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New organic-walled dinoflagellate cysts from the Cenomanian to Maastrichtian of the Trunch borehole, UK

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ABSTRACT – A high-resolution palynological study of Cenomanian to Maastrichtian chalks from the Trunch borehole (southeastern UK) has revealed twelve new species and one new subspecies of organic-walled dinoflagellate cysts: *Alterbidinium ioannidesii* sp. nov., *Cassiculosphaeridia alta* sp. nov., *Chatangiella eminens* sp. nov., *Cordosphaeridium catherineae* sp. nov., *Eatonicysta exilis* sp. nov., *Eatonicysta*? *mutabilireta* sp. nov., *Hystrichostrogylon robustum* sp. nov., *Membranilarnacia wilsonii* sp. nov., *Nelsoniella incomposita* sp. nov., *Odontochitina diducta* sp. nov., *Spiniferites jarvisii* sp. nov., *Spiniferites multispinulus* sp. nov. and *Spiniferites ramosus aquilus* subsp. nov. Two new genera, *Dimidium* gen. nov. and *Whitecliffia* gen. nov. are described to necessitate the new combinations (with a former name in parentheses) of *Dimidium striatum* gen. et comb. nov. (*Pterodinium*? *striatum*) and *Whitecliffia spinosa* gen. et comb. nov. (*Thalassiphora*? *spinosa*). *J. Micropalaeontol.* **29**(1): 51–72, May 2010.

KEYWORDS: *new species & genera, Trunch borehole, dinoflagellate cysts, taxonomy, Upper Cretaceous*

INTRODUCTION

Following their inception in the Triassic, dinoflagellate cysts from the Upper Cretaceous remain arguably the least well known, with many undescribed and poorly understood forms (Costa & Davey, 1992). Recent studies on Upper Cretaceous sequences have described many new taxa (Prössl, 1990; Kirsch, 1991; Schiøler, 1993, Slimani, 1994, 2001; Schiøler *et al*., 1997, Prince *et al*., 1999, 2008; Pearce *et al*., 2003) but focus on sections with a relatively short stratigraphic range and/or with a relatively wide sampling interval. The palynology of a continuous Cenomanian to lower Maastrichtian core at Trunch (southeast UK; Fig. 1), the most extensive section from onshore UK, has been studied at a 1–2 m sample resolution and yielded two new genera, twelve new species and one new subspecies of organic-walled dinoflagellate cysts, which are described here.

MATERIALS AND METHODS

The Trunch borehole (Norfolk, UK; TG 2933 3455; N 52°51′34″ E 01°24′19″; Fig. 1) was continuously cored in 1975 by the British Geological Survey (BGS; then the Institute of Geological Sciences) to sample the Chalk at its most complete development in Britain. The 10-inch diameter core recovered a thick Quaternary cover and 468 m of Cenomanian–lower Maastrichtian Chalk (Wood *et al*., 1994), including 246 m of Campanian strata. The chalk samples from the borehole were taken from composite bags of 10 cm intervals, no cut round of core was preserved. Palynological processing techniques follow those of Pearce *et al*. (2003). Graphic logs of the core were drawn by Jarvis *et al*. (2002, 2006) based on the lithostratigraphy and macrobiostratigraphy of Gallois & Morter (1976) and Wood *et al*. (1994), and form the basis of the borehole stratigraphy shown in Figure 2.

SYSTEMATIC DESCRIPTIONS

Division **Dinoflagellata** (Bütschli, 1885) Fensome *et al*., 1993
Subdivision **Dinokaryota** Fensome *et al*., 1993
Class **Dinophyceae** Pascher, 1914
Subclass **Peridiniphycidae** Fensome *et al*., 1993
Order **Gonyaulacales** Taylor, 1980
Suborder **Gonyaulacineae** (Autonym)
Family **Gonyaulacaceae** Lindemann, 1928
Subfamily **Cribroperidinioideae** Fensome *et al*., 1993
Genus *Cordosphaeridium* Eisenack, 1963a

Type species. *Cordosphaeridium inodes* (Klumpp, 1953: 391, pl. 18, figs 1–2) Eisenack, 1963a

Cordosphaeridium catherineae sp. nov.
(Pl. 1, figs 10–13; Fig. 3)

Derivation of name. In honour of Dr Catherine Emma Stickley, University of Tromsø (Norway), for her contributions to integrated palynological/diatom studies of both hemispheres.

Diagnosis. A species of *Cordosphaeridium* with taeniate, solid, fibrous processes that are widest proximally, narrow medially before dividing into 2–5 isolated processes of constant width that terminate in a bifurcation.

Holotype. MPK 13889; e/f ref: R51/2; Plate 1, figs 10–13; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 270.9–271.0 m, Burnham–Flamborough Chalk (undifferentiated), low *Gonioteuthis quadrata* Zone (mid-lower Campanian).

Description. Medium-sized, chorate dinoflagellate cyst with a sub-spherical body. Wall two-layered comprised of an endophragm and fibrous periphram that are closely appressed. Taeniate intratabular processes arise from the periphragm and appear to be solid. Processes are widest proximally (up to 14 μm), narrow medially where 2–5 isolated processes, with a relatively constant width (1 μm), are developed and terminate distally in a bifurcation. Proximal process width is directly proportional to the size of the corresponding paraplate such that

