

Organic-walled marine microplankton from the Barremian and Aptian of the North Sea Region - biostratigraphy and taxonomy

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ABSTRACT: Quantitative palynofloral analysis of 42 core chip samples from upper Barremian and Aptian sediments of the Heselton No. 2 shallow borehole (Speeton Clay Formation, Eastern England) and Gannet Field well 22/26a-2 (Valhall Formation, United Kingdom Sector, Central North Sea) has yielded very rich and diverse marine assemblages composed largely of dinocysts and acritarchs. The high biostratigraphic resolution achieved has allowed detailed correlation between the sections analysed and with third-party data from the Wiechendorf 1/86 borehole (Lower Saxony Basin), a distance of approximately 700 km; the positions and extent of several hiatuses have been assessed within this framework. The Barremian/Aptian boundary has been discussed and “conventional” palynological criteria assessed with respect to contrary microfaunal and nannofloral evidence. Close spacing of samples has allowed some assessment of inter- and intra-species trends and, although palaeoenvironmental change profoundly influences assemblages, specific controls remain poorly understood. Over-prescriptive generic placement of taxa based on what are essentially subjective criteria is critically discussed. The zonation scheme proposed by Duxbury (2001) has been re-visited and significantly refined; recognition of additional marker events has allowed further sub-division of several zones to subzonal level, allowing a better understanding of late Barremian palynostratigraphy. Seventy-nine key palynofloral events have now been recognised between the late Barremian and “mid” Aptian, including many first occurrences. One genus, 23 species and 2 subspecies of dinocysts are described as new, nine new combinations have been effected and the diagnoses of two species have been emended; one species has been reduced to sub-species rank.

Key words: Palynology, zonation, dinocysts, Barremian, Aptian, Speeton Clay, U.K., Saxony.

INTRODUCTION

The Speeton Clay Formation ranges in age from late Berriasian to Albian (ammonite and belemnite dating), and is about 300 ft (91 m) thick at its type locality in Filey Bay, east Yorkshire coast, England. It consists of a series of light to dark grey clays, marls and limestones outcropping between the Kimmeridge Clay to the north and Chalk to the south (Duxbury 2018, text-fig. 1). Since the first detailed description of the Speeton Clay by Lamplugh (1889), many authors have contributed to the understanding of this section. Several more recent accounts provide a succinct summary of this work, including Duxbury (1977, 1980, 2018), Harding (1990), Rutledge (1994), Mitchell and Underwood (1999) and Hart et al. (2009), and these details are not repeated here.

The current study presents a detailed palynofloral analysis of upper Barremian to “mid” Aptian sediments in the Heselton No. 2 borehole, a 30 metre piston-core obtained by the British Geological Survey (BGS) in 1991, about 15 km inland from the Speeton coastal outcrop (text-figs. 1, 2). Twenty-one conventional core samples have been analysed, all within the Speeton Clay Formation, and each yielded a rich and diverse palynoflora.

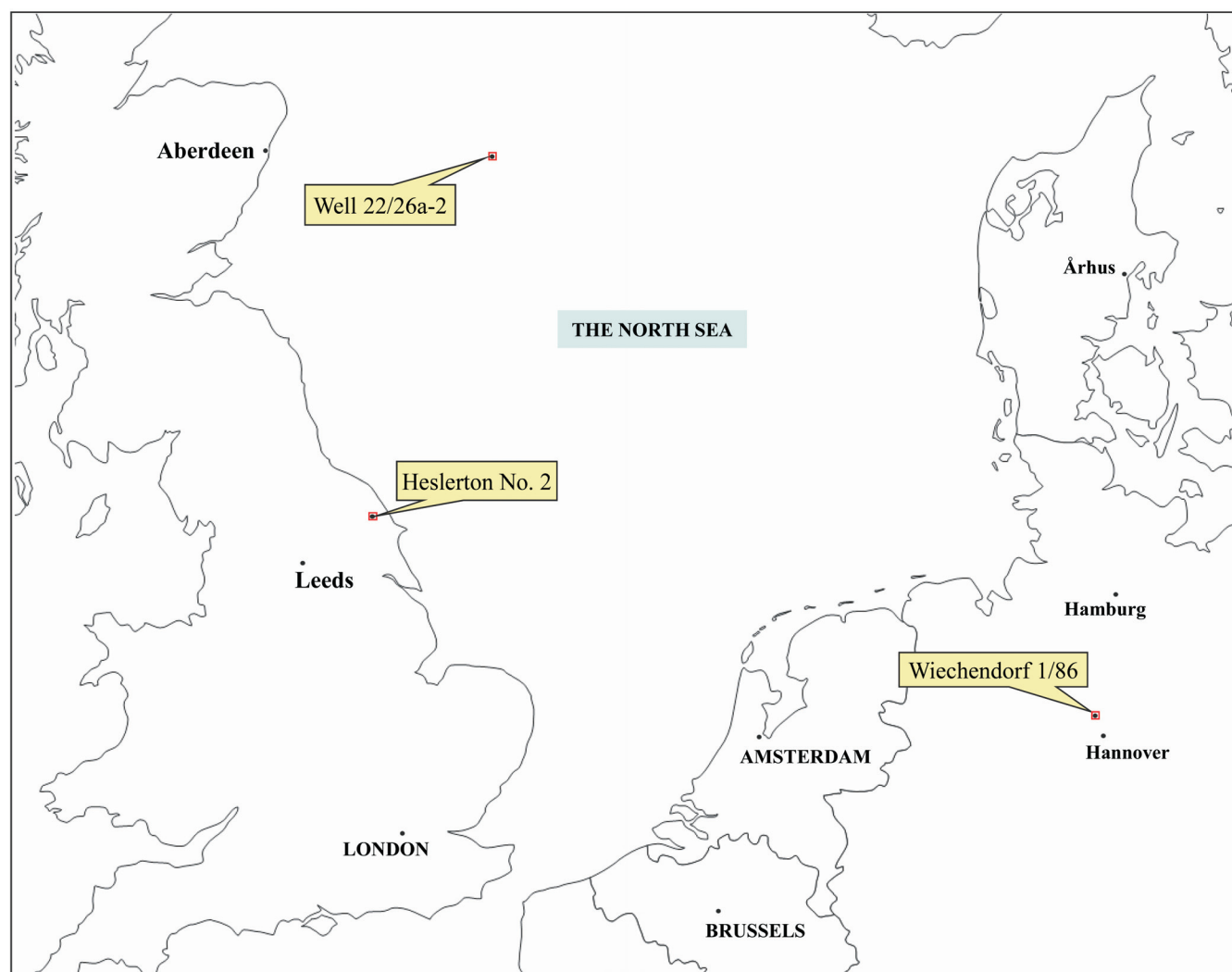
The Barremian/Aptian boundary interval was described in bed-by-bed detail for the Speeton coastal section by Mitchell and Underwood (1999), who combined fragmentary outcrop evidence. The transitory, rarely-exposed nature of outcrops in this part of the Speeton coastal section is illustrated by the ab-

sence of records of the ammonite *Prodeshayesites* (basal Aptian marker) prior to Mitchell and Underwood’s study. Although Mitchell and Underwood (op. cit.) took large samples, they did not retain any outcrop material, so that palynofloras from this part of the Speeton outcrop are as yet unstudied.

Several dinocyst species known to be restricted to the late Barremian were absent from the Heselton No. 2 core, indicating a significant hiatus. To determine if this was correct, twenty-one conventional core samples were analysed for comparison from the more complete upper Barremian interval of UKCS Central North Sea Gannet Field well 22/26a-2 (text-figs. 1, 7). Recovered palynofloras were again numerous and well-preserved.

Duxbury (2001) established a palynofloral zonation scheme for the Valanginian to basal Cenomanian, using North Sea wells in UKCS quadrants 13 and 14. Thirty-two zones were defined in the Valanginian to Albian interval, based on the recognition of over 170 palynofloral events. Resolution within upper Barremian and lower Aptian sections was, at that time, based largely on key events in cuttings suites and so relied particularly on species last occurrences.

Whilst the Duxbury (2001) scheme was fully applicable here, quantitative analysis of conventional core material has allowed the recognition of several first appearance datums (FADs), together with further last appearance datums (LADs) and acme events, adding further refinement. These additional events are



TEXT-FIGURE 1
Location map showing the wide geographic distribution of sections analysed in the current study.

discussed in the text and illustrated in text-figure 9; all samples are quoted at drilled depths throughout the text.

A multi-disciplinary attempt to characterise the Barremian/Aptian boundary of the Lower Saxony Basin was co-ordinated by Kemper, including geophysical, ammonite, microfaunal, nannofloral and palynofloral data, compiled in *Geologisches Jahrbuch Reihe A, Heft 141* (1995). Conventional core from the Wiechendorf 1/86 borehole was analysed in that work, including the Barremian/Aptian boundary. Data from Lister and Batten (1995 - Wiechendorf 1/86) have been compared with the Heslerton No. 2 and 22/26a-2 palynofloras in the present study (text-fig. 8).

The multi-disciplinary approach applied in the Lower Saxony Basin studies highlighted the difficulty in resolving the Barremian/Aptian boundary (Kemper 1995, p. 54). Palynofloral, nannofloral and microfaunal picks for that boundary disagreed, but although the last two were considered feasible by Kemper (op. cit.), he felt the “conventional” palynofloral mark-

ers of Lister and Batten (1995) to be untenable; this mis-match is further discussed here.

A thin “mid” Aptian interval in the Heslerton No. 2 borehole (text-fig. 6) again yielded rich palynofloras and these have been compared with similar assemblages in the South of England (Duxbury 1980, Lister and Batten 1988) and the Lower Saxony Basin (Heilmann-Clausen and Thomsen 1995; Lister and Batten 1995).

MATERIALS AND METHODS

Conventional core samples from the Heslerton No. 2 shallow borehole and UKCS Central North Sea well 22/26a-2 were analysed here (details below). All samples were prepared according to standard palynological methodology: 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 or Schultze reagent and preparation of slides. Samples were overwhelmingly dominated by miospores, particularly bisaccate pollen. After an initial 500 specimen per sample count of all taxa, the count of dinocysts

TABLE 1
Ammonite Zonation of the NW European Aptian (from Kemper 1995 and Erba 1996).

Two-fold subdivision (used here)	Three-fold subdivision (e.g. Kemper 1995)
	<i>Hypacanthoplites jacobi</i> UPPER APTIAN

UPPER APTIAN	<i>Parahoplites nutfieldensis</i> MIDDLE APTIAN
	<i>Epicheloniceras martinoides</i> -----
	<i>Tropaeum bowerbanki</i>
	<i>Deshayesites deshayesi</i> LOWER APTIAN
LOWER APTIAN	<i>Deshayesites forbesi</i>
	<i>Prodeshayesites fissicostatus</i>

and acritarchs was increased to 500 per sample in order to achieve numerically consistent marine assemblages.

For consistency with common use, the chronostratigraphy applied uses a two-fold sub-division of the Barremian, as opposed to the three-fold sub-division used in previous studies of the Speeton Clay (Duxbury 1977, 1980) and the Central North Sea (Duxbury 2001), so that the upper Barremian here includes all of the “middle” Barremian (essentially Speeton Cement Beds equivalents). In the Aptian, only two sub-divisions are applied here, which is usual for the Boreal Aptian, although Kemper (1995) preferred a three-fold division in Germany (see Erba 1996, Figure 3). These schemes are summarised in Table 1.

Dinocyst evidence from the highest two samples analysed from the Heslerton No. 2 borehole, at 11.50 m and 10.85 m, suggests a position close to the lower/upper Aptian boundary (using a two-fold subdivision), and possibly spanning it. Because of this uncertainty, these samples have been assigned an informal “mid” Aptian age here, which should not be confused with the formal middle Aptian applied by authors including Kemper (1995).

Where reference is made to Barremian ammonite zones, the scheme summarised in Rawson and Jeremiah (2001, Table 1) has been used (reproduced as Table 2 below), although their tentative placement of the *elegans* Zone at the top of the lower Barremian is unusual – this interpretation was also used by Jeremiah (2001, figures 7, 9). In the present study, for reasons discussed below and because of the closeness of the Heslerton No. 2 borehole to the Speeton coastal outcrop, the lower/upper Barremian boundary is placed within the *elegans* Zone and this is reflected in Table 2.

The “Speeton model” is illustrated in Harding (1990, text-fig. 3), Duxbury (2001, Figure 16) and Table 2 here, where the *elegans* Zone spans the lower/upper Barremian boundary (a boundary placed at the base of the Cement Beds at Speeton) following the German belemnite zonation (i.e., top *Aulacoteuthis* belemnite Zone = top lower Barremian).

The position of the *elegans* Zone at Speeton was discussed by Rawson and Mutterlose (1983), in their detailed description of Barremian cephalopod assemblages, and a small mis-match was noted between Speeton and German ammonite and belemnite

TABLE 2
Ammonite Zonation of the NW European Barremian (modified after Rawson and Jeremiah 2001, Table 1).

	<i>Parancyloceras bidentatum</i>
UPPER BARREMIAN	<i>Simancyloceras stolleyi</i>
	<i>Simancyloceras pingue</i>
	<i>Paracrioceras denckmanni</i>
-----	<i>Paracrioceras elegans</i>
	<i>'Hoplocrioceras' fissicostatum</i>
LOWER BARREMIAN	<i>'Hoplocrioceras' rarocinctum</i>
	<i>Simbirskites (Craspedodiscus) variabilis</i>

assemblages. Rawson and Mutterlose (op. cit., p. 144) stated, “The only anomaly is the small overlap at Speeton between the base of the *elegans* Zone and the top of the *Aulacoteuthis* Zone. This could reflect lack of detailed stratigraphical control in Germany, for in many sections there ammonites are as rare as at Speeton”.

Both the top of the *Aulacoteuthis* Zone and base *elegans* Zone are still placed at the lower/upper Barremian boundary in Germany, as illustrated by Kakabadze and Hoedemaeker (2010, p. 2), so that the mis-match between Speeton and German schemes persists. Comparing the Rawson and Jeremiah (2001) and Kakabadze and Hoedemaeker (op. cit.) schemes, the *elegans* Zone could be placed either at the base of the upper Barremian or at the top of the lower Barremian.

Rawson (1995) drew the base of the upper Barremian at the base of the *denckmanni* Zone, while suggesting that the boundary could be a little lower, “in or at the base of the *elegans* Zone”.

A more extreme placement of the *elegans* Zone was suggested by Kemper (1995, Figure 1) in a scheme including both the *elegans* and overlying *denckmanni* zones within the lower Barremian; this model would place a significant part of the Cement Beds at Speeton within the lower Barremian (although the exact top *denckmanni* Zone level at Speeton is unclear), and is not followed here.

Palynofloral zones applied to the current study are those of Duxbury (2001), with some refinement based on current observations (text-fig. 9). Because of the rarity of ammonite-dated boreal Barremian sections and particularly their almost total lack of ammonite/dinocyst calibration, no attempt has been made here to relate upper Barremian palynofloral zones to the “standard” ammonite scheme (Table 2). Similarly, although the ammonite stratigraphy across the Barremian/Aptian boundary is well understood (Kemper 1995), microfossil (including palynofloral) calibration of this boundary remains unresolved (see remarks under “Wiechendorf 1/86” below and Kemper 1995).

BACKGROUND

Heslerton No. 2 borehole

Twenty-one core samples between 29.85 m and 10.85 m from the upper Barremian and Aptian (Speeton Clay Formation) of the Heslerton No. 2 borehole (text-figs. 2, 6) have been included

in the current study, covering the lower part of the sections described in the nannofloral work of Rutledge (1994) and Jeremiah (2001). The last author has shown the section as high as 3.60 m in Heslerton No. 2 to be of a latest Early Albian age (Jeremiah, op. cit., p. 80). Detailed analysis of all samples was undertaken to resolve key events, to characterise the Barremian/Aptian boundary level and to subdivide the studied section into the palynofloral zones of Duxbury (2001). Key events are plotted in text-figure 2 against the lithology of Rutledge (1994, Figure 1.5) ex Rawson (unpublished).

Lithologically, the section represented by the Heslerton No. 2 core is very similar to the intermittently exposed uppermost part of the Filey Bay coastal succession, as described by Swinnerton (1935), Kaye (1964) and Mitchell and Underwood (1999).

There was no evidence in Heslerton No. 2 for palynofloral zones LKP23 or LKP24 (see notes under well 22/26a-2, below). This, and the major assemblage change observed, indicate a significant hiatus between the 19.00 m and 17.75 m samples, with Zone LKP25 resting on Zone LKP22 (see comments under well 22/26a-2 and on Wiechendorf 1/86, below).

Several age-diagnostic ammonites were recorded from Heslerton No. 2, including *Aconoceras nisoides* (at 12.30 m, 13.10 m and 13.60 m), indicative of a latest Barremian or earliest Aptian age, and *Parancyloceras bidentatum/scalare* (at 21.10 m), which suggests a late Barremian (?*bidentatum* Zone) age; the present study agrees with these broad age assignments. Although the dark, pyritic clay between approximately 17.75 m and 14 m was originally thought to be equivalent to the lower Aptian Fischeischiefer (see Rutledge 1994), palynofloral evidence suggests a slightly older age; there was no direct palynofloral evidence for the Fischeischiefer in the current study and a hiatus is interpreted. If that unit were present in Heslerton No. 2 it would be very thin, confined to the interval between the 14.95 m and 13.95 m samples.

A broad late Barremian to early Aptian age has been assigned to the interval 17.75 m to 14.95 m in the present study (see comments on Wiechendorf 1/86 below), with lower Aptian sediments positively identified as deep as 13.95 m.

Mitchell and Underwood (1999) described in detail the Aptian and Albian lithological and faunal stratigraphy of the type Speeton Clay Formation and stated that, "The Barremian-Aptian boundary is marked by the appearance of abundant examples of the ammonite *Prodeshayesites* and a marked lithological change from black shale to sandy mudstone".

Prodeshayesites was not reported by Rutledge (op. cit.) in Heslerton No. 2, but the up-section transition from very dark pyritic clay to medium-dark, non-glaucconitic clay at about 14 m (text-fig. 2), and the presence of *Aconoceras nisoides* as deep as 13.60 m is similar to the Barremian/Aptian transition described by Mitchell and Underwood (op. cit.) at Speeton. This is consistent with "conventional" palynofloral evidence in the present study which would place that boundary between the 14.95 m and 13.95 m samples, although in the light of Kemper (1995) the section as deep as 17.75 m may be entirely within the Aptian (see Heslerton No. 2 under "Stratigraphic Comments", below).

Rutledge (1994, p. 230) reported, "A considerable nannofloral turnover across a sharp lithological contact at 12.07 m", and in

his Figure 3.8, he tentatively inferred an intra-lower Aptian hiatus between the *forbesi* and *deshayesi* zones at that level; a similar age was concluded by Jeremiah (2001, Table C1). The nannofloral turnover around 12.07 m was similarly reflected as a marked palynofloral assemblage change between the 12.20 m and 11.50 m samples, suggesting the absence of a significant part of the lower Aptian (text-figs. 6, 8).

No detailed attempt has been made in the current study to interpret observed palynofloras palaeoenvironmentally, although significant variations in both the marine and terrestrial assemblages were recorded (see text-fig. 10). The main focus of this study has been on the marine component but, unfortunately, current understanding of the palaeoenvironmental significance of particular Early Cretaceous dinocyst and acritarch species and of variations in relative numbers of such taxa is somewhat rudimentary. Analysis of miospore assemblage changes can provide some insights (as outlined in the SporomorphEcogroup approach of Abbink 1998), but this is largely beyond the scope of the current work, although samples at 17.00 m and 13.20 m show strong peak upland/minimum lowland and peak lowland/minimum upland signals, possibly reflecting levels of maximum transgression and maximum regression respectively – these horizons are indicated in Text-figure 2, and the quantitative miospore data are presented in Text-figure 10.

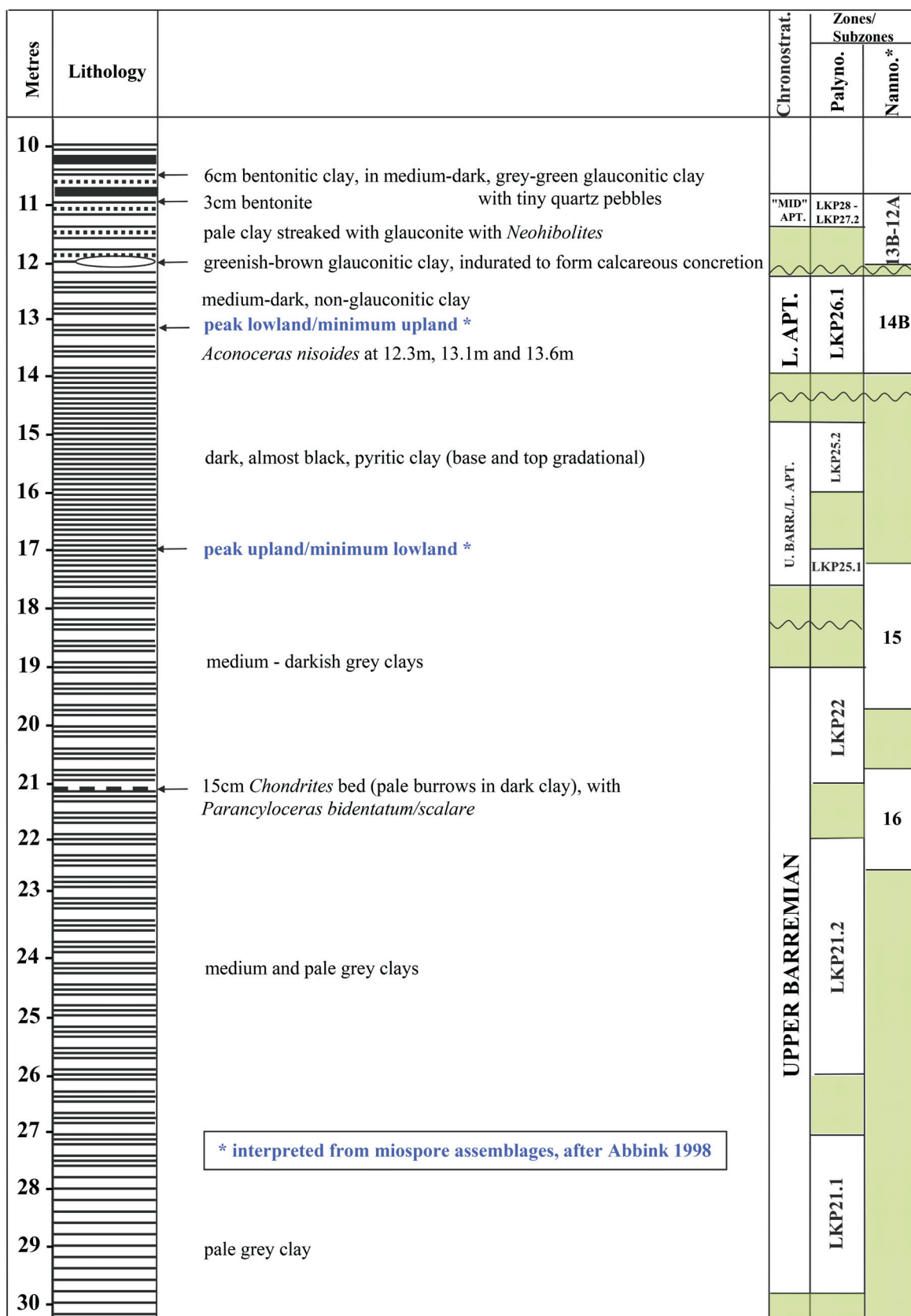
UK Central Graben well 22/26a-2

Twenty-one conventional core samples between 11,245.00 ft and 11,143.00 ft from the upper Barremian interval (Valhall Formation, pars.) of well 22/26a-2 have been included in the current study (text-figs. 2, 7). This core was previously analysed for nannofossils by Jeremiah (1991, Figure 15), who placed the V3/V4 lithological boundary (Johnson and Lott 1993) at about 11,235 ft (electric log depth – text-fig. 7). The V3/V4 boundary was placed at the "middle"/upper Barremian boundary by Johnson and Lott (op. cit., p. 48), and this corresponds well to observations here for well 22/26a-2, as the top "middle" Barremian marker, LAD *Rhynchodiniopsis fimbriata* (Duxbury 1980; 2001) was at 11,230.00 ft (text-fig. 7).

The transition across the V3/V4 boundary in well 22/26a-2 from a lower-gamma section into higher gamma shales and the LAD of *R. fimbriata* at 11,230.00 ft (text-fig. 7) suggest that the V3/V4 boundary is equivalent to the transition from the Middle B (Cement Beds) to Upper B Beds (Lamplugh 1889) in the Speeton coastal outcrop. The absence of *R. fimbriata* from all Heslerton No. 2 samples suggests that the "middle" Barremian was not penetrated to the base of that borehole.

There is a small discrepancy, however, between the range of *Rhynchodiniopsis fimbriata* observed here and at Speeton – in well 22/26a-2, the total range of *R. fimbriata* was between 11,235.00 ft and 11,230.00 ft, apparently (from log data) at the base of Unit V4, whereas at Speeton it is restricted to the Cement Beds (Unit V3 on current evidence). This could be explained by a small positive core depth to electric log depth slippage. Although no such slippage was recorded on the Shell UK data base (M. Vieira, pers. comm.), it is unlikely that the range of *R. fimbriata* would be significantly different between Speeton and the Heslerton No. 2 borehole.

Ammonites are very rare in the Cement Beds, although Rawson and Mutterlose (1983, Figure 1) tentatively placed the *elegans/denckmanni* zonal boundary at the base of their Bed 48, formally Cement Bed ζ (see Duxbury 1980, text-fig. 2). The



TEXT-FIGURE 2

Stratigraphy of the Heslerton No. 2 borehole between 10 m and 30 m, after Rutledge (1994) ex Rawson (unpublished) and palynofloral interpretation.

* Nannofloral zones after Jeremiah (2001).

FAD of *R. fimbriata* was recorded significantly higher than Cement Bed ζ by Duxbury (1980, text-fig. 3) and its FAD in well 22/26a-2, at 11,235.00 ft, therefore suggests a *denckmanni* or younger age. This fits well with nannofloral dating of a belemnite from 11,236.17 ft (see discussion below).

Rawson and Jeremiah (2001) recorded a single *Duvalia* sp. (a belemnite characteristic of the Tethyan Realm) at 11,236.17 ft, associated with an influx of the nannofossil *Isocrystallithus dispar*, a stratigraphically restricted event in the North Sea dated as late Barremian and, “probably equating to the *Simancylloceras pingue* ammonite zone” (Rawson and Jeremiah, op. cit., p. 55). The *I. dispar* influx characterises nannofloral Subzone 17A of Jeremiah (2001), although it is difficult to correlate it with the ammonite zonation. Jeremiah (op. cit., p. 64, 65) assigned a *?pingue* Zone age to the whole of Zone LK17, but then placed Subzones LK17A and 17B into *?pingue* and *?denckmanni* zones respectively. However, in his Text-figure 7, the whole of Zone LK17 is placed within the upper part of the *denckmanni* Zone. Because of this uncertainty, a broad *denckmanni/pingue* age must be assigned at 11,236.17 ft.

In addition to the influx at 11,236.17 ft, a further Tethyan incursion was noted in this well by Jeremiah (2001, p.63), characterised by influxes of the nannofossils *Micrantholithus stellatus* (between 11,154.00 ft and 11,137 ft) and *Conusphaera rothi* (between 11,154.00 ft and 11,147.00 ft). These are associated at 11,152.00 ft with flattened late Barremian heteromorph ammonites, including the genera *Camereiceras*, *Hemihoplites* and *Heteroceras*, indicative of the Tethyan *Hemihoplites feraudinianus* ammonite Subzone (see Reboulet et al. 2014, Table 1b), equivalent to the Boreal *stolleyi* Zone (Rawson and Jeremiah 2001; Jeremiah 2001).

As in Heselton No. 2, no detailed attempt has been made here to interpret observed palynofloras palaeoenvironmentally, although fully quantitative data for both marine and miospore taxa are included in Text-figure 11.

SYSTEMATICS

Several previously undescribed and stratigraphically valuable taxa were recorded during the present study, and the following section includes descriptions of one new genus, 23 new species and 2 new subspecies. Nine new combinations have been effected and the diagnoses of two species have been emended; one species has been reduced to sub-species rank. Taxa are treated alphabetically below.

All type and figured taxa, including holotypes, are curated at the Natural History Museum, Cromwell Road, London SW7 5BD. England Finder (E.F.) references are included for holotypes and paratypes in Type Locality data, and for all figured specimens in text figure and plate captions.

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

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

Remarks: This genus has been extensively discussed by various authors, notably Sarjeant (1985) and Lucas-Clark (1987), both of whom recognised the difficulties inherent in consistently differentiating it from similar genera.

