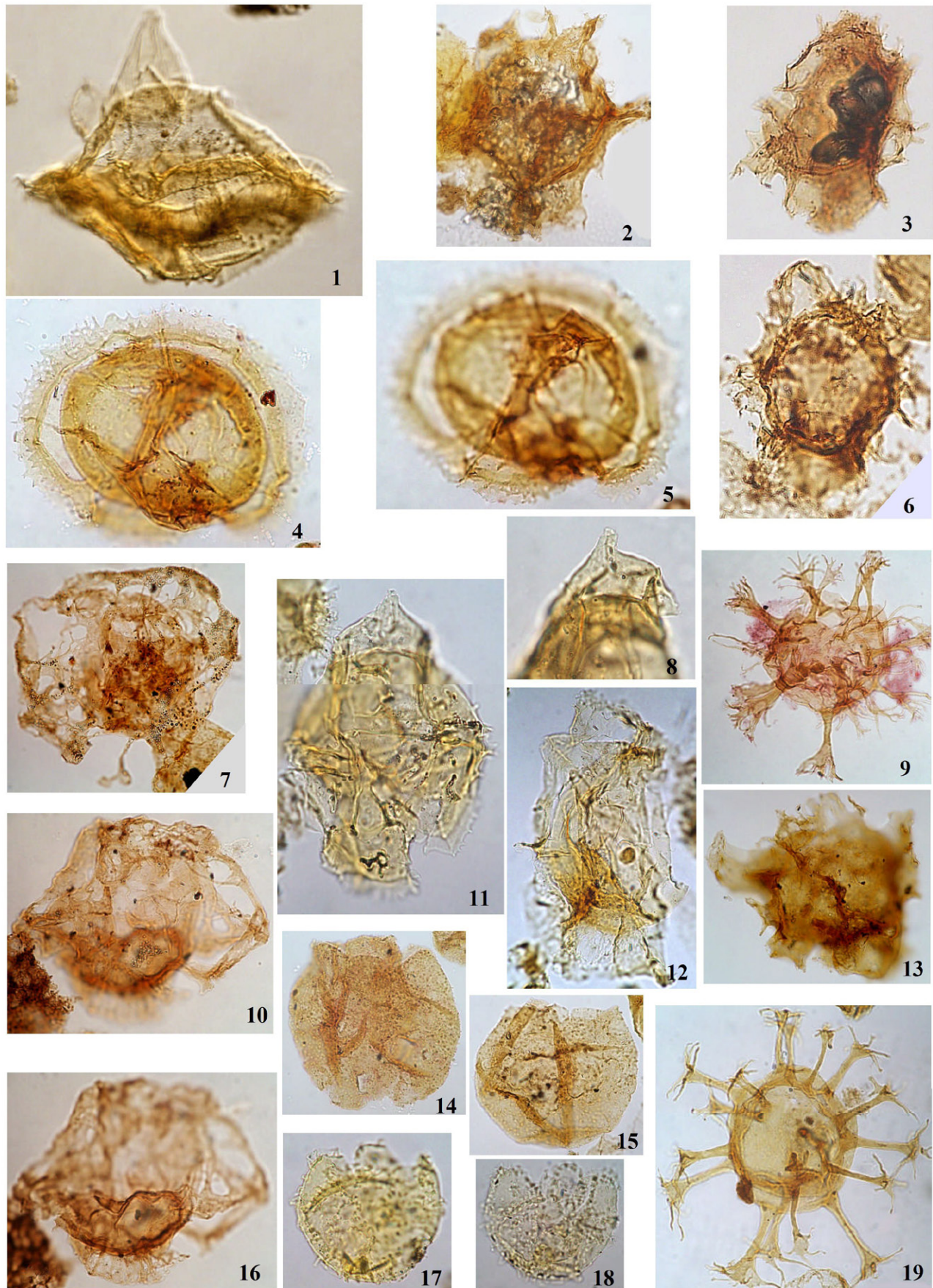


PLATE 19

All specimens from Vergol except Figures 9 and 10 which are from La Charce. Photographs $\times 475$ except for Figures 3, 4, 6, 8-10, 20-22 which are $\times 700$.

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| <p>1, 5 <i>Systematophora? scoriacea</i> from Bed V94M, lower Valanginian.</p> <p>2 <i>Systematophora</i> sp. A of Monteil 1993 from Bed B97M, upper Berriasian.</p> <p>3, 9, 10 <i>Dapsilidium duma</i> from the lower Valanginian. Figure 3 from Bed V84M, lower Valanginian, and Figures 9 and 10 (the latter a particularly elongate specimen) from Bed LCH164M and Bed LCH128M respectively, both upper Valanginian.</p> <p>4 <i>Impletosphaeridium multifurcillatum</i> from Bed V132M, upper Valanginian.</p> | <p>6, 8 <i>Impletosphaeridium tribuliferum</i> from Bed B113M, upper Berriasian.</p> <p>7, 11-16 <i>Systematophora? cf. scoriacea</i>. Figures 7 and 16 from Beds V123M and V132M respectively, upper Valanginian. Figures 11-13, 15 from Bed V94M and Figure 14 from Bed V88, all lower Valanginian.</p> <p>17-19 <i>Hystriosphera schindewolfii</i>. Figures 17, 18 from Beds V91M and V97M respectively, lower Valanginian, and Figure 19 from Bed V101M, upper Valanginian.</p> <p>20-22 <i>Hystriosphera diversum</i>. Figures 20, 21 from Bed B134M, upper Berriasian and Figure 22 from Bed B138M, lower Valanginian.</p> |
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PLATE 20

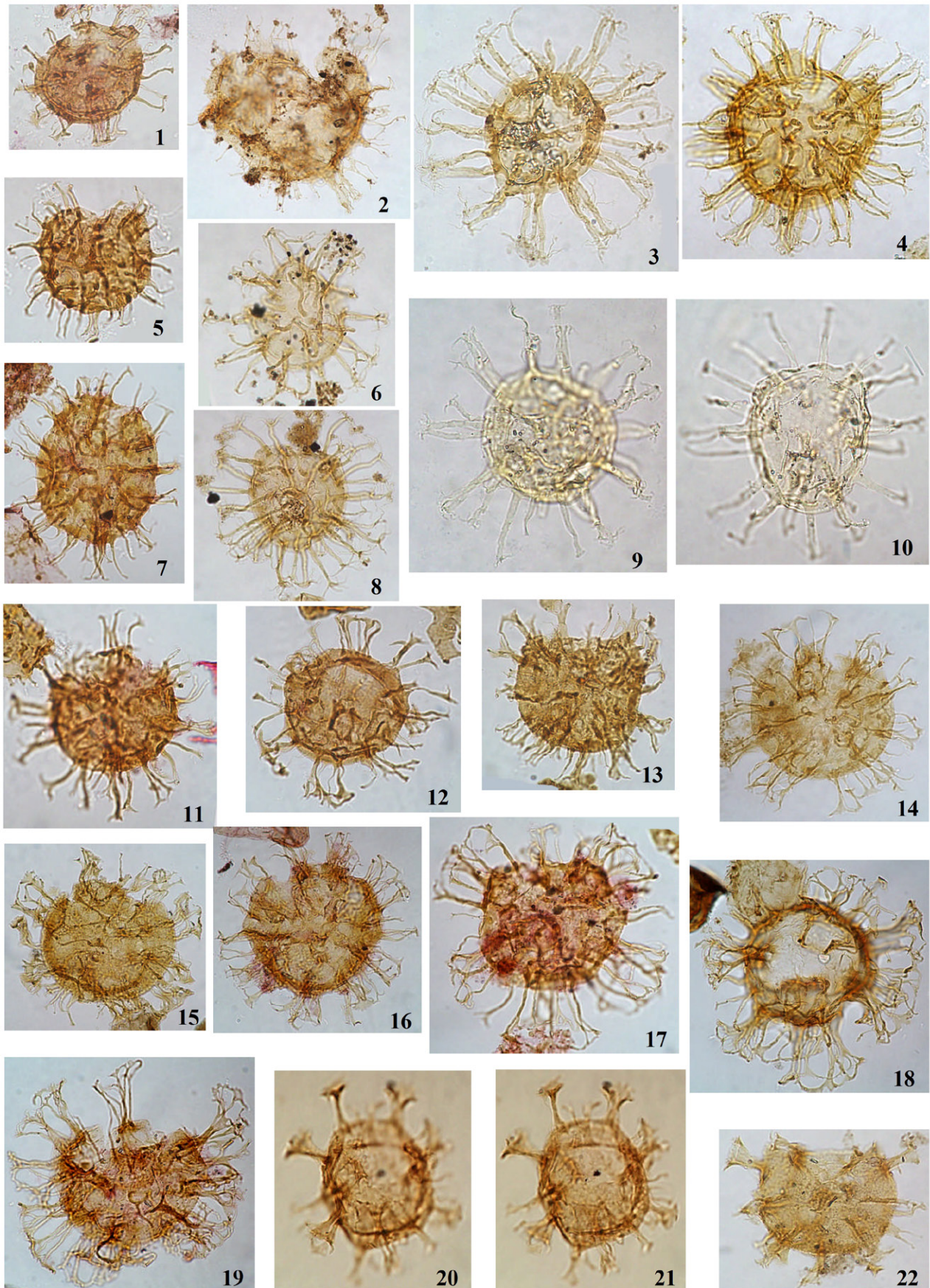
All specimens from La Charce except Figures 13, 14, 16-18 which are from Vergol. Photographs $\times 700$ except for Figures 13, 14, 16-18 which are $\times 475$.

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| <p>1-4, 6 <i>Impagidium</i> LC1 from Bed LCH203M, lower Hauterivian.</p> <p>5, 7, 8, <i>Hapsocysta peridictya</i> from the lower Hauterivian. Figures 9-12 5, 7, 8, 11 specimens at the base of its range with much-reduced trabecular height, Bed LCH208M. Figures 9, 10, 12 more typical specimens from Bed LCH220.</p> <p>13, 14, 16 <i>Pseudoceratium pelliferum</i> subsp. <i>pelliferum</i>.</p> | <p>Figures 13, 16 from Bed V101M and Figure 14 from Bed V111M, upper Valanginian.</p> <p>15 <i>Wrevittia diutina</i> subsp. <i>tabulacornuta</i> from Bed LCH213M, lower Hauterivian.</p> <p>17, 18 <i>Pseudoceratium pelliferum</i> subsp. <i>radiculatum</i> n. subsp. from Beds B138M and B136M respectively, lower Valanginian. Figure 18 holotype.</p> |
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PLATE 21

A selection of scolecodonts from Vergol. Photographs $\times 700$.