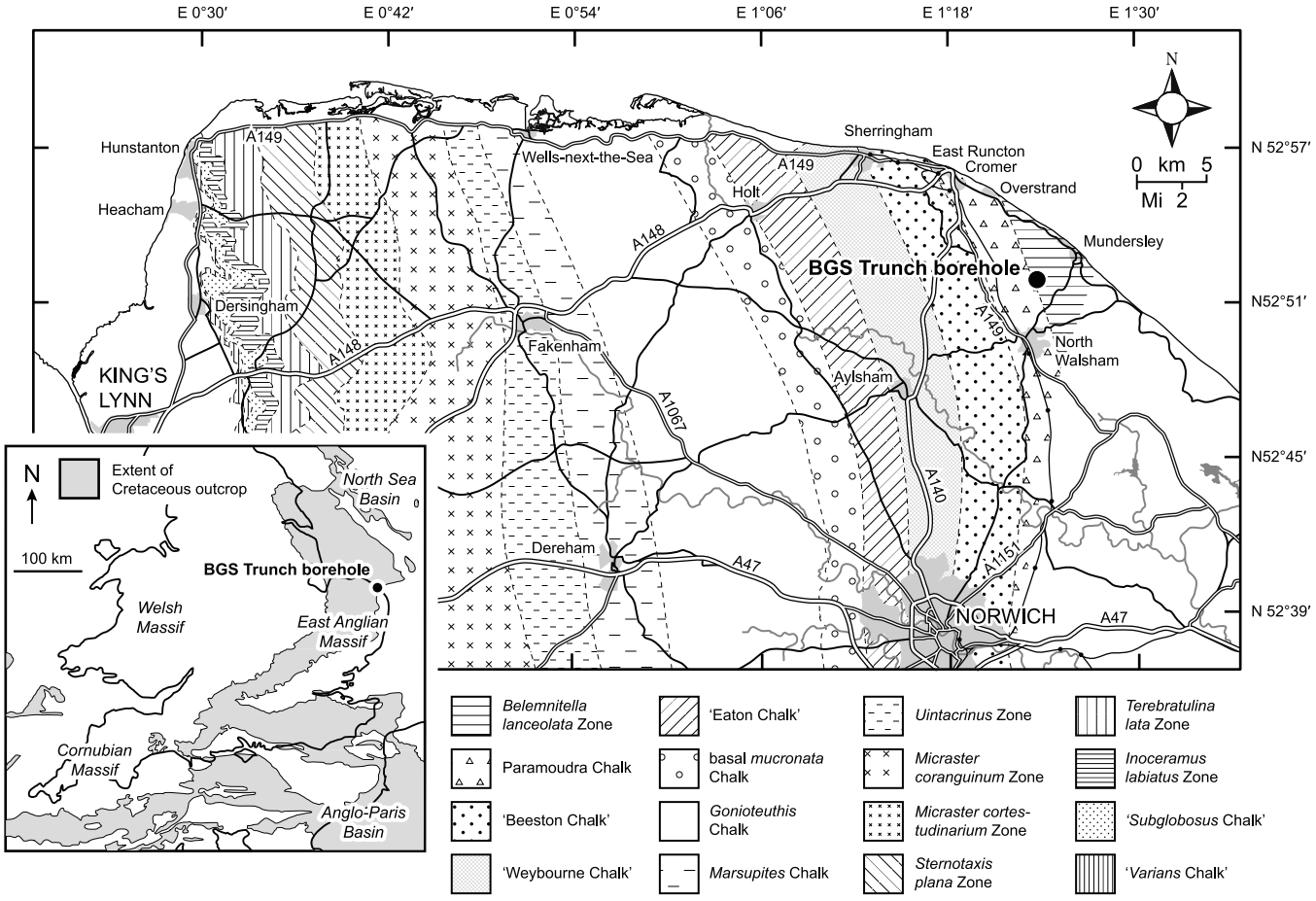


Fig. 1. Location map of the BGS Trunch borehole. Lithostratigraphy and macrofossil zones taken from Peake & Hancock (1961). Inset map modified from Rawson (1992).

the largest processes occupy the larger reflected paraplates. As a result, the pre- and postcingular processes are the widest and the process occupying the 1′′′′ paraplate at the antapex is slender and typically the longest (33 μm); the parasulcal processes do not vary significantly in width. Occasionally, two processes may occur on a single paraplate, particularly 4′′′. Twenty-four to twenty-six processes define the paratabulation 4′, 6′′, 5–6c, 5–6′′′, 1p, 1′′′′, 2s (as?, ras?; Fig. 3). The archaeopyle is precingular (Type 1P, operculum detached) and formed by the loss of the third precingular paraplate (3′′).

Dimensions. Holotype: central body (w/l) 43 × 42 μm, process length (max) 33 μm; range: central body (w/l) 35(45.1)50 × 32(40.7)51 μm, process length (max) 18(21.8)33 μm. 15 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Uintacrinus socialis* Zone (mid-upper Santonian) to the low *Gonioteuthis quadrata* Zone (mid-lower Campanian; Fig. 2).

Remarks. The species superficially resembles *Florentinia* Davey & Verdier, 1973 but differs by possessing solid processes. Furthermore, according to Stover & Evitt (1978), more than one process per paraplate may be present in *Cordosphaeridium*, as is the case with 4′′ in *C. catherineae* sp. nov.

Comparison. Differs from other species of *Cordosphaeridium* that also possess wide bases by possessing long processes that become isolated medially. Although the processes in *C. inodes* (Klumpp, 1953: 391, pl. 18, figs 1–2) Eisenack, 1963a may be also taeniate, they are hollow and open distally. *Cordosphaeridium fibrospinosum* Davey & Williams, 1966b (86, pl. 5, fig. 5) possesses broad processes with an ovoidal cross-section but lacks the isolated processes that develop distally. *C. exilimurum* Davey & Williams, 1966b (87–88, pl. 11, fig. 2) possesses tubiform processes and is distinctively thin-walled.

Subfamily **Gonyaulacoideae** (Autonym)
Genus *Hystrichostrogylon* Agelopoulos, 1964

Type species. *Hystrichostrogylon membraniphorum* Agelopoulos, 1964 (674, text-fig. 1).

Hystrichostrogylon robustum sp. nov.
(Pl. 5, figs 4–7)

Derivation of name. From the latin *robustus*, meaning strong, powerful or firm referring to the nature of processes.

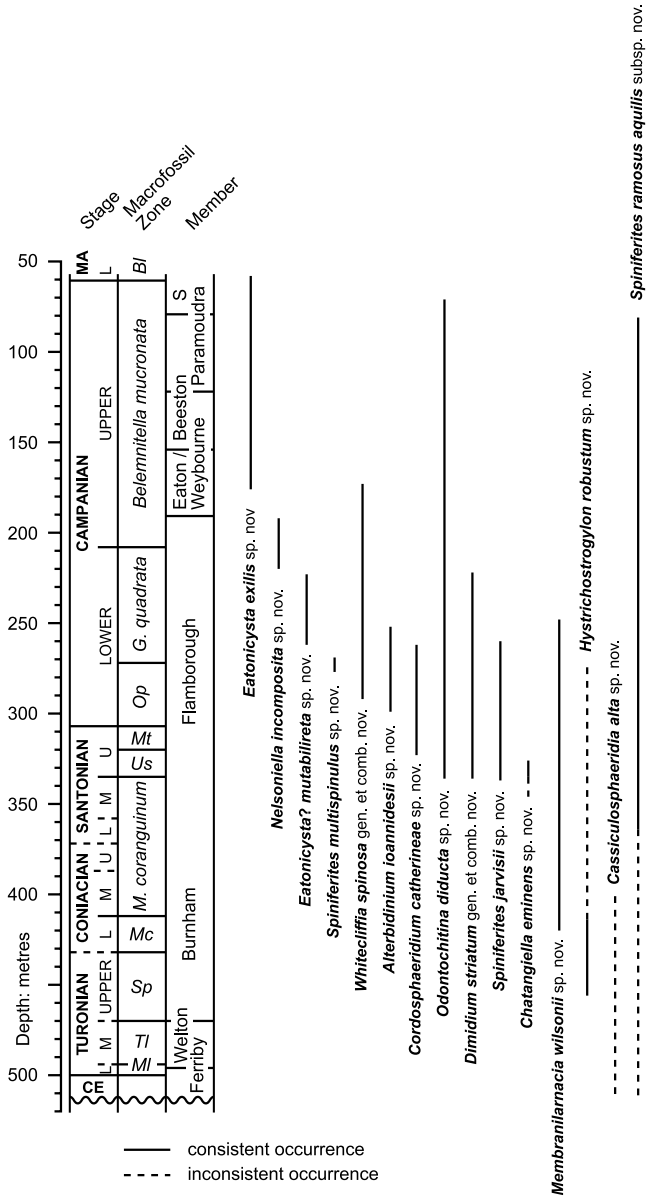


Fig. 2. Summary stratigraphic range chart of the species discussed in the text. Boundaries based on the graphic logs of Jarvis *et al.* (2002, 2006). Abbreviations – *Bl*, *Belemnella lanceolata*; *G. quadrata*, *Gonioteuthis quadrata*; *M. coranguinum*, *Micraster coranguinum*; *Mc*, *Micraster cortestudinariuum*; *Ml*, *Mytiloides labiatus*; *Mt*, *Marsupites testudinarius*; *Sp*, *Sternotaxis plana*; *Tl*, *Terebratulina lata*; *Us*, *Uintacrinus socialis*; L, lower; M, middle; U, upper; S, Sidestrand; CE, Cenomanian; MA, Maastrichtian.