The German Aptian type material of the type species, *Apteodinium granulatum* Eisenack 1958 was re-examined by Sarjeant (op. cit.), who concluded that “Eisenack’s diagnosis was too vague to be helpful”, and that, “Of all published records subsequent to Eisenack’s work, only two - those by Gocht (1959) and by Foucher and Taugourdeau (1975) - are shown by illustrations to refer to *Apteodinium granulatum*, as here redefined”. Sarjeant (op. cit.) emended the diagnoses of *Apteodinium* and *A. granulatum*, restricting the type material of the latter to Eisenack (1958, Plate 23, Figures 8–11).

Lucas-Clark (op. cit.) also emended the diagnoses of *Apteodinium* and *A. granulatum*, based primarily on Californian Albian material, accepting many authors’ attributions to *A. granulatum*, several previously rejected by Sarjeant (op. cit., p. 81, 83). The concepts of both *Apteodinium* and *A. granulatum* were broadened significantly by Lucas-Clark, reflecting the wide range of forms encompassed by her revised definitions. The range of forms included in *A. granulatum* by Lucas-Clark (op. cit. pl. 4, figs. 1–15) is considered here to be unreasonable, and far beyond Sarjeant’s or Eisenack’s concept of that species.

In her description of *A. granulatum* Lucas-Clark (op. cit.) stated that it differs from other species of *Apteodinium* in, “the degree of development of ornament or thickness of the spongy outer layer of wall”. Neither Eisenack’s original nor Sarjeant’s revised diagnosis of *A. granulatum* mentioned a spongy outer layer and Sarjeant, in contrasting *Apteodinium* and *Archeotectatum* Habib (1972) pointed out that the latter, “has a thick, spongy (sic) wall”, implying that the former does not. However, re-illustration of the type material by Jan du Chêne et al. (1986a, p. 57) and their description of *A. granulatum* (op. cit., Table 14) as “spongio-fibreux” clarifies the wall structure of this species and further confirms Lucas-Clark’s description. In the present study, specimens assigned to *Apteodinium granulatum* are restricted to those very similar to Eisenack’s type material.

Apteodinium bulla Duxbury n. sp.

Plate 13, Figures 1, 6, 9

Holotype: Plate 13, Figures 1, 6

Paratype: Plate 13, Figure 9.

Type Locality: Late Barremian-aged core chips from well 22/26a-2. Holotype: 11,167.00 ft E.F. N47.2. Paratype: 11,159.00 ft E.F. H53.0.

Derivation of Name: From the Latin *bull*a, a boss, stud - in reference to the characteristic apical horn termination of this species.

Diagnosis: A large, fairly thick-walled, spheroidal species, autophragm only, with an irregularly granular to vermiculate surface and a squat, conical apical horn. The horn is ornamented, similarly to the rest of the body surface and is typically surmounted by a small feature ranging from a pedunculate “blob” to a small, solid cylinder. The cingulum and adcingular areas are rarely indicated by faint partial tabulation marked by some alignment of body ornament, while a marked reduction in ornament marks the sulcus. Archeopyle single-plate precingular (3”).

Dimensions: Holotype: Length - 106 μ m. Width - 101 μ m. Paratype: Length - 114 μ m. Width - 114 μ m.

Overall: 129 (117) 106 μm \times 124 (110) 99 μm .

Specimens Measured: 14.

Remarks: This species has a short stratigraphic range, restricted in the present study to the 11,167.00 ft and 11,159.00 ft samples (intra-late Barremian age) in well 22/26a-2. In its large size, *Apteodinium bulla* n. sp. resembles *Apteodinium grande* Cookson and Hughes 1964 and *Apteodinium* cf. *grande sensu* Duxbury 2001 but differs from both in its very distinctive granular/vermiculate body ornament and in possessing a characteristic terminal boss at the tip of the apical horn. Because of its spheroidal shape the orientation of this species tends to be very variable.

***Apteodinium granulatatum* Eisenack 1958**

Plate 13, Figures 2, 3

Apteodinium granulatatum EISENACK 1958, p. 386–387, pl. 23, figs. 8–14

Apteodinium cf. *granulatatum* Eisenack 1958 in DUXBURY 2018, pl. 14, figs. 8, 11

Remarks: Duxbury (2018, text-fig. 10 and Plate 14, Figures 8, 11) described discrete, major influxes of “*Apteodinium* cf. *granulatatum* Eisenack 1958” within the lower Valanginian and lower Hauterivian. Large numbers of this taxon were also recorded here, within the upper Barremian. In the light of the excellent illustrations of Eisenack’s type material in Jan du Chêne et al. 1986a, specimens previously allocated to *A.* cf. *granulatatum* are now recognised as very similar to the holotype of *A. granulatatum* (Eisenack 1958, Plate 23, Figure 9) and are assigned to that species.

***Apteodinium mutabile* Duxbury n. sp.**

Plate 14, Figures 1, 2, 5, 8, 11, 12

?*Apteodinium granulatatum* Eisenack 1958 in ALBERTI 1961, pl. 4, figs. 4–6

Holotype: Plate 14, Figure 5

Paratype: Plate 14, Figures 11, 12

Type Locality: Heselton No. 2 at 26.00 m (core chip), late Barremian age. Holotype: E.F. T37.4. Paratype: E.F. T27.1

Derivation of Name: From the Latin *mutabilis*, changeable - in reference to the variability in morphology of this species.

Diagnosis: A thin-walled, ovoidal to ellipsoidal species, autophragm only, with a smooth to rarely microrugulate surface and a prominent apical horn. The horn is bifurcated, consisting of a hollow, distally-closed elongation of the main cyst, surmounted by a short spike or relatively broad, flexible extension. Conspicuous folds cover the surface of the cyst and these are frequently developed into prominent outgrowths, particularly on the hypocyst. The form and number of outgrowths varies markedly between specimens. Archeopyle single plate precingular (3”).

Dimensions (including outgrowths): Holotype: Length - 89 μm . Width - 58 μm . Paratype: Length - 68 μm . Width - 73 μm .

Overall: 91 (77) 68 μm \times 73 (60) 53 μm .

Specimens Measured: 5.

Remarks: This is a rare and unusual species exhibiting a wide morphological range, from relatively simple specimens (Plate 14, Figure 1) limited to surficial folds to specimens with several prominent outgrowths (Plate 14, Figures 11, 12), particularly on the hypocyst. Complex specimens can be reminiscent of the pareodiniacean *Cantulodinium speciosum* Alberti 1961, but differ in having a single plate (3”) archeopyle, as opposed to the intercalary archeopyle of *C. speciosum*.

The dimensions of this species vary significantly and relate directly to the degree and locations of outgrowth development. Despite the sometimes complex morphology, there appears to be only a single cyst wall.

Apteodinium mutabile was restricted to the late Barremian, occurring between 26.00 m and 20.00 m in Heselton No. 2 (more extreme specimens between 26.00 m and 22.95 m), and possibly encompasses specimens illustrated by Alberti (1961, Plate 4, Figures 4–6) as *Apteodinium granulatatum*, also from the late Barremian. Sarjeant (1985, p. 83) included one of Alberti’s specimens (Alberti 1961, Plate 4, Figure 5) within *Apteodinium thelium* Sarjeant 1985, but this is rejected here. Although the age range of *A. thelium* quoted by Sarjeant is late Barremian to late Aptian, this appears to be only because of the inclusion of Alberti’s specimen; all of Sarjeant’s (op. cit.) type material for *A. thelium* is from the late Aptian.

***Apteodinium paeminosum* Duxbury n. sp.**

Plate 14, Figures 7, 9, 10, 13

Holotype: Plate 14, Figures 9, 13

Paratypes: Plate 14, Figures 7, 10

Type Locality: Heselton No. 2 at 11.50 m (core chip), “mid” Aptian. Holotype: E.F. J47.2. Paratype: E.F. O25.1

Derivation of Name: From the Latin *paeminosus*, uneven, rough - in reference to the surface ornament of this species.

Diagnosis: A large, thin-walled, spheroidal to ovoidal species, autophragm only, with an irregular surface ornament of low relief, consisting of slightly raised maculae to very rare conical. The unornamented, prominent apical horn is elongate conical and can have a distally closed extension. Indications of tabulation are absent, except for a large single-plate archeopyle (3”) and the cyst wall is often folded around the assumed circular area. Further folding reflects the delicate nature of this species.

Dimensions: Holotype: Length - 89 μm . Width - 81 μm . Paratype: Length - 81 μm . Width - 89 μm .

Overall: 96 (87) 73 μm \times 89 (75) 63 μm .

Specimens Measured: 11.

Remarks: This is a large form but significantly smaller and thinner walled than *Apteodinium bulla* n. sp., *Apteodinium grande* and *Apteodinium* cf. *grande sensu* Duxbury (2001), differing from each in having low ornament of slightly raised maculae to very rare conical. It differs further from *A. bulla* in having an unornamented apical horn and in its absence of tabulation except where indicated by the archeopyle.

Apteodinium paeminosum is restricted in the present study to the 11.50 m and 10.85 m samples (“mid” Aptian) in Heselton No. 2, being particularly common at the deeper level.

***Apteodinium parvigranulatum* Duxbury n. sp.**

Plate 14, Figures 3, 4, 6

Holotype: Plate 14, Figure 4.

Type Locality: Well 22/26a-2 at 11,179.50 ft (core chip), late Barremian age. Holotype: E.F. R50.2.

Derivation of Name: From the Latin parvus, little and granulum, a small seed - in reference to the surface ornament of this species.

Diagnosis: A thin-walled, ovoidal to ellipsoidal species, autophragm only, with a dense, very finely granular surface ornament and a prominent apical horn. The horn is hollow, distally closed, triangular in longitudinal section and can be simple or possess a short apical extension. There is no indication of tabulation, except for the single plate precingular archeopyle (3").

Dimensions: Holotype: Length - 68 µm. Width - 51 µm.

Overall: 86 (73) 61 µm × 71 (58) 48 µm.

Specimens Measured: 22.

Remarks: This species is restricted to usually small, "simple" forms possessing a thin autophragm covered in small granules and is thereby distinguished from Eisenack's type material of *Apteodinium granulatum*, as resolved by Sarjeant (1985). Although the morphology of *A. parvigranulatum* differs significantly from *A. granulatum*, it has no doubt been commonly assigned to the latter species by other authors.

Apteodinium parvigranulatum is similar in size to *Apteodinium mutabile* but the latter species is smooth-walled, highly folded and tends to have variously-developed outgrowths.

In having ornament over the entire surface and in lacking any trace of tabulation (except for the archeopyle), *A. parvigranulatum* is similar to *Apteodinium paeminosum*. It differs in being generally smaller, more elongate and in possessing dense, finely granular surface ornament; *A. paeminosum* has an irregular surface ornament of low relief, consisting of slightly raised maculae, with very rare coni.

Apteodinium parvigranulatum was restricted to the late Barremian here, occurring between 28.00 m and 19.00 m in Heselton No. 2 and between 11,235.00 ft and 11,179.50 ft in well 22/26a-2.

Genus ***Batioladinium*** Brideaux 1975

Necrobroomea WIGGINS 1975, p. 111

Type: Alberti 1961, Plate 5, Figure 2, as *Broomea jaegeri*.

Remarks: This genus was relatively uncommon in the present study and was represented by only three long-ranging species, *Batioladinium jaegeri* (Alberti 1961) Brideaux 1975, *B. longicornutum* (Alberti 1961) Brideaux 1975 and *B. micropodum* (Eisenack and Cookson 1960) Brideaux 1975.

Batioladinium longicornutum is smooth (Harding 1990, p. 46) and the antapical horns, are well-developed (Plate 6, Figure 16), of approximately equal length and can carry ragged ornament. The FAD of this species is within the lower Valanginian, palynofloral Subzone LKP8.3 (Duxbury 2018), and its LAD

was considered a near top-Barremian marker, top Zone LKP24, in Duxbury (2001, p. 128 and Figure 16). In the present study it has been shown to range slightly higher, to the top of Zone LKP25. Zone LKP25 has been re-assigned a late Barremian to early Aptian age on third party evidence from the Lower Saxony Basin (see remarks under "Wiechendorf 1/86", below).

Batioladinium micropodum was described by Eisenack and Cookson (1960, p. 8, 9) as having, "Shell-membrane rather thick, coarsely and closely granular", and this characteristic appears to be unique within this genus; in the present study, *B. micropodum* is limited to specimens having particularly dense surface ornament (Plate 6, Figures 2, 9). The present author agrees with Wiggins (1975, p. 111) in considering *Broomea* (now *Batioladinium*?) *pellifera* Alberti 1961 a taxonomic junior synonym of *Batioladinium micropodum* – Alberti's holotype (op. cit., Plate 5, Figure 11) is very similar to and of the same age (late Barremian) as the specimen figured in Plate 6 Figures 2, 9 here as *B. micropodum*.

Davey (1974, p. 64) included several of Alberti's figured specimens of *Batioladinium jaegeri* (Alberti op. cit. Plate 5, Figures 3-7) in *Batioladinium micropodum* (as "*Broomea*" *micropoda*), but not Alberti's other figured specimens, which include the holotype (Alberti op. cit., Plate 5, Figure 2). In his remarks on *B. micropodum*, Davey (op. cit., p. 64) stated that "the apical horn is variable but is usually short", presumably his reason for not transferring specimens of *B. jaegeri* figured by Alberti (op. cit.) with longer apical horns, including the holotype. In the present study, specimens assigned to *B. jaegeri* (Plate 10, Figure 14) have a characteristic "fish-tail" antapex, well-illustrated in all of Alberti's figured specimens, and they are either smooth or lightly ornamented, both features in contrast to the dense ornament of *B. micropodum*. Davey's inclusion of several of Alberti's figured specimens of *Batioladinium jaegeri* into *Batioladinium micropodum* is therefore rejected here.

Genus ***Biorbifera*** Habib 1972

Type: Habib 1972, Plate 10, Figure 3, as *Biorbifera johne-wingii*.

***Biorbifera barremiana* Duxbury n. sp.**

Plate 3, Figures 5, 12, 19

Holotype: Plate 3, Figure 19.

Type Locality: Heselton No. 2 at 26.00 m (core chip), late Barremian age. Holotype: E.F. N45.4.

Derivation of Name: From "Barremian" - in reference to the observed range of this species.

Diagnosis: A small, spheroidal to ovoidal species with a wide cingulum and broadly rounded poles. The cyst surface bears dense granules or coni associated with relatively widely-spaced, short, broadly-tapering, acuminate spines which are occasionally linked by slender trabeculae close to their contact with the main body. The cingulum is devoid of spines. The hypocyst is significantly longer than the epicyst. Archeopyle epicystal, operculum attached.

Dimensions: Holotype: Length - 30 µm. Width - 25 µm.

Overall: 30 (27) 25 µm × 25(24) 23 µm.

Specimens Measured: 3.

Remarks: This very small species is similar to *Biorbifera johnewingii* Habib 1972 in the absence of apical or antapical projections, in having a cover of spines and in displaying an epicystal archeopyle. It is also similar in having a denser cover of much shorter ornament, not recognised by Habib (op. cit.) but clearly shown by Below (1987, Plate 27, Figures 1-7, 13, 14, 19, 20). Below (op. cit.) also showed that spines can be absent from the cingular area of *B. johnewingii*, just as in *B. barremiana* n. sp.

In contrast to *B. johnewingii*, *B. barremiana* has a much more rounded outline, with little or no indentation of the cingulum and significantly fewer spines. Also, Habib (1976, p. 384) stated that, "In most cases, the distribution of the spinate processes is nontabular, with fewer processes present on the cingulum. In others, however, cyst tabulation is expressed by peritabular and intratabular arrangement of the processes, outlining plates of the precingular, cingular, postcingular, and antapical series". No clear indication of tabulation has been observed in *B. barremiana*, possibly because of the less dense spine cover.

A further feature of *B. barremiana* which was not demonstrated in *B. johnewingii* either by Habib (1972, 1976) or Below (1987) is the lateral connection of some spines by slender "bars" a short distance from the cyst surface. This feature is seen on the epicyst of the holotype of *B. barremiana* (Plate 3, Figure 19).

Genus *Carpodinium* Cookson and Eisenack 1962 emend. Leffingwell and Morgan 1977

Type: Cookson and Eisenack 1962, Plate 1, Figures 6-9, as *Carpodinium granulatum*.

***Carpodinium glabrum* Duxbury n. sp.**

Plate 16, Figures 1-3, 5, 6

Carpodinium granulatum Cookson and Eisenack 1962 emend. Leffingwell and Morgan 1977 in DUXBURY 1980, pl. 3, fig. 7

Holotype: Plate 16, Figures 1, 5.

Type Locality: Heslerton No. 2 at 29.85 m (core chip), late Barremian age. Holotype: E.F. B38.0.

Derivation of Name: From the Latin *glabrum*, hairless, smooth – in reference to the lack of ornament.

Diagnosis: A smooth, elongate ovoidal species with a hyaline endocyst and a prominent apical horn. Wall layers closely appressed over most plates, but with marked suturocavation. Small, circular holes are occasionally present within the main plate areas. Sutural crests are regularly to irregularly denticulate, marking a tabulation of '?', 6", ?c, 5 - 6", 1p, 1pv, 1"', and denticles surrounding the antapical plate may be significantly better-developed than elsewhere. A prominent ventral pericoel displays three or more perforations of varying sizes, presumably reflecting the perisulcal plates, so that in some cases this produces a ventral "string bag" effect. The archeopyle is single-plate precingular (3").

Dimensions: Holotype: Length - 66 µm. Width - 46 µm.

Overall: Length - 66 (65) 63 µm; Width - 46 (41) 35 µm.

Specimens Measured: 8.

Remarks: No determination of the apical or cingular series has been possible here. Although cingular crests are often well developed, the cingulum tends to be featureless with wall layers closely appressed.

In their comprehensive emendation and comments on *Carpodinium granulatum*, Leffingwell and Morgan (1977, p. 297, 298) described a wide morphological range, similar in several respects to *Carpodinium glabrum*. However, their description of sutural crests of the antapical plate, "developed weakly, if at all" contrasts with those of *C. glabrum*, which bears prominent, denticulate crests (Plate 16, Figures 1, 3). Also, their descriptions and graphical illustrations (op. cit. text-fig. 6) show none of the ventral cavation or fenestration typical of *C. glabrum*.

The specimens referred to *Carpodinium granulatum* by Duxbury (1980) are included in *Carpodinium glabrum* here; the characteristic ventral pericoel is clearly illustrated in Duxbury (op. cit., Plate 3, Figure 7).

The age range of *C. glabrum* appears to be restricted within the late Barremian and in the present study it occurred only in the deepest 4 samples analysed in Heslerton No. 2 and in a single sample (11,210.00 ft) in well 22/26a-2, in both cases assigned to palynofloral Subzone LKP21.1. This is well below the Aptian inception of *Carpodinium granulatum* in Australia noted by Leffingwell and Morgan (op. cit., p. 301) and figured by Morgan (1980, Figure 8). An English late Aptian FAD was recorded for *C. granulatum* in Duxbury 1983, text-figs. 2-4.

***Cassiculosphaeridia* Davey 1969**

Type: Davey 1969, Plate 4, Figure 3, as *Cassiculosphaeridia reticulata*.

Remarks: It is difficult to consistently distinguish at generic or specific level various forms with circular to subcircular outlines, a surface reticulum developed to varying degrees and a tetratabular apical archeopyle. Such forms have a very long stratigraphic range and are morphologically relatively "simple", so that their separation depends on which criteria are considered by each author to be taxonomically important.

In his description of *Cassiculosphaeridia*, Davey (1969, p. 141) noted the similarity of his genus to *Ellipsoidictyum cinctum* Klement 1960, the first differing in lacking "all signs of a tabulation", whereas in *Ellipsoidictyum* "there is an obvious cingulum". This was only partly supported by Harding (1990, p. 49) in his emendation of *Cassiculosphaeridia magna* Davey 1974, who described the cingulum as, "Usually undifferentiated, but sometimes delineated by quasi-parallel orientation of septa". In the present study a very similar species, *Cassiculosphaeridia calvata* n. sp. displays a marked cingular bulge produced by wall layer separation, and in this case a "cingular zone" can be further enhanced by surface ornament (Plate 12, Figure 12).

Ellipsoidictyum imperfectum (Brideaux and McIntyre 1975) Lentini and Williams 1977 was described (as *Dictyopyxidina imperfecta*) from the Aptian to middle Albian of Canada. Characteristics described for *E. imperfectum* (Brideaux and McIntyre 1975, p. 25) included, "a low, perfect to imperfect, reticulate network....a sinistral cingulum, and sulcal region, outlined respectively by a transverse, elongate pair of low ridges and an absence or reduction of the reticulum..... tabulation not determinable".

Although Davey (1969) was referenced elsewhere in Brideaux and McIntyre (op. cit.) those authors did not compare *E. imperfectum* with the similar species *Cassiculosphaeridia reticulata*, the type species of *Cassiculosphaeridia*. However, the main differences appear to be the presence in *E. imperfectum* of a cingulum and reduction of the surface reticulum in the sulcal area; reference to a cingulum reinforces Davey's (1969, p. 141) separation of *Ellipsoidictyum* from *Cassiculosphaeridia*.

Further species similar to *Cassiculosphaeridia reticulata* include *Ellipsoidictyum sagena* (Duxbury 1980) Below 1982a and *Ellipsoidictyum imperfectum*. Below (1982a, p. 346) transferred *Lithodinia sagena* Duxbury 1980 to *Ellipsoidictyum*, and Williams et al. (1993, p. 56) also suggested this transfer, as "The reticulate ornamentation precludes retention in *Lithodinia*". This transfer is accepted here.

Harding (1990, p. 35) described in detail *Ellipsoidictyum sagena* (as *Meiourogonyaulax sagena*), but without reference to Below (1982a) or to the genus *Ellipsoidictyum*.

The wall structure of this group of cysts has been variously described. Davey (1969, p. 141) stated that *Cassiculosphaeridia* has "two layers", with the "Periphragm giving rise to low crests or membranes which form a reticulate pattern"; this suggests an endophragm/periphragm relationship. A similar relationship was described for *Ellipsoidictyum imperfectum* (as *Dictyopyxidina imperfecta*) by Brideaux and McIntyre (1975, p. 25), who stated, "Wall two-layered; endophragm simple; periphragm forming a low, perfect to imperfect, reticulate network".

Courtinat (1989, p.182) considered *Cassiculosphaeridia* to be a taxonomic junior synonym of *Valensiella* Eisenack 1963 emend. Courtinat 1989. However, Slimani (1994) rejected this, observing that in his own (Campanian to Danian) material re-worked specimens of *Valensiella ovulum* (the type species) possessed an ectophragm, something not observed by Courtinat (op. cit.), although this was observed by Deflandre (1947) in his original diagnosis, as confirmed by Stover and Evitt (1978, p. 86).

Slimani's rejection of Courtinat's proposal therefore appears to rest on the absence of an ectophragm in *Cassiculosphaeridia*, although Harding (1990, p. 48) described *Cassiculosphaeridia* with, "an autophragm (bearing nontabular muri or septa in the form of a pseudo-reticulum) supporting an ectophragm". This suggests that to Harding (op. cit.) the presence of an ectophragm does not exclude species from *Cassiculosphaeridia* - Harding's work was not discussed by Slimani (op. cit.).

The structure of *Ellipsoidictyum sagena* appears to support Harding's interpretation (autophragm plus ectophragm) as, in all respects other than the presence of delicate, denticulate crests running across the reticulation, that species is very similar to *Ellipsoidictyum imperfectum* and *Cassiculosphaeridia reticulata* (see Below 1982a, p. 346). The tabulation of *E. sagena* (see Harding 1990; p. 35) is therefore expressed entirely over the ectophragm surface. This might also suggest that the "transverse, elongate pair of low ridges" (Brideaux and McIntyre 1975; p. 25) marking the cingulum in *E. imperfectum* are entirely within the autophragm.

In the present study, species of *Cassiculosphaeridia* and *Ellipsoidictyum* are separated according to the development of tabulation and nature of the reticulum as follows:

Cassiculosphaeridia reticulata Davey 1969 – cysts bearing a complete surface reticulation, lacking any signs of tabulation and with no obvious cingulum but with a delicate ectophragm.

Ellipsoidictyum imperfectum (Brideaux and McIntyre 1975) Lentin and Williams 1977 – cysts with a low, "perfect to imperfect" reticulum, a cingulum but no clear tabulation and with the reticulum reduced or absent in the sulcal area.

Ellipsoidictyum sagena (Duxbury 1980) Lentin and Williams 1981 – cysts with a complete to degenerate surface reticulum and an ectophragm crossed by denticulate crests marking a typically gonyaulacacean tabulation.

This approach allows an ectophragm in both *Cassiculosphaeridia* and *Ellipsoidictyum*, contradicting Slimani's separation of the first from *Valensiella* and Stover and Evitt's (1978, p. 43) description of the latter as, "autophragm only", although the inclusion of these forms in *Cassiculosphaeridia* and *Ellipsoidictyum* does not necessarily accurately reflect these Early Cretaceous species' relationships to each other.

The type species of *Ellipsoidictyum*, *E. cinctum* Klement 1960 was described from the Oxfordian and may bear a more remote relationship to *E. imperfectum* and *E. sagena* than those species bear to each other and to *Cassiculosphaeridia reticulata*. The FAD of the last species was recorded only to the base of the Valanginian in Duxbury (2018), suggesting that "*Cassiculosphaeridia*-like" taxa as discussed here might be restricted entirely to the Cretaceous and might be better separated from superficially similar Jurassic species.

***Cassiculosphaeridia calvata* Duxbury n. sp.**

Plate 12, Figures 3, 6, 9, 12

Holotype: Plate 12, Figures 3, 6, 9.

Type Locality: Heslerton No. 2 at 26.00 m (core chip), late Barremian age. Holotype: E.F. Y29.4.

Derivation of Name: From the Latin *calvatus*, made bare, bald - in reference to the reduced ornament.

Diagnosis: A large species of *Cassiculosphaeridia* characterised by significant reduction or loss of reticulation in the mid-dorsal and mid-ventral areas. Clear separation of autophragm and ectophragm is observed, particularly around the cingulum, producing a prominent paracingular bulge. Archeopyle tetratabular apical with the operculum usually lost.

Dimensions: Holotype: Length - 81 µm; Width - 101 µm.

Overall: Length - 81 (79) 76 µm; Width - 101 (96) 89 µm.

Specimens Measured: 4 (all with operculum detached).

Remarks: Harding (1990, p. 51) referred to the extinction of *Cassiculosphaeridia magna* Davey 1974 "during Hauptblatterton event times", early Barremian, contrary to quoted ranges in Davey (1974) and Duxbury (1980) which included occurrences of a late Barremian age. He speculated that, "The anomalous ranges cited by Davey and Duxbury may well refer to records of a similar large reticulate dinocyst which occurs

sporadically from the end of the Hauptblatterton event into late Barremian time. This form has an apical archeopyle (tA), but is also characterised by a prominent paracingular bulge and a noticeable sulcal groove”.

Although not illustrated by Harding, the “similar large reticulate dinocyst” referred to by him was noted in the current study and is described here as *Cassiculosphaeridia calvata*. The stratigraphic range of *C. calvata* is confined to the late Barremian in Heselton No. 2 (26.00 m to 22.00 m samples), whereas *C. magna* ranges only as high as the 27.05 m sample. The transition between the two species appears therefore to be within the late Barremian, a younger level than suggested by Harding (op. cit., p. 51).

This species represents the youngest occurrence of large *Cassiculosphaeridia* spp. and its development is interpreted as a response to environmental pressures (currently unresolved) on the very long-ranging species *Cassiculosphaeridia magna* towards the top of its range. The transition from *Cassiculosphaeridia magna* to *C. calvata* appears to involve a “loosening” of the ectophragm layer and loss of the characteristic clear surface reticulation. Ultimately, only hints of the original reticulation are retained, confined to the cingulum and cyst margin, with the mid-dorsal and mid-ventral areas clear. The cingular bulge produced by wall layer separation is particularly notable.

Chlamydophorella Cookson and Eisenack 1958 emend. Duxbury 1983

Chlamydophorella COOKSON and EISENACK 1958, p. 56
Gardodinium ALBERTI 1961, p. 18

Type: Cookson and Eisenack 1958, Plate 11, Figure 1, as *Chlamydophorella nyei*.

Remarks: The large morphological range of this genus was noted in Duxbury 1983 (p. 41) and numerous specimens with a similarly wide range were recorded in the present study. These have not been fully sub-divided here, as there appears to be no stratigraphic value in doing so and because gradations between particular morphotypes are common. However, *Chlamydophorella membranoperforata* Below 1982a is exceptional in being particularly distinctive with its elongate shape and relatively coarsely reticulate ectophragm and in offering some stratigraphic value.

Chlamydophorella membranoperforata Below 1982a
Plate 1, Figure 18. Plate 18, Figure 20

Chlamydophorella membranoperforata BELOW 1982a, p. 345, fig. 3.