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| <p>1-5, 9 Specimens from Bed V88 (Barrande layer B4), lower Valanginian. Figures 2 and 9 are particularly good semi-articulated examples.</p> <p>6 From Bed B129M, upper Berriasian.</p> <p>7 From Bed B113M, upper Berriasian. A possible <i>Pterogenys</i> sp.</p> | <p>8 From Bed V97M, uppermost lower Valanginian, <i>inostranze-wi</i> Zone.</p> <p>10 An excellent semi-articulated example from Bed V123M, upper Valanginian.</p> |
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APPENDIX 1 – Species List

An alphabetical list is included below for taxa referred to in the text, text-figures and plate descriptions; illustrations in the present work have plate and figure numbers indicated in brackets. For the most part, citations follow Fensome et al. 2019.

- Adnatosphaeridium caulleryi* (Deflandre) Williams and Downie 1969
- Amphorulacysta metaelliptica* (Dodekova 1969) Williams and Fensome 2016 (Pl. 1, Figs. 1-3, 7)
- Aprobolocysta extrema* Duxbury 2001 (Pl. 9, Figs. 16, 17. Pl. 12, Fig. 6)
- Aprobolocysta humilis* Duxbury n. sp. (Pl. 12, Figs. 1-3)
- Aprobolocysta pustulosa* Smith and Harding 2004 (Pl. 12, Fig. 10)
- Aprobolocysta reticulata* (Stover and Helby 1987) Duxbury 2018 subsp. *reticulata* autonym (Pl. 9, Figs. 8, 9, 13)
- Aprobolocysta reticulata* (Stover and Helby 1987) Duxbury 2018 subsp. *imparilis* n. subsp. (Pl. 9, Figs. 11, 12, 18, 19)
- Aprobolocysta trycheria* Pourtoy 1988 (Pl. 9, Figs. 6, 7)
- Apteodinium deflandrei* (Clarke and Verdier 1967) Lucas-Clark 1987 (Pl. 8, Figs. 22, 23)
- Avellodinium falsificum* Duxbury 1977 (Pl. 14, Fig. 17)
- Avellodinium lepidum* Backhouse 1988 (Pl. 14, Fig. 8)
- Batioladinium inaequalis* Duxbury 2023 (Pl. 9, Figs. 10, 14)
- Batioladinium longicornutum* (Alberti 1961) Brideaux 1975 (Pl. 9, Fig. 15)
- Batioladinium micropodum* (Eisenack and Cookson 1960) Brideaux 1975 (Pl. 10, Fig. 18)
- Batioladinium* cf. *micropodum* (Eisenack and Cookson 1960) Brideaux 1975 (Pl. 10, Fig. 13)
- Batioladinium radiculatum* Davey 1982 (Pl. 9, Fig. 20)
- Batioladinium varigranulosum* (Duxbury 1977) Davey 1982 (Pl. 9, Figs. 1-5)
- Bicornus obscurus* Duxbury n. gen n. sp. (Pl. 4, Figs. 7-9, 11-13, 15, 16)
- Biorbifera johnewingii* Habib 1972 (Pl. 10, Figs. 4, 8, 12)
- Bourkidinium elegans* Torricelli 1997 (Pl. 12, Fig. 11)
- Bourkidinium granulatum* Morgan 1975 (Pl. 12, Figs. 4, 5)
- Callaiosphaeridium asymmetricum* (Deflandre and Courteville 1939) Davey and Williams 1966b
- Callaiosphaeridium* sp. (Pl. 13, Fig. 15)
- Cassiculosphaeridia magna* Davey 1974 (Pl. 7, Fig. 17)
- Cassiculosphaeridia reticulata* Davey 1969 (Pl. 8, Figs. 14, 16, 19, 20)
- Cauca maculosa* Duxbury 2018 (Pl. 11, Fig. 4)
- Cauca redacta* Duxbury n. sp. (Pl. 11, Figs. 8, 11, 12, 15, 16)
- Chlamydophorella ambigua* (Deflandre 1937) Stover and Helby 1987 subsp. *ambigua* autonym (Pl. 5, Fig. 23, 24, 26)
- Chlamydophorella caminus* Duxbury n. sp. (Pl. 5, Figs. 13, 17)
- Chlamydophorella ordinalis* (Davey 1974) Davey 1978 (Pl. 18, Figs. 17, 18)
- Chlamydophorella pyriformis* (Vozzhennikova 1967) Davey 1978
- Chlamydophorella trabeculosa* (Gocht 1959) Davey 1978
- Chytroeisphaeridia conspicua* Duxbury n. sp. (Pl. 3, Figs. 1-4)
- Chytroeisphaeridia scabrata* Pocock 1972
- Circulodinium hirtellum* Alberti 1961 (Pl. 13, Fig. 7. Pl. 17, Fig. 4, 7)
- Codoniella campanulata* (Cookson and Eisenack 1960) Downie and Sarjeant 1965
- Codoniella prisca* Duxbury n. sp. (Pl. 8, Figs. 15-17)
- Codoniella psygma* Davey 1979a
- Cribroperidinium colum* Duxbury 2001 (Pl. 6, Fig. 14)
- Cribroperidinium sepimentum* Neale and Sarjeant 1962 (Pl. 17, Figs. 15, 16)
- Ctenidodinium elegantulum* Millioud 1969
- Cyclonephelium maugaad* Below 1981 (Pl. 8, Fig. 24. Pl. 15, Fig. 4)
- Cymososphaeridium validum* Davey 1982 (Pl. 1, Figs. 9, 13, 14)
- Cymososphaeridium validum "regulare"* (informal taxon) (Pl. 1, Fig. 17)
- Dapsilodinium? deflandrei* (Valensi 1947) Lentin and Williams 1981 (Pl. 10, Fig. 21)
- Dapsilodinium duma* (Below 1982c) Lentin and Williams 1985 (Pl. 19, Figs. 3, 9, 10)
- Dapsilodinium multispinosum* (Davey 1974) Bujak et al. 1980
- Dapsilodinium warrenii* (Habib 1976) Lentin and Williams 1981 (Pl. 13, Figs. 1, 4)
- Diacanthum aculeatum* (Klement 1960) Duxbury n. comb.
- Diacanthum brixii* (Below 1982a) Duxbury n. comb.
- Diacanthum coummia* (Below 1981a) Duxbury n. comb.
- Diacanthum crestatum* (Jain 1977) Duxbury n. comb.
- Diacanthum daveyi* (Jan du Chêne et al. 1986b) Duxbury n. comb.
- Diacanthum evittii* (Dodekova 1969) Duxbury n. comb.
- Diacanthum hollisteri* Habib 1972 (Pl. 6, Figs. 8, 12, 17, 22)
- Diacanthum konarae* (Dodekova 1992) Duxbury n. comb.
- Diacanthum mazaganense* (Below 1984) Duxbury n. comb.
- Diacanthum sousense* (Below 1981) Duxbury n. comb.
- Diacanthum tenuiceras* (Eisenack 1958) Stover and Evitt 1978
- Diacanthum victorii* (Pöthe de Baldi and Ramos 1983) Duxbury n. comb.
- Dichadogonyaulax bensonii* Monteil 1992a (Pl. 2, Figs. 14, 15, 17-19)
- Dichadogonyaulax* cf. *bensonii* Monteil 1992a (Pl. 2, Fig. 5)
- Dingodinium cerviculum* Cookson & Eisenack 1958 (Pl. 5, Figs. 10, 14, 22)
- Dingodinium jurassicum* Cookson & Eisenack 1958 (Pl. 5, Figs. 11, 12, 15, 16)
- Dingodinium? spinosum* (Duxbury 1977) Davey 1979b
- Dingodinium albertii* Sarjeant 1966c
- Dingodinium? globosum* Duxbury n. sp. (Pl. 5, Figs. 1-4, 6, 7)
- Dingodinium tuberosum* (Gitmez 1970) Fisher and Riley 1980
- Dinogymnium aerlicum* Londeix et al. 1996 subsp. *aerlicum* autonym (Pl. 5, Figs. 8, 9)
- Dinogymnium aerlicum* subsp. *curvispinum* Duxbury n. subsp. (Pl. 4, Figs. 1-5)
- Dinogymnium circulos* Duxbury n. sp. (Pl. 4, Figs. 17, 18, 22)
- Dinogymnium rotundum* Duxbury n. sp. (Pl. 4, Figs. 20, 21, 23, 24)
- Discorsia nannus* (Davey 1974) Duxbury 1977 (Pl. 7, Figs. 15, 18)
- Dissiliodinium curiosum* Burger and Sarjeant 1995 (Pl. 15, Figs. 12, 13, 15, 16)
- Dissiliodinium globulum* Drugg 1978
- Downiesphaeridium chems* (Below 1982c) Duxbury n. comb. (Pl. 13, Figs. 10, 13)
- Downiesphaeridium flexuosum* (Davey et al. 1966) Islam 1993 (Pl. 13, Figs. 2, 3)
- Downiesphaeridium obtusum* Duxbury n. sp. (Pl. 13, Figs. 6, 9)
- Druggidium apicopaucicum* Habib 1973 (Pl. 8, Figs. 1-4, 6)
- Druggidium* cf. *apicopaucicum* Habib 1973 (Pl. 8, Figs. 5, 7, 10, 11, 14)
- Druggidium deflandrei* (Millioud 1969) Habib 1973 *sensu* Habib 1973 (Pl. 8, Figs. 8, 9, 12)