Diagnosis. A species of *Hystrichostrogylon* with short, robust processes.

Holotype. MPK 13890; e/f ref: P40/2; Plate 5, figs 4–7; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 432.3–432.4 m, Burnham–Flamborough Chalk (undifferentiated), high *Sternotaxis plana* Zone (high upper Turonian).

Description. Medium-sized, camocavate, spiniferate, dinoflagellate cyst. The central body episome is prolate ellipsoid and the hyposome is roughly spherical to minorly oblate ellipsoid. The wall is two-layered, comprised of a thin (~0.5 μm) and smooth endophragm and a thin (~0.5 μm) and smooth periphragm, which are separated ventrally and appressed elsewhere. Short (~13 μm long), stout trifurcating gonal processes (1–2 μm wide) and up to 3 bifurcating or simple intergonal processes arise from the periphram. Bi- and trifurcating processes terminate distally with a minute (1 μm long) bifurcation. The longest processes are united proximally by a sutural crest and occur where the wall layers are appressed, and become shorter and lacking, or with much reduced, sutural crests where the wall layers are separated ventrally. As such, the paratabulation is incompletely developed. The archaeopyle is precingular (Type 1P, operculum detached) and formed by the loss of the third precingular paraplate (3″). A mid-ventral opisthopyle may be present in the periphragm.

Dimensions. Holotype: central body (w/l) 42 × 52 μm, including pericoel (w/l) 66 × 53 μm, process length (max.) 13 μm; range: central body (w/l) 41(42.7)46 × 37(47.3)53 μm, including pericoel (w/l) 46(56.7)70 × 44(53.2)66 μm, process length (max.) 6(11)16 μm, 9 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Sternotaxis plana* Zone (high upper Turonian) to the low *Gonioteuthis quadrata* Zone (mid-lower Campanian; Fig. 2).

Comparison. *Hystrichostrogylon robustum* sp. nov. is most closely comparable with *H. membraniphorum* Agelopoulos, 1964 (674, text-fig. 1–2) but differs by possessing shorter processes (although there is a slight overlap in the 13–29 μm range for *H. membraniphorum*), and an incomplete but more strongly developed paratabulation. *Hystrichostrogylon borisii* Schiøler, 1993 (106, 108, pl. 1, figs 7–9; pl. 2, figs 1–3) and *H. membraniphorum granulatum* Heilmann-Clausen in Heilmann-Clausen & Costa, 1989 (468, pl. 18, figs 1–3) have an ornamented endophragm, but which is smooth in *H. robustum* sp. nov. Differs from *H. coninckii* Heilmann-Clausen in Thomsen & Heilmann-Clausen, 1985 (353, 355, pl. 7, figs 9–12; text-figs 10A–F), *H. clausenii* Bujak, 1994 (125, 127, pl. 1, figs 4–6) and *H. holohymenium* Islam, 1983 (238, 240, pl. 3, figs 5–7) in the position of the pericoel.

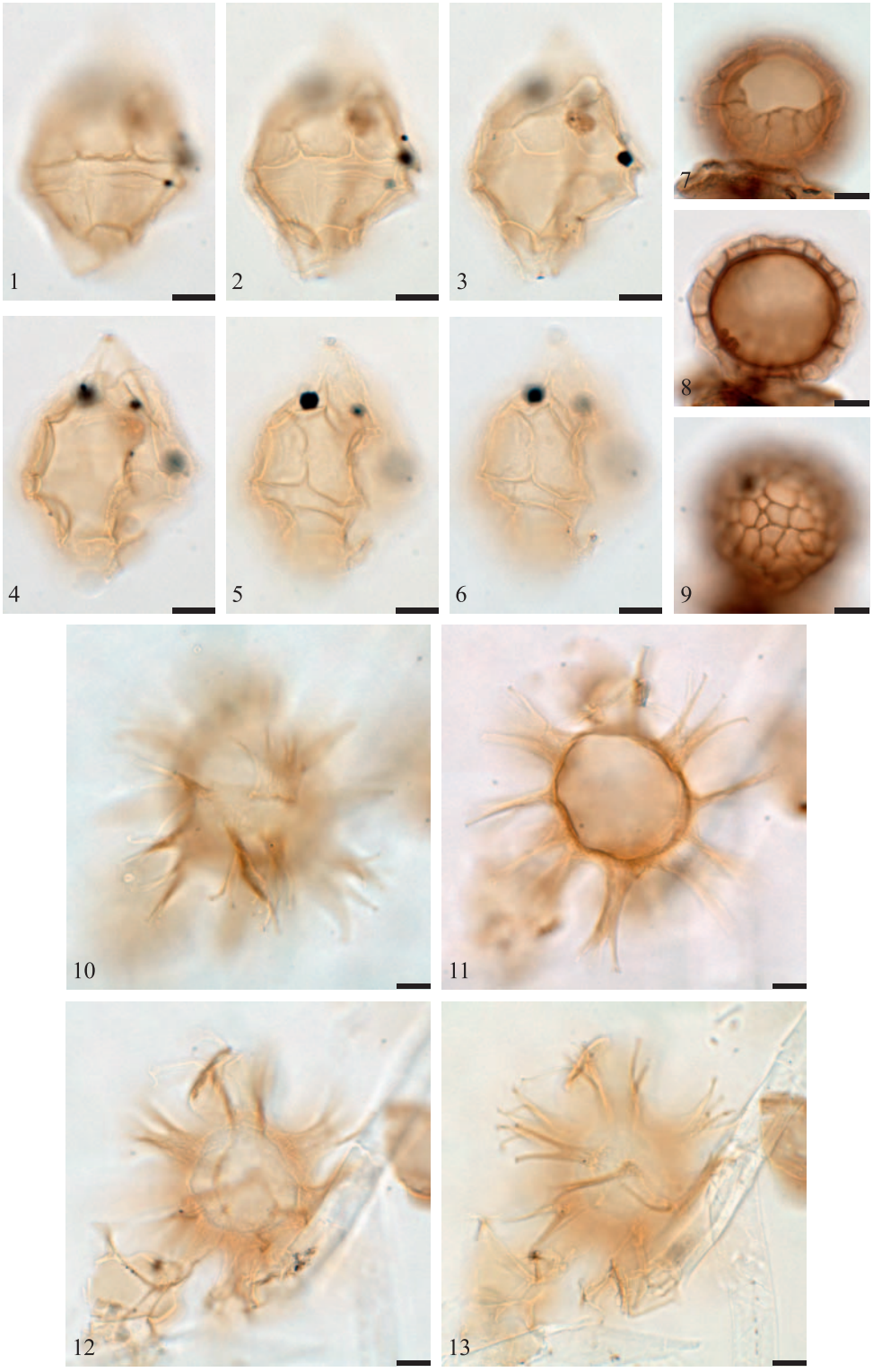
Genus *Spiniferites* Mantell, 1850

Type species. *Spiniferites ramosus* (Ehrenberg, 1838, pl. 1, fig. 5 designated by Davey & Williams, 1966a: 32) Mantell, 1854

Spiniferites jarvisii sp. nov.
(Pl. 6, figs 2–5)

Derivation of name. In honour of Professor Ian Jarvis, Kingston University (London, UK) for his invaluable contribution to Cretaceous stratigraphy.

Diagnosis. A species of *Spiniferites* that possesses a thick endophragm that becomes thinner towards the paraplate margins.