Remarks: In the present study, *C. membranoperforata* was recorded throughout much of the section analysed in well 22/26a-2 (11,230.00 ft to 11,143.00.0 ft) but in Heselton No. 2 it ranged no higher than 16.00 m, confirming its LAD close to the Barremian/Aptian boundary (text-fig. 6). In both 22/26a-2 and Heselton No. 2, the oldest common occurrence of this species was within palynofloral Zone LKP22 (intra-late Barremian age), and this event is considered a key correlation point between those wells (text-fig. 8).

The stratigraphic distribution of *C. membranoperforata* outside of the study area is difficult to assess, as it is rarely differentiated. It was not noted by Lister and Batten (1995), Heilmann-Clausen and Thomson (1995) or Harding (1990), although the last author appears to have included it within *Chlamydo-*

phorella nyei Cookson and Eisenack 1958 (see Harding, op. cit.; Plate 26, Figures 9-16).

Cribroperidinium Neale and Sarjeant 1962 emend. Davey 1969, 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, Plate 19, Figure 4; text-figure 3a–b, as *Cribroperidinium sepimentum*

Remarks: This genus was restricted by Helenes (1984, p. 112) to acavate cysts, stating the following, “Autophragm only, it may be differentiated into a homogeneous and structureless inner part and a vesicular to “spongy looking” outer part, but without separation between layers”. Similarly, Fensome et al. (1993, p. 89) referred to *Cribroperidinium* as “acavate”.

In the present study, *Cribroperidinium cornutum* Davey 1974 is included in this genus although it has two wall layers. Helenes (op. cit., p. 128) listed *C. cornutum* as a provisionally assigned species, pending “clarification of wall structure and complete paratabulation pattern”. *Cribroperidinium hadrum* (Sarjeant 1966a) n. comb. emend. also appears to have a second wall layer, although in this case not so obviously as in *C. cornutum*.

Cribroperidinium cornutum Davey 1974

Plate 9, Figures 3, 5, 6. Plate 11, Figures 1, 5, 9

Cribroperidinium cornutum DAVEY 1974, p. 48–49, pl. 2, figs. 1–5

Remarks: The present study encompasses the stratigraphic range of this species, which is entirely within the late Barremian interval, allowing its morphological development to be assessed by direct observation. Plate 9 illustrates a possible morphological sequence from *Cribroperidinium sepimentum* Neale and Sarjeant 1962, through a taxon very similar to *C. cornutum* but acavate (informally termed *Cribroperidinium* cf. *sepimentum*) to *C. cornutum sensu stricto*.

Older specimens of *C. cornutum* show less well-developed cavation, largely confined to the cingular area and antapex, whereas younger material displays cingular, ventral hypocystal and, in extreme cases, cornucavation, sometimes extending onto the ventral epicyst. The style of cavation demonstrated by *C. cornutum* suggests an endophragm/periphragm relationship rather than autophragm/ectophragm.

Tabulation is marked in *C. cornutum* by denticulate crests which reduce in cavate areas to lines of denticles; the narrow cingulum encircles the cyst along the distal edge of the cingular cavation as lines of such denticles and a clear break in the cingular cavation marks the sulcus. Sutural crest height is similarly reduced, particularly where ventral cavation occurs.

The complete paratabulation pattern of *C. cornutum* has not been elucidated here, but it appears to be similar to *C. sepimentum*, the type species. Current observations suggest that this species should be included within *Cribroperidinium*, although it is unusual in possessing cavation. In all other respects it is typical of the genus and in the present study it is seen to be very close to the type species.

Duxbury (2001, p. 113) referred to some resemblance of *Scrinioidinium barremianum* Duxbury 2001 to *C. cornutum*, in

its overall size, shape and cavation, and the present study further confirms this. Specimens intermediate to these species (here termed *Cribroperidinium* cf. *cornutum*) were recorded at the inception level of *S. barremianum* (11,167.00 ft in well 22/26a-2), having the rounded outline and distal apical horn perforations typical of *S. barremianum*, but displaying a clear tabulation. This suggests that *S. barremianum* might represent a late development within the "*C. cornutum* lineage". A representative sample of *C. cf. cornutum* is illustrated in Plate 9, Figures 4, 7, 8, 9.

It has been shown, therefore, that there appears to be a direct lineage from *Cribroperidinium sepimentum*, through *C. cf. sepimentum*, *C. cornutum sensu stricto* and *C. cf. cornutum* to *Scriniodinium barremianum*. This process involved an initial reduction in size (from *C. sepimentum*), development of cavation, formation of characteristic apical horn perforations and loss of surface features.

***Cribroperidinium echinatum* Duxbury n. sp.**

Plate 7, Figures 5, 9. Plate 8, Figures 10, 11, 15, 16

Cribroperidinium aceras (Eisenack 1958) Sarjeant 1985 in HEILMANN-CLAUSEN and THOMSEN 1995, pp. 292, 293, pl. 6, figs. 1-5

Holotype: Plate 7, Figures 5, 9.

Type Locality: Heslerton No. 2 at 11.50 m (core chip), "mid" Aptian. Holotype: E.F. T55.4.

Derivation of Name: From the Latin echinatus, prickly - in reference to the spiny nature of this species.

Diagnosis: A thick-walled, spheroidal to ovoidal proximate cyst, autophragm only, the epicyst slightly shorter than the hypocyst. Prominent slender, tapering, acuminate spines cover the cyst and a tabulation typical of the genus is outlined by low, spiny ridges. Some intratabular alignment of spines is apparent. No clear apical projection. The archeopyle is formed by loss of a single precingular plate (3"), operculum free.

Dimensions: Holotype: 51 × 48 µm.

Overall: 66 (56) 51 µm × 61 (52) 43 µm.

Specimens Measured: 8.

Remarks: This distinctive, small species of *Cribroperidinium* is characterised mainly by its spiny nature and usually clear tabulation, marked by spiny ridges. Its secondary, intratabular spine alignment is again typical of the genus. The presence of overt tabulation precludes the inclusion of this species in *Elimatia* Duxbury n. gen., the last being characterised by evenly distributed spines which can be reduced or absent in "bald" areas, but without clear tabulation.

Although Heilmann-Clausen and Thomsen (1995, p. 292) stated that Sarjeant's (1985) emendation of *Cribroperidinium aceras* (Eisenack 1958) Sarjeant 1985 had allowed them to firmly identify specimens from the Ahlum-1 borehole as *C. aceras*, their illustrations (op. cit., Plate 6, figures 1 - 5) do not support this, and their material is here included within *Cribroperidinium echinatum* n. sp.

Sarjeant re-studied and re-illustrated Eisenack's type material (Eisenack 1958, Plate 21, Figures 1, 2) and Sarjeant (1985,

Plate IV, Figures 1, 2 and Plate V, Figures 5, 6, text-fig. 2), accepting and describing *C. aceras* as a valid species, but this is difficult to support. The similarity of Eisenack's *C. aceras* type material to *Cribroperidinium orthoceras* (Eisenack 1958) Davey 1969 is inescapable (see Eisenack 1958, Plate 21, Figures 3-11 and Plate 24, Figure 1, and Sarjeant 1985, Plate I, Figures 1, 4, Plate II, Figures 1, 2, Plate III, Figures 1, 4 and text-fig. 1). This might suggest that Eisenack's *C. aceras* type specimens are physically damaged *C. orthoceras* (i.e., lacking the apical horn), in which case Eisenack's original and Sarjeant's subsequent illustrations of the holotype appear to show an inverted specimen (well-illustrated in Sarjeant 1985, Plate IV, Figures 1, 2).

In the current study, *Cribroperidinium orthoceras*, and possibly *C. aceras*, are considered taxonomic junior synonyms of *Cribroperidinium edwardsii* (Cookson and Eisenack 1958) Davey 1969, the first synonymy following Davey and Verdier (1971).

***Cribroperidinium episomum* (Sarjeant 1966a) n. comb. emend.**

Plate 10, Figures 4, 5, 8, 12

Gonyaulacysta episoma SARJEANT 1966a, p. 118, 119, pl. 13, figs. 9, 10, text-fig. 27

Gonyaulacysta boreas DAVEY 1974, p. 52, 53, pl. 4, figs. 1-4; pl. 7, fig. 5.

Millioudodinium? boreas (Davey 1974) STOVER and EVITT 1978, p. 174

Millioudodinium episomum (Sarjeant 1966a) STOVER and EVITT 1978, p. 173

~~non~~ *Gonyaulacysta episoma* Sarjeant 1966a in MORGAN 1980, pl. 14, figs. 1-6

Rhynchodiniopsis episoma (Sarjeant 1966a) SARJEANT 1982, p. 35

Cribroperidinium boreas (Davey 1974) HELENES 1984, p. 121

Leptodinium episomum (Sarjeant 1966a) HELENES 1984, p. 131

Emended Diagnosis: A spheroidal to ovoidal dinocyst with a broad apical horn. The cyst wall is of moderate thickness and fibroperforate, free of ornament or bearing intratabular, lightly-striate spines or tubercles. Sutural crests are relatively high, narrow and markedly fenestrate; individual fenestrations can be large, are generally oval and can extend from the cyst wall to the crestal margin, which is smooth. The cingulum divides the cyst into approximately equal halves; the displacement of the cingulum along the sulcus approximates the cingulum width. The reflected tabulation is 4', 6", ?c, 6", 1p, 1p.v., 1". A precingular archeopyle is formed by the detachment of plate 3".

Remarks: Very similar descriptions of this species were offered by Sarjeant (1966a, p. 118, 119 - as *Gonyaulacysta episoma*) and Davey (1974, p. 52, 53 - as *Gonyaulacysta boreas*), with both authors emphasising the importance of the distinctive overall shape, tabulation and type of sutural crests. Remarkably, both authors also cited the similar crests of *Cribroperidinium? scottii* (Cookson and Eisenack 1958) Stover and Evitt 1978 and further similarities exhibited by *Tehamadinium tenuiceras* (Eisenack 1958) Jan du Chêne et al. 1986b. However, Davey (op. cit.) did not discuss *C. episomum per se*.

The sutural crests of this species are particularly characteristic and were well illustrated by Davey (1974, Plate 4, Figure 4). Davey (op. cit., p. 53) described crestal perforations as, "so large that often the crests appear to consist of small membranous processes which are linked distally by trabeculae", and Sarjeant (1966a, p. 118) described, "Crests consisting of rows of thin spinelets connected distally by trabeculum". The size

ranges quoted for this species by Sarjeant (op. cit., p. 118) and Davey (op. cit., p. 52) are very similar.

Towards the top of its range, this species can be larger and more ornate than older material, although still with characteristically entire distal margins to the crests.

Cribroperidinium episomum was described by Sarjeant (op. cit.) from the late Barremian of the West Heselton No. 1 borehole, where it was abundant and Davey (op. cit.) described it, as *Gonyaulacysta boreas*, from the late Barremian of the Speeton Clay outcrop. It was restricted to the late Barremian to early Aptian interval in the present study, ranging as young as palynofloral Zone LKP25.

***Cribroperidinium hadrum* (Sarjeant, 1966a) n. comb. emend.**
Plate 8, Figures 1–6

Gonyaulacysta hadra SARJEANT 1966a, p. 119–121, pl. 14, fig. 1, text-fig. 28

Millioudodinium hadra (Sarjeant 1966a) STOVER and EVITT 1978, p. 173

Rhynchodiniopsis hadra (Sarjeant 1966a) SARJEANT 1982, p. 35

Leptodinium? hadrum (Sarjeant 1966a) HELENES 1984, p. 131

Emended Diagnosis: A very large, ovoidal, proximate cyst with a prominent, tapering, blunt-ended apical horn approximately one quarter of the cyst length. Autophragm very thick and fibro-perforate, without surface ornament and forming a broad, rounded apical protuberance. A very thin outer membrane covers the cyst and bears low surface ridges outlining a tabulation typical for the genus. Some separation of wall layers can be particularly prominent around the cingulum and at the antapex; the longer, distal part of the apical horn appears to be constructed of this outer layer. Archeopyle large, single-plate precingular (3"), operculum free.

Remarks: The questionable transfer of this species to *Leptodinium* Klement 1960 by Helenes (1984, p. 131) is rejected here. His comment that “Sarjeant’s (in Davey et al. 1966) text-figure 28 suggests the presence of quadrate X and Z paraplates” is negated by Sarjeant’s comment (1966a, p. 120) that, “Text-figure 28 was prepared from study of several specimens and is unlikely to be accurate in detail”. In the present study, despite the common occurrence of this species, distortion of the low sutural ridges has also precluded detailed analysis of the tabulation. However, the general form and (where discernible) tabulation of this species allows its positive assignment to *Cribroperidinium*.

Cribroperidinium hadrum is characterised by its very large size, thick autophragm and lack of prominent surface ornament. The surface of other large species, including *Cribroperidinium edwardsii* (Cookson and Eisenack 1958) Davey 1969 tends to be covered with verrucae, short spines or tubercles which are often aligned. Fourteen specimens were measured here, with the following dimensions – length 162(138)104 µm x breadth 129(113)89 µm, very similar to those quoted by Sarjeant (1966a, p. 120).

This species is also characterised by what appears to be a thin, “loose-fitting”, finely-wrinkled outer membrane over which run very low ridges marking the tabulation. This membrane might generally be termed an ectophragm, as described by Evitt (1985, p. 65) although it is typically separate from the autophragm around the cingulum (suturocavation beneath each

cingular ridge) and at the antapex. Also, the long apical horn appears to be mainly formed by this outer layer (Plate 8, Figures 1, 3, 5).

Divergence of wall layers in *Cribroperidinium* has been discussed above for *C. cornutum*, a species which also shows cingular and antapical wall separation; this feature is much more extreme in *C. cornutum* than in *C. hadrum*.

Helenes’s (1984, p. 112) description of the wall structure of *Cribroperidinium* as autophragm which may be differentiated into a homogeneous and structureless inner part and a vesicular to “spongy looking” outer part, without separation of layers does not accurately describe *C. hadrum* or *C. cornutum*. It is the opposite particularly of what is seen in *C. hadrum*, which has a thick “spongy-looking” inner and a very thin outer layer as noted by Sarjeant (1966a, p. 120), who described “two distinct layers; a fairly thin periphragm and a thicker endophragm”.

Cribroperidinium hadrum was described by Sarjeant (1966a, p. 119–121) from the late Barremian of the West Heselton No. 1 borehole, where it was “quite frequent”. It was common to very common here, with a very restricted stratigraphic range (palynofloral Subzone LKP25.1) in Heselton No. 2 (17.75 m and 17.00 m samples) and an isolated occurrence at the same level (11,143.00 ft) in well 22/26a-2.

***Cribroperidinium ornatum* Duxbury n. sp.**
Plate 10, Figures 1–3, 6, 9

Holotype: Plate 10, Figures 1–3.

Type Locality: Well 22/26a-2 at 11,181.33 ft (core chip), late Barremian age. **Holotype:** E.F. K48.0.

Derivation of Name: From the Latin orno, ornatus, decorate, furnish - in reference to the surface complexity of this species.

Diagnosis: A moderately thick-walled, spheroidal proximate cyst, autophragm only, the epicyst slightly shorter than the hypocyst. A fairly coarse, spiny reticulum covers the surface and a tabulation apparently typical of the genus is outlined by relatively high, distally-entire, fenestrate sutural crests. Reticular spine height equals that of the sutural crests. A prominent, spiny apical horn is invariably present. The archeopyle is formed by loss of a single precingular plate (3"), operculum free.

Dimensions: Holotype: 73 × 78 µm.

Overall: 81 (73) 68 µm × 78 (68) 63 µm.

Specimens Measured: 7.

Remarks: This very distinctive species of *Cribroperidinium* is characterised mainly by its fairly coarse, spiny surface reticulum and the distally entire, fenestrate sutural crests. The overall shape of this species and its distinctive sutural crests are reminiscent of *Cribroperidinium episomum*. In addition, *C. episomum* can bear a few intratabular, lightly striate spines very similar to, but much rarer than, those of *C. ornatum*.

In its reticulate surface ornament and spines, *C. ornatum* resembles *Cribroperidinium spinoreticulatum* (McIntyre and Bridaux 1980) Århus 1992 and *Cribroperidinium comptum* (Duxbury 1980) Lentin and Williams 1981, although the more rounded shape, coarser surface reticulum, longer spines and dis-

tally-entire, fenestrate sutural crests set *C. ornatum* apart from the last two species.

Cribroperidinium ornatum was recorded from only one sample, at 11,181.33 ft (late Barremian) in well 22/26a-2.

Genus *Cyclonephelium* Deflandre and Cookson 1955

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

Remarks: Like Harding (1990, p. 19), the present author recognises the wide range of cyst morphologies encompassed within this genus and the difficulty in differentiating effectively between taxa. Harding (op. cit.) recognised three species of *Cyclonephelium*, *C. distinctum* Deflandre and Cookson 1955 and the informal taxa, *Cyclonephelium* sp. I and *Cyclonephelium* sp. II.

One reason for Harding's informal treatment appears to be Evitt's (1985, p. 214) comment that variability is likely to reflect palaeoenvironmental conditions. However, the effects of changing palaeoenvironmental conditions on dinocyst assemblages would presumably extend beyond a particular genus, affecting many taxa, with adaptation to these changes reflected in various intra-specific trends. An example of this concerns *Muderongia* Cookson and Eisenack 1958 and similar genera, including *Vesperopsis* Bint 1986 and *Nyktericysta* Bint 1986, where differences in the number of wall layers, degree of wall layer separation, surface ornament and style of excystment (adnate or free operculum) are considered particularly important. Which, if any, dinocyst characteristics are particularly palaeoenvironmentally sensitive is difficult to assess at present (see remarks under *Muderongia patula* Duxbury n. sp., below).

In the present study, one of Harding's informal taxa, *Cyclonephelium* sp. II appears to be a particularly valuable marker, having a very restricted age range within the late Barremian, and this species is formalised below, as *Cyclonephelium crebrum* Duxbury n. sp.

Cyclonephelium crebrum Duxbury n. sp.

Plate 16, Figures 7, 11–13

Cyclonephelium sp. II HARDING 1990, p. 20, pl. 3, figs. 7–9

Holotype: Plate 16, Figures 12, 13.

Type Locality: Heselton No. 2 at 22.95 m (core chip), late Barremian age. Holotype: E.F. R42.1.

Derivation of Name: From the Latin *creber*, thick, crowded, packed, close set – in reference to the surface ornament.

Diagnosis: A dorso-ventrally flattened, single-walled species, sub-circular in outline with a prominent left antapical bulge. The surface is covered with numerous short, capitate spines which are much reduced or absent in the mid-dorsal area and which are transected by a deep, diagonal depression on the ventral surface. Increases in ornament height occur on the left antapical bulge and its right antapical equivalent. Ventral reduction in ornament height continues beyond the sulcus so that in lateral view a break in ornament usually occurs at the cyst margin. Archeopyle tetratabular apical with the operculum usually lost, leaving a zig-zag margin with slight sutural splitting suggesting six precingular plates. No tabulation apparent except for the archeopyle margin.

Dimensions: Holotype: Length - 73 μ m. Width - 78 μ m.

Overall: Length - 84 (73) 63 μ m; Width - 86 (77) 63 μ m.

Specimens Measured: 4 (operculum detached).

Remarks: As noted by Harding (1990, p. 20), this species is usually rare, occurring in low numbers in Heselton No. 2 between 26.00 m and 20.00 m (late Barremian), being consistently present between 26.00 m and 22.95 m; a similar, very short range to that reported by Harding. It was more common at the top of its range at 11,181.33 ft and 11,179.50 ft in well 22/26a-2, however. It is a distinctive form, particularly in having a very dense cover of spines and a well-defined sulcal/post-sulcal "bald" area. The wide geographic range of this species reported by Harding (op. cit.) and its very short stratigraphic range suggest that it might be a valuable marker for the late Barremian; its LAD in well 22/26a-2 falls within palynofloral Subzone LKP23.1.

This species is similar to *Cyclonephelium distinctum* Deflandre and Cookson 1955 but, as noted by Harding (1990, p. 20), "with a greater density of more slender processes concentrated in marginate areas" (compare Plate 16, Figures 7, 11–13 with Plate 16, Figure 4).

Genus *Diphasiosphaera* Duxbury 1980

Type: Duxbury 1980, pl. 1, fig. 5; text-fig. 6, as *Diphasiosphaera stolidota*.

Remarks: The genus *Diphasiosphaera* Duxbury 1980 was considered by Stover and Williams (1987, p.81) to be a taxonomic junior synonym of *Hystrichostrogylon* Agelopoulos 1964 emend. Stover and Evitt 1978, and the type species description was emended by Harding (1990, p. 29) as *Hystrichostrogylon stolidota* (Duxbury) Stover and Williams 1987. This transfer is rejected here and the genus *Diphasiosphaera* is retained for forms with total separation of the wall layers, except for, "the archeopyle margin and that portion of the paracingulum directly beneath it" (Duxbury 1980). In addition, the type species, *D. stolidota*, invariably bears a prominent, coronate apical projection (Plate 5, Figures 7, 10, 11), a feature largely lacking from Harding's material. *Hystrichostrogylon* is considered here to be a taxonomic junior synonym of *Achomosphaera*, as recognised by Eaton (1970), and therefore of *Spiniferites* - see discussion under that genus, below; it is partially cavate, usually in discrete ventral and antapical regions, as illustrated in his type material by Agelopoulos (1964, p. 674, text-figs. 1, 2), re-orientated correctly by Eaton (op. cit., Plate 1, figures 7–10). Harding's emendation of *Diphasiosphaera stolidota* (as *Hystrichostrogylon*) may have been based largely on a different cavate taxon, possibly close to *Endoscrinium bessebae* Below 1981 (see notes under *D. stolidota*, below).

Fensome et al. (1993) questionably assigned *Hystrichostrogylon* to their Subfamily Gonyaulacoideae (together with *Spiniferites* and *Achomosphaera*), on the basis of its general morphology (similar to *Spiniferites*), not on the basis of tabulation, "which is not clear". They tentatively placed *Diphasiosphaera* in their Subfamily Uncertain, stating that they did not consider it a taxonomic junior synonym of *Hystrichostrogylon*.

Eaton (1976, Figure 5) re-oriented the type species of *Hystrichostrogylon*, *H. membraniphorum* Agelopoulos 1964, showing that the "apical" archeopyle described by Agelopoulos (1964, p. 674) was mid-dorsal precingular and that the charac-

teristic pericoel development was restricted to the ventral and antapical regions. Following Davey and Verdier (1971, p. 34), Eaton (op. cit., p. 237) considered that, “pericoel development in this group of dinoflagellate cysts does not warrant special taxonomic treatment” and, because of the lack of tabulation in the type material, Eaton implicitly transferred *H. membrani-phorum* to *Achomosphaera* Evitt 1963, a genus here synonymised with *Spiniferites*.

Although Eaton’s photographs (1976, Plate 1, figures 7 - 10) and his Text-figure 5 clearly show the close resemblance of *H. membrani-phorum* to “the typical Palaeogene form of *Achomosphaera ramulifera*”, his implied synonymy of *Hystrichostrogydon* with *Achomosphaera* was rejected by Stover and Evitt (1978, p. 165) because, “the morphological characteristics of *Hystrichostrogydon* are sufficiently distinctive”.

Diphasiosphaera appears to have originated from the genus *Spiniferites* Mantell 1850 by total separation of the wall layers, except for, “the archeopyle margin and that portion of the paracingulum directly beneath it” (Duxbury 1980, p. 115), and is therefore considered part of the Subfamily Gonyaulacoideae here. Its origin is clearly within the *Spiniferites* Complex which is considered to include only partial cavation, mainly restricted to the ventral surface (see *Spiniferites caminus*, below).

Diphasiosphaera stolidota Duxbury 1980
Plate 5, Figures 7, 10, 11

Diphasiosphaera stolidota DUXBURY 1980, p. 116, 117, pl. 1, figs. 5, 9, text-fig. 6

Remarks: Harding’s emendation of this species is rejected here, as he described the “rare development” of an apical prominence, cavation which “is often complete” and “L-type ventral paratabulation”. All specimens assigned to *D. stolidota* here possess a coronate apical structure, and some dorsal contact between the wall layers.

Although Harding (1990, Figure 11) included a reconstruction of the ventral tabulation of *Diphasiosphaera stolidota* (as *Hystrichostrogydon stolidota*), suggesting a clear L-type organisation, this L-type organisation is not clear in Harding’s photographic illustrations (op. cit. Plate 11, Figures 1-8). It would be an unusual arrangement, as he recognised in stating (p. 30), “almost all of the *Spiniferites* Complex cysts have S-type ventral organisation”. In view of his broad interpretation of this species, it is probable that most specimens included by Harding should not be assigned to it, and may include *Endoscrinium bessebae* Below 1981.

Harding’s comment (1990, p. 30) that, “this species is common in the early Barremian of most sections studied (except for Speeton which may explain why Duxbury believed it to be restricted to the Cement Beds)” is inconsistent with current observations and with evidence from numerous Central North Sea wells, where *D. stolidota* has a younger base, ranging in age from the “middle” Barremian (included in the late Barremian here) to the early Aptian. This may be a further indication that many of the specimens included in *D. stolidota* (as *H. stolidota*) by Harding should not have been assigned to that species.

Genus ***Druggidium*** Habib 1973 emend. Harding 1986
Type: Habib 1973, pl. 1, fig. 3; text-fig. 3, as *Druggidium apicopaucicum*.

Remarks: Harding (1986, p. 19) rejected the transfer by Lejeune-Carpentier and Sarjeant (1983, p. 2, 4) of *Phanerosdinium fourmarierii* Lejeune-Carpentier 1951 and *P. laeve* Lejeune-Carpentier 1951 to *Druggidium* on various tabulation criteria, but also stated, “it is of importance to note that all of the positively identified species of *Druggidium* are restricted to the pre-Aptian Early Cretaceous, whereas *P. fourmarierii* and *P. laeve* were described from the Senonian”.

This last statement suggests a possible age-differentiation of genera, although more recently, *Druggidium discretum* and *D. meerensis* have been described from the late Maastrichtian and Danian by Slimani and Louwey (2011). The archeopyle type of the last two species is described as, “precingular or combination, involving apical, anterior intercalary and precingular plates” (Slimani and Louwey 2011, p. 43), conforming to Harding’s (1986, p. 18, 19) emendation of *Druggidium*.

Although Fensome et al. (1993, p. 73 and text-fig. 75D) described only a precingular archeopyle in *Druggidium*, both Harding (1986, p. 18) and Slimani and Louwey (2011, p. 43) included the possibility of a combination archeopyle comprising apical, intercalary and precingular plates.

Harding’s (1986, p. 18, 19) emendation of *Druggidium*, Slimani’s (1994, p. 24) emendation of *Microdinium* and Slimani and Louwey’s (2011, p. 43, 44) descriptions of *Druggidium discretum* and *D. meerensis* – see also Remarks under *Fibradinium* Morgenroth 1968, below – clearly differentiate *Druggidium* from *Microdinium*, the latter having an apical-intercalary archeopyle (i.e., no involvement of the precingular series).

In his conclusions concerning *Druggidium*, Harding (1986, p. 26) stated that, “The intraspecific variability of archeopyle type shows this character to be of little taxonomic value, whereas accurately determined paratabulation features appear to be a much more reliable taxonomic criterion”. He also emphasised the value of SEM analysis, “when interpreting such details as the eipycystal paratabulation of certain partiform gonyaulacoid dinocysts: such features as the apical and anterior intercalary paraplates would be beyond the resolution of the light microscope”. This re-iterates Evitt’s comment concerning his *Microdinium* Complex (Evitt 1985, p. 216), that “Examination with the SEM will be essential to resolve many structural details”.

The present study was restricted to transmitted light microscopy, allowing limited analysis of the very small species of *Druggidium* recovered; no detailed morphological interpretations have been possible, particularly of epicystal areas.

Druggidium augustum Harding 1986
Plate 3, Figures 13–15

Druggidium augustum HARDING 1986, p. 20–21, pl. 2, Figures 1–9; text-fig. 3

Remarks: An influx of small, thin-walled, ovoidal forms was restricted to the 16.00 m sample in Heslerton No. 2. Cysts vary from specimens which are finely granulate over the entire surface (Plate 3, Figures 13, 14) to others with isolated areas devoid of ornament (Plate 3, Figure 15). Tabulation is indistinct and there was little size variation in the specimens measured, which have an average length and width of 30 µm and 25 µm re-

spectively (10 specimens), very close to Harding's (1986) averages for this species.

In most respects, specimens recorded here agree closely with Harding's type material from the Otto-Gott brickpit, near Hannover, although there are a few differences, particularly minor indentations of the cingulum and immediately posterior to it. Harding (1986, p. 22) specified, "no indentation seen in ambital view" for the cingulum of *D. augustum*, and his illustrations (Harding op. cit., text-fig. 3 and Plate 2) support this. He also stated (Harding op. cit., p. 20), "Greatest width just posterior to the paracingulum". Although specimens observed here show some cingular indentation, they are broadest across the cingulum, and tend to have a slight depression immediately posterior to it.