- Egmontodinium toryna* (Cookson and Eisenack 1960) Davey 1979b (Pl. 2, Figs. 6, 7)
- Elimatia discus* (Harding 1990 ex Harding in Williams et al. 1998) Duxbury 2019 (Pl. 12, Figs. 12, 17)
- Ellipsoidictyum minusculum* Duxbury n. sp. (Pl. 7, Figs. 4, 5, 9, 10-13)
- Epitricysta vinckensis* Stover and Helby 1987b
- Exiguiphaera asketa* Duxbury 2018 (Pl. 7, Fig. 21)
- Exiguiphaera lita* Duxbury 2023 (Pl. 7, Fig. 24)
- Exiguiphaera phragma* Duxbury 1979 (Pl. 7, Figs. 22, 23)
- Exochosphaeridium robustum* Backhouse 1988 (Pl. 14, Figs. 3, 18)
- Fibradinium variculum* Stover and Helby 1987c (Pl. 6, Figs. 13, 16, 18, 21)
- Fibradinium annetorpense* Morgenroth 1968
- Foucheria modesta* Monteil 1992 (Pl. 13, Figs. 5, 11)
- Gochteodinia brevispina* Duxbury n. sp. (Pl. 8, Figs. 13, 18)
- Gochteodinia minuta* Duxbury 2023 (Pl. 8, Fig. 19)
- Gochteodinia? variabilis* Duxbury n. sp. (Pl. 3, Figs. 5, 9, 10, 14)
- Halophoridia caperata* (Srivastava 1984) Duxbury n. comb. - acritarch (Pl. 14, Figs. 12-15)
- Halophoridia merraba* (Srivastava 1984) Duxbury n. comb. - acritarch
- Halophoridia xena* Cookson & Eisenack 1962a - acritarch
- Hapsocysta minuta* Duxbury n. sp. (Pl. 8, Figs. 21, 25. Pl. 15, Figs. 8, 9)
- Hapsocysta peridictya* (Eisenack and Cookson 1960) Davey 1979a (Pl. 20, Figs. 5, 7, 8, 9-12)
- Heslertonella heslertonensis* (Neale and Sarjeant 1962) Sarjeant 1966b (Pl. 11, Fig. 6)
- Heslertonella inferior* Duxbury n. sp. (Pl. 11, Figs. 1-3, 5, 7)
- Heslertonella reticulata* Duxbury 2023 (Pl. 11, Fig. 10)
- Heslertonella senecta* Harding 1990 ex Harding in Williams et al. 1998
- Heslertonella striata* (Clarke & Verdier 1967) Duxbury n. comb.
- Hystrichodinium furcatum* Alberti 1961 (Pl. 11, Fig. 14)
- Hystrichodinium pulchrum* Deflandre 1935 (Pl. 11, Fig. 9)
- Hystrichodinium ramoides* Alberti 1961
- Hystrichodinium voigtii* (Alberti 1961) Davey 1974 (Pl. 11, Fig. 13)
- Hystrichosphaeridium arborispinum* Davey and Williams 1966b
- Hystrichosphaeridium diversum* Duxbury 2018 (Pl. 19, Figs. 20-22)
- Hystrichosphaerina schindewolfii* Alberti 1961 (Pl. 19, Figs. 17-19)
- Impagidinium diversum* Duxbury 2001
- Impagidinium* LC1 (informal taxon) (Pl. 20, Figs. 1-4, 6)
- Impletosphaeridium multifurcillatum* (Prössl 1990 ex Prössl 1992) Williams et al. 1998 (Pl. 19, Fig. 4)
- Impletosphaeridium transfodum* Morgenroth 1966
- Impletosphaeridium tribuliferum* (Sarjeant 1962) Islam 1993 (Pl. 19, Figs. 6, 8)
- Isthmocystis distincta* Duxbury 1979 (Pl. 17, Figs. 2, 3, 5, 6)
- Kleithriasphaeridium corrugatum* Davey 1974 (Pl. 14, Fig. 2)
- Kleithriasphaeridium eoinodes* (Eisenack 1958) Davey 1974
- Kleithriasphaeridium fasciatum* (Davey and Williams 1966b) Davey 1974 (Pl. 14, Figs. 4, 5)
- Kleithriasphaeridium telaspinosum* (Fisher and Riley 1980) Lentini and Williams 1981
- Kleithriasphaeridium porosispinum* Davey 1982 (Pl. 2, Figs. 13, 17)
- Kleithriasphaeridium simplicispinum* (Davey and Williams 1966b) Davey 1974 (Pl. 14, Fig. 1)
- Mendicodinium reticulatum* Morgenroth 1970
- Mendicodinium* "granular" (informal taxon) (Pl. 15, Figs. 1, 2, 10)
- Mendicodinium* "reticulate" (informal taxon) (Pl. 15, Figs. 3, 5-7)
- Muderongia dedecosa* (Gocht 1957) Duxbury 2023 (Pl. 16, Fig. 3)
- Muderongia extensiva* Duxbury 1977 subsp. *extensiva* autonym (Pl. 16, Fig. 12)
- Muderongia extensiva* Duxbury 1977 subsp. *spinosa* n. subsp. (Pl. 16, Figs. 7, 8, 10)
- Muderongia mcwhaei* Cookson and Eisenack 1958
- Muderongia perforata* Alberti 1961 (Pl. 16, Fig. 6)
- Muderongia simplex* Alberti 1961 (Pl. 16, Figs. 9, 11)
- Nelchinopsis kostromiensis* (Vozzhennikova 1967) Wiggins 1972 (Pl. 5, Fig. 5)
- Nematosphaeropsis scala* Duxbury 1977 (Pl. 2, Figs. 2, 3)
- Occisucysta duxburyi* Jan du Chêne et al. 1986b
- Occisucysta tentorium* Duxbury 1977 (Pl. 18, Figs. 1, 4, 5)
- Oligosphaeridium complex* (White 1842) Davey and Williams 1966 (Pl. 18, Fig. 19)
- Oligosphaeridium diluculum* Davey 1982
- Oligosphaeridium distinctum* Duxbury 2018
- Ovoidinium? glebulentum* Duxbury n. sp. (Pl. 13, Figs. 8, 12, 16)
- Ovoidinium diversum* Davey 1979a
- Palaecysta integra* Chen 2013
- Palaecysta pectita* Chen 2013
- Palaecysta palmula* (Davey 1982) Williams and Fensome 2016 (Pl. 1, Fig. 16)
- Palleodinium digitatum* n. gen. n. sp. (Pl. 14, Figs. 9, 10. Pl. 17, Fig. 13)
- Perisseiasphaeridium cretaceum* Duxbury 2018 (Pl. 18, Fig. 9)
- Phoberocysta latissima* Duxbury n. sp. (Pl. 16, Figs. 1, 2, 5)
- Phoberocysta neocomica* (Gocht 1957) Millioud 1969 (Pl. 16, Fig. 4. Pl. 17, Figs. 8, 11)
- Polygonifera staffinensis* (Gitmez 1970) Davey 1982
- Prolixosphaeridium basifurcatum* Dodekova 1969
- Prolixosphaeridium conulum* Davey 1969a
- Prolixosphaeridium deirense* Davey et al. 1966
- Prolixosphaeridium mixtispinosum* (Klement 1960) Davey et al. 1969
- Prolixosphaeridium prolatum* Duxbury n. sp. (Pl. 12, Figs. 14-16)
- Protobatioladinium lindiense* Schrank 2005
- Protobatioladinium modestum* Duxbury n. sp. (Pl. 3, Figs. 6-8, 11-13, 15-17)
- Protobatioladinium westburiensis* Nohr-Hansen 1986
- Protoellipsodinium seghire medaure* Below 1981 (Pl. 10, Figs. 1, 2, 5, 6)
- Protoellipsodinium touile mugatae* Below 1981 (Pl. 10, Figs. 3, 9, 10, 17 and 22)
- Protoellipsodinium vacuolatum* Duxbury 2018
- Protoellipsodinium* cf. *vacuolatum* (Pl. 10, Figs. 7, 11)
- Pseudoceratium aulaeum* Harding 1990 ex Harding in Williams et al. 1998
- Pseudoceratium iehiense* Helby 1987
- Pseudoceratium pelliferum* Gocht 1957 subsp. *pelliferum* autonym (Pl. 20, Figs. 13, 14, 16)
- Pseudoceratium pelliferum* Gocht 1957 subsp. *radiculatum* Duxbury n. subsp. (Pl. 20, Figs. 17, 18)
- Pseudoceratium weymouthense* Helby 1987
- Pterodinium striatum* (Eisenack and Cookson 1960) Duxbury n. comb.
- Resticulasphaera fasciculata* Duxbury n. sp. (Pl. 10, Fig. 14-16, 19, 20)
- Resticulasphaera medusae* Harding 1990 ex Harding in Williams et al. 1998
- Rhombodella vesca* Duxbury 1980 (Pl. 15, Figs. 11, 14) - acritarch
- Rhombodella* cf. *vesca* (Pl. 6, Fig. 19) - acritarch
- Rhombodella natans* Cookson & Eisenack 1962 - acritarch