Explanation of Plate 1.

figs 1–6. *Alterbidinium ioannidesii* sp. nov. (holotype), MPK 13899, e/f ref: K38/3: **1,** proximal dorsal view showing the well-developed parasutural ridges; **2–3,** proximal mid-dorsal views clearly showing an omphalus; **4–5,** internal mid-ventral view (reversed) showing the apical horn; **6,** internal ventral view (reversed) showing the depressed parasulcus. **figs 7–9**. *Cassiculosphaeridia alta* sp. nov. (holotype), MPK 13897, e/f ref. P65: **7,** external ventral view; **8,** ambital view showing the crests; **9,** internal dorsal view (reversed) showing the well-developed and irregular reticulum. **figs 10–13**. *Cordosphaeridium catherineae* sp. nov. (holotype), MPK 13889; e/f ref. R51/2: **10,** internal dorsal view (reversed) showing the taeniate solid paracingular processes and pair of isolated processes on the 4‴ paraplate; **11,** ambital view showing the distinctive antapical process; **12,** external mid-ventral view; **13,** external ventral view. Scale bar 10 μm.

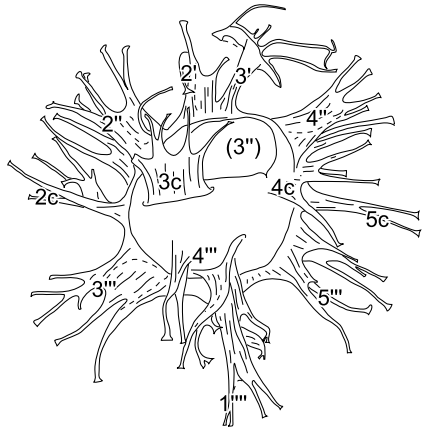


Fig. 3. Inferred paratabulation of the dorsal surface of *Cordosphaeridium catherineae* sp. nov. based on the arrangement of processes using Kofoid-notation, demonstrating that the cyst conforms to standard gonyaulacoid tabulation. Note the distinctive elongated antapical process.

Holotype. MPK 13891; e/f ref: X25/2; Plate 6, figs 2–5; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 307.9–308.0 m, Burnham–Flamborough Chalk (undifferentiated), high *Marsupites testudinarius* Zone (high upper Santonian).

Description. Small to medium-sized spiniferate chorate dinoflagellate. The central body episome is prolate ellipsoid and the hyposome is roughly spherical to minorly oblate ellipsoid. The wall is two-layered, with a thick and smooth endophragm (~1.5 μm) that is thinned towards the margin of the paraplates and a smooth and thin periphragm (~0.5 μm) that forms the processes. The processes are gonal, approximately half the diameter of the central body in length, and trifurcate distally (with furcations up to 5 μm in length) before terminating in a minute bifurcation (1–2 μm long). Parasutural crests are highest against the processes and up to 2 μm high in between and clearly delineating the standard gonyaulacacean paratabulation. The paracingulum is distinctly laevorotatory by twice the width of the paracingulum; the parasulcus is straight and lacks clearly developed parasutural crests. The lateral margins of the sixth precingular paraplate taper apically and the paraplate appears to have a rectilinear contact with the apical series. The archaeopyle is precingular (Type 1P, operculum detached) and formed by the loss of the third precingular paraplate (3″).

Dimensions. Holotype: central body (w/l) 31 × 33 μm, process length (max.) 16 μm; range: central body (w/l) 31(36.6)40 × 33(41.8)50 μm, process length (max.) 14(16.8)20 μm, 10 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Micraster coranguinum* Zone (high middle Santonian) to the lower *Gonioteuthis quadrata* Zone (mid-lower Campanian; Fig. 2).

Comparison. Differs from other species of *Spiniferites* by possessing a thick endophragm that thins towards the margin of the paraplates. The mostly closely related species is *Pterodinium crassimuratus* (Davey & Williams, 1966a: 39, pl. 1, fig. 11) Thurow *et al*., 1988 that also possesses the characteristic thinning of the endophragm, but differs in lacking processes that project beyond the parasutural crests.

Spiniferites multispinulus sp. nov.
(Pl. 7, figs 1–6)

Derivation of name. *multi* and *spine* referring to the two intergonal processes per septum.

Diagnosis. A species of *Spiniferites* consistently possessing two intergonal spines on the pre- and postcingular paraplates which are close to half the diameter of the central body in length.

Holotype. MPK 13892; e/f ref: P48; Plate 7, figs 1–6; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 269.9–270.0 m, Burnham–Flamborough Chalk (undifferentiated), low *Gonioteuthis quadrata* Zone (mid-lower Campanian).

Description. Small to medium-sized, spiniferate chorate dinoflagellate with a prolate ellipsoid central body. The wall is two-layered, comprising a thin (~0.5 μm) and smooth endophragm and a thin (~0.5 μm) and smooth periphragm, the latter of which develops partially hollow processes. Trifurcating gonal and bifurcating intergonal processes are typically around half the diameter of the central body in length (with furcations up 6 μm in length), and terminate in a minute bifurcation (<1 μm long). Gonal processes often possess a single vacuole at the mid-length. Two intergonal processes are consistently present on the lateral boundaries of the larger pre- and postcingular paraplates. The processes are united proximally by well-developed parasutural crests, highest against the processes and which may reach 6 μm high in between, particularly those at the paracingulum, and clearly delineate the standard gonyaulacacean paratabulation. The paracingulum is weakly laevorotatory, typically by one paracingulum width; the parasulcus lacks clearly developed parasutures. The archaeopyle is precingular (Type 1P, operculum detached) and formed by the loss of the third precingular paraplate (3″).

Dimensions. Holotype: central body (w/l) 30 × 37 μm, process length (max.) 15 μm; range: central body (w/l) 30(35.1)42 × 37(39.3)43 μm, process length (max.) 12(14.9)18 μm, 10 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Offaster pilula* Zone (mid-lower Campanian) to low *Gonioteuthis quadrata* Zone (mid-lower Campanian; Fig. 2).

Remarks. *Spiniferites multispinulus* sp. nov. is most closely comparable to *Spiniferites twistringiensis* (Maier, 1959) Fensome

et al., 1990. According to the original description of the junior synonym *Hystrichosphaera ramosa* subsp. *multibrevis* Davey & Williams (1966a: 35–36), *S. twistringiensis* has by implication, short and solid processes that are much less than half the diameter of the central body in length, with a considerable variation in the number of intergonal processes (up to three). In contrast, *S. multispinulus* sp. nov. has partially hollow processes that are relatively longer and appears to be a stable form with a consistent number of processes. Furthermore, on inspection of the holotype of *H. ramosus multibrevis* (Davey & Williams 1966a, pl. 4, fig. 6), few of the parasutures appear to possess more than one intergonal process (and this is also the case for the drawn specimen; (Davey & Williams 1966a, fig. 9) and, therefore, it appears distinctly less 'spiny' than *S. multispinulus* sp. nov. Moreover, the crests are clearly higher in *S. multispinulus*, particularly between paraplates on the precingular and postcingular series, and vacuoles are not present on *H. ramosus multibrevis*. Finally, *S. twistringiensis* was recorded consistently from the Cenomanian to lower Maastrichtian in the Trunch borehole, while *S. multispinulus* sp. nov. is recorded only over an 8 m interval across the *Offaster pilula*/*Gonioteuthis quadrata* zonal boundary, making it a potentially useful marker. These observations are considered sufficient to treat *S. multispinulus* sp. nov. as a new species.