The influx of *D. augustum* observed at 16.00 m in Heselton No. 2 is close to the Barremian/Aptian boundary (text-fig. 6 and comments on "Wiechendorf 1/86", below) and is associated with a marked increase in acanthomorph acritarchs (17% of the marine component). This occurrence contrasts with Harding's observations, as he cited the age range of this species as latest Hauterivian to latest early Barremian at Gott, Speeton and Hunstanton (Harding, op. cit., p. 22).

Despite the slight morphological differences between current observations and Harding's type material, specimens observed in the present study are considered sufficiently similar to be assigned to *D. augustum*. Although Harding (1986) considered *D. augustum* to have its LAD in the latest early Barremian, the full stratigraphic range is unclear; his reference (Harding op. cit., p. 17) to Rawson and Mutterlose (1984 as 1983) might suggest that nothing was examined younger than the basal Cement Beds at Speeton. This would imply that the youngest material examined in Harding 1986 was of an earliest late Barremian age, intra-elegans ammonite zone, and so significantly older than the influx of *D. augustum* recorded in the present work. Although Gott, Speeton and Hunstanton were also analysed in Harding (1990), *D. augustum* was not reported in that study.

***Druggidium ornatum* Duxbury n. sp.**

Plate 3, Figures 1, 2, 8, 9, 16, 20

?*Druggidium* cf. *apicopaucicum* Habib 1973 *sensu* HARDING 1986, pl. 3, fig. 15

Holotype: Plate 3, Figures 16, 20

Type Locality: Heselton No. 2 at 24.00 m (core chip), late Barremian age. Holotype: E.F. G46.0.

Derivation of Name: From the Latin ornatus, decorated – in reference to the surface ornament.

Diagnosis: A small, elongate ovoidal species with tabulation apparently typical for the genus, sometimes expressed as low surface ridges but indistinct. A broad, distinct cingulum is very high on the cyst, reflecting a squat epicyst and a much longer hypocyst. Surface ornament invariably present varying from fine granulation over the entire cyst to sparser distribution with isolated areas devoid of ornament; lineation of the surface ornament sometimes observed. The archeopyle includes two precingular plates which can remain adherent and which may be entirely smooth.

Dimensions: Holotype: Length - 41 µm. Width - 25 µm.

Overall: Length - 41 (39) 35 µm; Width - 25 (25) 23 µm.

Specimens Measured: 4.

Remarks: This is a rare species, occurring sporadically in the present study between the 29.85 m and 19.00 m samples in Heselton No. 2 (late Barremian). It is considered possibly conspecific with that recorded by Harding (1986, Plate 3, Figure 15) as *Druggidium* cf. *apicopaucicum* Habib 1973, although Harding (op. cit.) did not comment on his taxon.

The species closest to *D. ornatum* n. sp. appears to be *Druggidium apicopaucicum* Habib 1973, but the indistinct tabulation and surface ornament of the former clearly distinguish it. Also, although Habib (op. cit., p. 52) gave a range of Berriasian to Barremian for *D. apicopaucicum*, Habib and Drugg (1983, p. 629) quote an age range of early Valanginian to late Hauterivian, significantly older than anything analysed here.

Millioud's illustrations of the type material of *Druggidium deflandrei* (Millioud 1969) Habib 1973 (Millioud, op. cit.; Plate 2, Figures 5-7) bear superficial resemblance to *D. ornatum*, although the detailed morphology is difficult to assess. However, Millioud (op. cit., p. 429) stated, "sutures low, probably perforate. Wall finely vacuolar and sometimes scabrate", which is very similar to Habib's interpretation of this species (Habib 1973) and his description (op. cit., p. 52), "Tract surface alveolate; alveolae commonly restricted to zones near the plate boundaries". In contrast, Below's illustrations (1987, Plate 17, Figures 7-15) appear to show a different species entirely, squat and with denticulate crests. His emendation of this species (Below 1987, p. 58, as *Raphidodinium deflandrei*) is therefore rejected here.

***Druggidium rhabdoreticulatum* Habib 1973**

Plate 3, Figures 3, 4, 6, 7, 10

Druggidium rhabdoreticulatum HABIB 1973, p. 53, pl. 2, figs. 3-7

Remarks: Small, ovoidal to ellipsoidal forms with a fine reticulum of variable height covering the cyst surface and obscuring the tabulation to varying degrees have been assigned here to *Druggidium rhabdoreticulatum* Habib 1973. A "raised membrane that covers the tract" (Habib 1973, p. 53) was not observed, however. Selectively reduced reticular height in some specimens can be associated with granular intra-plate areas (Plate 3, Figure 6). Partial tabulation, apparently typical for the genus was occasionally expressed by low surface ridges running across the reticulate surface. Two precingular plates appear to be detached in archeopyle formation; these may be lost or remain adherent.

There was little size variation in the specimens observed, with an average length and width of 28 µm and 23 µm respectively. This is below the 40 x 29 µm range for the maximum diameter of *D. rhabdoreticulatum* quoted by Habib (1973, p. 53) and compared to measurements calculated from Habib's light micrographs (Habib op. cit., Plate 2, Figures 3-7). In discussing *Druggidium* sp., Harding (1986, p. 24) considered that the dimensions stated by Habib (op. cit.) in his species descriptions and determinable from the light micrographs of *Druggidium deflandrei* seem to be erroneous; Harding's specimens were again smaller than dimensions quoted by Habib. A similar error might explain the apparent size differences for *D. rhabdoreticulatum* noted here.

In most respects, other than Habib's quoted dimensions, specimens recorded here agree closely with Habib's type material. A Valanginian to Albion range was quoted for this species by Habib (1973, p. 54), and this was further refined to a "Hauterivian (probably late Hauterivian)" FAD by Habib and Drugg (1987, p. 756). The last authors also found that, except for a single, isolated occurrence, the youngest persistent occurrence of *D. rhabdoreticulatum* was in their *Odontochitina operculata* Zone (Habib and Drugg 1987, p. 756, 757), of a late Hauterivian to earliest Aptian age.

As with *Druggidium augustum* Harding 1986, the presence of *D. rhabdoreticulatum* was very restricted in the present study, being largely confined to the 17.75 m sample in Heslerton No. 2 (late Barremian to early Aptian age), where it constituted 17% of the dinocyst assemblage, associated with a major influx of acanthomorph acritarchs (39% of the marine component). Single occurrences of *D. rhabdoreticulatum* were also observed at 17.00 m, 19.00 m and 25.10 m, but it was otherwise absent.

Genus *Elimatia* Duxbury n. gen.

Type: Davey 1974, p.63, Plate 7, Figures 2, 3 as *Trichodinium speetonense*.

Derivation of Name: From the Latin *elimatus*, finished, elaborated, adorned – in reference to the characteristic spines.

Diagnosis: Spheroidal to ovoidal dinocysts, autophragm only. Surface fibroreticulate and produced into short, acuminate spinules which are evenly distributed or which can be reduced or absent in "bald" areas. Tabulation is absent or partly outlined by aligned spinules and/or occasional very low ridges. Sulcal area sometimes less-densely spinose with a pronounced flagellar scar. An apical structure can be present, usually formed by fused clusters of longer spinules. Archeopyle single-plate precingular (presumed 3").

Remarks: This genus has been described in order to accommodate species previously included in *Trichodinium* Eisenack and Cookson 1960 emend. Clarke and Verdier 1967, but which vary significantly from the type species *T. pellitum* Eisenack and Cookson 1960.

As described and illustrated in Eisenack and Cookson (1960, p. 5, 6 and Plate 2, Figures 4 - 7), the genus *Trichodinium* included three significantly different morphotypes, connected only by characteristics broadly applicable to a number of genera. This was partially addressed by Clarke and Verdier (1967, p. 18, 19), who's emendation specified only a precingular archeopyle, sculpture of, "generally short hairs, spines or small flat-topped processes" and a small apical horn. The latter authors contrasted *Trichodinium* with *Apteodinium* in its apical horn type, "commonly formed by the coalescence of several hairs or bristles in the apical region", and in its "type of sculpture".

Although he did not formally address this issue, Morgan (1980, p.33) did recognise the need to reconsider *Trichodinium* after re-examination of the holotype of the type species, *T. pellitum*. Morgan (op. cit.) stated that, "the holotype and other specimens seen have a dense cover of intratabular hairs, with bare parasutural areas"; this is significantly at variance with most species included in this genus to date. Morgan (op. cit.) also pointed out that *Trichodinium paucispinum* Eisenack and Cookson 1960, has "a two plate precingular archeopyle, and the few spines appear to be parasutural". The last species was trans-

ferred to *Pervosphaeridium* Yun Hyesu 1981 by Jan du Chêne et al. (1986a).

In the present study and following the observations of Morgan (1980, p. 33), *T. pellitum*, the type species of *Trichodinium* (Eisenack and Cookson 1960, Plate 2, Figure 4), is recognised as markedly different from several taxa previously included in that genus; these taxa have been transferred to *Elimatia* Duxbury n. gen. No comprehensive treatment is attempted here of several other species which still remain in *Trichodinium* (see Williams et al. 2017), although it is possible that *Trichodinium* might be monotypic considering the very distinctive characteristics of *T. pellitum*.

The third species described by Eisenack and Cookson (op. cit.), *Trichodinium intermedium*, was synonymised with *Trichodinium castanea*, by implication in Clarke and Verdier (1967, p.19), although this was rejected by Morgan (1980, p. 33), and Morgan (op. cit.) is followed here. Of Eisenack and Cookson's three original morphotypes, *T. intermedium* is the only one here transferred to *Elimatia* n. gen.

The type material for *Trichodinium castanea* Deflandre 1935 ex Clarke and Verdier 1967 was from a ?Senonian flint erratic, and the published range covers much of the Cretaceous. Other species unquestionably included in *Elimatia* here are, however, all typical of Lower Cretaceous sediments. Because of this discrepancy, pending further review, *T. castanea* has not been transferred to *Elimatia* here.

Harding (1990, p. 37–39) introduced the concept of "true" and "false" apical horns in his treatment of four species of *Trichodinium*, *T. calvus* Harding 1990, *T. ciliatum* (Gocht 1959) Eisenack and Klement 1964, *T. discus* Harding 1990 and *T. speetonense* Davey 1974. Although Harding didn't define "true" and "false", the first appears to be similar to that displayed by several species of *Cribroperidium* and *Apteodinium* whereas "false" horns are formed by apical tufts of particularly long spinules, which can be fused to varying degrees.

Trichodinium calvus appears to be the only species of this type with a "true" horn and is possibly a taxonomic junior synonym of *Apteodinium? albertii* Lentin and Williams 1981. In his description of *A.? albertii* (as *Pareodinia spinosa*), Alberti (1961, p. 24) refers to a pointed apical horn and very small surface spines 1.5 to 2 µm long, and his illustration (op. cit. Plate 4, Figure 16) suggests some reduction of this ornament on the epicyst; Alberti's material was of a late Barremian age. All of these features closely match Harding's (1990, p. 37) observations on *T. calvus*, also from the late Barremian.

In the present study, *Trichodinium ciliatum*, *T. discus* and *T. speetonense* are all readily transferred to *Elimatia*. *Trichodinium calvus* is also transferred to that genus, as *Elimatia albertii* (Lentin and Williams 1981) n. comb., although recognising that its "true" apical horn is atypical (see Plate 12, Figures 5, 7).

Duxbury (1980, p. 122, 123) described the "*Trichodinium*-type" body ornament of *Cribroperidium comptum* (Duxbury) Stover and Evitt 1978, and this has been confirmed in the current study, together with the possession in some specimens of a tapering, "true" apical horn, very similar to that of *Elimatia albertii* (compare Plate 12, Figures 1, 5, 7). The LAD of *C. comptum* was at 27.05 m in Heslerton No. 2 and its range over-

laps the late Barremian inception of *E. albertii*, allowing a possible linking of the two species.

Other accepted species

Elimatia albertii (Lentin and Williams 1981) **n. comb.**

Pareodinia spinosa ALBERTI 1961, p. 24, Plate 4, Figure 16
Apteodinium? spinosum (Alberti 1961) STOVER and EVITT 1978, p. 142 (combination illegitimate - junior homonym of *Apteodinium spinosum* Jain and Millepieid 1975)
Apteodinium? albertii LENTIN and WILLIAMS 1981, p. 15 (substitute name for *Apteodinium spinosum*)
Trichodinium calvus HARDING 1990, p. 37, pl. 19, figs. 7–12

Remarks: see comments above.

Elimatia ciliata (Gocht 1959) **n. comb.**

Apteodinium ciliatum GOCHT 1959, p. 65, pl. 8, figs. 5, 6

Remarks: Although Clarke and Verdier (1967, p. 19) believed *Trichodinium castanea* to be the taxonomic senior synonym of this species, it is retained here following Harding (1990, p. 38), for the reasons outlined by the latter author.

Elimatia discus (Harding 1990 ex Harding in Williams et al. 1998) **n. comb.**

Trichodinium discus Harding 1990b, p. 38, pl. 18, figs. 7–13 ex HARDING in WILLIAMS et al. 1998, p. 615

Elimatia intermedia (Eisenack and Cookson 1960) **n. comb.**

Trichodinium intermedium EISENACK and COOKSON 1960, p. 6, pl. 2, figs. 5–6

Remarks: Morgan (1980, p. 33) rejected the synonymy of this species with *T. castanea*, as proposed by Clarke and Verdier (1967, p. 19), and this rejection is supported here. One of Morgan's reasons was that "at least in Australia, *T. intermedium* (Barremian to Cenomanian) has a longer range than *T. castaneum* (Late Aptian to Cenomanian)". The Cenomanian was the youngest Stage included in Morgan's (1980) work.

Similarly, in his remarks on *Elimatia ciliata* (as *Trichodinium ciliatum*), Harding (1990, p. 38) rejected the synonymy of that species with *T. castanea*, also by Clarke and Verdier (1967, p. 19). Harding (op cit.) did not record *T. castanea* in the boreal Barremian, suggesting a possible post-Barremian base range similar to that in Australia.

Elimatia speetonense (Davey 1974) **n. comb.**

Plate 10, Figures 7, 11. Plate 12, Figures 10, 11

Trichodinium speetonense DAVEY 1974, p. 63, pl. 7, figs. 2, 3

Holotype: Davey 1974, Plate 7, Figures 2, 3. The holotype of this, the type species of *Elimatia* n. gen. is curated at the Natural History Museum, Cromwell Road, London, with the reference number NHMUK PM FD 728(2).

Remarks: This distinctive species was well described by Davey (1974, p. 63) and Harding (1990, p. 38, 39) and minimal discussion is necessary here.

In his diagnosis of this species, Davey (op. cit.) noted that larger spines are often "perforate proximally". This feature was also noted in the present study although, rather than spine perforation, it appears to represent the occasional distal linkage of usually two spines, particularly around the cingular area. It is not a common feature and was not described by Harding (op. cit.).

Conversely, Davey suggested that there is "no definite alignment" of spines, but Harding noted that, "Paratabulation can be partially discerned on many specimens, outlined by aligned spinules". Current observations accord with Harding's description (see Plate 12, Figures 10, 11 here).

Genus ***Ellipsoidictyum*** Klement 1960

Type: Klement 1960, Plate 6, Figures 15, 16, as *Ellipsoidictyum cinctum*.

Remarks: See remarks under *Cassiculosphaeridia* Davey 1969, above.

Ellipsoidictyum imperfectum (Brideaux and McIntyre 1975) Lentin and Williams 1977 subsp. *quadrum* **n. subsp.**

Plate 17, Figure 1, Plate 18, Figures 1, 6, 10

Ellipsoidictyum imperfectum (Brideaux and McIntyre 1975) Lentin and Williams 1977 in BELOW 1982a, fig. 8 only

Holotype: Plate 18, Figures 1, 6, 10

Paratype: Plate 17, Figure 1

Type Locality: Heslerton No. 2 at 11.50 m (core chip), "mid" Aptian. Holotype: E.F. F47.3. Paratype: E.F. N25.4

Derivation of Name: From the Latin quadrus, square - in reference to the outline of this subspecies.

Diagnosis: A subspecies of *Ellipsoidictyum imperfectum* with significant elevation of the reticular height along linear features which appear to be sutural and to mark an indistinct gonyaulacoid tabulation. The linear features are highest in presumed gonal areas, particularly on the hypocyst, and their crests are smooth or may have some minor irregularity. In optical section, the cyst has an angular, often quadrate appearance. Archeopyle tetratabular apical.

Dimensions: Holotype (complete): 61 × 63 µm.

Paratype (operculum missing): 53 × 63 µm.

All measured specimens with operculum missing: 58 (54) 48 µm × 63 (55) 48 µm.

Specimens Measured: 10.

Remarks: This subspecies was restricted to the 11.50 m and 10.85 m samples from Heslerton No. 2, where it was common; its FAD may prove to be a valuable "mid" Aptian marker.

Ellipsoidictyum imperfectum subsp. *quadrum* n. subsp. is closely similar to *E. imperfectum* subsp. *imperfectum*, as described by Brideaux and McIntyre (1975, p. 25, 26), differing only in the presence of distinctive raised linear features. Dorso-ventral compression is typical, and some specimens display significant reduction in reticulation which, together with the high linear features, presumably delineates gonyaulacoid tabulation.

A specimen of a late Aptian age from Sarstedt figured by Below (1982a, Figure 8) as *E. imperfectum* has been assigned to this subspecies, although its tabulation appears to be unusually clearly-marked compared to the Heslerton No. 2 material.

Genus *Exochosphaeridium* Davey, Downie, Sarjeant and Williams 1966 emend. Helenes 2000

Type: Davey, Downie, Sarjeant and Williams 1966, Plate 2, Figures 9–10, as *Exochosphaeridium phragmites*.

Remarks: The type species of this genus, *Exochosphaeridium phragmites* Davey et al. 1966, was described from the Cenomanian of the Fetcham Mill borehole and illustrated in Davey et al. 1966, Plate 2, Figures 8–10. The holotype (op cit., Figures 9, 10) is a large specimen which appears to be significantly different to the much smaller paratype (op. cit., Figure 8), and probably represents a different species. The overall diameter of the holotype of *E. phragmites* (measured from the photographic illustrations) is approximately $100 \times 90 \mu\text{m}$, whereas the paratype measures $52 \times 54 \mu\text{m}$.

Exochosphaeridium crassum Duxbury n. sp.

Plate 13, Figures 4, 5, 7, 8

Holotype: Plate 13, Figures 4, 7.

Paratype: Plate 13, Figure 5, 8.

Type Locality: Well 22/26a-2 at 11,235.00 ft (core chip), late Barremian age. Holotype: E.F. U27.0. Paratype: E.F. V34.3

Derivation of Name: From the Latin *crassus*, thick, fat, stout - in reference to the main body of this species.

Diagnosis: A thick-walled, spheroidal to ovoidal chorate cyst bearing numerous long, tapering, fairly rigid and acuminate spines of equal length and with a low apical bulge. The surface of the cyst is fibro-perforate with striations running into the spine bases. Spines can merge proximally but only rarely and can form what appear to be intratabular clusters. There is no clear indication of tabulation except for a single plate archeopyle, presumed mid-dorsal precingular (3"). A prominent, solid apical horn is consistently present; this may furcate at any point along its length and commonly displays short spines distally.

Dimensions: Holotype: $76 \times 73 \mu\text{m}$.

Paratype: Overall - $73 \times 63 \mu\text{m}$.

All measured specimens: 78 (73) $66 \mu\text{m} \times 76$ (69) $63 \mu\text{m}$.

Specimens Measured: 11.

Remarks: *Exochosphaeridium crassum* n. sp. is similar in some respects to the holotype of *Exochosphaeridium phragmites* Davey et al. (1966, Plate 2, Figures 9, 10), although it is thick-walled, significantly smaller and has spines only rarely joined proximally, as opposed to the "often confluent" (Davey et al. 1966, p. 165), proximally joined, blade-like processes of *E. phragmites*.

The prominent, solid apical projection of *E. crassum* n. sp. may be formed by the lateral merger of several spines and could therefore be a "false" horn in the sense of Harding (1990, p. 37–39). However, Helenes (2000, p. 138) in his generic description notes that in *Exochosphaeridium*, "The P (1pr) structure is represented by a spine at the tip of the apical horn", presumably implying a "true" apical horn.

This species has a very restricted range in the present study, being observed only in well 22/26a-2 at 11,235.00 ft and 11,230.00 ft, palynofloral Zone LKP20.

Genus *Fibradinium* Morgenroth 1968

Type: Morgenroth 1968, Plate 42, Figure 4, as *Fibradinium annetorpense*.

Remarks: Below (1987, p. 36) considered *Fibradinium* and *Microdinium* Cookson and Eisenack 1960 to be taxonomic junior synonyms of *Phanerodinium* Deflandre 1937a. However, Lentin and Williams (1989, p. 289) noted that the type of *Phanerodinium*, *P. cayeuxii* Deflandre 1936 ex Deflandre 1937a is embedded in flint so that the archeopyle is difficult to interpret; they recommended that only *Phanerodinium cayeuxii* and *P. setiferum* Deflandre 1937a should be included in *Phanerodinium*. This difficulty was re-stated by Fensome et al. (1993, p. 74) and Williams et al. (2017, p. 638, 639).

Both the generic diagnosis of *Phanerodinium* and the description of *P. cayeuxii* were subsequently emended by Slimani (1994, p. 43–45) and a single-plate precingular archeopyle (?3") described, although the configuration of apical and/or anterior intercalary plates was uncertain. Loss of a single plate (4") was subsequently demonstrated by Slimani and Louwye (2011, p. 48, 49) in two further species of *Phanerodinium*, *P. belgicum* Slimani and Louwye 2011 and *P. fourmarieri* Lejeune-Carpentier 1951 emend. Slimani and Louwye 2011. The absence of anterior intercalary plates, "is now known to characterise the genus" (Harding 1986, p. 19).

Slimani (1994, p. 14, 15) described the taxon "*Fibradinium annetorpense*?" as essentially similar to Morgenroth's original illustrations of *F. annetorpense* (particularly his text-figs. 1 and 2), but differing in details of the tabulation, having an archeopyle formed by loss of apical and intercalary plates, losing 9 small plates in total. In addition, Slimani (op. cit., p. 24) emended the genus *Microdinium* Cookson and Eisenack 1960 to emphasise the apical-intercalary archeopyle, type (tAtl)a, also composed "usually" of 9 small plates. This suggests clear differences in tabulation and archeopyle type between *Fibradinium* and *Microdinium* (apical-intercalary) and *Phanerodinium* (precingular, no anterior intercalary plates), which justify the rejection of Below's (1987, p. 36) synonymisation of these genera.

Slimani's observations (1994, p. 15) led him to ask whether there might not be (translation), "some intraspecific variability within *F. annetorpense*; if yes, the separation of the genus *Fibradinium* and the genus *Microdinium* would become impossible". If the last two genera were combined, *Fibradinium* would take priority, confirming Below's 1987 (p.36) implied synonymy of these genera. However, Slimani (op. cit.) did not formally synonymise these two genera and in a subsequent paper, Slimani and Louwye (2011) referred to "*Microdinium* Cookson and Eisenack 1960 emend. Slimani 1994" and assigned two new species of *Druggidium* to "the *Microdinium* Complex of Gp-cysts", implicitly accepting *Microdinium* as separable from *Fibradinium*. They offered no discussion of this acceptance.

Fibradinium variculum Stover and Helby 1987

Plate 2, Figures 9, 10, 13. Plate 3, Figures 17, 18

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

Remarks: 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 (1987, p. 267) for *F. variculum* is apical, type [tA], whereas Slimani (1994) describes the loss of apical and intercalary plates, 9 in total, in *F. annetorpense*? (see above). The operculum of this species is “normally free” (Stover and Helby op. cit., p. 267), and because of its small size and lack of tabulation and since very small intercalary plates are often difficult to resolve without SEM analysis, the true archeopyle type might be more complex than Stover and Helby described.

Specimens of *F. variculum* recorded here were very similar to the type material, tending to have a rounded-triangular hypocyst similar to illustrations in Stover and Helby (1987 Figures 7C and 7D). The sulcal depression is particularly pronounced, with a marked adcingular narrowing of the sulcal groove (Plate 2, Figure 9 and Plate 3, Figure 18 here, and Figure 7F in Stover and Helby op. cit.). The lack of surface features has precluded any assessment of the tabulation or of the archeopyle type.

Genus *Florentinia* Davey and Verdier 1973 emend. Duxbury 1980
Type: Davey and Verdier 1973, Plate 2, Figures 1, 3, as *Florentinia laciniata*.

Remarks: In proposing their new combination, *Kleithriasphaeridium mantellii*, Fensome et al. (2016) reiterated the recommendation of Fensome and Williams (2005, p. 48) that taxa with simple tubular processes and precingular rather than combination archeopyles, such as *Florentinia cooksoniae*, should be transferred to *Kleithriasphaeridium*. Fensome and Williams (2005, p. 48) noted that previously *Florentinia* included “forms with simple tubular processes such as *Florentinia aculeata* and *Florentinia cooksoniae*, as well as more ‘classic’ *Florentinia* types, such as *Florentinia laciniata* and *Florentinia ferox*, with more complicated processes”; this approach was again taken by Fensome and Williams (2019).

However, in their synopsis of *Kleithriasphaeridium*, Fensome and Williams (op. cit., p. 117) referred to “simple, tubular, hollow and open or closed” processes and, “Archeopyle usually precingular but occasionally combination apical-precingular, with formulas P3” or A(1'-4') + P3””, although in their comments, they stated that *Kleithriasphaeridium* bears “a precingular archeopyle”.

In their description of *Florentinia*, Fensome and Williams (op. cit., p. 84) stated, “Processes dividing upwards into two or more distally free, blade-like, tapering or truncated branches” and, “Archeopyle precingular, with formula P3” or combination precingular-apical, with formula A(1'-4')+P3””. In their comments they stated that, “The core group of species thus circumscribed seem to represent a morphological plexus that ranges from species like *Florentinia tenera* (broad, sometimes bulbous processes that are not truly subdivided but have aculeae perched on their distal rims)....”.

There are obvious clear similarities between Fensome and Williams’ (op. cit.) concepts of *Florentinia* and *Kleithriasphaeridium*, but their main dividing line appears to be the

possession by *Florentinia* of distally divided processes, “emphasizing forms with mesotabular processes that tend to be united basally but that subdivide along their length to produce a variable number of free distal elements” (Fensome and Williams op. cit., p. 84). This “core group” might be difficult to maintain, however, when *Florentinia tenera*, a species without “truly subdivided” processes is included.

In addition, it is clear from the illustration of the holotype of *Florentinia mantellii* (Davey and Williams 1966, Plate 6, Figure 6) that most processes of that species divide distally (see also Plate 21, Figure 12 here) conforming to the genus *Florentinia* by Fensome and Williams’ own criteria. The transfer of *Florentinia mantellii* to *Kleithriasphaeridium* by Fensome et al. 2016 is therefore rejected.

It was also suggested by Fensome and Williams (op. cit., p. 119) that *Kleithriasphaeridium readei* (Davey and Williams 1966) Davey and Verdier 1976 is “similar to *Kleithriasphaeridium mantellii* but with nontabular surface ridges that extend onto the processes”, but this is clearly not the case. *Kleithriasphaeridium readei* differs from *F. mantellii* in having distally-open, tubular processes bearing distal fringing spinules and it appears to be very similar in morphology to the type species, *Kleithriasphaeridium corrugatum* Davey 1974, although it occurs much younger. Re-orientation of the holotype of *F. mantellii* also shows a low apical bulge, absent from *K. readei*.

The concept of *Florentinia* applied in the present study is that expressed by Duxbury (1980, p. 119); this encapsulates all of the characteristic features considered important by Fensome and Williams (2019). The transfer of several taxa from *Florentinia* to *Kleithriasphaeridium* by Fensome et al. (2016) and Fensome and Williams (2019) may be questioned, however, as it tends to blur the boundary between these genera, particularly by extending the morphological concept of the latter genus significantly beyond ‘classic’ *Kleithriasphaeridium* types, such as *Kleithriasphaeridium corrugatum* and *Kleithriasphaeridium fasciatum* (Davey and Williams 1966, p. 90, Plate 7, Figures 5–6) Davey 1974.

Florentinia globosa Duxbury n. sp.