- Rigaudella filamentosa* (Cookson and Eisenack 1958) Below 1982b
- Rotosphaeropsis thula* (Davey 1982) Riding and Davey 1989
- Scriniodinium dictyotum* Cookson and Eisenack 1960
- Scriniodinium elimatum* Duxbury 2018 (Pl. 17, Figs. 9, 10, 12, 14)
- Spiculodinium alatum* (Duxbury 1977) Duxbury 2018
- Spiculodinium?* *inordinatum* Duxbury n. sp. (Pl. 18, Fig. 2, 3, 6, 12, 13)
- Spiculodinium neptuni* (Eisenack 1958) Duxbury 2018
- Spiculodinium verdieri* (Below 1982c) Duxbury 2018
- Spiniferites modestus* Duxbury 2023 (Pl. 2, Figs. 4, 8)
- Spiniferites primaevus* (Duxbury 1977) Monteil 1992b (Pl. 2, Figs. 10, 11, 13)
- Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990 (Pl. 2, Fig. 1)
- Stephanelytron cretaceum* Duxbury 1983 (Pl. 5, Figs. 18, 19)
- Subtilisphaera perlucida* (Alberti 1959) Jain and Millepieid 1973
- Subtilisphaera terrula* (Davey 1974) Lentin and Williams 1976 (Pl. 4, Fig. 6, 10, 14, 19)
- Systematophora areolata* Klement 1960
- Systematophora* cf. *areolata* Klement 1960 in Davey 1982 (Pl. 1, Figs. 11, 12, 15)
- Systematophora complicata* Neale and Sarjeant 1962 (Pl. 1, Figs. 5, 6)
- Systematophora?* *daveyi* Riding and Thomas 1988 (Pl. 1, Figs. 4, 8)
- Systematophora?* *scoriacea* (Raynaud 1978) Monteil 1992b (Pl. 19, Figs. 1, 5)
- Systematophora?* cf. *scoriacea* (Pl. 19, Figs. 7, 11-16)
- Systematophora* sp. A Monteil 1993 (Pl. 19, Fig. 2)
- Tanyosphaeridium hirsutum* Duxbury n. sp. (Pl. 12, Figs. 7-9, 13)
- Tenua* sp. cf. *Tenua colliveri* (Cookson & Eisenack 1960) Fensome et al. 2019 (Pl. 18, Figs. 14, 15)
- Thalassiphora?* *charollaisii* Monteil (in press) (Pl. 18, Figs. 7, 10, 16)
- Tubotuberella apatela* (Cookson and Eisenack 1960) Ioannides et al. 1977
- Valensiella* sp. cf. *Valensiella ovula* (Deflandre 1947) Eisenack 1963 (Pl. 7, Figs. 1-3, 6-8)
- Valensiella prenannus* Duxbury 2023 (Pl. 14, Figs. 11, 16)
- Vexillocysta retis* Harding 1990
- Vexillocysta colligata* (Morgan 1980) Duxbury 2018 (Pl. 8, Fig. 20)
- Vexillocysta spinosa* Duxbury 2018 (Pl. 13, Fig. 14)
- Wallodinium cylindricum* (Habib 1970) Duxbury 1983
- W. cylindricum* (Habib 1970) Duxbury 1983 subsp. *ornatum* n. subsp. (Pl. 2, Figs. 9, 12, 16)
- W. krutzschii* (Alberti 1961) Habib 1972
- W. luna* (Cookson and Eisenack 1960) Lentin and Williams 1973
- Wrevittia* sp. cf. *Wrevittia cassidata* (Eisenack and Cookson 1960) Helenes and Lucas-Clark 1997 (Pl. 18, Fig. 8, 11)
- Wrevittia* cf. *cassidata sensu* Duxbury 2019
- Wrevittia* cf. *cassidata sensu* Duxbury 2023
- Wrevittia diutina* (Duxbury 1977) Helenes and Lucas-Clark 1997 subsp. *patula* Duxbury 2023 (Pl. 6, Figs. 1-4, 5, 6, 9)
- Wrevittia diutina* (Duxbury 1977) Helenes and Lucas-Clark 1997 subsp. *tabulacornuta* (Prössl 1990 ex Prössl 1992) Williams et al. 1998 (Pl. 14, Figs. 6, 7. Pl. 20, Fig. 15)
- Wrevittia helocoidea* grp.
- Wrevittia?* *perforobtusata* (Duxbury 1977) Helenes and Lucas-Clark 1997 (Pl. 6, Figs. 7, 11)
- Wrevittia speciosa* (Harding 1990) Duxbury 2019

APPENDIX 2 – Species Details

Slides containing the type and figured specimens from Vergol and La Charce illustrated in the present study are housed at the Muséum d'histoire naturelle (MHN), Route de Malagnou 1, Geneva. The following is a list of these slides, including data on specimens and England Finder (E.F.) co-ordinates. Slide references at the Geneva MHN are of the format MHNG-GEPI-2024-xxxxx, where "xxxxx" refers to individual slide numbers; for the current study, numbers 20001 to 20090, listed below. A further set of slides covering the Vergol and La Charce sections analysed in the current study is stored in the collection of the Marine Palynology and Paleoceanography group, Utrecht University, The Netherlands, under code 000.000.017.384.

Slides/MHNG Refs.	Taxa	E.F. Ref.	Illustrations
Vergol Outcrop			
B97M (2)/20001	1 <i>Systematophora</i> sp. A	H55.3	Pl.19, Fig. 2
B113M (1)/20002	1 <i>I. tribuliferum</i>	N40.0	Pl.19, Fig. 6
B113M (2)/20003	1 <i>D. obtusum</i>	M44.1	Pl.13, Fig. 9
	2 <i>I. tribuliferum</i>	Q35.0	Pl.19, Fig. 8
	3 scolecodont	K50.1	Pl.21, Fig. 7
B121M (R2)/20004	1 <i>A. metaelliptica</i>	C41.0	Pl.1, Figs. 7, 10
	2 <i>S.? daveyi</i>	B42.0	Pl.1, Fig. 8
B125M (2)/20005	1 <i>W. diutina diutina</i>	M43.2	Pl.6, Fig. 20
B129M (1)/20006	1 scolecodont	W40.1	Pl.21, Fig. 6
B129M (2)/20007	1 <i>A. humilis</i>	J45.0	Holotype Pl.12, Figs. 1, 2 Pl.12, Fig. 15 Pl.13, Fig. 14
	2 <i>P. prolatum</i>	T41.3	
	3 <i>V. spinosa</i>	N40.3	
B131M (R1)/20008	1 <i>S. complicata</i>	U38.3	Holotype Holotype Pl.1, Fig. 5 Pl.10, Fig. 14 Pl.12, Fig. 13 Pl.12, Fig. 16 Pl.14, Fig. 13 Pl.14, Fig. 14 Pl.16, Fig. 9 Pl.10, Fig. 19
	2 <i>R. fasciculata</i>	U40.1	
	3 <i>T. hirsutum</i>	W42.1	
	4 <i>P. prolatum</i>	Q42.2	
	5 <i>H. caperata</i>	H52.1	
	6 <i>H. caperata</i>	Y43.4	
	7 <i>M. simplex</i>	F52.0	
	8 <i>R. fasciculata</i>	U49.3	
B131M (R3)/20009	1 <i>E. asketa</i>	K54.0	Pl.7, Fig. 21
B134M (1)/20010	1 <i>H. diversum</i>	G52.4	Pl.19, Figs. 20, 21
B136M (1)/20011	1 <i>A. humilis</i>	L31.1	Pl.12, Fig. 3
B136M (R1)/20012	1 <i>C. conspicua</i>	C42.2	Paratype Holotype Pl.3, Fig. 1 Pl.5, Fig. 8 Pl.10, Figs. 8, 12 Pl.10, Fig. 21 Pl.20, Fig. 18
	2 <i>D. aerlicum aerlicum</i>	O34.1	
	3 <i>B. johnnewingii</i>	J70.1	
	4 <i>D.? deflandrei</i>	U41.2	
	5 <i>P. pelliferum radiculatum</i>	T56.0	
B136M (R2)/20013	1 <i>P. cretaceum</i>	C45.0	Pl.18, Fig. 9
B138M (2)/20014	1 <i>B. obscurus</i>	P36.2	Paratype Pl.4, Figs. 7, 8 Pl.4, Fig. 9 Pl.4, Figs. 12, 13 Pl.4, Fig. 16 Pl.12, Fig. 14 Pl.13, Fig. 8
	2 <i>B. obscurus</i>	Q47.4	
	3 <i>B. obscurus</i>	V33.1	
	4 <i>B. obscurus</i>	R59.0	
	5 <i>P. prolatum</i>	R41.0	
	6 <i>O.? glebulentum</i>	C42.3	

B138M (3)/20015	1	<i>H. diversum</i>	M37.4		Pl.19, Fig. 22
	1	<i>P. pelliferum radiculatum</i>	P37.0		Pl.20, Fig. 17
B142M (2)/20016	1	<i>T.? charollaisii</i>	O53.4		Pl.18, Fig. 7
	2	<i>T.? charollaisii</i>	Q56.1		Pl.18, Figs. 10, 16
B151M (1b)/20017	1	<i>B. obscurus</i>	D47.0	Holotype	Pl.4, Figs. 11, 15
V5M (1)/20018	1	<i>E. lita</i>	P61.0		Pl.7, Fig. 24
	2	<i>A. extrema</i>	K41.0		Pl.12, Fig. 6
	3	<i>T. hirsutum</i>	U56.4		Pl.12, Fig. 8
V5M (2)/20019	1	<i>E. toryna</i>	H52.2		Pl.2, Fig.7
V10M (1)/20020	1	<i>A. extrema</i>	T56.4		Pl.9, Fig. 17
V10M (2)/20021	1	<i>A. pustulosa</i>	K48.1		Pl.12, Fig. 10
	2	<i>O.? glebulentum</i>	P41.2	Holotype	Pl.13, Figs. 12, 16
V14M (3)/20022	1	<i>K. fasciatum</i>	O48.2		Pl.14, Figs. 4, 5
V19M (1)/20023	1	<i>W. cretacea</i>	X39.1		Pl.6, Fig. 15
	2	<i>F. modesta</i>	K64.3		Pl.13, Fig. 5
V19M (2)/20024	1	<i>D. bensonii</i>	K56.3		Pl.2, Figs.14, 15
	2	<i>D. aerlicum aerlicum</i>	L60.1		Pl.5, Fig. 9
	3	<i>H. inferior</i>	E59.1	Holotype	Pl.11, Figs. 3, 7
V26M (1)/20025	1	<i>E. toryna</i>	O41.0		Pl.2, Fig. 6
	2	<i>S.? inordinatum</i>	O38.0	Holotype	Pl.18, Fig. 3
	3	<i>S.? inordinatum</i>	G61.4		Pl.18, Fig. 13
V26M (2)/20026	1	<i>P. seghiris medaure</i>	O47.0		Pl.10, Fig. 1
V26M (4)/20027	1	<i>S.? inordinatum</i>	V41.3		Pl.18, Fig. 2
V31M (3)/20028	1	<i>A. extrema</i>	K51.2		Pl.9, Fig. 16
	2	<i>P. latissima</i>	M46.1	Paratype	Pl.16, Fig. 1
	3	<i>P. latissima</i>	H47.0	Holotype	Pl.16, Fig. 2
	4	<i>P. latissima</i>	R52.1		Pl.16, Fig. 5
V36M (1)/20029	1	<i>S.? inordinatum</i>	K43.2		Pl.18, Fig. 6
V36M (2)/20030	1	<i>P. seghiris medaure</i>	G41.4		Pl.10, Figs. 2, 6
V36M (3)/20031	1	<i>F. modesta</i>	K47.0		Pl.13, Fig. 11
V42M (1)/20032	1	<i>D. hollisteri</i>	M54.4		Pl.6, Figs. 17, 22
V45M (1)/20033	1	<i>D. apicopaucicum</i>	E36.2		Pl.8, Figs. 1, 2
	2	<i>D. apicopaucicum</i>	Q41.3		Pl.8, Figs. 3, 4
V48M (1)/20034	1	<i>D. rotundum</i>	X28.4		Pl.4, Figs. 23, 24
	2	<i>D. apicopaucicum</i>	P53.1		Pl.8, Fig. 6
V59M (1)/20035	1	<i>S.? inordinatum</i>	K29.0		Pl.18, Fig. 12
V59M (2)/20036	1	<i>V. colligata</i>	S28.1		Pl.8, Fig. 20
V84M (1)/20037	1	<i>D. duma</i>	H49.4		Pl.19, Fig. 3