Comparison. Differs from all other species of *Spiniferites* by consistently possessing two intergonal processes on the lateral margins of the pre- and postcingular paraplates.

Spiniferites ramosus aquilus sp. nov.
(Pl. 7, figs 7–12)

Derivation of name. From the latin *aquilus*, meaning dark-coloured, blackish, referring to the densely reticulate endophragm.

Diagnosis. A species of *Spiniferites* possessing a densely and minutely reticulate periphragm imparting a distinctively dark aspect under transmitted light microscopy.

Holotype. MPK 13893; e/f ref: M56/2; Plate 7, figs 7–12; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 415.9–416.0 m, Burnham–Flamborough Chalk (undifferentiated), high *Micraster cortestudinarium* Zone (high lower Coniacian).

Description. Small to medium-sized spiniferate chorate dinoflagellate. The central body episome is prolate ellipsoid and the hyposome is roughly spherical to minorly oblate ellipsoid. Wall two-layered, comprised of a thin endophragm (~0.5 μm), which is very finely reticulate such that the wall appears blackish under transmitted light microscopy. The periphragm is thin (~0.5 μm) and smooth from where hollow (at least proximally) processes are developed. The processes are short (~10 μm long), gonal and trifurcate distally (3–4 μm in length) terminating in a minute (<1 μm long) bifurcation. The processes are united proximally by well-developed parasutural crests that are highest against the gonal processes and up to 4 μm in between; clearly delineating the standard gonyaulacacean paratabulation. The paracingulum is distinctly laevorotatory by over twice the width of the paracingulum; the parasulcus is straight and lacking clearly delineated paraplates other than the posterior sulcal paraplate. The sixth precingular paraplate is distinctly triangular with a rectilinear contact with the apical series. The archaeopyle is precingular (Type 1P, operculum detached) and formed by the loss of the third precingular paraplate (3″).

Dimensions. Holotype, central body (w/l) 31 × 36 μm, process length (max.) 10 μm; range, central body (w/l) 31(35)38 × 35(39)41 μm, process length (max.) 9(9.8)12 μm, 10 specimens measured.

Stratigraphic range. Ferriby Chalk, *Mantellioceras mantellii* Zone (lower Cenomanian) to the Paramoudra Chalk, high *Belemnitella mucronata* Zone (high upper Campanian; Fig. 2).

Remarks. The endocyst ornamentation is suggested to be reticulate rather than granulate since, where the cross-section of the surface can be seen (i.e. at the ambitus), the wall appears to have a negative ornament.

Comparison. Differs from *Spiniferites ramosus reticulatus* (Davey & Williams 1966a: 38, pl. 1, figs 2–3) Lentin & Williams, 1973 by possessing a more finely reticulate endophragm that results in a distinctively darkened aspect and a paratabulation clearly demarcated by the smooth parasutural crests.

Subfamily **Leptodinioideae** Fensome *et al*., 1993
Genus *Dimidium* gen. nov.

Type species. *Gonyaulacysta striatum* Clarke & Verdier, 1967 (31, pl. 4, figs 11–13; pl. 5, fig. 15; text-fig. 12).

Derivation of name. From the latin *dimidius* meaning halved or divided in half, referring to the epicystal archaeopyle.

Diagnosis. Proximate dinoflagellate cysts with an epicystal archaeopyle, parasutural crests not (or rarely) exceeding ¼ body width, clearly expressing an exsert first apical homologue (*1′), L-Type and sexiform paraplate patterns and slight dextral torsion.

Description. Medium-sized sub-spheroidal to oblate proximate dinoflagellate cyst lacking apical or antapical horns. The wall is single-layered and comprised of an autophragm that forms parasutural crests. The paratabulation is indicated by the low parasutural crests, less than ¼ body diameter in height, which conform to the standard gonyaulacoid formula 4′, 6″, 6c, 5–6s (as, ras, rs, ls, ps), 6‴, 1p, 1⁗ (Fig. 4), and display an L-Type ventral pattern, and sexiform hypocystal paraplate arrangement. Slight dextral torsion exists such that the vertical midlines through the 3″ and 4‴ paraplates are not in-line, and the 3″/4″ suture bisects the right lateral margin of the 5‴ paraplate. The archaeopyle is polyplacoid epitractal (Type tAtP), the operculum is occasionally adnate ventrally, but more usually detached and contiguous.

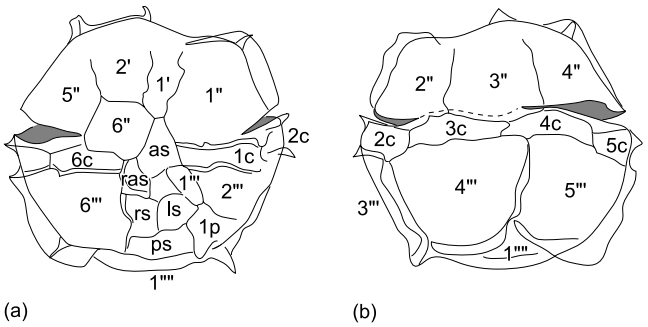


Fig. 4. Inferred tabulation of *Dimidium striatum* gen. et comb. nov., based on crest arrangement using Kofoid notation demonstrating that the cyst conforms to standard gonyaulacoid paratabulation: (**a**) ventral surface; (**b**) dorsal surface. The dashed line indicates the probable extent of the archaeopyle resulting in a ventrally adnate operculum.

Comparison. *Dimidium* most closely resembles *Heslertonia* Sarjeant, 1966 but differs in possessing parasutural crests that are much lower than ¼ body width. Ornamentation height (i.e. processes or crests) is probably an unsuitable generic level discriminator but the precedent stems back to an original difference between *Pterodinium* Eisenack, 1958 and *Leptodinium* Klement, 1960. However, *Heslertonia* is classified in the Order Gonyaulacales, but unassigned to a suborder or family (Fensome *et al*., 1993) since by implication the ventral and hyposomal paraplate configuration have not been determined. In contrast, *Dimidium* gen. nov. is clearly L-Type and sexiform with a slight dextral torsion. Since the orientation of the paraplates is well understood in *Dimidium* gen. nov., it is considered grounds to treat it distinct from *Heslertonia*, in the same way that Stover & Evitt (1978) erected *Impagidinium* when the paratabulation of *Pterodinium* was unknown. Differs from *Ctenidodinium* Deflandre, 1939 in lacking anterior intercalary paraplates and from *Dichadogonyaulax* Sarjeant, 1966 in lacking a preapical structure (pr) separating the second from the fourth apical homologues. It differs from *Dinopterygium* Deflandre, 1935 by possessing a sexiform rather than quinqueform hypocystal paraplate pattern and in the position of the principal archaeopyle suture that is immediately anterior to the paracingulum rather than within the paracingulum. It differs from species of *Impagidinium* Stover & Evitt, 1978, *Leptodinium* Klement, 1960 and *Pterodinium* Eisenack, 1958 primarily by possessing an epicystal archaeopyle.

Dimidium striatum (Clarke & Verdier, 1967) gen. et comb. nov.
(Pl. 2, figs 7–12; Pl. 3. figs 1–5; Fig. 4)

1967 *Gonyaulacysta striata* Clarke & Verdier: 31, pl. 4, figs 11–13, text-fig. 12.
1969 *Leptodinium striatum* (Clarke & Verdier) Sarjeant: 13.
1985 *Leptodinium striatum* (Clarke & Verdier) Sarjeant: 72.
1981 *Heslertonia rugula* Yun: 72–73, pl. 8, figs 2a–b.
1981 *Pterodinium striatum* (Clarke & Verdier) Yun: 12, pl. 8, figs 5a–b, 6a–b
1986 *Pterodinium striatum* (Clarke & Verdier) Yun; Jan du Chêne *et al*.: 274, pl. 88, figs 9–11.
1999 *Pterodinium*? *striatum* (Clarke & Verdier) Yun; Prince *et al*.: 166.