Plate 19, Figure 11; Plate 21, Figures 1–6

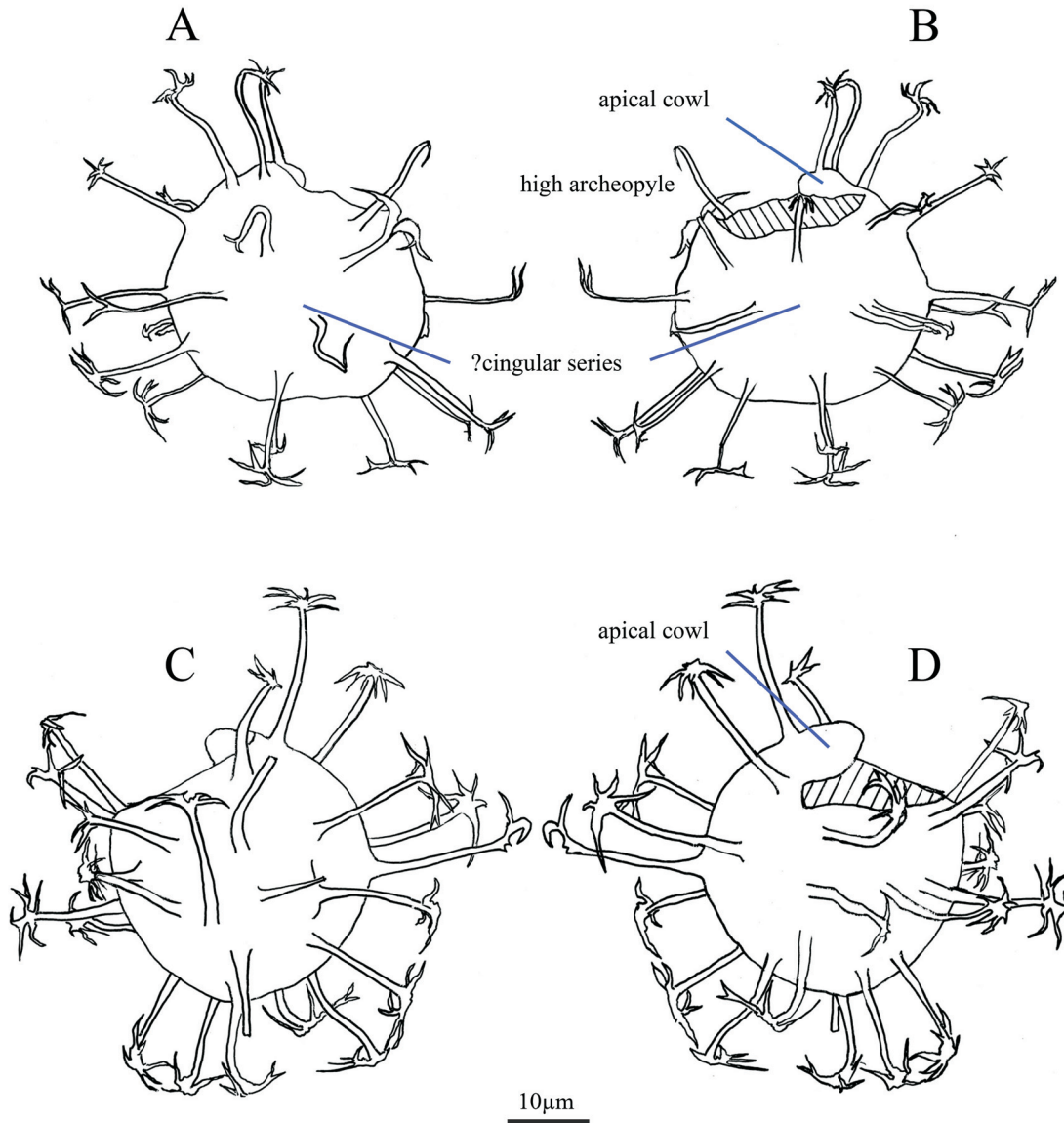
Holotype: Plate 21, Figures 3, 5, 6.

Paratype: Plate 21, Figure 1, 2, 4.

Type Locality: Heslerton No. 2 at 12.20 m (core chip), early Aptian age. Holotype: E.F. T46.0. Paratype E.F. M51.4.

Derivation of Name: From the Latin *globosus*, round as a ball, spherical – in reference to the main body of this species.

Diagnosis: A smooth, fairly thick walled, chorate cyst with a spheroidal endocyst. Smooth, mesotabular, hollow, distally open and slightly flared processes extend from the cyst surface, where clearly defined, finely granular patches are present below process bases. Tabulation of the formula 4", 6", 6", 1p.v., 1" is indicated by process distribution and by a precingular archeopyle (3"). Process length increases slightly between the epicyst and hypocyst, but process breadth varies significantly, being least at the apex and greatest in the postcingular area, where processes are typically much broader than that at the antapex. Distal process margins bear short spines or tubules and closure of some process terminations can produce a “club-like”



TEXT-FIGURE 3

Gochteodinia? phoenix (Duxbury 1980) n. comb. emend. Two specimens from the upper Barremian of well 22/26a-2 at 11,181.33 ft. A, B at E.F. O29.4, FD1127(12) and C, D at E.F. K56.0, FD1127(13). These specimens are also figured in Plate 20, figures 1–5.

appearance. Processes can display large lateral fenestrations, most typically in the postcingular series.

Dimensions: Holotype: Central body - $53 \times 46 \mu\text{m}$

Overall: $91 \times 81 \mu\text{m}$.

All measured specimens: Central body - 66 (53) $46 \mu\text{m} \times 58$ (48) $41 \mu\text{m}$.

Overall: 104 (96) $76 \mu\text{m} \times 96$ (84) $58 \mu\text{m}$.

Specimens Measured: 12.

Remarks: *Florentinia globosa* n. sp. is large and fairly thick-walled, and it lacks cingular processes, contrasting with

Florentinia mantellii (Davey and Williams 1966) Davey and Verdier 1973 and *F. striata* n. sp. The significant differences in process breadth, particularly between the broad postcingular series and the narrower antapical process are sometimes striking, and set this species apart from *Florentinia deanei* (Davey and Williams 1966) Davey and Verdier 1973, *F. abjuncta* Duxbury 1983 and *F. interrupta* Duxbury 1980. The last two species also display typically “disrupted” processes, except for that at the antapex.

There is some similarity between *F. globosa* and *Florentinia cooksoniae* (Singh 1971) Duxbury 1980, but Singh (1983, p. 147) listed several features which set the last species apart, including the lack of secondary tubules, a distinct apical boss and slender cingular and sulcal processes “when present”; the last

comment suggests that Singh considered the presence or absence of cingular or sulcal processes to be variable within the same species. Also, the spheroidal shape of *F. globosa* results in its random orientation whereas *F. cooksoniae* is elongate (as illustrated in Singh 1983, Plate 52) and appears usually to possess a particularly large antapical process (Singh 1971, p. 329).

***Florentinia striata* Duxbury n. sp.**

Plate 21, Figures 9–11

Holotype: Plate 21, Figures 10, 11.

Type Locality: Well 22/26a-2 at 11,235.00 ft (core chip), late Barremian age. Holotype: E.F. V29.0.

Derivation of Name: From the Latin *striata*, striped – in reference to the main body and processes of this species.

Diagnosis: A fairly thick-walled chorate cyst with a spheroidal to ovoidal endocyst. Hollow, mesotabular, distally open and parallel-sided processes extend from the surface and finely-granular patches may be present below process bases; the distal margins of these processes are crenellated, surmounted by short, flat-ended projections. Postcingular processes are typically much broader than that at the antapex. Slender, capitate or distally branched cingular processes are also present. Striations run along the entire length of the larger processes and over the cyst surface, where they form a complex network of low ridges. Tabulation of the formula 4', 6", 6c, 6"', 1p.v., 1''' is indicated by process distribution and by a precingular archeopyle (3"). Process length increases slightly between the epi- and hypocyst, but process breadth varies significantly.

Dimensions: Holotype: Central body - 51 × 48 µm.

Overall: 84 × 84 µm.

All measured specimens: Central body - 68 (53) 41 µm × 71 (51) 38 µm.

Overall: 101 (87) 73 µm × 94 (83) 71 µm.

Specimens Measured: 10.

Remarks: *Florentinia striata* is similar to *Florentinia interrupta* Duxbury 1980 in having striate processes but differs in possessing tubular processes with flat-ended projections around the their distal margins; the processes of *F. interrupta* furcate in a complex manner and divide into several capitate elements. *Florentinia striata* also resembles *Florentinia globosa* in showing significant differences in process breadth, in its tendency to random orientation and in possessing broader postcingular processes than at the antapex. It differs in possessing cingular processes and in its characteristic surface striation.

Genus *Gochteodinia* Norris 1978 emend. Below 1990

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

***Gochteodinia? phoenix* (Duxbury 1980) n. comb.**

Plate 20, Figures 1–7, 9–13. Text-figure 3

Hystrichosphaeridium? phoenix DUXBURY 1980, p. 124, 125, pl. 13, figs. 5, 6; text-fig. 9

Surculosphaeridium? phoenix (Duxbury 1980) LENTIN and WILIAMS 1981, p. 271

Hystrichosphaeridium? phoenix Duxbury in BELOW 1982a, p. 350, Figure 10

?Kleithriasphaeridium sarmentum (Davey 1979) BELOW 1982b in Prössl 1990, pl. 9, fig. 6

Cymososphaeridium? phoenix (Duxbury 1980) Fauconnier in FAU-CONNIER and MASURE 2004, p. 159

Remarks: The difficulty in placing this species generically was noted by Duxbury (1980, p. 125) and is reflected in the several genera to which it has subsequently been questionably assigned by various authors. Comparisons have been made to the genera *Melitasphaeridium* Harland and Hill 1979, *Hystrichosphaeridium* Deflandre 1937b and *Kiokansium* Stover and Evitt 1978, based on the process type and the small, usually smooth central body (Duxbury 1980, p. 124, Below 1982a, p. 350). Tentative transfers to *Surculosphaeridium* Davey et al. 1966 and *Cymososphaeridium* Davey, 1982 have also been made. These genera include tetratabular apical (*Hystrichosphaeridium*, *Surculosphaeridium*, *Cymososphaeridium*) single-plate precingular (*Kleithriasphaeridium*, *Melitasphaeridium*) and two-plate precingular (*Kiokansium*) archeopyles.

Observations in the present study have allowed further resolution of the archeopyle type, suggesting that most of these assignments and suggested archeopyle types may be incorrect. Plate 20 presents a number of specimens showing that on excystment this species lost (separately) two polygonal plates whilst retaining an apical “cowl” which is sometimes surmounted by a low apical bulge; all genera with apical or single-plate precingular archeopyles may therefore be discounted. The loss of two individual opercular plates might allow an assignment to *Kiokansium*, and this was suggested as most possible by Duxbury (op. cit., p. 125), who stated, “The presence of solid processes tends to suggest that *H.? phoenix* may be closer to the *B. polypes/T. hydra* group of cysts than to others”.

However, the position of the archeopyle in this species is relatively very high on the cyst compared to that of *Kiokansium unituberculatum* (Tasch in Tasch et al. 1964) Stover and Evitt 1978 (compare Plate 7, Figure 4 with Plate 20, Figure 3 and text-fig. 3B, D here) and *Taleisphaera hydra* (see Below 1982b, Figure 3). Although a complete tabulation scheme has not been interpreted, in “simpler” examples, process numbers are reduced, suggesting that the “high” archeopyle in *G.? phoenix* may be the result of the entire precingular series remaining in place.

The overall structure of this species, except that it is spheroidal and therefore possesses no pronounced apical horn, appears to be very similar to that of some species of *Gochteodinia*, particularly *Gochteodinia villosa* (Vozzhennikova 1967) Norris 1978 subsp. *multifurcata* Davey 1982 and *G. judilentinae* McIntyre and Brideaux 1980; the processes are particularly close to those of the last species.

A specimen of *Gochteodinia* sp. D3E from the lower Valanginian of the Speeton coastal outcrop is illustrated in Plate 20, Figure 8 for comparison, and this relatively rounded taxon displays several features similar to those observed in *G.? phoenix*. This small, “true” *Gochteodinia* has “V - shaped” archeopyle margins, a low, bluntly-rounded apical termination and, because of the much reduced horn, a similarly “high” position of the large two-plate archeopyle (in this case intercalary).

Inclusion of a species without a pronounced apical horn in *Gochteodinia* must be questioned, although that of *Gochteo-*

dinia sp. D3E is much reduced. Also, there are precedents for including forms with and without apical projections, for example within the genera *Aprobolocysta* Duxbury 1977 and *Batioladinium* Brideaux 1975.

***Gochteodinia* sp. D3E**

Plate 20, Figure 8

Description: A small, rotund species with a short, bluntly-rounded apical horn. The entire cyst surface is finely and evenly granular and bears short, distally-tapering, flat-ended processes. Archeopyle large, two-plate intercalary.

Remarks: A single specimen of this species, measuring 40x34 µm, has been recorded from the lower Valanginian (Bed D3E) of the Speeton coastal outcrop. It is included here only for comparison with *Gochteodinia? phoenix*.

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

Type: Ehrenberg 1837, Plate 1, Figure 16, as *Xanthidium tubiferum*.

Hystriospheraeridium arborispinum Davey and Williams 1966
Plate 18, Figures 15, 16, 18, 19

Hystriospheraeridium arborispinum DAVEY and WILLIAMS 1966, p. 61, pl. 9, figs. 5,10

Remarks: In his remarks on *H. arborispinum*, Harding (1990, p. 41) stated that, "This species has an extremely erratic distribution in late Barremian time, usually occurring in low abundance in great contrast to its importance in the Hauptblatterton and its equivalents". This was not the case in the present study, however, where *H. arborispinum* was common to abundant as high as 27.05 m in Heslerton No. 2 (intra-Zone LKP21). In well 22/26a-2, *H. arborispinum* was common as high as 11,210.00 ft (top Zone LKP21) and it was abundant between 11,181.33 ft and 11,167.00 ft (Zone LKP23), a part of the section missing from Heslerton No. 2.

A marked downhole increase in *H. arborispinum* has been consistently recorded by the present author in the UK Central North Sea, associated with the LAD of *Cerbia magna* Duxbury 2001, and these events have been used here to define the top of new palynofloral Subzone LKP24.1 (see "Refinement of the Duxbury 2001 Scheme, Zones LKP25 to LKP20", below). Subzone LKP24.1 is interpreted to occur within the sample gap between 11,167.00 ft and 11,159.00 ft in well 22/26a-2 (text-fig. 7).

Significant morphological variation was noted within this species, including the presence of particularly large, elongate specimens, although these are much rarer than more "normal" forms. Except for an increase in size and elongation, these unusual specimens are morphologically identical to others; this morphotype is contrasted with more typical forms in Plate 18, Figures 15, 16, 18 and 19.

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

Type: Morgenroth 1966, Plate 10, Figure 5, as *Impletosphaeridium transfodum*.

Impletosphaeridium multifurcillatum (Prössl 1990 ex Prössl 1992) Williams et al. 1998
Plate 7, Figures 2, 3, 6, 7, 10, 11

Cleistosphaeridium multifurcillatum PRÖSSL 1990, p. 100, 101, pl. 9, figs. 2, 8, 11 (not validly published)

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

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

Remarks: This species has been retained in the genus *Impletosphaeridium* Morgenroth 1966 pending further study, although there was no evidence in the current study for the type tA archeopyle described by Prössl (1990, p. 100, 101). In very rare specimens, the archeopyle appears to be two-plate precingular (see Plate 7, Figure 11), similar to that of *Kiokansium* Stover and Evitt 1978.

However, the spherical shape of this species and the tendency of distal spines to lie parallel to the cyst surface or to recurve are also reminiscent of *Gochteodinia? phoenix* (Duxbury 1980) n. comb. Like *Impletosphaeridium multifurcillatum*, *G.? phoenix* has solid processes of equal length, which vary in number although they are invariably fewer than those of *I. multifurcillatum*. In addition, very rare specimens have been observed with what appear to be opercular plates only partially detached (see Plate 7, Figure 2), and these appear to be lost singly, as in the possible intercalary archeopyle of *G.? phoenix*.

The small size and spiny nature of *Impletosphaeridium multifurcillatum* can make it difficult to separate from other, similar-sized chorate dinocysts, particularly in poorly-preserved assemblages. In the present study, *I. multifurcillatum* was restricted to the interval 11,235.00 ft to 11,230.00 ft in well 22/26a-2, associated with common to abundant small representatives of *Palaecysta silybum* (Davey 1979) Williams and Fensome 2016, a form which can appear superficially similar but has a clear tetratabular apical archeopyle and "process complexes" (see Plate 19, Figures 12, 13 for small examples of *P. silybum*).

Genus ***Kiokansium*** Stover and Evitt 1978 emend. Duxbury 1983

Type: Tasch et al. 1964, Plate 3, Figure 8, as *Hystriospheraeridium unituberculatum*.

Remarks: This genus is restricted to taxa with a spheroidal to elongate ellipsoidal test bearing solid, distally acuminate or branched spines and a two-plate precingular archeopyle (Duxbury 1983, p. 48). As discussed by Williams et al. 2017 (p. 13), the International Code of Nomenclature (ICN) requires that the type species of *Kiokansium* is *K. unituberculatum* (Tasch in Tasch et al. 1964) Stover and Evitt 1978 (= *K. polypes* of previous usage), and this is accepted here.

In the present study only one species, *Kiokansium unituberculatum* has been positively assigned to this genus. The elongate species *Kiokansium prolatum* Duxbury 1983 was not recorded, and specimens attributed to that species by Heilmann-Clausen and Thomsen (1985, Plate 13, Figures 11–13) are here attributed to extreme forms of *Protoellipsodinium clavulus* Davey and Verdier 1974 emend Duxbury 1983 subsp. *spinigerus* Brideaux 1977 n. stat.

The absence of *K. prolatum* from the present study is interpreted as evidence that the youngest sample analysed (10.85 m in Heslerton No. 2) is no younger than the earliest late Aptian, as Duxbury 1983 (text-fig. 34) illustrated a near-base *martinioides* ammonite zone FAD for that species.

The morphological range of *Kiokansium unituberculatum* as interpreted here is significant, including forms with long, very slender spines to those with shorter, relatively broad spines and densely granular body ornament. No sub-division has been attempted here as there does not seem to be clear separation of these forms morphologically or temporally. The morphological range observed in the present study is illustrated in Plate 7, Figures 4, 8, 12, 14, 15, 18.

Genus *Meiourogonya* Sarjeant 1966a

Type: Valensi 1953, Plate 12, Figures 12, 13, as *Gonyaulax* sp.

Meiourogonya *lacunosa* Duxbury n. sp.

Plate 17, Figures 2-5, 8, 11, 13

Holotype: Plate 17, Figures 8, 11

Paratype: Plate 17, Figures 2-4.

Type Locality: Heselton No. 2 at 19.00 m (core chip), late Barremian age. Holotype E.F. K44.0, Paratype E.F. S51.4.

Derivation of Name: From the Latin *lacunosus*, full of hollows, cavities – in reference to the wall structure of this species.

Diagnosis: A large, thick-walled dinoflagellate cyst, subcircular in outline with finely and irregularly perforate “septa” forming a reticulum over much of the cyst surface, producing a pitted appearance. Tabulation of the formula $?', 6'', ?c, 6''', 1p, ?p.v., 1'''$ is marked by low sutural ridges and by ectophragm folding along sutures. The height of the surface reticulum is particularly pronounced at the apex (producing a low, rounded prominence), around the cingulum and towards the antapex. There is a marked offset of cingular terminations and a clear sulcal furrow. The archeopyle is apical and the zig-zag archeopyle margin displays a distinct but shallow sulcal notch.

Dimensions: Holotype (complete): Length - 86 μ m. Width - 81 μ m. Paratype (operculum lost): Length - 66 μ m. Width - 86 μ m.

Complete specimens (2 recorded): 86 (77) 68 μ m \times 81 (70) 58 μ m.

Overall (operculum lost): Length - 73 (68) 63 μ m; Width - 86 (74) 58 μ m.

Specimens Measured: 5.

Remarks: This species is recognisable even from fragmentary specimens, being covered in what appear to be subcircular pits resulting from the apparent thinning of the cyst wall at the centre of each mesh of the surface reticulum. The wall structure is similar to that in some species of *Cassiculosphaeridia* Davey 1969, particularly as described by Harding (1990, p. 49), for *C. magna* Davey 1974 emend. Harding 1990, although the presence of clearly-defined tabulation in *M. lacunosa* excludes this species from *Cassiculosphaeridia*.

A similarly clear tabulation over a reticulate surface is observed in *Ellipsoidictyum sagera* (Duxbury 1980) Below 1982a, but that is a much smaller species with sutures usually, “delineated by single rows of pointed and occasionally ribbed denticles” (Harding 1990, p. 35).

Meiourogonya *lacunosa* is restricted to the 19.00 m sample (late Barremian) in the Heselton No. 2 borehole and to the interval 11,190.00 ft to 11,154.00 ft in well 22/26a-2.

Meiourogonya *stoveri* Millioud 1969

Meiourogonya *stoveri* MILLIoud 1969, pl. 3, figs. 1-3.

Remarks: This species was generally rare in the present study, except for a significant increase in numbers at its youngest occurrence, within the early Aptian interval of Heselton No. 2, where a particularly large and ornate form was recorded; this has been described below as a new sub-species.

Meiourogonya *stoveri* subsp. *grandis* Duxbury n. subsp.

Plate 17, Figures 6, 9, 12

Holotype: Plate 17, Figure 6.

Paratype: Plate 17, Figures 9, 12.

Type Locality: Heselton No. 2 (core chips). Holotype at 13.20 m, early Aptian age, E.F. P51.3, Paratype at 12.20 m, early Aptian age, E.F. L39.0.

Derivation of Name: From the Latin *grandis*, great - in reference to the very large size of this subspecies.

Diagnosis: A very large, thick-walled dinoflagellate cyst, subcircular to pentagonal in outline with fairly coarse reticulate ornament typically confined to penitabular areas. Tabulation of the formula $?', 6'', ?c, 6''', 1p, 1p.v., 1'''$ is marked by distally entire crests which are higher on the hypocyst and particularly prominent towards the antapex, giving the cyst an angular outline. The sulcus broadens antapically and has a deep central groove. The archeopyle is apical and the zig-zag archeopyle margin displays a distinct but shallow sulcal notch.

Dimensions: Holotype: Length - 84 μ m. Width - 91 μ m. Paratype: Length - 73 μ m. Width - 84 μ m.

Complete specimen (2 recorded): 99 (96) 94 μ m \times 96 (96) 96 μ m.

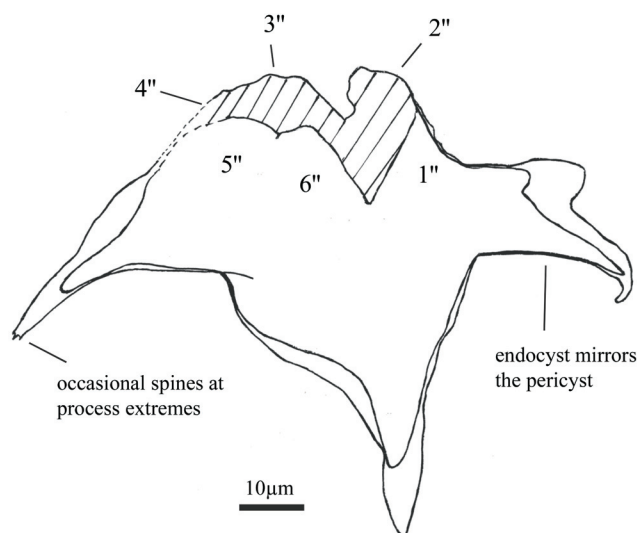
Overall (operculum lost): Length - 94 (78) 63 μ m; Width - 104 (90) 78 μ m.

Specimens Measured: 16.

Remarks: This subspecies is typical of the species in its often subcircular outline, thick wall, crests which are highest towards the antapex and sulcus broadening antapically. However, it differs in its significantly greater size (complete specimens about 20% larger than Millioud's type material) and in the coarseness of its reticulate ornament, which can cover plates but which tends to be concentrated in penitabular areas, leaving conspicuous “bald” areas. Some suturocavation can be observed, with the crestal membrane distinctly perforate.

Meiourogonya *stoveri* subsp. *grandis* tends to angularity, often superficially similar to that of *Ellipsoidictyum imperfectum* subsp. *quadrum* (compare Plate 17, Figure 6 with Plate 17, Figure 1 and Plate 18, Figures 1, 6, 10).

This subspecies was restricted to the latest Barremian to early Aptian interval in the present study (14.95 m to 12.20 m in Heselton No. 2), whereas specimens assigned to *M. stoveri* subsp. *stoveri* were observed no higher than 17.00 m, where they were rare. Millioud (1969, p. 429) described *M. stoveri* as,



TEXT-FIGURE 4

Muderongia patula n. sp. (holotype) from the upper Barremian of Heselton No. 2 at 27.05 m, E.F. Y45.0, FD1116(4). This specimen is also figured in Plate 23, Figure 7.

“sporadically present in the Barremian and in the lower Aptian”.

Genus *Muderongia* Cookson and Eisenack 1958

Type: Cookson and Eisenack 1958, Plate 6, Figure 2, as *Muderongia mcwhaei*.

Remarks: The genus *Muderongia* was rare in the present study, being represented by only three species, *Muderongia imparilis* Duxbury 1980, *M. staurota* Sarjeant 1966b and *M. patula* Duxbury n. sp. The first was consistent only in the older late Barremian in Heselton No. 2 (as young as the 28.00 m sample) but with an isolated occurrence in the 24.00 m sample, and *M. staurota* ranged up to a level close to the Barremian/Aptian boundary (17.00 m sample).

The third species recorded is described below.

Muderongia patula Duxbury n. sp.

Plate 23, Figures 1–3, 7; text-figure 4

Holotype: Plate 23, Figure 7.

Type Locality: Heselton No. 2 at 27.05 m (core chip), late Barremian age. Holotype: E.F. Y45.0.

Derivation of Name: From the Latin patulus, open, spread out, broad – in reference to the relative width of this species.

Diagnosis: A smooth, delicate, proximate and cornucavate cyst with two wall layers clearly represented. The two lateral horns are of approximately equal length and may be anteriorly rounded or have a distinct precingular projection and deep cingular notch; long postcingular projections occur on both lateral horns. A well developed left antapical horn contrasts markedly with a rudimentary right antapical horn development or rounded right antapical area. There is no clear tabulation except

for a narrow, faint cingulum. Rare denticles may occur towards horn extremities. The endocyst is well defined, having long lateral and left antapical projections but a rounded right antapex. Notching of the endocystal lateral projections can occur, reflecting the cingular notches in the pericyst. The archeopyle is apical, with the operculum usually lost.

Dimensions: Holotype: Length - 78 μm. Width - 104 μm.

Overall: Length - 91 (75) 63 μm; Width - 104 (90) 76 μm.

Specimens Measured: 5.

Remarks: *Muderongia patula* is a rare but very distinctive species very similar in outline to *Vesperopsis longicornis* (Batten and Lister 1988) Harding 1990, which differs in possessing an autophragm only (Harding 1990, p. 21, Lister and Batten 1988, p. 27). The possession of autophragm only or endophragm plus periphragm is currently considered generically significant, although perhaps paleosalinity differences might have played a role. *Vesperopsis longicornis* was described (Batten and Lister op. cit.) from the Vectis Formation (Wealden, fresh water to low salinity) of the Isle of Wight, and Harding (1990, p. 21) noted that it occurred in flood abundance in the highest part of the Weald Clay in the Warlingham borehole, Surrey. Wilpshaar and Leereveld (1994) noted that high abundances of their *Muderongia* Group (including *Odontochitina* and *Phoberocysta*) have been reported in sediments representing variable salinity conditions (e.g. Lister and Batten 1988).

Although the surface of *M. patula* n. sp. is smooth, small denticles can occur towards horn extremities (Plate 23, Figure 3 and text-fig. 4), a feature also reported for *Muderongia australis* Helby (1987, p. 300-303) and illustrated in his Figure 3C.

Genus *Oligosphaeridium* Davey and Williams 1966

Original type: White 1842, Plate 4, Figure 11, as *Xanthidium tubiferum* var. *complex*.

Neotype: Davey and Williams 1966, Plate 7, Figure 1, designated by Davey and Williams (1966, p. 71).

Oligosphaeridium magnum Duxbury n. sp.

Plate 15, Figures 1–5, 8, 13

Holotype: Plate 15, Figure 1

Type Locality: Well 22/26a-2 at 11,179.50 ft (core chip), late Barremian age. Holotype E.F. J34.3.

Derivation of Name: From the Latin magnus, large, great, in reference to the very large size of this species.

Diagnosis: A large, thin-walled species with a smooth, spheroidal main body. Hollow, mesotabular processes of equal length but variable breadth indicate a tabulation scheme of 4', 6", 0c, 6", 1p, 1"". Processes taper, being narrowest at about half their length. Distal terminations vary on individual specimens from complex margins with long fringing spines to regularly or irregularly fenestrate. Some processes bear longitudinal perforations which may penetrate the distal margin, effectively removing one side of the process. The archeopyle involves the loss of four apical plates with some additional splitting along precingular sutures.

Dimensions: Holotype - Central body - $63 \times 86 \mu\text{m}$. Overall - $134 \times 139 \mu\text{m}$

Other measured specimens: Central body - 91 (77) $63 \mu\text{m} \times 94$ (79) $63 \mu\text{m}$.