V88 (1)/20038	1	<i>S. cf. areolata</i>	O49.3		Pl.1, Fig. 11
	2	<i>S. cf. areolata</i>	P40.1		Pl.1, Fig. 15
	3	<i>S. twistringiensis</i>	M51.4		Pl. 2, Fig. 1
	4	<i>W. cylindricum ornatum</i>	B49.0	Holotype	Pl. 2, Fig. 12
	5	<i>C. colum</i>	N36.3		Pl. 6, Fig. 14
	6	<i>R. cf. vesca</i>	U44.0		Pl. 6, Fig. 19
	7	<i>R. vesca</i>	B44.3		Pl. 15, Fig. 14
	8	<i>S. elimatum</i>	O31.1		Pl. 17, Fig. 10
	9	<i>S.? cf. scoriacea</i>	H42.0		Pl. 19, Fig. 14
	10	scolecodont	E43.3		Pl.21, Fig. 5
	11	<i>S.? daveyi</i>	N40.0		Pl.1, Fig. 4
V88B/20039	1	<i>A metaelliptica</i>	R49.0		Pl.1, Fig. 1
	2	<i>A metaelliptica</i>	V48.0		Pl.1, Fig. 2
	3	<i>C. prisca</i>	K46.3	Paratype	Pl.8, Fig.16
V88 (schulze)/20040	1	<i>A metaelliptica</i>	V46.0		Pl.1, Fig. 3
	2	<i>D. bensonii</i>	U51.0		Pl.2, Fig. 18
	3	<i>D. bensonii</i>	T44.0		Pl.2, Fig. 19
	4	<i>Chlamydophorella</i> sp. A	E38.3		Pl.5, Figs. 21, 25
	5	<i>C. ambigua ambigua</i>	P56.3		Pl.5, Fig. 24
	6	<i>C. ambigua ambigua</i>	F47.0		Pl.5, Fig. 26
	7	<i>H. minuta</i>	W49.0	Holotype	Pl.8, Fig. 25
	8	<i>B. cf. micropodum</i>	E39.4		Pl.10, Fig. 13
	9	<i>B. micropodum</i>	Q39.2		Pl.10, Fig. 18
	10	<i>D. warrenii</i>	U45.3		Pl.13, Fig. 1
	11	<i>D. warrenii</i>	S45.3		Pl.13, Fig. 4
	12	<i>D. flexuosum</i>	O46.3		Pl.13, Fig. 2
	13	<i>D. flexuosum</i>	P53.0		Pl.13, Fig. 3
	14	<i>D. obtusum</i>	F41.0	Holotype	Pl.13, Fig. 6
	15	<i>D. chems</i>	Q51.0		Pl.13, Fig. 10
	16	<i>D. chems</i>	O45.3		Pl.13, Fig. 13
	17	<i>E. robustum</i>	L41.3		Pl.14, Fig. 3
	18	<i>V. prenannus/D. nannus</i>	L44.0		Pl.14, Fig. 19
	19	scolecodont	Y40.1		Pl.21, Fig. 1
	20	scolecodont	H55.4		Pl.21, Fig. 2
	21	scolecodont	D41.2		Pl.21, Fig. 3
	22	scolecodont	F56.1		Pl.21, Fig. 4
	23	scolecodont	T52.3		Pl.21, Fig. 9
V91M (1)/20041	1	<i>V. cf. ovula</i>	N37.3		Pl.7, Fig. 1
	2	<i>V. cf. ovula</i>	C45.1		Pl.7, Fig. 6
	3	<i>D. cf. apicopaucicum</i>	S39.0		Pl.8, Figs. 7, 14
	4	<i>C. maugaad</i>	Q41.0		Pl.8, Fig. 24
	5	<i>T. hirsutum</i>	N31.0		Pl.12, Fig. 9
V91M (schulze)/20042	1	<i>P. palmula</i>	W57.0		Pl.1, Fig. 16
	2	<i>D. aerlicum curvispinum</i>	Q43.0		Pl.4, Fig. 5
	3	<i>D. circulos</i>	P44.0	Holotype	Pl.4, Fig. 22
	4	<i>D. ? globosum</i>	T48.4	Holotype	Pl.5, Figs. 1, 6
	5	<i>D. ? globosum</i>	P46.1		Pl.5, Fig. 4
	6	<i>D. ? globosum</i>	V54.0	Paratype	Pl.5, Fig. 7
	7	<i>D. cf. apicopaucicum</i>	D42.0		Pl.8, Figs. 5, 11
	8	<i>H. inferior</i>	G42.4		Pl.11, Figs. 1, 5
	9	<i>H. heslertonensis</i>	B40.0		Pl.11, Figs. 6
	10	<i>P. digitatum</i>	R48.2	Holotype	Pl.14, Fig. 10
	11	<i>H. schindewolfii</i>	U36.1		Pl.19, Fig. 17
V94M (1)/20043	1	<i>F. variculum</i>	R56.4		Pl.6, Fig. 16
	2	<i>V. cf. ovula</i>	K37.4		Pl.7, Fig. 8
	3	<i>S.? cf. scoriacea</i>	P50.0		Pl.19, Fig. 13

	4	<i>S.? cf. scoriacea</i>	K50.0		Pl.19, Fig. 15
V94M (schulze)/20044	1	<i>D. rotundum</i>	D40.4	Holotype	Pl.4, Fig. 21
	2	<i>C. ambigua ambigua</i>	S41.2		Pl.5, Fig. 23
	3	<i>E. minusculum</i>	L40.1		Pl.7, Figs. 10, 11
	4	<i>E. minusculum</i>	C55.2	Holotype	Pl.7, Figs. 12, 13
	5	<i>A. trycheria</i>	U54.0		Pl.9, Figs. 6, 7
	6	<i>C. hirtellum</i>	C39.1		Pl.13, Fig. 7
	7	<i>E. robustum</i>	Y47.1		Pl.14, Fig. 18
	8	<i>Mendico. "gran."</i>	P50.2		Pl.15, Fig. 1
	9	<i>C. hirtellum</i>	B57.1		Pl.17, Fig. 4
	10	<i>S.? scoriacea</i>	Q53.0		Pl.19, Fig. 1
	11	<i>S.? scoriacea</i>	U48.2		Pl.19, Fig. 5
	12	<i>S.? cf. scoriacea</i>	Y46.0		Pl.19, Fig. 11
	13	<i>S.? cf. scoriacea</i>	K38.0		Pl.19, Fig. 12
V97M (A)/20045	1	<i>D. circulos</i>	V35.3		Pl.4, Figs. 17, 18
	2	<i>D. hollisteri</i>	N37.4		Pl.6, Figs. 8, 12
	3	<i>C. prisca</i>	B36.3		Pl.8, Fig. 15
	4	<i>C. prisca</i>	K41.2	Holotype	Pl.8, Fig. 17
	5	<i>B. varigranosum</i>	O65.3		Pl.9, Fig. 2
	6	<i>C. maculosa</i>	G41.1		Pl.11, Fig. 4
	7	<i>C. redacta</i>	P45.4	Holotype	Pl.11, Figs. 11, 12
	8	<i>C. redacta</i>	J44.3		Pl.11, Fig. 15
	9	<i>C. redacta</i>	R37.4	Paratype	Pl.11, Fig. 16
	10	<i>P. neocomica</i>	M42.0		Pl.16, Fig. 4
	11	<i>P. digitatum</i>	C47.3	Paratype	Pl.17, Fig. 13
	12	<i>H. schindewolfii</i>	H45.2		Pl.19, Fig. 18
	13	scolecodont	F33.0		Pl.21, Fig. 8
	14	<i>B. johnewingii</i>	U38.0		Pl.10, Fig. 4
	15	<i>R. fasciculata</i>	H46.4	Holotype	Pl.10, Figs. 15, 16
	16	<i>H. voigtii</i>	F37.4		Pl.11, Fig. 13
	17	<i>K. corrugatum</i>	N52.0		Pl.14, Fig. 2
	18	<i>R. vesca</i>	D48.0		Pl.15, Fig. 11
V97M (schulze)/20046	1	<i>M. dedecosa</i>	U53.0		Pl.16, Fig. 3
V101M (1)/20047	1	<i>C. validum</i>	N50.0		Pl.1, Fig. 9
	2	<i>V. cf. ovula</i>	P49.0		Pl.7, Fig. 7
	3	<i>D. cf. apicopaucicum</i>	S31.0		Pl.8, Fig. 10
	4	<i>H. minuta</i>	G43.2	Paratype	Pl.8, Fig. 21
	5	<i>Callaiosphaeridium</i> sp.	S36.0		Pl.13, Fig. 15
	6	<i>P. pelliferum pelliferum</i>	R50.2		Pl.20, Fig. 13
	7	<i>B. varigranosum</i>	H53.0		Pl.9, Fig. 3
	8	<i>C. maugaad</i>	T37.2		Pl.15, Fig. 4
V101M (schulze)/20048	1	<i>S. cf. areolata</i>	D36.0		Pl.1, Fig. 12
	2	<i>B. varigranosum</i>	L54.0		Pl.9, Fig. 1
	3	<i>B. varigranosum</i>	N38.1		Pl.9, Fig. 5
	4	<i>B. granulatum</i>	E55.0		Pl.12, Fig. 5
	5	<i>T. hirsutum</i>	R51.3	Paratype	Pl.12, Fig. 7
	7	<i>P. pelliferum pelliferum</i>	S52.3		Pl.20, Fig. 16
V102M (1)/20049	1	<i>V. cf. ovula</i>	Q44.0		Pl.7, Fig. 3
	2	<i>P. touile mugatae</i>	N42.1		Pl.10, Figs. 17, 22
	3	<i>H. minuta</i>	W51.0		Pl.15, Figs. 8, 9
V102M (schulze)/20050	1	<i>E. minusculum</i>	F39.3	Paratype	Pl.7, Figs. 4, 5, 9
	2	<i>P. seghiris medaure</i>	W42.4		Pl.10, Fig. 5