Type species. As for the genus.

Holotype. *Gonyaulacysta striata* Clarke & Verdier, 1967, plate 4, figs 11–13.

Locality and horizon: Culver Cliff, Isle of Wight, UK; Sample CV26, *Marsupites testudinarius* Zone (upper Santonian).

Dimensions. Type material of Clarke & Verdier (1967), holotype: overall (w/l): 55 × 66 μm, height of crests (max.): 11 μm; range: overall (w/l): 40–55 × 40–66 μm, height of crests (max.): 4–11 μm.

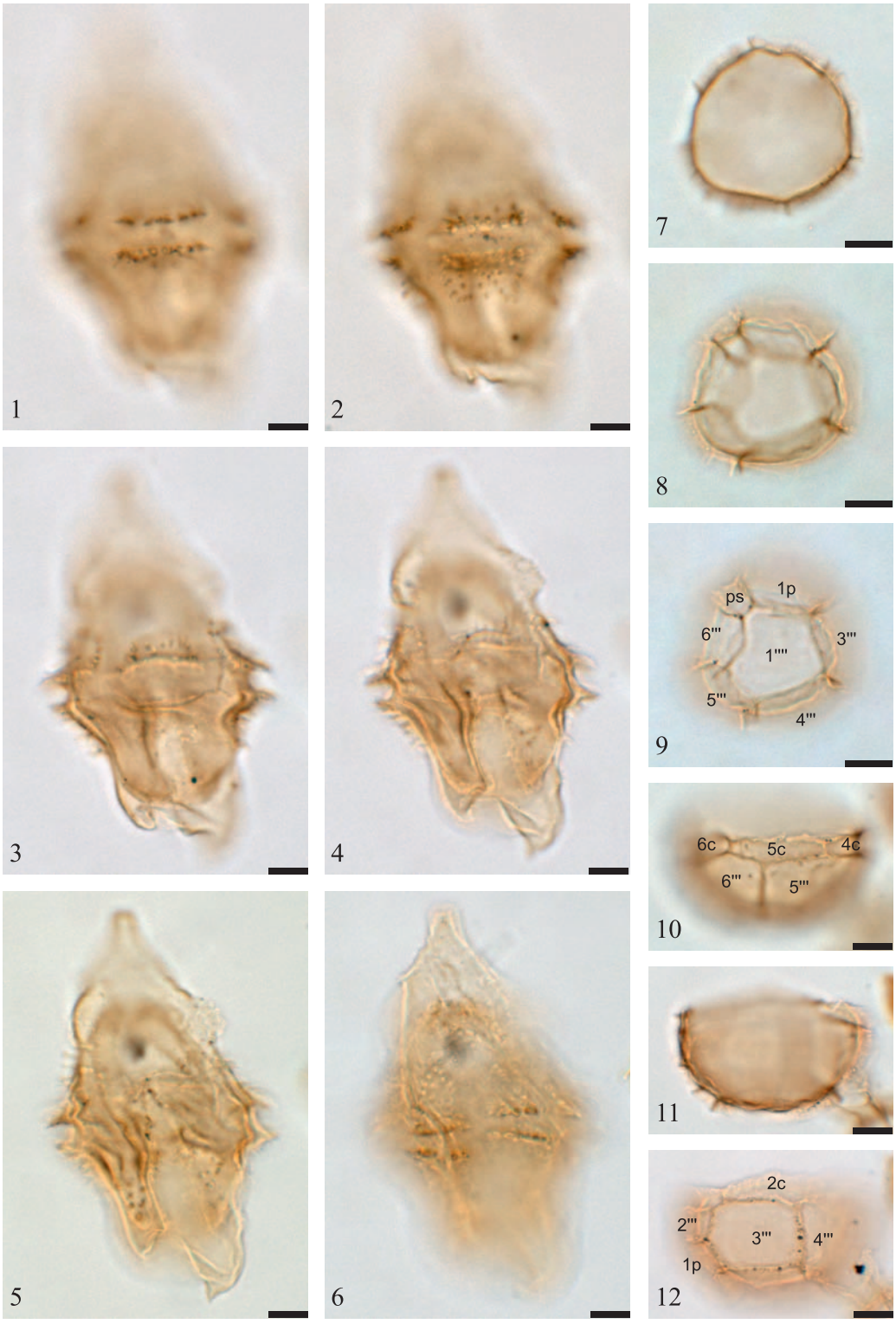
Trunch borehole material, range: central body (w/l) 28(41.3)50 × 41(43)46 μm, crest height (max) 1(1.7)2 μm, 7 specimens measured.

Stratigraphic range. Type section, as restudied by Prince *et al*. (1999): Broadstairs Chalk to Newhaven Chalk, high *Micraster coranguinum* Zone (high middle Santonian) to the *Offaster pilula* Zone (lower Campanian).

Trunch borehole material: Burnham–Flamborough Chalk (undifferentiated), high *Micraster coranguinum* Zone (high middle Santonian) to the high *Gonioteuthis quadrata* Zone (high lower Campanian; Fig. 2).