Overall - 152 (141) $129 \mu\text{m} \times 152$ (132) $101 \mu\text{m}$.

Specimens Measured: 10.

Remarks: The processes of this very large species vary significantly, flaring distally and showing a wide range of morphologies on individual specimens from simple to very complex. The presence on some processes of longitudinal holes sometimes penetrating the distal margin is a similar feature to that in *Perisseiasphaeridium cretaceum* Duxbury 2018 and *Oligosphaeridium distinctum* Duxbury 2018.

Specimens tend to be randomly-oriented because of the spheroidal shape of this taxon, and there was no evidence of tabulation other than for the process distribution and archeopyle.

This taxon was recorded between 11,181.33 ft and 11,173.00 ft in well 22/26a-2. It was rare except for a major influx at 11,179.50 ft; similar discrete major influxes have been observed at this level within the late Barremian elsewhere in the Central North Sea, where it is a valuable stratigraphic marker for palynofloral Subzone LKP23.1.

Genus *Palaecysta* Chen 2013

Type: Chen 2013, Plate 1, Figure 1, as *Palaecysta integra*.

Palaecysta silybum (Davey 1979) Williams and Fensome 2016 Plate 19, Figures 3, 6, 12, 13

Systematophora silyba DAVEY 1979, p. 433, 434, 436, pl. 48, figs. 7, 8; pl. 50, figs. 2, 3, 5, 6, 7-9.

Remarks: Specimens of *P. silybum* recorded here displayed a typically wide variation in processes (simple to branching) and in overall size, very similar to the original illustrations (Davey 1979). A significant increase in numbers of smaller forms with particularly simple processes (Plate 19, Figures 12, 13) was recorded in well 22/26a-2 between 11,235.00 ft and 11,230.00 ft, and this may be a valuable secondary marker for the upper part of palynological Zone LKP20 (text-fig. 7).

Genus *Pentadinium* Gerlach 1961 emend. Benedek et al. 1982

Type: Gerlach 1961, Plate 26, Figures 5, 6; text-figs. 6, 7, as *Pentadinium laticinctum*.

Remarks: The critical morphological feature separating *Pentadinium* from *Impagidinium* (and *Pterodinium*) appears to be the overtly pterocavate nature of the former, and this criterion is applied in the present study. However, Heilmann-Clausen and Thomsen (1995, p. 300 and 304) noted that *Impagidinium alectrolophum* (Sarjeant 1966a) Stover and Evitt 1978 and *Pentadinium omasum* Harding 1990 ex Harding in Williams et al. 1998 are morphologically very similar and this has been confirmed here (Plate 4, Figures 2, 3, 5, 6, 9). The pterocavate nature of *P. omasum* sets it apart from *I. alectrolophum*, but Heilmann-Clausen and Thomsen (op. cit., p. 300) suggested that there may be transitional forms.

In comparing the wall structure of *I. alectrolophum* with that of *P. omasum*, Heilmann-Clausen and Thomsen (op. cit., p. 304) stated that, "The endophragm of *P. omasum* is usually densely

packed with minute internal vesicles and has smooth surfaces", although in his diagnosis of *P. omasum*, Harding (1990, p. 36, 37) describes a "pseudopunctate 'orange-peel' type surface sculpture", and one of his illustrations (op. cit., Plate 17, Figure 3) shows this particularly well. This 'orange-peel' surface sculpture appears also to occur in *I. alectrolophum* (Plate 4, Figures 2, 3 here), although Harding (op. cit.) did not refer to it, and in *Pentadinium circumfoveolatum* (Prössl 1990 ex Prössl 1992) n. comb. (see comments below).

Pentadinium circumfoveolatum (Prössl 1990 ex Prössl 1992) n. comb.

Plate 4, Figures 4, 7, 8, 10, 11, 13, 14, 16, 17

?*Gonyaulacysta circumfoveolata* PRÖSSL 1990, p. 103, pl. 10, figs. 6-10 (not validly published)

?*Gonyaulacysta circumfoveolata* PRÖSSL 1992 nomen nudum, p. 114-115

Remarks: Prössl's (1990) description of this species accords closely with observations here. He described:

- a thin, smooth periphragm forming a short, truncate apical horn
- a thick endophragm
- intratabular ornament on larger plates interrupted by an ornament-free, sub-circular zone
- foveolae with the largest concentrated in central plate areas
- partial tabulation characterised by lack of endocystal ornamentation along sutures
- a single-plate precingular archeopyle (type P)

Heilmann-Clausen and Thomsen (1995, p. 295-297) interpreted the distinctive ornament of this species as "different-sized holes", mostly in the periphragm, sometimes so closely spaced that "the periphragm is better characterised as a reticulum". They interpreted larger holes in central plate areas as possible openings in the periphragm or "vacuoles in a foamy layer between the endo- and periphragm".

The prominent equatorial pericoel of this species was noted by Heilmann-Clausen and Thomsen (1995, p. 295) and this feature was confirmed in the present study, although in his original diagnosis, Prössl (1990, p. 103) described this species only as cavate and the cingular pericoel was not clear in his illustrations (op. cit., Plate 10, Figures 6-10).

Observations in the present study do not support Heilmann-Clausen and Thomsen's interpretation, as the "ornament" which they describe appears to be structural within the endophragm, not holes within the periphragm. The periphragm appears to be smooth over much of the cyst, although some faint texture (?microreticulate) can occur (Plate 4, Figure 17). The endophragm appears to be relatively thin and smooth along sutural lines, but has penitabular and plate-centred thickenings; the sub-circular zones noted by Prössl are between these areas of thickened endocyst.

The endocyst texture of *P. circumfoveolata* (Prössl 1990 ex Prössl 1992) n. comb. appears to be very similar to the "pseudopunctate 'orange-peel'" surface texture described and illustrated for *Pentadinium omasum* by Harding (1990, p. 36,

37) and shown here for *P. circumfoveolatum* in Plate 4, Figure 16. In *P. circumfoveolatum* the wall structure also includes vacuoles of various sizes.

The structure of *P. circumfoveolatum* is very similar to that of *P. omasum*, although the former ranges has its LAD in the late Barremian and the latter has its FAD in the “mid” Aptian in the current study. *Impagidinium alectrolophum* (Sarjeant 1966a) Stover and Evitt 1978, a species with a similar “pseudopunctate ‘orange-peel’” texture occurs throughout the ranges of these species.

The apical horn of *Pentadinium circumfoveolatum* was described by Prössl (op. cit.) as truncate and Heilmann-Clausen and Thomsen (op. cit.) described it only as “hollow”. In the present study, there was significant variation in horn development from very short, triangular examples (Plate 4, Figure 4) to well-developed structures having low sutural ridges, similar to horns exhibited by *Gonyaulacysta* Deflandre 1964 and *Wrevittia* Helenes and Lucas-Clark 1997. Well-developed horns of this type differ from the smaller horns observed in *P. omasum* (see Plate 4, Figure 5 here and Harding 1990, Plate 17).

The presence of a distinct equatorial pericoel and various other similarities between *P. omasum* and *P. circumfoveolatum* justify the transfer of the latter species to *Pentadinium*, despite sometimes significant differences in horn development between these taxa.

Genus *Protoellipsodinium* Davey and Verdier 1971

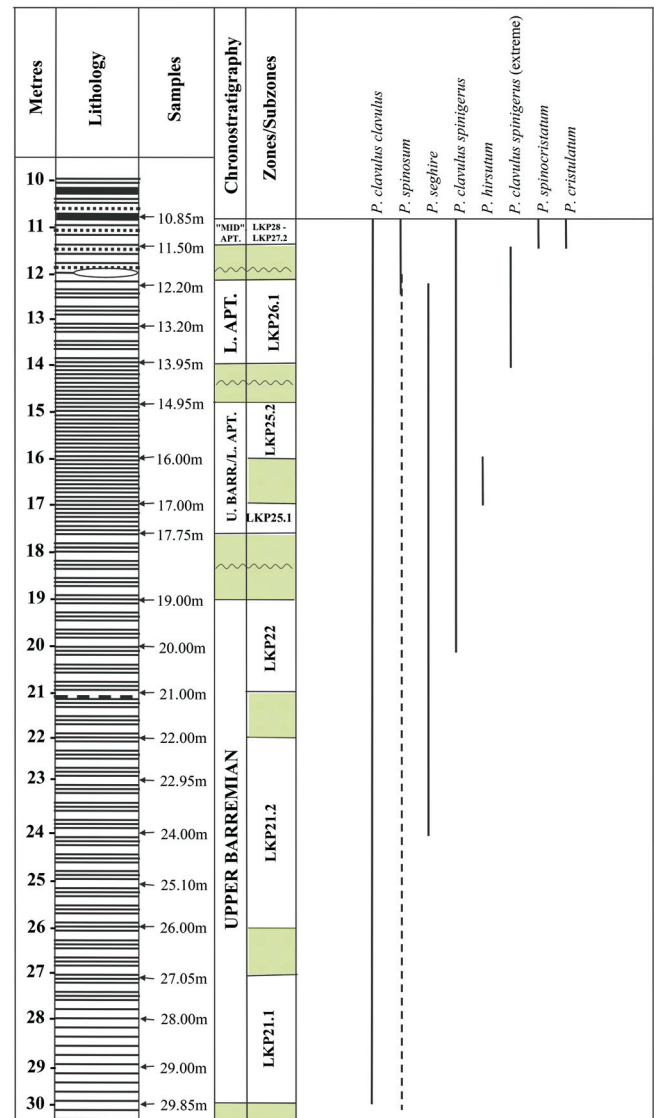
Type: Davey and Verdier 1971, Plate 5, Figure 2, as *Protoellipsodinium spinocristatum*.

Remarks: This genus was present throughout the studied interval, showing considerable morphological variation, whilst maintaining the basic features specified by Davey and Verdier (1971, p. 26) in their original generic description – elongate cyst, rounded apices without polar structures, precingular archeopyle, lack of tabulation other than sometimes represented by the cingulum and distally closed spines. Of the seven taxa assigned to this genus here, two species, *Protoellipsodinium cristulatum* and *P. hirsutum* are described as new. The distribution of *Protoellipsodinium* spp. in the current study is illustrated in text-figure 5.

The type species, *Protoellipsodinium spinocristatum*, has distinctive longitudinal ridges surmounted by acuminate spines, but this appears to be an unusual feature of the genus as a whole – only two species of the seven taxa recorded here, *P. spinocristatum* and *P. cristulatum* n. sp. display it, and both occur only in the highest two samples analysed from Heslerton No. 2 (“mid” Aptian).

Some proximal spine linkage is observed in the Valanginian species *Protoellipsodinium vacuolatum* Duxbury 2018, but that species lacks linear spine distribution, parallel to the long-axis, which is typical of *P. spinocristatum* and *P. cristulatum*. Some alignment of spine bases may also be observed in *Protoellipsodinium hirsutum* Duxbury n. sp., but without longitudinal ridges.

Other than *P. spinocristatum* and *P. cristulatum*, *Protoellipsodinium* spp. recorded here were unornamented except for spines which varied widely in length, number and distal structure (compare *Protoellipsodinium seghire* Below 1981 and extreme



TEXT-FIGURE 5

The distribution of *Protoellipsodinium* spp. in the Heslerton No. 2 borehole. The dashed line shows that the published range of *Protoellipsodinium spinosum* extends at least as old as the deepest sample analysed from Heslerton No. 2, although it was recorded only in the highest three samples in the present study.

forms of *P. clavulus* Davey and Verdier 1974 emend Duxbury 1983 subsp. *spinigerus* Brideaux 1977 n. stat.).

Protoellipsodinium clavulus Davey and Verdier 1974 emend Duxbury 1983

Protoellipsodinium clavulum DAVEY and VERDIER 1974, p. 637, pl. 93, fig. 7

Operculodinium? spinigerum BRIDEAUX 1977, p. 30, pl. 12, figs. 8, 9, pl. 13, figs. 1–11

Remarks: This species was discussed in Duxbury 1983 (pp. 53, 54) and the specific diagnosis was emended to include forms with much more elaborate distal process terminations than originally included by Davey and Verdier (1974, p. 637), who assigned to this species only specimens with spines which were “basically capitate”. In the current study, contrary to both the

original diagnosis and the emendation of Duxbury (1983), it is clear that process length can exceed half of the cyst width, particularly in younger examples with fewer processes, here included in *Protoellipsodinium clavulus* Davey and Verdier 1974 subsp. *spinigerus* Brideaux 1977 n. stat.

The sub-species *P. clavulus* subsp. *spinigerus* accommodates forms with more elaborate spine terminations, beyond those which are “basically capitate”. Although Duxbury (op. cit., p. 53) recognised a gradation between the simpler forms described by Davey and Verdier (1974) and those with multifurcate process terminations, the present study has shown that the more elaborate forms occur no older than the mid late Barremian, whereas *P. clavulus* with capitate spines ranges significantly older, to the base of the late Barremian.

***Protoellipsodinium clavulus* Davey and Verdier 1974 emend Duxbury 1983 subsp. *clavulus* autonym**
Plate 2, Figures 7, 8

Protoellipsodinium clavulum DAVEY and VERDIER 1974, p. 637, pl. 93, fig. 7
Protoellipsodinium clavulum Davey and Verdier 1974, in DUXBURY 1980, pl. 7, fig. 3
Protoellipsodinium cf. *spinosum* Davey and Verdier 1971, in BELOW 1981, pl. 11, fig. 12
Protoellipsodinium clavulum Davey and Verdier 1974, in DUXBURY 1983, pl. 5, fig. 16
Protoellipsodinium clavulum Davey and Verdier 1974, in PRÖSSL 1990, pl. 5, fig. 10

Remarks: This sub-species is restricted to the “simpler” morphotypes of *P. clavulus*, as originally described by Davey and Verdier (1974, p. 637), which have capitate distal spine terminations or very rudimentary furcation. It is a long-ranging taxon, with an age range from the early Barremian (Prössl 1990) to the early Albian (Duxbury 1983, Prössl 1990), and was recorded throughout the section analysed in the present study.

***Protoellipsodinium clavulus* Davey and Verdier 1974 emend Duxbury 1983 subsp. *spinigerus* Brideaux 1977 n. stat.**
Plate 2, Figures 11, 12, 14, 15; Plate 3, Figures 21, 22

Operculodinium? spinigerum BRIDEAUX 1977, p. 30, pl. 12, figs. 8, 9, pl. 13, Figures 1–8
Protoellipsodinium clavulum DAVEY and VERDIER 1974, in Duxbury 1983, pl. 5, fig. 19
Protoellipsodinium clavulum Davey and Verdier 1974, in PRÖSSL 1990, pl. 5, fig. 11
Protoellipsodinium clavulum Davey and Verdier 1974, in HEILMANN-CLAUSEN and THOMSEN 1995, pl. 12, fig. 11
Kiokansium prolatum, in HEILMANN-CLAUSEN and THOMSEN 1995, pl. 13, figs. 11–13

Remarks: The holotype of this sub-species, figured as *Operculodinium? spinigerum* by Brideaux (1977, Plate 12, Figures 8, 9 and Plate 13, Figures 1–4) falls at one extreme of the morphological range of this subspecies, having long, relatively few processes with several slender distal spines. Similar forms were illustrated by Heilmann-Clausen and Thomsen (1995, Plate 13, Figures 11–13) as *Kiokansium prolatum* Duxbury 1983.

Although elaborate specimens with more numerous, shorter processes and with varying numbers of distal spines occur as old as the late Barremian, the extreme forms illustrated by Brideaux (1977) and Heilmann-Clausen and Thomsen (1995), and those figured in Plate 2, Figures 14, 15 here are all re-

stricted to the Aptian. The latter type is included in *P. clavulus* subsp. *spinigerus* here, but its range is separated-out as *P. clavulus spinigerus* (extreme) in text-figure 5.

***Protoellipsodinium cristulatum* Duxbury n. sp.**
Plate 2, Figures 3–6

Holotype: Plate 2, Figure 3.

Type Locality: Heselton No. 2 at 11.50 m (core chip), “mid” Aptian. Holotype: E.F. E39.4.

Derivation of Name: From the Latin *cristula*, a small tuft, comb, plume - in reference to the characteristic crests of this species.

Diagnosis: A smooth, ellipsoidal, thin-walled species with rounded apical and antapical poles. Longitudinal ridges cover the surface of the cyst, and these bear fairly high, serrated crests for much of their length, grading into short, broad-based, acuminate spines at the poles. The archeopyle involves the displacement of a single plate, presumably the mid-dorsal precingular (3”).

Dimensions: Holotype: Length - 56 µm. Width - 41 µm.

Overall: Length - 66 (57) 48 µm; Width - 41 (39) 35 µm

Specimens Measured: 7.

Remarks: *Protoellipsodinium cristulatum* has longitudinal ridges, with serrated crests over much of its surface, although these grade to broad-based spines at the poles. In having a ridged surface it is most similar to *Protoellipsodinium spinocristatum*, although that species bears only acuminate spines, which may occasionally coalesce proximally, but without the crests typical of *P. cristulatum*.

In some respects, *P. cristulatum* and *P. spinocristatum* are similar to *Ellipsodinium rugulosum* Clarke and Verdier 1967, but differ in lacking the clear cingulum and reticulate sculpture specified for that genus by Clarke and Verdier (1967, p. 68). *Protoellipsodinium cristulatum* and *P. spinocristatum* also possess crests and/or spines along surface ridges, whereas the muri of *E. rugulosum* possesses only irregular distal margins (Clarke and Verdier op. cit., p. 69).

***Protoellipsodinium hirsutum* Duxbury n. sp.**
Plate 1, Figures 7, 8, 11, 12

Holotype: Plate 1, Figure 12.

Type Locality: Heselton No. 2 at 17.00 m (core chip), late Barremian age. Holotype: E.F. S54.0.

Derivation of Name: From the Latin *hirsutus*, hairy, bristly, rough, shaggy - in reference to the very numerous, flexuous spines of this species.

Diagnosis: A smooth, ellipsoidal, thin-walled species with rounded apical and antapical poles. Numerous slender, distally-tapering, capitate spines, about one quarter to one third the breadth of the cyst cover the cyst surface; these are usually proximally discrete but rare proximal linkage may occur. The archeopyle involves the displacement of a single plate, presumably the mid-dorsal precingular (3”).

Dimensions: Holotype: Central body - 48 × 35 µm. Overall - 61 × 48 µm.

All measured specimens: Central body - 51 (46) 41 μm \times 35 (31) 25 μm .

Overall: 61 (57) 46 μm \times 48 (45) 38 μm .

Specimens Measured: 10.

Remarks: *Protoellipsodinium hirsutum* is most similar to *P. clavulus* subsp. *clavulus* in bearing distally-tapering, capitate spines. It differs, however, in the very large number (several hundred) of spines present and in their flexuous nature. This was a relatively rare species in the current study, and is restricted in age to the late Barremian to early Aptian of Heslerton No. 2 (17.00 m and 16.00 m samples).

Genus *Pterodinium* Eisenack 1958

Type: Eisenack 1958, Plate 24, Figure 6; text-fig. 6, as *Pterodinium aliferum*

Pterodinium bab Below 1981

Plate 4, Figure 12

Pterodinium bab BELOW 1981, p. 113, pl. 7, figs. 10a–b, 11a–c; pl. 14, figs. 9, 12a–c, 13; text-figs. 72a–d, 73a–c

Impagidinium ordocaviopse IOSIFOVA 1996, p. 219, 221, pl. 1, figs. 1a–c, 2a–c, 4a–c, 5a–c; text-figs. 7A–D

Remarks: Iosifova described *Impagidinium ordocaviopse* from the ?Hauterivian of the Moscow Basin, including morphotypes with relatively high, distally smooth or wavy sutural crests bearing large perforations aligned in rows. She compared this species with several others but did not refer to *Pterodinium bab* Below 1981, which was described from the Hauterivian of Morocco.

Below's "schematic" illustrations of crestal variation in *P. bab* suggest either very fenestrate crests with slender distal spines (Below op. cit., text-fig. 73a, b) or crests with relatively small, irregularly-distributed perforations (op. cit., text-fig. 73c). However, his photographic illustrations indicate much more variation, including a specimen (op. cit., Plate 14, Figure 13) with crests very similar to those described by Iosifova for *Impagidinium ordocaviopse*.

Although it seems that Below's material includes specimens with much more elaborate crestal fenestration than that described by Iosifova, the presence of less elaborate individuals included by Below in the same species suggests that *I. ordocaviopse* Iosifova 1996 may be considered a taxonomic junior synonym of *Pterodinium bab* Below 1981.

This appears to be a long-ranging species and in the present study it occurred as young as the 13.20 m sample (early Aptian) in Heslerton No. 2.

Pterodinium premnon Duxbury 1980

Plate 6, Figures 1, 5, 8

Pterodinium premnos DUXBURY 1980, p. 131, pl. 3, figs. 1, 2

Impagidinium phlyctaena STOVER and HELBY 1987, p. 268, 271, figs. 8A–P

Remarks: Stover and Helby (1987, p. 271) recognised the similarity between *Impagidinium phlyctaena* and *Pterodinium premnon* and they pointed out that in the original diagnosis of *P. premnon* (Duxbury 1980, p. 131), the hollow, plate-centred features typical of this species were described as, "one per paraplate area". This was interpreted by Stover and Helby (op.

cit., p. 271) as, "an intratabular projection on each paraplate". They stated (op. cit., p. 271) that *I. phlyctaena* "lacks intratabular features on the apical and cingular paraplates, and on some paraplates the features are large granules rather than processes" and that because the ventral aspect of *P. premnon* was not illustrated in Duxbury 1980, "no further comparison is possible". Thus they considered this feature to distinguish *P. phlyctaena* from *P. premnon*.

Although his work was not considered by Stover and Helby, Below (1981, pp. 115, 116) provided an expanded diagnosis and detailed description of *Pterodinium premnon* and his illustrations, particularly text-figure 76, confirm the absence of plate-centred structures from the apical and cingular plates. Below (op. cit.) restricted the distribution of the plate-centred features typical of *P. premnon* to plates 1"-5", 2-6" and 1"', very similar to the distribution described for *I. phlyctaena* by Stover and Helby (op. cit.). Moreover, Below's illustrations of *P. premnon* (op. cit. Plate 3, Figures 11, 12, Plate 14, Figures 10, 11 and text-fig. 76) show that the overall structure of *P. premnon* matches closely that of *I. phlyctaena*, as illustrated in Stover and Helby (op. cit., Figure 8). Consequently, *Impagidinium phlyctaena* is considered here to be a taxonomic junior synonym of *Pterodinium premnon* Duxbury 1980.

Specimens of *P. premnon* recorded in the present study lack plate-centred structures on the apical and cingular plates (like *I. phlyctaena* - see Plate 6, Figures 1, 5, 8) and accord closely with Below's illustrations.

Genus *Raphidodinium* Deflandre 1936 emend. Sarjeant and Downie 1982, emend. Below 1987

Type: Deflandre 1936, Plate 10, Figures 1, 2, 7, as *Raphidodinium fucatum*.

Remarks: The type species, *Raphidodinium fucatum*, was originally described from flint chips of a ?Senonian age (Deflandre 1936), allowing no detailed evaluation. The type material was re-analysed by Sarjeant and Downie (1982), who emended the generic diagnosis to emphasise the gonal position of the spines, the gonyaulacoid tabulation, poorly marked by raised crests or lines, a planar to feebly laevorotatory cingulum and a precingular archeopyle.

A further generic emendation by Below (1987, p. 57, 58) significantly increased the range of forms included in this genus and specified an archeopyle involving plates 3" and 4". Following Lentin and Williams (1989, p. 121), Below's transfer of *Druggidium* to this genus is rejected here.

Raphidodinium minor Duxbury n. sp.

Plate 1, Figures 15–17

Holotype: Plate 1, Figure 15.

Paratype: Plate 1, Figure 17.

Type Locality: Heslerton No. 2 at 21.00 m (core chip), late Barremian age. Holotype: E.F. S41.0. Paratype: G40.2.

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

Diagnosis: A small, thin-walled dinocyst, elongate ovoidal to ellipsoidal with rounded polar areas. The cyst surface is finely granular and faint tabulation is outlined by very low ridges. A

prominent, fairly wide and indented cingulum with little sulcal offset is clearly marked, dividing the cyst unevenly, the epicyst being invariably shorter than the hypocyst. Long, flexuous, distally acuminate, solid gonol processes are present towards the apices but absent from much of the cyst. Equal numbers of processes can occur at the apex and antapex, but there are normally fewer at the apex; the maximum total number of spines observed is twelve.

Dimensions: Holotype: Central body - $25 \times 18 \mu\text{m}$; Overall - $48 \times 38 \mu\text{m}$.

Paratype: Central body - $33 \times 18 \mu\text{m}$; Overall - $58 \times 43 \mu\text{m}$.

All measured specimens: Central body - 33 (26) $20 \mu\text{m} \times 18$ (16) $15 \mu\text{m}$.

Overall - 58 (51) $43 \mu\text{m} \times 43$ (36) $30 \mu\text{m}$.

Specimens Measured: 8.

Remarks: Although the archeopyle type of *Raphidodinium minor* is unknown, there is a marked similarity between this small, thin-walled species and *R. fucatum*, particularly in the possession of a small number of long gonol processes, an elongate central body, a clear “feebly laevorotatory” cingulum and low ridges marking faint tabulation. It differs, however, in possessing a more elongate central body and in having its spines polarised, with no cingular processes observed.

The number of spines possessed by *Raphidodinium minor* appears to be greater than those demonstrated for *R. fucatum*. Sarjeant and Downie (1982) described “typically or constantly nine” (3 apical, 4 cingular and 2 antapical) processes for *R. fucatum*, whereas *R. minor* possesses up to twelve with no cingulars. The specimen of *R. fucatum* illustrated by Setoyama et al. (2013, Figure 5.23) has even fewer processes (?), although some processes loss may have occurred due to breakage.

Sarjeant and Downie (op. cit.) quoted an age range for *R. fucatum* of late Turonian to early Maastrichtian in France, Belgium and the North Sea Basin. Therefore there is a significant time interval between that species and *R. minor*, which was restricted to a very short interval within the late Barremian of Heslerton No. 2 (21.00 m to 19.00 m) and to a single sample, at 11,187.00 ft in well 22/26a-2.

Spiniferites Mantell 1850 emend Sarjeant 1970
Spiniferites MANTELL 1850, p. 191
Hystrichosphaera WETZEL 1933 ex Deflandre 1937b, 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, Plate 1, Figure 15, as *Xanthidium ramosum* - lectotype designated by Davey and Williams (1966, p. 32)

Remarks: Duxbury (1983) synonymised *Achomosphaera* with *Spiniferites*, following Reid (1974) and May (1980) for reasons explained in Duxbury 1983 (p. 54, 55), and that approach has again been followed here. Comments below therefore include species elsewhere included in *Achomosphaera*.

In their “Comparison” under *Spiniferites* Stover and Evitt (1978, p. 190) encapsulated the difficulty in sustaining both

Achomosphaera and *Spiniferites*, by stating, “*Spiniferites* differs from *Achomosphaera* in that parasutural ridges or septa connect the bases of processes. Such features are normally not present in *Achomosphaera*, which, however, may have faint linear markings between processes. Transitional forms are known, and their assignment to either genus is largely subjective”. Generic differentiation based on the difference between “faint linear markings” and “ridges” is clearly unsustainable.

Following Eaton’s (1976, p. 237) transfer of *Hystrichostrogylon membraniphorum* Agelopoulos, 1964 (the type species) to *Achomosphaera*, the genus *Hystrichostrogylon* is synonymised with *Spiniferites* here. Eaton transferred *H. membraniphorum* to *Achomosphaera* because of the lack of tabulation in the type material, but Stover and Evitt (1978, p. 164) stated that in *Hystrichostrogylon*, “faint parasutural lines or ridges may be present on periphragm”, exactly their criteria for separation of *Spiniferites* from *Achomosphaera*.

The presence (consistent to occasional) of an apical horn is a feature of several species of *Spiniferites* recorded in the current study, including *Spiniferites caminus* n. sp., *Spiniferites ornatus* n. sp. and *Spiniferites ramuliferus*, and this may prompt comparisons with the monospecific genus *Spiniferella* Stover and Hardenbol 1994. However, it is not the very prominent apical horn of the type, *Spiniferella cornuta* (Gerlach 1961) Stover and Hardenbol 1994, that distinguishes *Spiniferella* from *Spiniferites* but its, “relatively large last precingular paraplate that is subquadrangular to pentangular rather than subtriangular. Thus the ventral epicystal paraplate relationships of *Spiniferella* are like those of *Leptodinium* Klement 1960 emended Sarjeant 1982” (Stover and Hardenbol op. cit., p. 38).

Although further genera may be taxonomic junior synonyms of *Spiniferites* (see Williams et al. 2017, p. 753, 754), none are proposed here beyond those listed above, as they bear little relevance to the current study.