	3	<i>H. pulchrum</i>	H56.4		Pl.11, Fig. 9
	4	<i>M. extensiva spinosa</i>	F54.4		Pl.17, Fig. 1
V107M (1)/20051	1	<i>W. cylindricum ornatum</i>	E32.3		Pl.2, Fig. 9
	2	<i>D. ? globosum</i>	M34.0		Pl.5, Figs. 2, 3
	3	<i>V. cf. ovula</i>	G52.2		Pl.7, Fig. 2
	4	<i>C. reticulata</i>	L34.0		Pl.7, Figs. 16, 19
	5	<i>M. extensiva spinosa</i>	K49.0	Holotype	Pl.16, Fig. 8
	6	<i>P. neocomica</i>	N32.0		Pl.17, Fig. 8
	7	<i>T. cf. colliveri</i>	C44.3		Pl.18, Fig. 15
V107M (schulze)/20052	1	<i>C. caminus</i>	M35.0		Pl.5, Fig. 17
	2	<i>E. phragma</i>	S51.4		Pl.7, Figs. 22, 23
	3	<i>C. redacta</i>	N39.4		Pl.11, Fig. 8
	4	<i>K. simplicispinum</i>	V53.0		Pl.14, Fig. 1
	5	<i>M. extensiva spinosa</i>	E47.2	Paratype	Pl.16, Figs. 7, 10
	6	<i>O. tentoria</i>	R43.2		Pl.18, Figs. 4, 5
V111M (1)/20053	1	<i>W. cylindricum ornatum</i>	U40.0		Pl.2, Fig. 16
V112M (1)/20054	1	<i>S. exsanguia</i>	L37.1		Pl.6, Fig. 10
	2	<i>A. reticulata imparilis</i>	F32.4	Holotype	Pl.9, Figs. 11, 12
	3	<i>P. touile mugataë</i>	U48.1		Pl.10, Figs. 9, 10
	4	<i>M. simplex</i>	M43.0		Pl.16, Fig. 11
V112M (schulze)/20055	1	<i>A. reticulata imparilis</i>	L56.0		Pl.9, Fig. 18
	2	<i>A. reticulata imparilis</i>	S50.0	Paratype	Pl.9, Fig. 19
	3	<i>A. lepidum</i>	H46.1		Pl.14, Fig. 8
V116M (2)/20056	1	<i>P. pelliferum pelliferum</i>	K36.3		Pl.20, Fig. 14
V120M (0)/20057	1	<i>C. validum</i>	N34.2		Pl.1, Fig. 13
	2	<i>C. validum</i>	N52.4		Pl.1, Fig. 14
V123M (1)/20058	1	<i>D. aerlicum curvispinum</i>	N52.1		Pl.4, Fig. 3
	2	<i>D. aerlicum curvispinum</i>	D44.1		Pl.4, Fig. 4
	3	<i>S.? cf. scoriacea</i>	K53.4		Pl.19, Fig. 7
V123M (schulze)/20059	1	<i>N. scala</i>	B56.2		Pl.2, Figs. 2, 3
	2	<i>D. nannus</i>	G37.2		Pl.7, Fig. 18
	3	<i>M. perforata</i>	S40.0		Pl.16, Fig. 6
	4	scolecodont	U45.0		Pl.21, Fig. 10
V124M (1)/20060	1	<i>D. aerlicum curvispinum</i>	W35.3	Holotype	Pl.4, Figs. 1, 2
	2	<i>D. rotundum</i>	Q34.1		Pl.4, Fig. 20
	3	<i>F. variculum</i>	W37.0		Pl.6, Figs. 18, 21
	4	<i>D. deflandrei ssu Habib</i>	P46.4		Pl.8, Fig. 8
	5	<i>D. deflandrei ssu Habib</i>	Q44.1		Pl.8, Fig. 12
	6	<i>A. reticulata reticulata</i>	K40.3		Pl.9, Fig. 13
	7	<i>R. fasciculata</i>	B44.4		Pl.10, Fig. 20
	8	<i>Mendico. "retic."</i>	W49.1		Pl.15, Figs. 3, 6
V124M (schulze)/20061	1	<i>W. diutina patula</i>	N57.1		Pl.6, Figs. 1, 2
	2	<i>W. diutina patula</i>	P55.4		Pl.6, Figs. 3, 4
	3	<i>F. variculum</i>	P43.0		Pl.6, Fig. 13
	4	<i>G. brevispina</i>	V38.0	Paratype	Pl.8, Fig. 18
	5	<i>H. inferior</i>	K46.1	Paratype	Pl.11, Fig. 2
	6	<i>H. caperata</i>	G47.0		Pl.14, Fig. 12
	7	<i>H. caperata</i>	O46.2		Pl.14, Fig. 15
	8	<i>Mendico. "retic."</i>	J40.0		Pl.15, Fig. 5
	9	<i>Mendico. "retic."</i>	P47.0		Pl.15, Fig. 7

V127M (2)/20062	1	<i>M. extensiva extensiva</i>	Q60.2		Pl.16, Fig. 12
V132M (1)/20063	1	<i>S. primaevus</i>	S42.0	Holotype	Pl.2, Figs. 10, 11
	2	<i>S. terrula</i>	N36.0		Pl.4, Figs. 6, 10
	3	<i>S. terrula</i>	R32.1		Pl.4, Figs. 14, 19
	4	<i>C. caminus</i>	S48.4		Pl.5, Fig. 13
	5	<i>S. cretaceum</i>	B43.3		Pl.5, Figs. 18, 19
	6	<i>C. reticulata</i>	X44.0		Pl.7, Fig. 14
	7	<i>C. reticulata</i>	C31.1		Pl.7, Fig. 20
	8	<i>C. magna</i>	C46.0		Pl.7, Fig. 17
	9	<i>A. reticulata reticulata</i>	P43.0		Pl.9, Figs. 8, 9
	10	<i>B. longicornutum</i>	D47.0		Pl.9, Fig. 15
	11	<i>P. touile mugataë</i>	E38.3		Pl.10, Fig. 3
	12	<i>E. discus</i>	J30.4		Pl.12, Fig. 17
	13	<i>V. prenannus</i>	S31.4		Pl.14, Fig. 16
	14	<i>A. falsificum</i>	T51.3		Pl.14, Fig. 17
	15	<i>C. hirtellum</i>	X49.2		Pl.17, Fig. 7
	16	<i>P. neocomica</i>	V48.0		Pl.17, Fig. 11
	17	<i>O. complex</i>	R48.0		Pl.18, Fig. 19
	18	<i>I. multifurcillatum</i>	G36.2		Pl.19, Fig. 4
V132M (schulze)/20064	1	<i>D. cf. bensonii</i>	T33.0		Pl.2, Fig. 5
	2	<i>N. kostromiensis</i>	X40.2		Pl.5, Fig. 5
	3	<i>D. cerviculum</i>	S32.0		Pl.5, Fig. 10
	4	<i>D. cerviculum</i>	V45.2		Pl.5, Figs. 14, 22
	5	<i>Chlamydophorella</i> sp. A	Q48.0		Pl.5, Fig. 20
	6	<i>D. nannus</i>	S38.4		Pl.7, Fig. 15
	7	<i>B. inaequalis</i>	V45.0		Pl.9, Fig. 10
	8	<i>B. inaequalis</i>	D40.1		Pl.9, Fig. 14
	9	<i>H. reticulata</i>	U44.0		Pl.11, Fig. 10
	10	<i>H. furcatum</i>	O39.0		Pl.11, Fig. 14
	11	<i>B. granulatum</i>	Q53.0		Pl.12, Fig. 4
	12	<i>Mendico. "gran."</i>	X39.0		Pl.15, Fig. 10
	13	<i>T. cf. colliveri</i>	N48.1		Pl.18, Fig. 14
	14	<i>S.? cf. scoriacea</i>	T38.2		Pl.19, Fig. 16

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LCH107M (1)/20065	1	<i>I. distincta</i>	Q31.2		Pl.17, Figs. 2, 5
	2	<i>I. distincta</i>	S28.4		Pl.17, Figs. 3, 6
LCH128M (1)/20066	1	<i>D. deflandrei</i> ssu Habib	M49.2		Pl.8, Fig. 9
	2	<i>D. duma</i>	O50.4		Pl.19, Fig. 10
LCH141M (1)/20067	1	<i>K. porosispinum</i>	L49.1		Pl.2, Figs. 13, 17
	2	<i>E. discus</i>	H42.2		Pl.12, Fig. 12
LCH149M (1)/20068	1	<i>W.? perforobtusata</i>	P33.2		Pl.6, Figs. 7, 11
	2	<i>S. elimatum</i>	J33.0		Pl.17, Fig. 9
	3	<i>S. elimatum</i>	K49.0		Pl.17, Fig. 12
	4	<i>S. elimatum</i>	T34.1		Pl.17, Fig. 14
LCH160M (1)/20069	1	<i>G. minuta</i>	X37.0		Pl.8, Figs. 19
LCH164M (1)/20070	1	<i>C. conspicua</i>	G40.2	Holotype	Pl.3, Fig. 2
	2	<i>C. conspicua</i>	M31.4		Pl.3, Figs. 3, 4
	3	<i>C. conspicua</i>	G26.0	Paratype	Pl.3, Fig. 17
	4	<i>D. duma</i>	O44.2		Pl.19, Fig. 9