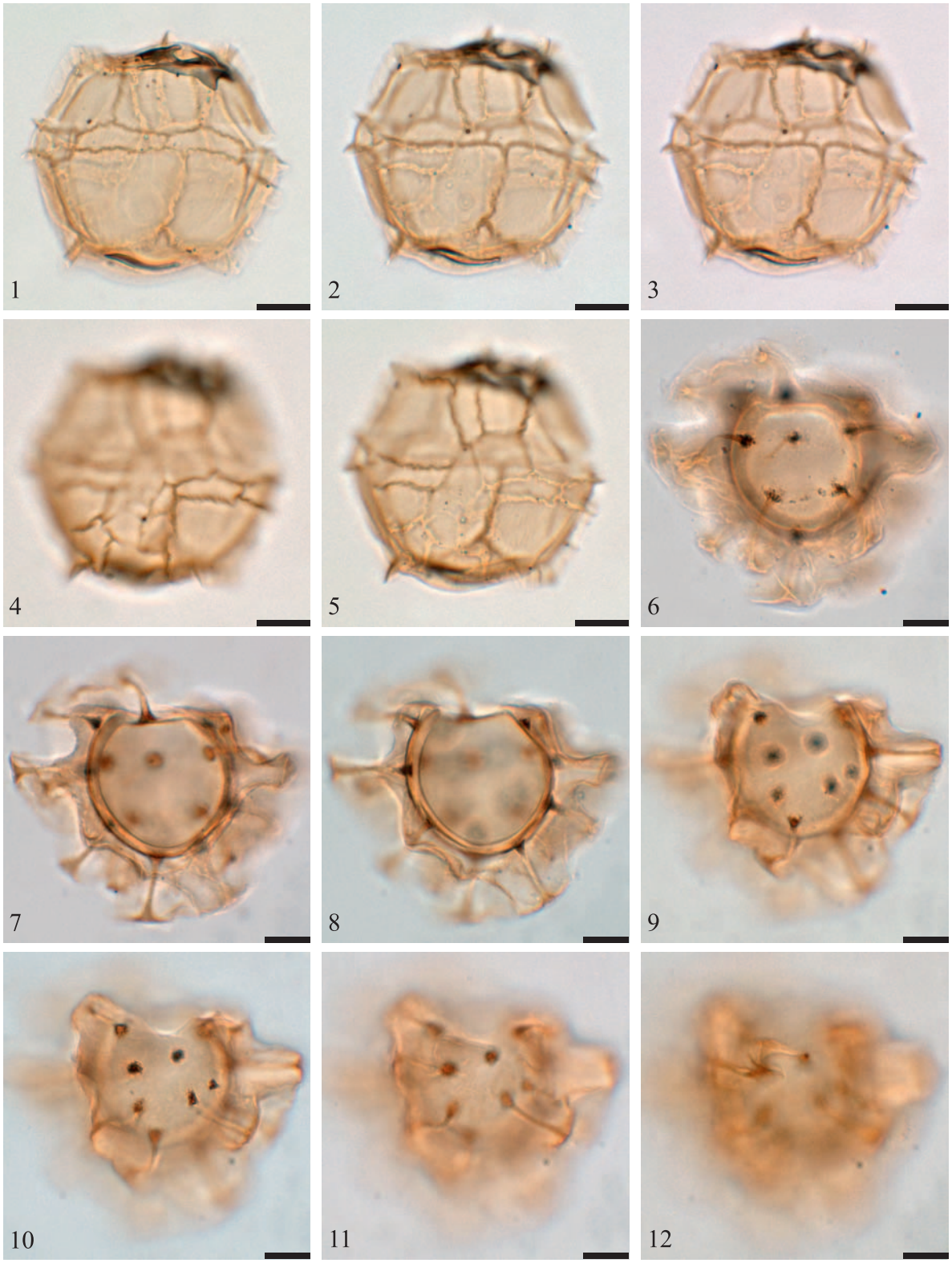
Remarks. Clarke & Verdier (1967: 31–32) first described this species as: 'A species of *Gonyaulacysta* having no apical horn but possessing thin, often striate ledges ... plates smooth, bordered by ledges up to 5 μm high ... the precingular archaeopyle is not an obvious feature'. In the measurement of an undisclosed number of specimens, the range of crest height was stated to be 4–11 μm, exceeding that stated in the description, and in the holotype the maximum crest height of 11 μm is less than ¼ the shortest dimension of the central body (i.e. breadth 55 μm). Sarjeant (1969: 12) transferred the form to *Leptodinium striatum* without discussion, and emended the generic description: '... height of crests always less (and typically markedly less) than ¼ of shell width. A precingular single-plate archaeopyle ... may not be present'. A range of surface ornamentation was accepted (but he did not specify striate!). It is unknown which criteria Sarjeant used to justify the transfer, but it may be partly due to the relative height of the parasutural crests of *Pterodinium*, which, according to the basic description of Eisenack (1958: 395), were described only as 'broad'.

Yun (1981) emended the generic description of *Pterodinium* by quantifying crest height as ¼ of the body size, which are uniform in height on an individual specimen, and then proposed the combination *Pterodinium striatum* based on crest heights of 10–17 μm. Yun's maximum crest height exceeds ¼ of the largest body dimension (51 μm); however, it is not known if this is typical since the shortest crest height is also less than ¼ the shortest body diameter (42 μm). The paratabulation was described with the formula: 3′, 1a, 6″, 6c, 5‴, 1p, 1⁗; but critically the archaeopyle type was not recognized. From the same material, Yun (1981) also described a very similar new species *Heslertonia regula*, for otherwise identical species with an epicystal archaeopyle, possessing occasionally striate crests (stated to be up 13 μm high). The average maximum crest height from 18 specimens of 9.7 μm is less than ¼ the average shortest



Explanation of Plate 2.

figs 1–6. *Chatangiella eminens* sp. nov. (holotype), MPK 13900, e/f ref. P60: **1,** internal dorsal view (reversed) showing the fusing of some of the spines on the paracingulum; **2–3,** internal mid-dorsal view showing the intratabular clustering of spines; **4,** ambital view showing the peri-archaeopyle and the distinctively long spines on the lateral margins; **5,** mid-ventral view showing the deeply depressed parasulcal area; **6,** external ventral view showing the intratabular clustering of spines. **figs 7–9**. *Dimidium striatum* gen. et comb. nov.: **7,** ambital view showing short paracingular spines; **8,** external mid-hypocystal view; **9,** external antapical view showing the 6-sided 1'''' paraplate, and the clearly sexiform hypocystal configuration. **figs 10–12**. *Dimidium striatum* gen. et comb. nov.: **10,** internal right lateral view (reversed); **11,** ambital view showing the striated periphragm and short processes; **12,** external left lateral view. Scale bar 10 μm.



Explanation of Plate 3.

figs 1–5. *Dimidium striatum* gen. et comb. nov.: **1,** external dorsal view showing the crenulated parasutural crests; **2,** external mid-dorsal view; **3,** ambital view; **4,** internal mid-ventral view (reversed) showing the well-differentiated plates in the parasulcus; **5,** internal ventral view (reversed) showing the distinctive square-shaped 6″ with a geniculate contact with 1′ and 4′ and L-Type ventral paraplate configuration. **figs 6–12**. *Eatonicysta exilis* sp. nov. (holotype), MPK 13894, e/f ref. O30: **6,** external dorsal view; **7,** external mid-dorsal view showing the solid processes; **8,** ambital view; **9–11,** internal mid-ventral views (reversed); **12,** internal ventral view (reversed) showing the nature of the process endings. Scale bar 10 μm.

body dimension of 48 μm (although only just exceeds that in the holotype). Therefore, *H. rugula* is considered a synonym of *D. striatum*. The photograph of the detached epicyst of *H. regula* (Yun, 1981, pl. 8, fig. 8) suggests that *D. striatum* has an exsert first apical homologue (*1′), typical of the subfamily Goniodomoideae (Autonym), but differs from others in that subfamily by possessing a sexiform rather than quinqueform hypocystal pattern.

Comparison. From the dimensions above, it is clear the crest heights of *Dimidium striatum* from the Trunch borehole are lower than those from the type material of Clarke & Verdier (1967). Given the comparable first occurrences of the species, it would not be reasonable to differentiate these forms on crest height alone since crest height in many species is related to (supporting) processes' height, which has been shown to be a function of salinity (Ellegaard, 2000; Mertens *et al*., 2009; Rochon *et al*., 2009). This might be expected since the type area and the Trunch borehole are located in different basins. Significant salinity variations through the Upper Cretaceous at Trunch have been suggested by Whatley *et al*. (2003). *Dimidium striatum* gen. et comb. nov. appears to most closely resemble *Heslertonia striata* (Eisenack & Cookson, 1960: 9, pl. 3, fig. 10–11) Norvick in Norvick & Burger (1976), which also possesses a striate autophragm, but which differs in possessing stronger striations and higher parasutural crests that exceed ¼ body diameter. Furthermore, *Heslertonia striata* is most commonly recorded from the Albian and Cenomanian of Australia (i.e. Eisenack & Cookson, 1960; Norvick & Burger, 1976; Burger, 1980; McMinn & Burger, 1986) but has been recorded in the Northern Hemisphere from Finland (Uutela, 1989), Germany (Below & Kirsch, 1997) and Spain (Mao & Lamolda, 1998; Lamolda & Mao, 1999) but critically not above the lower Turonian. The disparate temporal range of *H. striata* and *D. striatum* gen. et comb. nov. provides supporting evidence for these as separate species.