Spiniferites caminus Duxbury n. sp.
 Plate 6, Figures 3, 4, 6, 7, 10, 11, 13

Holotype: Plate 6, Figures 6, 7, 11.

Paratype: Plate 6, Figure 13.

Type Locality: Heslerton No. 2 at 27.05 m (core chip), late Barremian age. Holotype: E.F. M52.0. Paratype: E.F. X41.0.

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

Diagnosis: A species with a smooth, ovoidal endocyst and a smooth, complex pericyst. Wall layers are closely attached in dorsal and antapical areas, with the pericyst forming short gonol and sutural processes proximally connected by curved crests of varying height. Process terminations usually bifurcate (sutural) and trifurcate (gonol), although both can be distally simple. A large pericoel characterises the ventral surface, displaying a large mid-ventral claustrum. A prominent, parallel-sided to distally-flaring apical horn is invariably present, usually flat-ended but sometimes bearing short spines at its distal extreme. The archeopyle is single plate precingular (3”).

Dimensions: Holotype: $66 \times 66 \mu\text{m}$.

Paratype: $58 \times 51 \mu\text{m}$.

Overall: 71 (63) 58 μm \times 66 (58) 51 μm .

Specimens Measured: 11.

Remarks: *Spiniferites caminus* possesses several characteristics similar to *Diphysiosphaera stolidota*, particularly the distinct apical horn, fairly thick, smooth cyst wall and partial cavation. In the present study, the stratigraphic range of *S. caminus* is within the older late Barremian of Heslerton No. 2, between 29.85 m and 27.05 m, immediately preceding *D. stolidota*, suggesting that *S. caminus* might be the precursor of that species.

***Spiniferites ornatus* Duxbury n. sp.**

Plate 5, Figures 1–6, 8, 9, 12

Spiniferites? sp. 1 in HEILMANN-CLAUSEN and THOMSEN 1995, p. 307, pl. 10, figs. 1–4

Holotype: Plate 5, Figures 1–4

Paratype: Plate 5, Figures 5, 6, 8, 9

Type Locality: Heslerton No. 2 at 13.20 m (core chip), early Aptian age. Holotype: E.F. V39.0. Paratype: Q28.1

Derivation of Name: From the Latin *ornatus*, adorned - in reference to the surface ornament.

Diagnosis: A species with a thick, fibro-perforate endocyst and a thinner, microperforate pericyst forming short trifurcate gonial and bifurcate sutural processes. Tabulation is marked by low ridges and suturocavation is common, often best developed around the cingulum. A prominent ventral pericoel can occur, displaying a large mid-ventral claustrum. An apical horn is often present, flat-ended or bearing a terminal spike. The archeopyle is single plate precingular (3").

Dimensions: Holotype: 83 \times 71 μm .

Paratype: 71 \times 71 μm .

Overall: 83 (67) 56 μm \times 73 (64) 48 μm .

Specimens Measured: 20.

Remarks: *Spiniferites ornatus* was recorded by Heilmann-Clausen and Thomsen (1995, p. 307) and referred informally to *Spiniferites?* sp. 1. They suggested that all specimens are pterocavate, but this does not appear to be the case, although the prominent suturocavation consistently displayed can be best developed around the cingulum.

An apical horn often occurs in this species and, in forms with a prominent cingular pericoel, it can resemble some species of *Pentadinium*, although the consistent occurrence of gonial and sutural processes excludes it from that genus.

Spiniferites ornatus is distinctive, involving a thick, fibro-perforate endophragm, which can appear densely granular or fibroreticulate, and a thinner, microperforate periphragm; the periphragm surface often appears microreticulate.

The observed age range of *S. ornatus* is of an early Aptian age in the Heslerton No. 2 borehole, being restricted to the 13.95 m, 13.20 m and 12.20 m samples. This age appears to be consistent with Heilmann-Clausen and Thomsen (op. cit.), who recorded it only from the early and (formal) middle Aptian of the Ahlum 1 borehole.

***Spiniferites ramuliferus* (Deflandre 1937b) Reid 1974**

Plate 22, Figure 8, Plate 23, Figure 10

Hystrichosphaera cf. *ramosa* (Ehrenberg) in DEFLANDRE 1935, pl. 5, fig. 11

Hystrichosphaeridium ramuliferum DEFLANDRE 1937b, p. 74, pl. 14, figs. 5, 6, pl. 17, fig. 10

Baltisphaeridium ramuliferum (Deflandre) in DOWNIE and SARJEANT 1963, p. 92

Achomosphaera ramulifera (Deflandre) in EVITT 1963, p. 163

Spiniferites ramuliferus (Deflandre) in REID 1974, p. 608, pl. 4, figs. 39, 40

Remarks: Considerable morphological variability was observed within this species in the present study, although the absence of sutural crests or ridges, or their very faint expression was consistent. Specimens illustrated in Plate 22, Figure 8 and Plate 23, Figure 10 illustrate some of this variation, including an essentially pentagonal process arrangement in the former and an apical horn and small ventral pericoel in the latter.

This species was recorded throughout the Heslerton No. 2 section, but no deeper than 11,235.00 ft in well 22/26a-2, together with the FAD of *Rhynchodiniopsis fimbriata* and at a level immediately above the *denckmanni/pingue* ammonite zone age assigned at 11,236.17 ft on nannofossils (re-interpreted from Rawson and Jeremiah 2001). Duxbury (1980, text-fig. 3) did not record *S. ramuliferus* with *R. fimbriata*, suggesting that the first species may have a slightly older FAD in well 22/26a-2 than at Speeton (see comments regarding *R. fimbriata* under "Background", above). Duxbury (2001) placed the FAD of *S. ramuliferus* in the upper part of Zone LKP19, towards the base of the "middle" Barremian (included in the upper Barremian here). Although the exact zonal position of the FAD of *Spiniferites ramuliferus* is unclear (lowest LKP20 or highest LKP19), it is nevertheless of an older late Barremian age.

***Spiniferites speetonensis* Duxbury 1980**

Plate 7, Figures 13, 16

Spiniferites speetonensis DUXBURY 1980, p. 131–132, pl. 11, figs. 1, 2, 4

Remarks: Specimens of this species recorded here accord closely with material described in Duxbury 1980, possessing gonial and sutural processes with distally perforate to fenestrate extremities and, in some cases, a ventral pericoel with claustrum. Although Duxbury (1980, p. 131) described "Short gonial (trifurcate) and parasutural (bifurcate) processes", the specimen illustrated in Plate 7, Figures 13, 16 has somewhat longer processes than are displayed by the holotype (Duxbury 1980, Plate 11, Figures 1, 2, 4).

The youngest occurrence of this species in the present study was at 16.00 m in Heslerton No. 2 (Zone LKP25), close to the Barremian/Aptian boundary, a level similar to that reported by Lister and Batten (1995, Figure 2B).

Genus *Surculosphaeridium* Davey, Downie, Sarjeant and Williams 1966 emend. Davey 1982.

Type: Sarjeant 1960, Plate 6, Figure 2, as *Hystrichosphaeridium cribrotubiferum*.

***Surculosphaeridium palmatum* Duxbury n. sp.**

Plate 19, Figures 1, 2, 4, 5, 7, 8

Holotype: Plate 19, Figures 4, 7

Paratype: Plate 19, Figure 8

Type Locality: Heslerton No. 2 at 27.05 m (core chip), late Barremian age. Holotype: E.F. X28.0. Paratype Heslerton No. 2 at 22.00 m (core chip), E.F. F41.2.

Derivation of Name: From the Latin *palmatus*, shaped like the palm of the hand - in reference to the distal process terminations.

Diagnosis: A small, fairly thick-walled chorate cyst, smooth walled and bearing long, solid, simple, mesotabular processes, in length about half of the main body diameter. Processes taper and then expand into broad distal terminations. Rarely, individual circular processes may bifurcate. Processes indicate a reflected tabulation pattern of 4', 6", 6c, 6"', 1p, 1'''. Distal terminations are palmate and in pre- and postcingular areas, the "heel" of each palm is adcingular. The archeopyle is tetratabular apical and the operculum is usually detached.

Dimensions: Holotype (operculum lost): Central body - $38 \times 38 \mu\text{m}$. Overall - $63 \times 71 \mu\text{m}$.

Paratype (complete): Central body - $43 \times 35 \mu\text{m}$. Overall - $73 \times 71 \mu\text{m}$.

Complete specimens: Central body - 43 (43) $43 \mu\text{m} \times 38$ (37) $35 \mu\text{m}$. Overall - 76 (75) $73 \mu\text{m} \times 71$ (71) $71 \mu\text{m}$.

Specimens measured: 2.

Operculum lost: Central body - 41 (38) $33 \mu\text{m} \times 41$ (38) $33 \mu\text{m}$. Overall - 76 (63) $51 \mu\text{m} \times 76$ (71) $61 \mu\text{m}$.

Specimens measured: 11.

Remarks: *Surculosphaeridium palmatum* is similar to *Surculosphaeridium trunculum* Davey 1979 and *S. longifurcatum* (Firtion 1952) Davey et al. 1966. It differs from *S. trunculum* in the simplicity of the processes, which are solid and without furcation, except for occasional bifurcation within the cingular series. In contrast, *S. trunculum* bears two process types, one bifurcating proximally and thinner processes, usually cingular, linked by medial bars. The palmate process terminations of *S. palmatum* contrast with those of *S. trunculum*, which "typically bifurcate or trifurcate and terminate with a small bifurcation or spinelets" (Davey 1979, p. 560).

Surculosphaeridium longifurcatum typically bears distally branching processes with those marking the cingulum characteristically deeply-furcate. The irregular distal process terminations of this species again contrast markedly with those of *S. palmatum*. Davey (1979, p. 560) considered *S. trunculum* to be "probably ancestral" to *S. longifurcatum*, with the last species ranging no older than the Albian (after Davey and Verdier 1971).

In the present study, *S. palmatum* ranges from 29.85 m to 16.00 m in Heslerton No. 2, upper Barremian, Zone LKP21 to the upper Barremian/lower Aptian, Zone LKP25.

Wrevittia Helenes and Lucas-Clark 1997

Type: Eisenack and Cookson 1960, Plate 1, Figure 4, as *Gonyaulax helicoidea*.

Remarks: Helenes and Lucas-Clark (1997) transferred several species from *Gonyaulacysta* Deflandre 1938 into their new

genera *Stanfordella* and *Wrevittia*, largely based on details of tabulation. They stated (op. cit., p. 179), "in this paper, we have transferred from *Gonyaulacysta* only those species whose morphology and paratabulation are sufficiently known, and conform to our definitions of *Stanfordella* and *Wrevittia*". They transferred *Gonyaulacysta cassidata* (Eisenack and Cookson 1960) Sarjeant 1966a into *Wrevittia* but not the similar species *Gonyaulacysta teichos* Davey 1974 or *G. speciosa* Harding 1990; the last species was not included at all in Helenes and Lucas-Clark (op. cit.) and the first was retained by them in *Gonyaulacysta*.

In discussing the tabulation of *Wrevittia*, Helenes and Lucas-Clark (1997, p. 186) stated, "The A/ai contact (hence separation of lu and li) is usually obvious and serves to separate this paratabulation from that of *Gonyaulacysta* and *Stanfordella*", and this distinction is clearly illustrated in Helenes and Lucas-Clark (op. cit., text-fig. 1). Detailed illustrations in Harding 1990 (Figures 14 and 15) of *Gonyaulacysta speciosa* and *G. teichos*, when interpreted in terms of Helenes and Lucas-Clark's defining criteria, suggest that these species should be assigned to different genera, since plates lu and li (=l' and 6" in Kofoid notation) are disconnected in *G. speciosa* whereas they touch in *G. teichos*. Although it is perhaps surprising that such similar taxa, both Barremian and both considered part of the "*Gonyaulacysta cassidata* lineage" by Harding (op. cit.) should merit separation into different genera, on the basis of Helenes and Lucas-Clark's criteria and of Harding's illustrations, *G. speciosa* is here transferred to *Wrevittia*, with *G. teichos* retained in *Gonyaulacysta* pending further study.

Wrevittia sp. cf. ***Wrevittia cassidata*** (Eisenack and Cookson 1960)

Helenes and Lucas-Clark 1997

Plate 13, Figures 10, 11

Remarks: In his comments on *Wrevittia teichos* (as *Gonyaulacysta teicha*), Harding (1990, p. 34) stated, "The possession of a strongly inflated apical pericoel indicates a close relationship with *Gonyaulacysta speciosus* sp. nov. and the *G. cassidata* lineage". The roots of this "lineage" appear to be in the lower Barremian, well before the FAD of *Wrevittia cassidata* (Aptian of Australia - Eisenack and Cookson 1960, p. 3 and Morgan 1980, Figure 8 and England - Duxbury 1983, text-fig. 3).

A further member of the "*G. cassidata* lineage" was recorded in the current study which did not appear to display defining characteristics of either *W. speciosa* or *G. teichos*. It varied from specimens with a smooth or lightly ornamented endocyst (Plate 13, Figure 11) to forms with a fairly dense cover of short conical (Plate 13, Figure 10), and it is informally referred to *Wrevittia* cf. *cassidata* here, pending a fuller assessment of its morphology.

This appears to be a stratigraphically valuable taxon, and its total range (Zones LKP21 and LKP22) is illustrated in text-figures 6, 7, 8 and 9.

Other species

Wrevittia speciosa (Harding 1990) **n. comb.**

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 (name not validly published in Harding 1990)

Remarks: see comments under *Wrevittia*, above.

STRATIGRAPHIC COMMENTS

Many palynofloral studies of the Boreal Barremian and Aptian stages have been undertaken, several of which are listed in Heilmann-Clausen (1987, text-fig. 3); these earlier contributions were necessarily more taxonomic than biostratigraphic, not surprising in view of the large number of new taxa encountered by earlier workers. Outstanding examples of these studies include Gocht (1957, 1959), Eisenack (1958), Alberti (1959, 1961), Neale and Sarjeant (1962), Davey and Williams (1966), Sarjeant (1966a, b) and Davey (1974).

A more stratigraphic approach was taken by later authors, who illustrated in detail the chronostratigraphic distribution of relevant taxa, by either compiling data from previous publications including Heilmann-Clausen (1987) and Pestchevitskaya (2007) or from first-hand analyses including Duxbury (1980, 1983), Heilmann-Clausen (1987), Harding (1990), Prössl (1990) and Lister and Batten (1995).

There have been varying degrees of success in terms of the consistent recognition and correlation of stratigraphically useful Boreal Barremian and Aptian events between outcrops or from outcrop to borehole sections, with notable attempts including Lister and Batten 1988 and Heilmann-Clausen and Thomsen (1995).

As noted by Harding (1990, p. 56, 57), in previous palynofloral studies the establishment of a formal zonation scheme for the Boreal Barremian and Aptian received little attention, being largely restricted to the broad scheme of Davey (1979). Duxbury (2001) established 15 zones for the Barremian and Aptian interval and this remains the most detailed Boreal scheme for this interval, justifying Harding's comment (1990, p. 56) that dinocysts can approach the "apparent resolution of cephalopod zonations". Direct linkage of palynofloral events to macrofossil zones is often difficult, however, because of the general rarity of macrofossils.

Results from the current study have allowed the direct comparison of palynofloral events in Heselton No. 2 and Central North Sea well 22/26a-2 with previously-reported analyses, particularly of outcrop and borehole data from Speeton (Duxbury 1980, Harding 1990) and the Lower Saxony Basin, including the Gott clay pit (Below 1982a; Harding 1990; Heilmann-Clausen and Thomsen 1995) and the Wiechendorf 1/86 borehole (Lister and Batten 1995).

Key palynofloral events recorded in the current study for the late Barremian and Aptian interval are summarised in text-figures 6, 7, 8 and 9 and these are briefly discussed below. Comprehensive species occurrence bar charts have been included for Heselton No. 2 and well 22/26a-2 in text-figures 10 and 11 respectively, providing absolute abundance counts of both marine and miopore taxa.

Heselton No. 2

The zonal sub-division of the section analysed is summarised using the modified Duxbury (2001) palynofloral scheme in text-figures 2, 6, 9 and 10.

The deepest section analysed here, between 29.85 m and 19.00 m has been assigned a late Barremian age, Zones LKP21 to LKP22, based on the LAD of *Aprobolocysta neista* at 19.00 m and the absence of *Rhynchodiniopsis fimbriata* throughout.

Confirmation of a late Barremian age to the base of the studied section included the occurrence of *Carpodinium glabrum*, *Cerbia tabulata*, *Odontochitina operculata*, *Palaeoperidinium cretaceum*, *Protoellipsodinium clavulus clavulus* and *Spiniferites ramuliferus* at 29.85 m.

The presence of *Carpodinium glabrum* is particularly significant since its oldest occurrence is in sample PAL 299, towards the top of the Cement Beds at Speeton (Duxbury 1980, text-figs. 2, 3, as *Carpodinium granulatum*), supporting a Zone LKP21 age to the base of the Heselton No. 2 core. The correlative significance of *C. glabrum* (as *C. granulatum*) was also recognised by Heilmann-Clausen and Thomsen (1995, p. 271, text-fig. 5).

A marked change in assemblage character was observed between the 27.05 m and 26.00 m samples, including significant up-section increases in *Cyclonephelium distinctum* and *Subtilisphaera perlucida* with corresponding reductions in *Odontochitina operculata* and *Hystriosphera arborispinum*.

The LADs of several taxa were recorded at 27.05 m, including *C. glabrum*, *Druggidium jubatum* and *Spiniferites caminus*, and taxa with their FADs at 26.00 m include *Cribroperidinium episomum* and *Cribroperidinium cornutum*. Combined with the overall change in assemblage character between 27.05 m and 26.00 m, this might suggest a small intra-Zone LKP21 hiatus or rapid palaeoenvironmental change. The LAD of *Cassiculosphera magna* was also recorded at 27.05 m, younger than suggested by Harding (1990 - see notes under *Cassiculosphera*, above and text-fig. 6).

Species ranging no higher than 19.00 m, included *Aprobolocysta neista* (see notes on this species under well 22/26a-2), *Cribroperidinium cornutum*, *Ellipsodinium reticulatum* and *Pseudoceratium solocispinum*, and the highest common occurrence of *Pseudoceratium pelliiferum* was also at that depth. The last two events indicate an age no younger than Zone LKP22. The oldest common occurrence of *Chlamydothorella membranoperforata* was at 21.00 m, at the base of Zone LKP22: this event was recorded at a similar level in well 22/26a-2 (text-fig. 7).

Several previously undescribed taxa were recorded within Zone LKP21 which to date are restricted to the Heselton No. 2 core, including *Muderongia patula* between 28.00 m and 25.10 m, *Biorbifera barremiana* at 26.00 m and 24.00 m and *Apteodinium mutabile* between 26.00 m and 22.95 m. Occurrences of *Raphidodinium minor* were restricted to only three samples, between 21.00 m and 19.00 m (Zone LKP22).

In addition, the informal taxon *Wrevittia* sp. cf. *Wrevittia cassidata* was restricted to the interval 26.00 m to 20.00 m (Zones LKP21 to LKP22). It was also recorded between 11,200.00 ft and 11,187.00 ft in well 22/26a-2 (Zone LKP22 - text-fig. 7).

A major assemblage change was recorded between the 19.00 m and 17.75 m samples, including marked up-section increases in *Impagidinium alectrolophum*, *Pentadinium omasum* and acanthomorph acritarchs and associated reductions in *Dingodinium albertii* and *Subtilisphaera perlucida*. In addition, the 17.75 m sample was characterised by large numbers of *Druggidium rhabdoreticulatum* and a major influx of *Cribroperidinium hadrum*. The last species was restricted to the 17.75 m and 17.00 m samples, associated with *Fromea complicata*, a

species particularly common at 17.00 m. The LAD of *Cribopteridinium episomum* was also at 17.75 m.

The restricted range of *Cribopteridinium hadrum* in Heslerton No. 2 strongly suggests that it is directly equivalent to about 19.25 m in the Shell West Heslerton No. 1 borehole, the type locality of *C. hadrum* (Sarjeant 1966a, p. 119–121). In addition, Lister and Batten (1995, p. 384) described, “forms comparable to *Leptodinium? hadrum*” as numerically significant between 99.87 m and 99.50 m in borehole Wiechendorf 1/86 in the Lower Saxony Basin, associated with common *Fromea fragilis*, a form similar to *F. complicata*. This is again considered equivalent to the restricted range of *C. hadrum* in Heslerton No. 2 (Subzone LKP25.1 - text-figs. 6, 9).

Several key late Barremian taxa were absent from Heslerton No. 2, collectively ranging between Zone LKP23 and Zone LKP24 (see notes under well 22/26a-2, below and text-figs. 6, 7, 9). This, and the major assemblage change observed, indicate a significant hiatus between the 19.00 m and 17.75 m samples, with Zone LKP25 resting on Zone LKP22.

An isolated occurrence of *Meiourugonyaulax lacunosa* at 19.00 m provides further evidence for a significant hiatus between 19.00 m and 17.75 m. A longer range, between Zones LKP22 and LKP24, was observed for this species in the more complete 22/26a-2 core (see notes below) and this again suggests that much of its range is missing between the 19.00 m and 17.75 m samples.

Duxbury (2001, p. 128) defined the top of Zone LKP24 on the LADs of *Cribopteridinium cornutum*, *Scriniodinium barremianum* and *Batioladinium longicornutum*, but it is now clear that these events are not isochronous. In the present study and in other Barremian/Aptian boundary studies, *B. longicornutum* ranges consistently younger than the other two species and, to reflect this, the top of Zone LKP24 is here re-defined on the LADs of *C. cornutum* and *S. barremianum*, with the LAD of *B. longicornutum* now included as a Zone LKP25 marker.

In Heslerton No. 2, the highest occurrences of *Batioladinium longicornutum*, *Hystriodinium furcatum*, *H. ramoides* and *Pentadinium omasum* were at 14.95 m, and the interval 17.75 m to 14.95 m has been assigned to Zone LKP25, of a late Barremian to early Aptian age (see notes on Wiechendorf 1/86, below). *Tehamadinium sousense* was present only at 13.95 m and 13.20 m, being particularly common at the deeper level. This is entirely within the early Aptian, an age very similar to that given in Below (1981, p. 61, 62).

A previously undescribed species, *Protoellipsodinium hirsutum*, was recorded only at 17.00 m and 16.00 m, and the highest occurrence of *Chlamyphorella membranoperforata* was at 16.00 m, confirming its LAD close to the Barremian/Aptian boundary.

The interval 13.95 m to 12.20 m has been assigned an early Aptian age in the present study, and palynofloras reflect a marked hiatus between 12.20 m and the base of the overlying interval (“mid” Aptian), at 11.50 m, confirming the evidence of Rutledge (1994, p. 230), of a “considerable nannofloral turnover across a sharp lithological contact at 12.07 m”. Rutledge (op. cit.) tentatively inferred an intra-lower Aptian hiatus between the *forbesi* and *deshayesi* zones at that level.

Assemblages between 13.95 m and 12.20 m were generally similar to those below, but they showed a marked increase in *Subtilisphaera perlucida* and a significant up-section increase in *Dingodinium cerviculum*, peaking at 12.20 m. The LAD of *S. perlucida* was at the top of the interval, where it was abundant. *Meiourugonyaulax stoveri* subsp. *grandis* n. subsp. and *Spiniferites ornatus* n. sp. were also characteristic of this interval.

Nyktericysta? vitrea was restricted to the interval 13.95 m to 12.20 m and the LADs of *Heslertonella heslertonensis* and *Avellodinium falsificum* were at 13.20 m. *Nyktericysta? vitrea* was shown to range no older than the *forbesi* ammonite zone in Duxbury 1983, and this base was confirmed in Lister and Batten (1988). Similarly, the LAD of *H. heslertonensis* has been proved to lie within the *forbesi* Zone by those authors. Duxbury (2001, Figure 16) placed the LAD of *Avellodinium falsificum* within the *fissicostatus* ammonite zone, but evidence from Heslerton No. 2 suggests a slightly younger LAD.

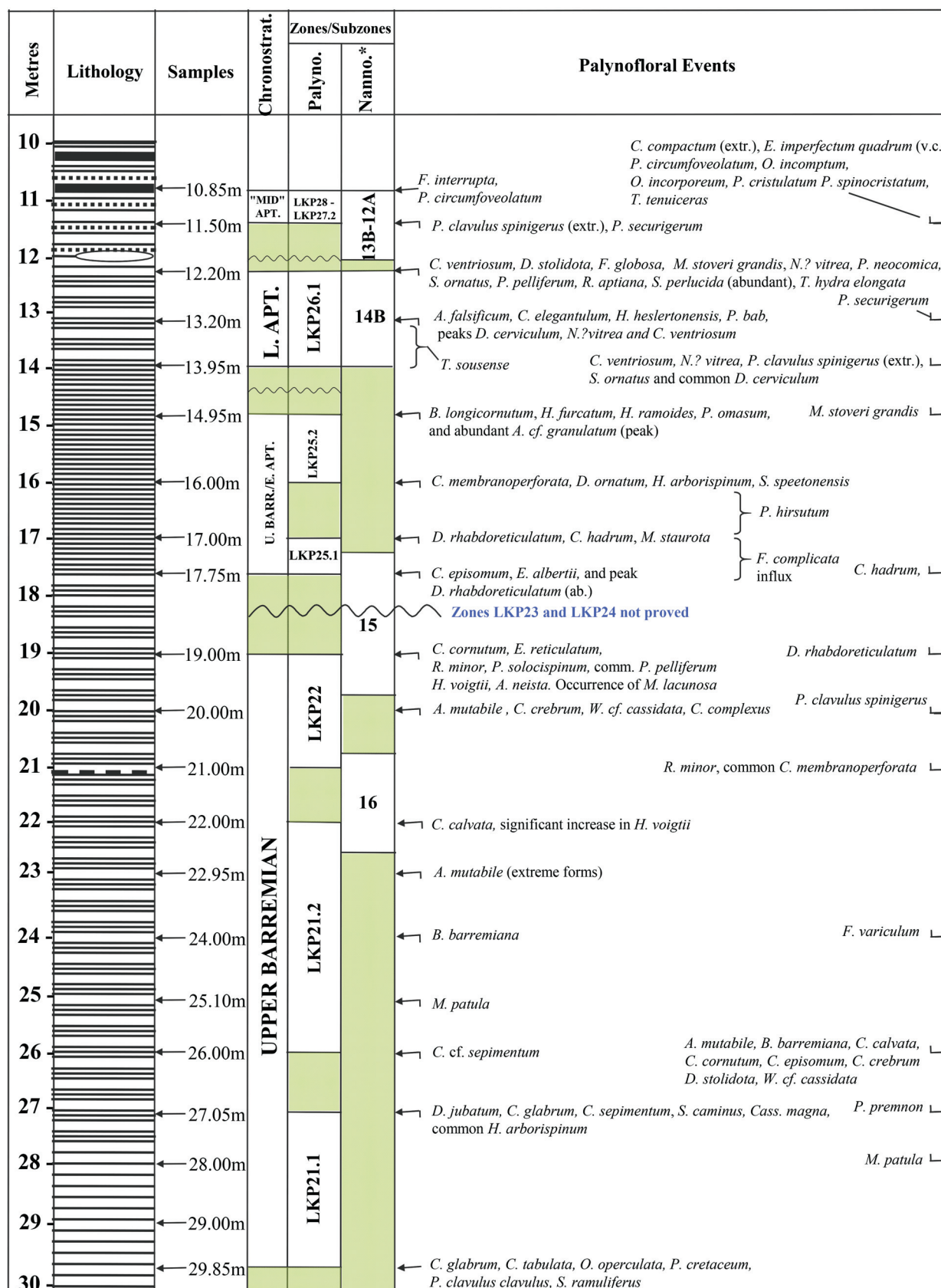
Several species ranged no higher than 12.20 m in Heslerton No. 2, including *Diphysiosphaera stolidota*, *Phoberocysta neocomica* and *Pseudoceratium pelliferum*, with the first two ranging no higher than the *forbesi* Zone (Duxbury 1983); *Pseudoceratium pelliferum* was shown to range as high as the *deshayesi* Zone by Duxbury (op. cit.), and this was again confirmed in Lister and Batten (1988).

The LAD of *Taleisphaera hydra* subsp. *elongata* was also at 12.20 m, although a slightly younger level within the Aptian is indicated by Heilmann-Clausen and Thomsen (1995, Figure 3), as they recorded the LAD of this taxon slightly higher than the FAD of *Pentadinium circumfoveolatum*, a species occurring only as deep as 11.50 m (“mid” Aptian) here.