LCH164M (2)/20071	1	<i>G.? variabilis</i>	B46.3	Holotype	Pl.3, Figs. 5, 9
	2	<i>G.? variabilis</i>	M48.3		Pl.3, Fig. 10
	3	<i>G.? variabilis</i>	R33.1	Holotype	Pl.3, Fig. 14
	4	<i>P. modestum</i>	S43.2		Pl.3, Fig. 8
	5	<i>P. modestum</i>	F48.4		Pl.3, Fig. 15
LCH170M (1)/20072	1	<i>W. cf. cassidata</i>	K39.3		Pl.18, Fig. 8
LCH173M (1)/20073	1	<i>P. modestum</i>	N38.3		Pl.3, Fig. 16
	2	<i>W. diutina patula</i>	L55.0		Pl.6, Figs. 5, 6, 9
LCH173M (2)/20074	1	<i>W. cf. cassidata</i>	M33.3		Pl.18, Fig. 11
LCH180M (1)/20075	1	<i>P. modestum</i>	M39.3		Pl.3, Fig. 7
	2	<i>P. modestum</i>	C31.3		Pl.3, Figs. 11, 12
	3	<i>P. digitatum</i>	W34.0		Pl.14, Fig. 9
	4	<i>C. sepimentum</i>	F55.2		Pl.17, Figs. 15, 16
LCH180M (2)/20076	1	<i>P. modestum</i>	T51.0		Pl.3, Fig. 13
LCH183M (1)/20077	1	<i>S. modestus</i>	V44.1		Pl.2, Figs. 4, 8
	2	<i>P. cf. vavuolatum</i>	U43.4		Pl.10, Fig. 7
	3	<i>S. modestus</i>	W28.4		Pl.10, Fig. 11
LCH187M (2)/20078	1	<i>P. modestum</i>	Q42.4		Pl.3, Fig. 6
LCH198M (2)/20079	1	<i>C. ordinalis</i>	G55.0		Pl.18, Fig. 17
LCH198M (3)/20080	1	<i>C. ordinalis</i>	G63.4		Pl.18, Fig. 18
LCH203M (1)/20081	1	<i>C. validum "regulare"</i>	G24.0		Pl.1, Fig. 17
LCH203M (2)/20082	1	<i>Impagidinium</i> LC1	K57.4		Pl.20, Fig. 1
	1	<i>Impagidinium</i> LC1	N36.0		Pl.20, Fig. 4
LCH203M (3)/20083	1	<i>Impagidinium</i> LC1	V52.0		Pl.20, Figs. 2, 3, 6
LCH208M (1)/20084	1	<i>B. elegans</i>	P52.0		Pl.12, Fig. 11
	2	<i>W. diutina tabulacornuta</i>	O47.4		Pl.14, Figs. 6, 7
	3	<i>H. peridictya</i>	U50.1		Pl.20, Fig. 5
	4	<i>H. peridictya</i>	E55.3		Pl.20, Fig. 7
	5	<i>H. peridictya</i>	G38.0		Pl.20, Figs. 8, 11
LCH208M (2)/20085	1	<i>Mendico. "gran."</i>	P43.3		Pl.15, Fig. 2
LCH213M (1)/20086	1	<i>W. diutina tabulacornuta</i>	H48.1		Pl.20, Fig. 15
LCH216M (1)/20087	1	<i>D. curiosum</i>	F44.3		Pl.15, Fig. 12
	2	<i>D. curiosum</i>	R42.1		Pl.15, Fig. 15
LCH216M (2)/20088	1	<i>V. prenannus</i>	B34.1		Pl.14, Fig. 11
	2	<i>D. curiosum</i>	K43.4		Pl.15, Fig. 13
	3	<i>D. curiosum</i>	U42.0		Pl.15, Fig. 16
LCH220M (1)/20089	1	<i>H. peridictya</i>	E56.4		Pl.20, Fig. 10
LCH220M (2)/20090	1	<i>A. deflandrei</i>	N46.2		Pl.8, Figs. 22, 23
	2	<i>H. peridictya</i>	H57.0		Pl.20, Figs. 9, 12

APPENDIX 3 – Further analysis of the Barrande layers

The Vergol/La Charce study presented above involved the analysis of only two of the four Barrande layers, B1 and B4. The following observations were made:

- there was a marked contrast in the palynofloras of layers B1 and B4 although dinoflagellate cysts predominated in both.
- the most common dinocyst taxa in layer B1 were *Circulodinium hirtellum*, *Muderongia simplex*, *M. extensiva* and *Systematophora? cf. scoriacea*.
- the most common dinocyst taxa in layer B4 were *Batioladinium cf. varigranosum*, *Chlamyphorella* spp., *Cribroperidinium* spp. and *Dapsiladinium warrenii*.
- dinocyst diversity increased significantly between layers B1 and B4 from 42 to 59 taxa and there was an associated reduction in the proportion of coastal:lowland miospores from 70:30 to 27:73.
- miospores were abundant in layer B4, dominated by bisaccate pollen but including common *Cyathidites* spp. They were relatively rare in layer B1.
- scolecodonts were present in layer B4 but not in layer B1.

The palaeoenvironmental implications of observed assemblages were briefly discussed and reference was made to the conclusions of Kujau et al. (2012), Mattioli et al. (2014) and Reboulet et al. (2003). It was noted that palaeoenvironmental trends suggested by certain dinocyst groups, as interpreted by Wilpshaar

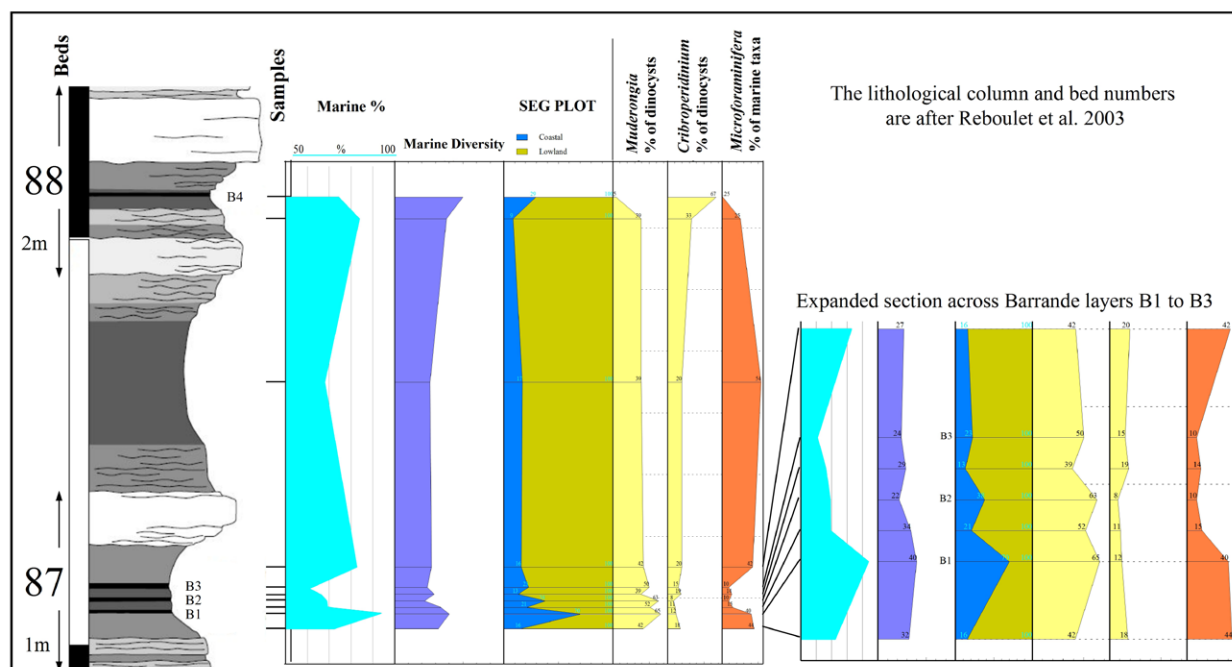
and Leereveld (1994), appeared to contradict changes in the observed Sporomorph EcoGroups of Abbink (1998), particularly the Coastal/Lowland curve.

In order to better resolve the interval containing the Barrande layers, eight further samples were processed by Dr. Nico Janssen of the TNO, Utrecht and forwarded to the author for analysis. The ten samples (including samples V87B1 and V88B4 from the original study) now spanning the Barrande layers at Vergol are illustrated in Figures A3-1 and A3-2; these are mostly clustered around the closely-spaced Barrande layers B1 to B3.

A count of 500 specimens/slide was made where possible for the new samples, but recovery was low for Barrande layers B2 (223 specimens) and B3 (281 specimens), probably due to dilution of the residue by abundant amorphous organic matter (granular AOM), presumably derived from degraded plant material but of unknown origin.

Several conclusions may be made from Figures A3-1 and A3-2:

1/. All samples are marine - the percentage of marine taxa ranges mainly between 60% and 80% but over 90% in Barrande layer B1. Dinocysts dominate, again bringing into question comments in Kujau et al (2012) about "limited dinoflagellate productivity for the four organic-rich Barrande layers". The reduction in dinosterane observed by Kujau et al (op. cit.) appears not to have been caused by dinoflagellate decline.



TEXT-FIGURE A3-1

Ten samples across the Barrande layers at Vergol plotted against the lithology and showing variations in marine influence and species diversity. A Sporomorph EcoGroup (SEG) column shows Coastal versus Lowland occurrences, a proxy for sea-level fluctuations. *Muderongia* Group and *Cribroperidinium* Group columns are plotted as percentages of total dinocysts and microforaminiferal occurrences shown are percentages of the whole marine assemblage.

2/. There is a clear trend of decreasing Coastal SEG relative to the Lowland SEG between Barrande layers B1 and B3. According to Abbink et al. 2004, this trend would reflect an overall fall in sea-level. Slight relative increases in the Coastal SEG at layers B1, B2 and B3 might suggest slight increases in sea-level at the Barrande levels within an overall trend of reducing sea level. A reduction in sea level would agree with Fig. 2 of Reboulet et al. 2003, where this part of the Vergol section is correlated with a regressive interval in the Carajuan section (Provence Platform).

3/. It was noted in the main study (above) that there was a major decrease in the *Muderongia* Group between Barrande layers B1 and B4. However, the new samples show that although there is a decline within Bed 87, a marked decrease is only seen in Barrande layer B4. Similarly, a significant increase in the *Cribroperidinium* Group was noted immediately below layer B4 but a major increase was seen only within layer B4, associated with a significant increase in the Coastal/Lowland curve.