The combined ranges of key taxa observed has therefore allowed a *forbesi* Zone, palynofloral Subzone LKP26.1 assignment for the interval 13.95 m to 12.20 m. This and the lack of convincing evidence for the Fischeischiefer in Heslerton No. 2 might suggest a hiatus between the 14.95 m and 13.95 m samples. The age of the Fischeischiefer was discussed for the southern margin of the Lower Saxony Basin by Lehmann et al. (2012), with various regional interpretations summarised in their text-figure 10. In their interpretation, the Fischeischiefer occurs in the lower part of their *fissicostatus* Zone (= *fissicostatus* and lowermost *forbesi* Zone of Southern England), an age very similar to that assumed for the North Sea Basin in Jeremiah (2001).

A minor hiatus between 14.95 m and 13.95 m might also be suggested by the FAD of *Cepadinium ventriosum* at the higher level, above the LAD of *Batioladinium longicornutum*, at 14.95 m. Both Heilmann-Clausen and Thomsen (1995) and Lister and Batten (1995) recorded *B. longicornutum* consistently higher than the FAD of *C. ventriosum* in the Lower Saxony Basin (see text-fig. 8).

Extreme forms of *Protoellipsodinium clavulus* subsp. *spinigerus*, as illustrated by Brideaux (1977, Plate 12, Figures 8, 9 and Plate 13, Figures 1–4) and Heilmann-Clausen and Thomsen (1995, Plate 13, Figures 11–13), and as shown in Plate 2, Figures 14, 15 here are restricted to the Aptian in Heslerton No. 2. The latter type is included in *P. clavulus* subsp. *spinigerus*, but its range is separated out as *P. clavulus spinigerus* (extreme) in text-fig. 5; this taxon ranges no deeper than 13.95 m.



TEXT-FIGURE 6

Key palynofloral events and interpreted stratigraphy of the Heselton No. 2 borehole. * Nannofloral zones after Jeremiah (2001)

Several taxa had their FADs at 11.50 m; these included *Protoellipsodinium spinocristatum*, *P. cristulatum* and *Tehamadinium tenuiceras*. In addition, *Pseudoceratium securigerum* and *Florentinia interrupta* ranged as high as 11.50 m and 10.85 m respectively. The combined ranges of these taxa suggest an early Aptian age, upper *deshayesi* to *bowerbanki* ammonite zones (Duxbury 1983) for this short interval; this differs from the late Aptian age assigned at 10.85 m by Jeremiah (2001, Table C1), but agrees with his early Aptian age assignment at 11.3 m.

The FADs of *Cyclonephelium compactum* (extreme - see Duxbury 1983), *Ovoidinium incomptum*, *O. incorporeum* and *Pentadinium circumfoveolatum* were also at 11.50 m, however. The FADs of the first three were recorded in the late Aptian of Southern England (Duxbury 1983; Lister and Batten 1988) and *P. circumfoveolatum* was assigned a late Aptian age by Prössl (1990) and Heilmann-Clausen and Thomsen (1995). The latter authors and Lister and Batten (op. cit.) also recorded the LAD of *Florentinia interrupta* within the late Aptian.

A major influx of *Ellipsoidictyum imperfectum* subsp. *quadrum* was observed at 11.50 m (the FAD of this taxon), and this might be a useful secondary marker close to the lower/upper Aptian boundary in this area, although this remains to be confirmed.

The age of the interval 11.50 m to 10.85 m is clearly close to the early/late Aptian boundary and may span it. In view of the uncertainty about the precise ranges of taxa recorded, the present author follows Jeremiah (2001) in assigning a "mid" Aptian age, within palynofloral Zones LKP27.2 to LKP28.

Well 22/26a-2

Seven palynological zones of a late Barremian age, informally named LKP19 to LKP25, were described for the UKCS Central North Sea by Duxbury (2001). The definitions of Zones LKP23 and LKP24 (Duxbury 2001, p. 128) included reference to three previously undescribed late Barremian-restricted taxa, *Cerbia magna*, *Impagidinium diversum* and *Scrinioidinium barremianum*, none of which was recorded in Heselton No. 2 in the present study, suggesting a probable hiatus. In order to test this, a more complete, cored section of a late Barremian age in UK Central Graben well 22/26a-2 was analysed for comparison. The zonal sub-division of this section is summarised using a modified Duxbury (2001) palynofloral scheme in text-figures 7, 8 and 11.

The deepest section analysed from well 22/26a-2, between 11,245.00 ft and 11,230.00 ft, has been assigned a late Barremian age, Zone LKP20, based on the presence of *Trabeculidium quinquetrum* at 11,245.00 ft, the FAD of *Pterodinium premnon* at 11,235.00 ft, the occurrences of *Rhynchodiniopsis fimbriata* between 11,235.00 ft and 11,230.00 ft and the LAD of *Cribroperidinium colum* at 11,230.00 ft. Several taxa present in the deepest sample analysed, at 11,245.00 ft, further confirmed this assignment, although they can range as old as Zone LKP19. Such taxa included *Prolixosphaeridium deirense* and *Odontochitina operculata*.

An influx of *Impletosphaeridium multifurcillatum* and a marked uphole increase in numbers of *Ctenidodinium elegantulum* were observed between 11,235.00 ft and 11,230.00 ft; neither of these events were seen in Heselton No. 2.

The LAD of *Gongylodinium brevispinosum* (another species not seen in Heselton No. 2) was also at 11,230.00 ft, suggesting that this might be a valuable alternative top Zone LKP20 marker. Occurrences of *G. brevispinosum* (as *Gongylodinium pauliae*) were recorded by Heilmann-Clausen and Thomsen (1995, Figure 3) as high as 236.00 m in the Ahlum-1 borehole, at the top of the lower Barremian. The age-discrepancy of this event compared to the present study is probably due to the placement by Kemper (1995, Figure 1) of the *elegans* and *denckmanni* ammonite zones within the lower Barremian (see notes under "Materials and methods", above).

Further evidence for the Zone LKP20 assignment between 11,245.00 ft and 11,230.00 ft included the FADs of *Exiguisphaera plectilis* and *Palaeoperidinium cretaceum* at 11,238.67 ft, immediately below the FAD of *Rhynchodiniopsis fimbriata*, exactly as recorded within the lower Cement Beds at Speeton (Duxbury 1980, text-fig. 3). Assemblages recorded between 11,245.00 ft and 11,230.00 ft in well 22/26a-2 are therefore older than anything seen in Heselton No. 2, although still within the late Barremian.

The interval 11,220.25 ft to 11,200.00 ft has been assigned a late Barremian age, Subzone LKP21.1, based on the LADs of *Cassiculosphaeridia magna* and *Spiniferites caminus* at 11,200.00 ft and the absence of *Rhynchodiniopsis fimbriata*.

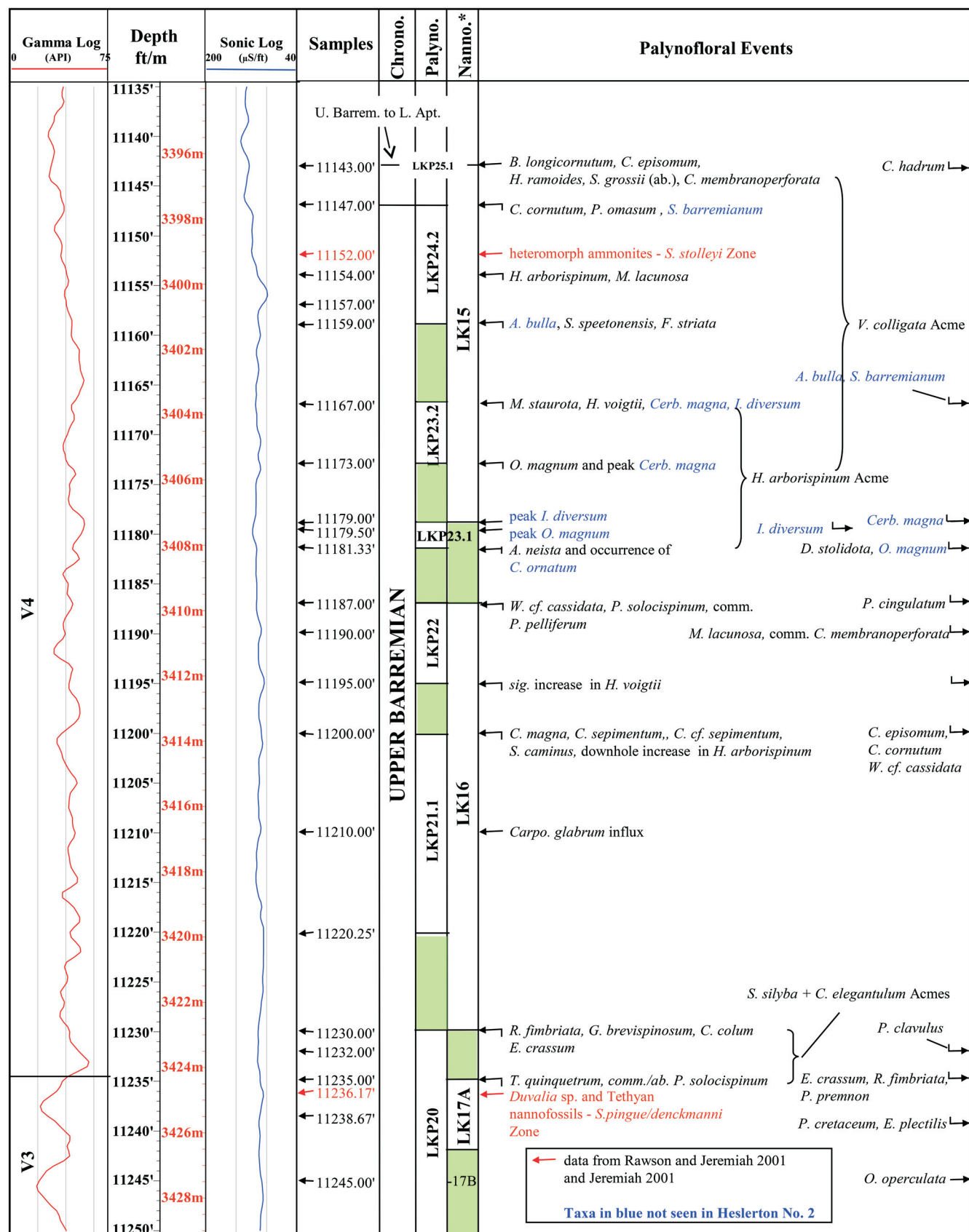
The FADs of *Cribroperidinium episomum* and *C. cornutum* were also at 11,200.00 ft, and an influx of *Carpodinium glabrum* occurred at 11,210.00 ft. All of these events were noted between 27.05 m and 26.00 m in Heselton No. 2, further confirming an intra-Zone LKP21 age towards the base of the Heselton No. 2 core.

In Heselton No. 2, the LADs of several taxa co-occurred at 19.00 m, including *Pseudoceratium solocispinum*, *Aprobolocysta neista* and *Cribroperidinium cornutum*. This contrasts with well 22/26a-2, in which the LADs of these taxa were discrete events, occurring at 11,187.00 ft, 11,181.33 ft and 11,147.00 ft respectively; the 11,147.00 ft sample is the top of Zone LKP24. Also, the LAD of *Aprobolocysta neista* in well 22/26a-2 was above the LAD of common *Pseudoceratium pelliiferum* (at 11,187.00 ft), a top Zone LKP22 event, suggesting that *A. neista* has its LAD in Zone LKP23. An isolated rare occurrence of *Raphidodinium minor* was restricted to the 11,187.00 ft sample.

The informal taxon *Wrevittia* cf. *cassidata* was restricted to the interval 11,200.00 ft to 11,187.00 ft, and a similar Zone LKP21 to LKP22 range was recorded between 26.00 m and 20.00 m in Heselton No. 2 (text-fig. 6). The oldest common occurrence of *Chlamydothorella membranoperforata* was at 11,190.00 ft, also within Zone LKP22 and a similar level for this event was noted in Heselton No. 2 (text-fig. 6).

Several taxa collectively ranging between Zones LKP23 and LKP24 were present in well 22/26a-2 but absent from Heselton No. 2, including *Oligosphaeridium magnum*, *Impagidinium diversum*, *Cerbia magna*, *Apteodinium bulla* and *Scrinioidinium barremianum*, and the first three were very common to abundant at 11,179.50 ft, 11,179.00 ft and 11,173.00 ft respectively.

Duxbury (2001, p. 128) defined Zone LKP23 as, "The interval from the first downhole occurrence of *Impagidinium diversum* to the highest occurrence of *Hystriodinium voigtii*" (the last



TEXT-FIGURE 7

Key palynofloral events and interpreted stratigraphy of well 22/26a-2. Taxa in blue were absent from the Heselton No. 2 borehole. * Nannofloral zones after Jeremiah (2001). V3 and V4 refer to the Valhall Formation lithostratigraphic sub-divisions of Johnson and Lott (1993).

being the top LKP22 marker) but very rare *H. voigtii* were recorded as high as 11,167.00 ft in well 22/26a-2, the same level as the LAD of *I. diversum*. Some reworking of *H. voigtii* is presumed.

Meiourgonyaulax lacunosa was recorded as high as 11,154.00 ft in well 22/26a-2, suggesting a range as high as Zone LKP24, much younger than the single occurrence recorded at 19.00 m in Heselton No. 2, which appears to represent only its base, with much of its range missing. As discussed above, a major hiatus is postulated in Heselton No. 2 between the 19.00 m and 17.75 m samples, with Zone LKP25 resting on Zone LKP22. Evidence from the 22/26a-2 core further confirms this and suggests that the section equivalent to the interval 11,187.00 ft to 11,147.00 ft in well 22/26a-2 is absent from Heselton No. 2 (text-figs. 6, 7, 8).

The palynoflora recovered from the highest sample analysed from well 22/26a-2, at 11,143.00 ft, included *Batioladinium longicornutum*, *Hystrichodinium ramoides*, *Cribroperidinium episomum*, rare *C. hadrum* and abundant *Sirmiodinium grossii*, proving a Subzone LKP25.1, late Barremian to early Aptian age (see notes on Wiechendorf 1/86, below).

The very restricted range of *C. hadrum* in Heselton No. 2 was discussed above, and its presence in well 22/26a-2 again suggests direct equivalence to the type horizon of *C. hadrum*, at 19.25 m in the Shell West Heselton No. 1 borehole (Sarjeant 1966a, p. 119–121) and to the interval 99.87 m to 99.50 m in borehole Wiechendorf 1/86 (text-figs. 6, 7, 8 and Lister and Batten 1995).

Wiechendorf 1/86

A multi-disciplinary attempt to characterise the Barremian/Aptian boundary in the Lower Saxony Basin was co-ordinated by Kemper, and compiled in Geologisches Jahrbuch Reihe A, Heft 141 (1995). The work was focused on three cores from the Wiechendorf 1/86, Hoheneggelsen KB9 and Ahlum 1 boreholes, in which no key ammonites were encountered; only the first two cored the Barremian/Aptian boundary.

As stated by Kemper (1995, p. 48), “an attempt was made to take ammonite-based boundaries known from a number of clay pits and locate them in drill cores by long-range correlation with the help of microfossils”. This is a sound approach, but there is some evidence from the individual papers that it was not strictly followed by the authors, either through individual choice (i.e., application of previously accepted norms for each microfossil discipline) or because the outcrops chosen offered inadequate macrofossil calibration.

The Wiechendorf 1/86 borehole was sited near the centre of the Lower Saxony Basin (text-fig. 1) and Lister and Batten (1995) analysed 37 samples of a late Barremian and Aptian age, recording rich and diverse dinocyst assemblages, comparable to those recovered from Heselton No. 2 and well 22/26a-2 in the current study. Semi-quantitative data presented in Lister and Batten 1995 (Figure 2) have allowed direct correlation of the following palynofloral events in Wiechendorf 1/86 and Heselton No. 2 (text-fig. 8):

FAD *Protoellipsodinium spinocristatum*
FAD *Tehamadinium tenuiceras*
FAD *Nyktericysta? vitrea*
FAD *Cepadinium ventriosum*
FAD *Tehamadinium sousense*

LAD *Cribroperidinium hadrum*
FAD *Cribroperidinium hadrum*
FAD *Cribroperidinium cornutum*
LAD *Pseudoceratium solocispinum*
LAD *Ellipsodinium reticulatum*
FAD *Cribroperidinium cornutum*
LAD *Druggidium jubatum*
occurrence of *Carpodinium glabrum*

Unfortunately, the various microfossil disciplines disagree on where the Barremian/Aptian boundary should be in Wiechendorf 1/86 (Kemper 1995). The level picked in Lister and Batten 1995, based on the deepest occurrence of *Cepadinium ventriosum*, is at about 86.00 m (A in text-fig. 8) but on foraminifera it is at 97.00 m (Kemper, op. cit., p. 54 - B in text-fig. 8) and on nannofossils (Cepek 1995) at about 105.00 m (C in text-fig. 8). Kemper (op. cit.) considered either the 97.00 m or 105.00 m picks to be possible, but he dismissed the higher (palynofloral) pick, stating that on various criteria, it “can not be correct and is therefore unacceptable”.

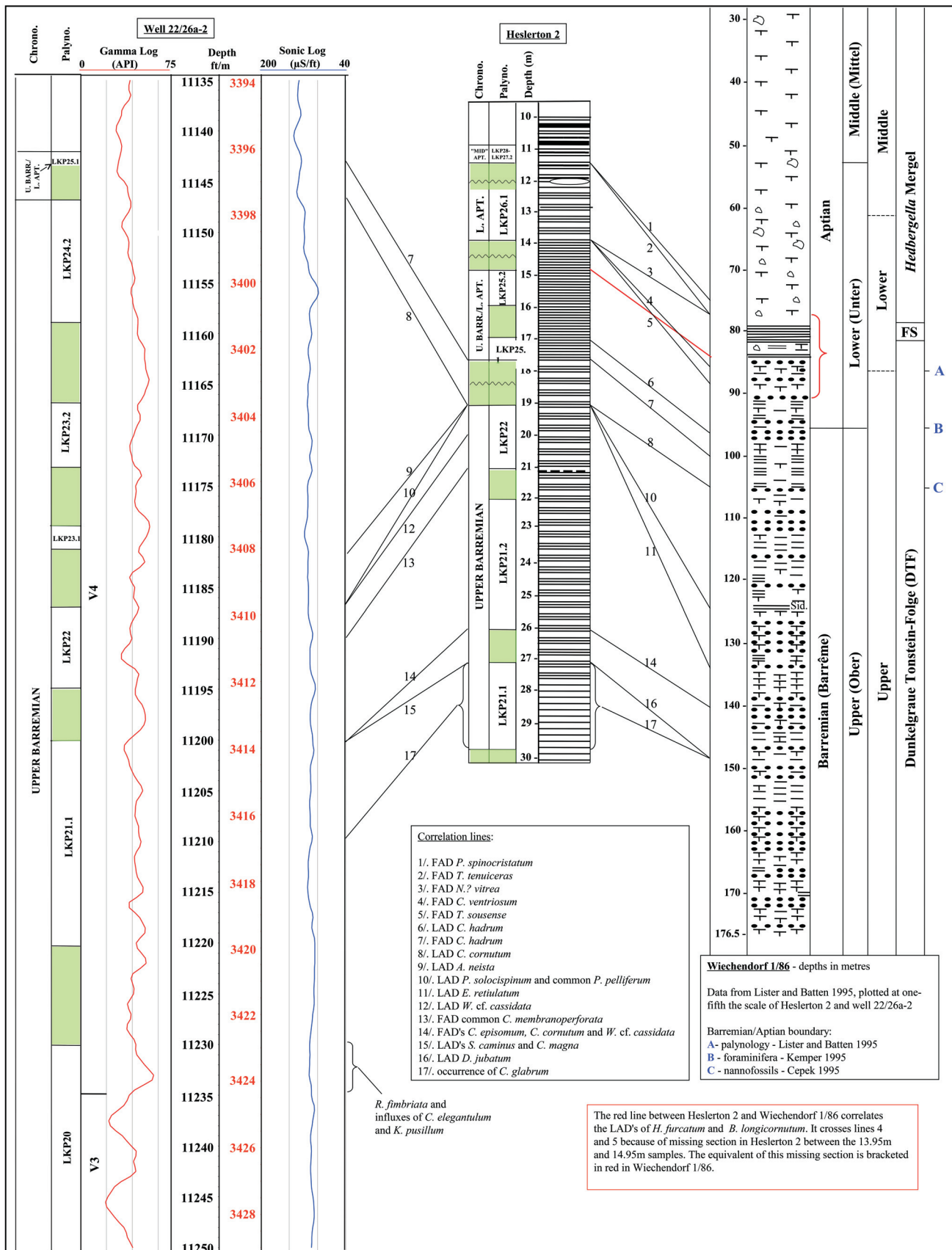
Kemper also stated (op. cit., p. 54) that in Wiechendorf 1/86 there was no dinoflagellate inception directly marking the Barremian/Aptian boundary, as *Cepadinium ventriosum* appears a few metres above it. Data presented in Lister and Batten (op. cit. Figure 2) but not highlighted in the text do, however, include distinct dinocyst markers close to the 97.00 m and 105.00 m Barremian/Aptian boundary picks:

97.00 m – Lister and Batten (op. cit., Figure 2C) recorded “*Leptodinium* sp. cf. *L. hadrum*” between approximately 100.00 m and 96.00 m, associated with an influx of the acritarch *Fromea fragilis* at the deeper level. This association is below the LADs of *Batioladinium longicornutum*, *Cribroperidinium episomum* (as *C. boreas*) and *Hystrichodinium furcatum*, and immediately above the LAD of *Cribroperidinium cornutum*, which is at 104.00 m. A very similar association was observed in Heselton No. 2 of *C. hadrum* at 17.75 m and 17.00 m, associated with an influx of *Fromea complicata* at the higher level, again below the LADs of *B. longicornutum* and *H. furcatum* and above *C. cornutum*. The *C. hadrum*/*Fromea* influxes are considered equivalent here.

105.00 m – this is very close to the LAD of *Cribroperidinium cornutum* (c. 104 m), a species shown to range to the eroded top of the Barremian, *Oxyteuthis depressa* belemnite zone (= *Parancyloceras bidentatum* ammonite zone) in Sarstedt (Gott clay pit - Below 1982a and Harding 1990), although at that locality the Barremian is overlain unconformably by upper Aptian clays (*Parahoplites nutfieldiensis* ammonite zone).

Considering the significant hiatus between 19.00 m and 17.75 m in the Heselton No. 2 borehole, it is not surprising that several distinctive species, including *Cerbia magna*, *Impagidinium diversum*, *Oligosphaeridium magnum*, *Aptea bulla* and *Scriniodinium barremianum*, were not recorded (text-figs. 6, 8). These taxa occur in well 22/26a-2 between the LADs of *Pseudoceratium solocispinum* and *Cribroperidinium cornutum* (text-figs. 7, 8).

It is surprising, however, that none of these “missing” species were (even informally) noted or illustrated in either Lister and Batten (1995) or Heilmann-Clausen and Thomsen (1995) in the Wiechendorf 1/86 or Ahlum 1 boreholes respectively. This is particularly true for Wiechendorf 1/86 which lies near the centre



TEXT-FIGURE 8
Correlation chart, well 22/26a-2, Heselton No. 2 and Wiechendorf 1/86. Data for the last borehole taken from Lister and Batten (1995).

of the Lower Saxony Basin and might be expected to have a more complete section. Using the LADs of *P. solocispinum* and *C. cornutum* (Events 10 and 8 respectively in text-fig. 8) as “brackets”, data from Lister and Batten (op. cit., p. 380 and Figure 2) might suggest that if these “missing” taxa were present, they might occur in Wiechendorf 1/86 between approximately 125.00 m and 104.00 m.

Whichever pick is preferred for the Barremian/Aptian boundary in Wiechendorf 1/86, the LAD of *C. cornutum* would be at or close to the top of the Barremian. If the 97 m level is preferred, then the *C. hadrum/Fromea* influx would be very close to the boundary. Although Sarjeant 1966a, p. 119 described *C. hadrum* (as *Gonyaulacysta hadra*) from the 19.25 m sample in the West Heselton No. 1 borehole as “Upper Barremian”, he gave no reason for this assignment.

In Heselton No. 2 there is a major hiatus so that the *C. hadrum/Fromea* influx rests on sediments of a Zone LKP22 age at 19.00 m, possibly reflecting a significant tectonic/erosive event (perhaps associated with the Barremian/Aptian boundary) between the 19.00 m and 17.75 m samples.

The evidence discussed above and first-hand observations here suggest that as the LAD of *C. cornutum* is a top Zone LKP24 marker (Duxbury 2001), Zone LKP25 (top defined on the LAD of *Hystrichodinium furcatum/ramoides*) could rest entirely (with a 105 m boundary pick in Wiechendorf 1/86) or partially (with a 97 m pick) at the base of the Aptian.

It follows also that taxa, “regarded as having become extinct at the end of the Barremian”, including *B. longicornutum* and *H. furcatum* (Lister and Batten 1995, p. 382) may range into the Aptian and that the FAD of *Cepadinium ventriosum* is an Aptian (but not base Aptian) event.

Refinement of the Duxbury 2001 Scheme, Zones LKP25 to LKP20

A detailed palynofloral zonation scheme for the Lower Cretaceous was presented in Duxbury 2001, and upper Berriasian to lower Hauterivian zones were significantly modified in Duxbury 2018. The current study has allowed additional refinement within the upper Barremian, recognising current uncertainty around the Barremian/Aptian boundary and using core samples to add stratigraphically significant FADs and acme occurrences.

The following zonal and subzonal definitions and comments represent a refinement of the zonal scheme presented in Duxbury (2001) for the upper Barremian (this includes the “Middle” Barremian in that work and in Duxbury 1977, 1980). As in that scheme, events are referred to in a down-section (or downhole) sense for ease of application to borehole analyses, although most modifications rely on the addition of FADs in core from Heselton No. 2 and well 22/26a-2. Key markers are illustrated in text-figure 9.

Recognition of additional marker events has allowed the sub-division of some zones to subzonal level and has added further to the already detailed upper Barremian scheme. As in Duxbury (2001, 2018), no attempt has been made here to make detailed comparisons between the refined LKP (Lower Cretaceous Palynology) scheme and those of previous authors.

Additional defining characteristics for upper Barremian Zones LKP25 to LKP20 are described below, including several new subzones; other zones described and illustrated in Duxbury (2001, 2018) are not repeated here.

Evidence cited above for the Barremian/Aptian boundary and summarised by Kemper (1995) has been accepted here, and a range of late Barremian to early Aptian has been assigned to Zone LKP25.

Zone LKP25

Age: early Aptian to late Barremian

Definition: The interval from the LADs of *Hystrichodinium furcatum*, *H. ramoides* and *Batioladinium longicornutum* to the LADs of *Cribroperidinium cornutum* and *Scriniodinium barremianum*.

Remarks: Duxbury (2001, p. 128) included the LAD of *Batioladinium longicornutum* as a top LKP24 marker but in other Barremian/Aptian boundary studies, including Lister and Batten (1995), *B. longicornutum* ranges as high as the LAD of the *Hystrichodinium furcatum/ramoides* grp. and significantly younger than *Cribroperidinium cornutum*. Therefore the top of Zone LKP25 has been re-defined here to reflect this.

Zone LKP25 can be subdivided into two subzones:

Subzone LKP25.2

Definition: The interval from the LADs of the *Hystrichodinium furcatum/ramoides* grp. and *Batioladinium longicornutum* to the LAD of *Cribroperidinium hadrum*.

Remarks: Lister and Batten (op. cit.) and Heilmann-Clausen and Thomsen (1995) also showed that *B. longicornutum* and the *Hystrichodinium furcatum/ramoides* grp. range marginally younger than *Cepadinium ventriosum*, proving the FAD of the last species is within Subzone LKP25.2.

The highest occurrence of *Cribroperidinium episomum* is near the top of this subzone and Lister and Batten (op. cit., Figure 2C) recorded it at the same level as the FAD of *C. ventriosum* in the Wiechendorf 1/86 borehole. The LADs of *Kleithria-sphaeridium fasciatum*, *Muderongia staurola* and common *Sirmiodinium grossii* are within Subzone LKP25.2, and the LADs of *Chlamyphorella membranoperforata* and *Protoellipsodinium hirsutum* are within the lower part of that subzone.

Pentadinium omasum ranges as high as 14.95 m in Heselton No. 2 (the same level as the LADs of *B. longicornutum* and the *Hystrichodinium furcatum/ramoides* grp.), and occurs through much of Subzone LKP25.2; Harding (1990, p. 37) considered it to be, “restricted to rocks of late Barremian age”.

Subzone LKP25.1

Definition: The interval from the LAD of *Cribroperidinium hadrum* to the LADs of *Cribroperidinium cornutum* and *Scriniodinium barremianum*.

Remarks: *Cribroperidinium hadrum* appears to have a very short range in both Heselton No. 2 and Wiechendorf 1/86 (Lister and Batten 1995, Figure 2C. “*Leptodinium* sp. cf. *L. hadrum*” of those authors is assumed to be *C. hadrum*), immediately above the LAD of *Cribroperidinium cornutum*, and in Heselton No. 2 it is common to abundant throughout its range.