Wilpshaar and Leereveld (1994) suggest that the *Muderongia* Group indicates nearer-shore settings than the *Cribroperidinium* Group in the Vocontian Basin, and this would agree with the Coastal/Lowland increase in Barrande layer B4. However, as noted in the main text, this does not appear to be a consistent relationship, and Figure A3/1 shows clearly that in Barrande layer B1 there is a converse relationship, with a peak in the Coastal/Lowland curve occurring at a peak in the *Muderongia* Group and relatively low numbers of *Cribroperidinium* spp.

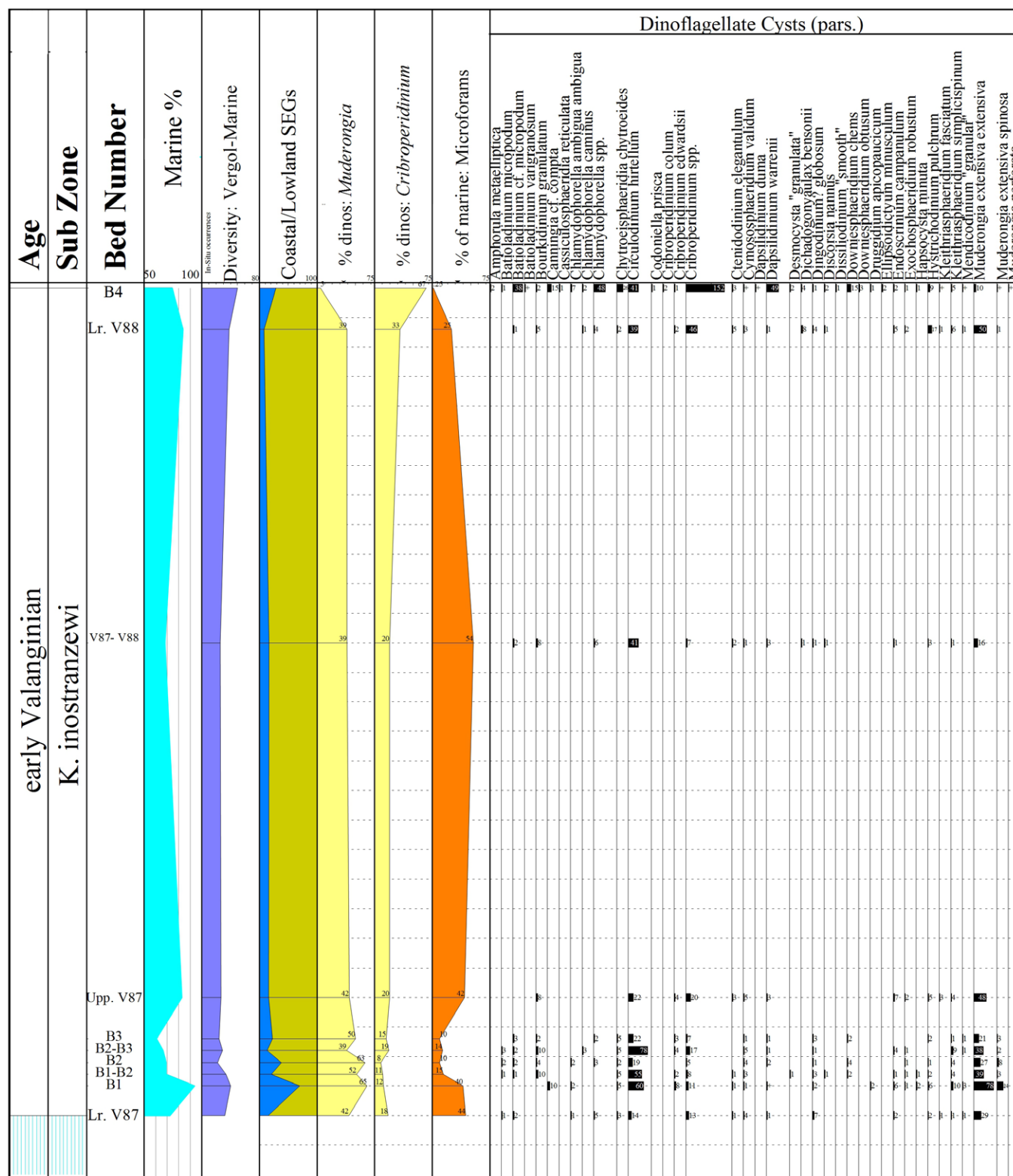
4/. The percentage of marine taxa is significant throughout, but this falls markedly from immediately above layer B1 to Barrande layer B3. This reduction is entirely due to a major reduction in microforaminiferal test linings (plotted separately in Figures

A3-1 and A3-2). A further, major reduction in microforaminiferal test linings was noted in Barrande layer B4.

Although no attempt has been made to separate individual microforaminiferal morphotypes here, their overall frequency appears to fall at sea level maxima and increase particularly in regressive phases, presumably demonstrating a preference for shallower settings. Lister and Batten (1988) stated that, "Foraminiferal test linings are also useful environmental indicators, being common in marine coastal and shallow shelf environments". The marked reductions in numbers around most of the Barrande layers at Vergol, associated with higher Coastal/Lowland miospore ratios may reflect such a preference and support a deeper setting. This does not explain the high percentage of microforaminifera in layer B1 however, associated with the highest Coastal/Lowland ratio recorded here. Variations in sea-bed oxygenation levels may also have some bearing on microforaminiferal numbers.

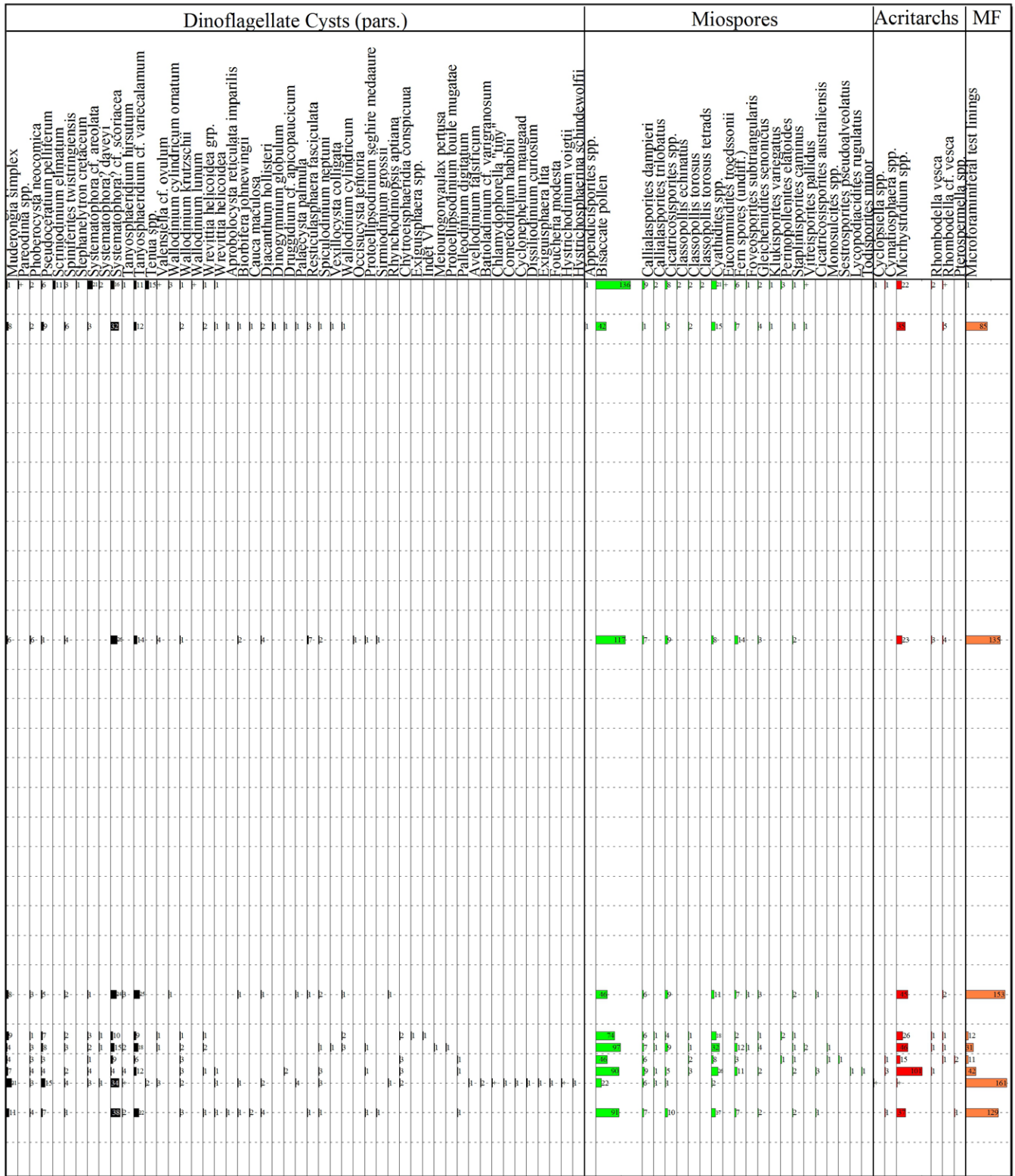
CONCLUSIONS

There are clearly significant differences between the palynofloral assemblages observed in and between the Barrande layers at Vergol, in contrast to the observations of Kujau et al. (2012) that, "no distinct difference between the four layers can be observed with respect to the biomarker patterns". Evidence here accords more closely with Reboulet et al. (2003), who described various differences between layers B1 to B3 and layer B4. However, although layers B1 to B3 and their associated marls do yield mutually similar palynofloras, there are some differences, most clearly shown in the marine diversity, Coastal/Lowland SEG and *Muderongia* % curves in Figures A3-1 and A3-2. These changes appear to be associated with a marine regression, and seem to reflect some palaeoenvironmental change even at such a small time-scale.



TEXT-FIGURE A3-2A
Stratigraphic occurrence and absolute abundance of palynomorphs in the ten samples spanning the Barrande layers.

B



TEXT-FIGURE A3-2B

Stratigraphic occurrence and absolute abundance of palynomorphs in the ten samples spanning the Barrande layers (continued).