Genus *Eatonicysta* Stover & Evitt, 1978

Type species. *Eatonicysta ursulae* (Morgenroth, 1966: 20, pl. 3, fig. 11) Stover & Evitt, 1978

Remarks. Williams & Downie (1966) described two varieties of their *Membranilarnacia reticulata* (now a junior synonym of *Eatonicysta ursulae*). The more common *M. reticulata* var. a lacks paracingular processes (but possibly possesses parasulcal processes), while four paracingular processes were observed on *M. reticulata* var. b (the presence or absence of parasulcal processes was not mentioned). Although the presence or absence of paracingular processes is regarded as a generic-level characteristic in many genera, it is, therefore, clearly not the case in *Eatonicysta*. Stover & Williams (1995) then emended the generic description of *Eatonicysta* as possessing a standard sexiform pattern with a paratabulation formula 4′, 6″, 0–6c, 5‴, lp, 1⁗, 0s.

Eatonicysta exilis sp. nov.
(Pl. 3, figs 6–12)

Derivation of name. From the latin *exilis* meaning thin or meagre, referring to the thin nature of the ectophragm.

Diagnosis. A species of *Eatonicysta* possessing a thin entire ectophragm and six paracingular processes.

Holotype. MPK 13894; e/f ref: O30; Plate 3, figs 6–12; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 93.9–94.0 m, Paramoudra Chalk, high *Belemnitella mucronata* Zone (high upper Campanian).

Description. Medium-sized chorate dinoflagellate cyst with an ovoidal central body. The body is two-layered with a smooth endophragm and periphragm, the latter of which forms processes that support a thin, loose and entire ectophragm. The processes are intratabular, solid, one per reflected paraplate and of consistent length. They are wide proximally (unconnected), narrowing at the mid-length, before widening and flaring distally. The paratabulation is indicated by intratabular processes that reflect the paraplate formula: 4′?, 6″, 6c, 6‴, 1p, 1⁗, 2s? (as, ps). The paracingulum is indicated by an equatorial alignment of processes, and the parasulcus by a deep notch anterior to the anterior sulcal paraplate. The archaeopyle is apical (Type tA, operculum detached) and formed by the loss of all apical paraplates.

Dimensions. Holotype, central body (w/l; excluding archaeopyle) 33 × 34 μm, processes' length (max.) 16 μm; range, central body (w/l; excluding archaeopyle) 26(34.6)43 × 18(33.2)44 μm, processes' length (max.) 13(17.3)21 μm. 10 specimens measured.

Stratigraphic range. Eaton–Weybourne Chalk (undifferentiated), low *Belemnitella mucronata* Zone (low upper Campanian) to the Sidestrand Chalk, low *Belemnitella lanceolata* Zone (lower Maastrichtian; Fig. 2).

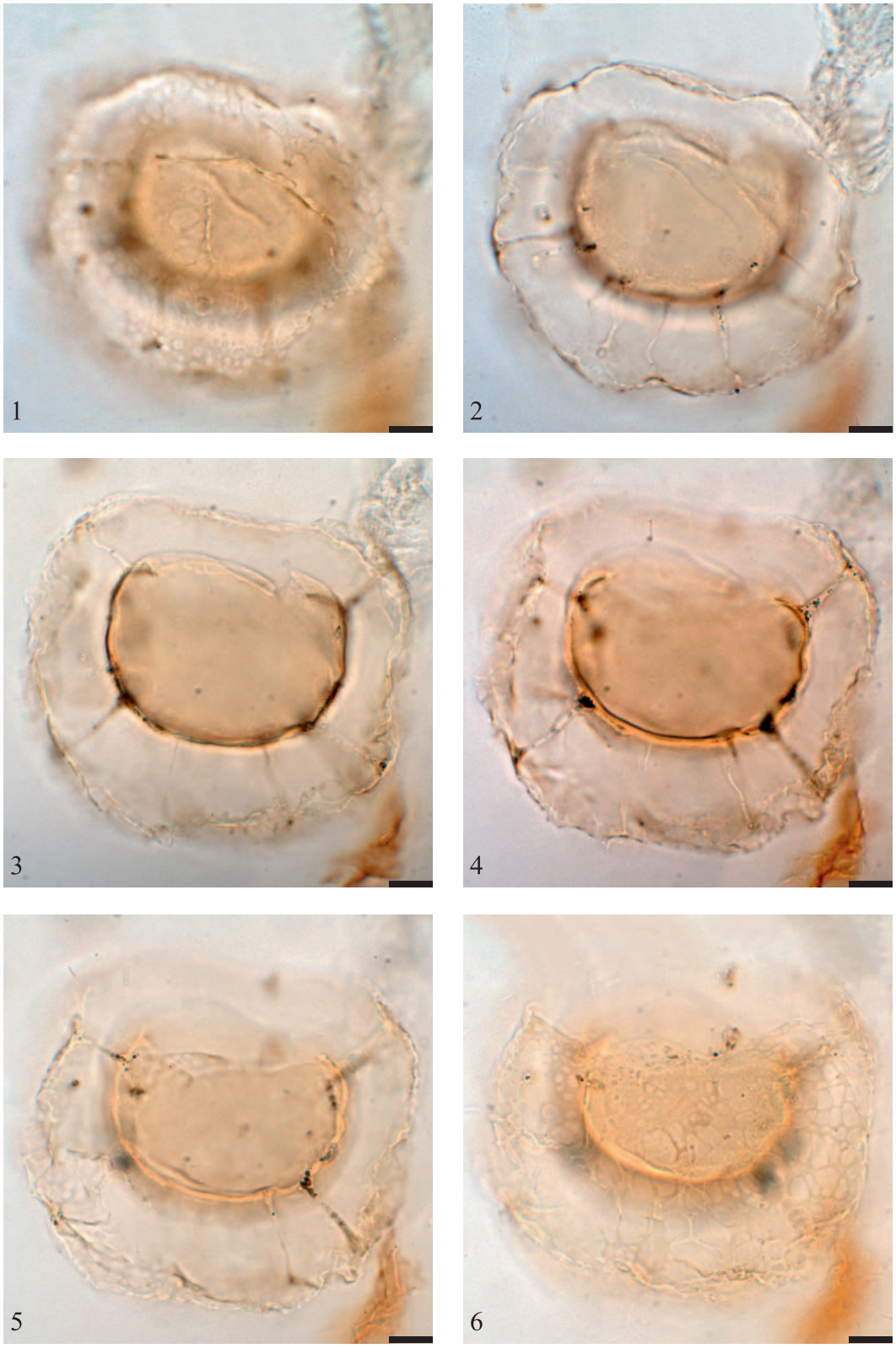
Remarks. *Eatonicysta exilis* sp. nov. possesses an anterior and posterior sulcal paraplate.

Comparison. Differs from *Eatonicysta*? *mutabilireta* sp. nov., *Eatonicysta ursulae* var. a *sensu* Williams & Downie (1966), *Membranilarnacia hapala* (Schiøler & Wilson, 1993: 346–347, pl. 2, figs 1–7; text-figs 12a–b) Lachkar & Masure in Fauconnier & Masure (2004) and *M. pterococcoides* (Wetzel, 1933b: 53, pl. 6, fig. 4) Eisenack, 1963b by possessing paracingular processes. Differs from *Eatonicysta ursulae* var. b *sensu* Williams & Downie (1966) by possessing 6 rather than 4 paracingular processes and in possessing an entire ectophragm.

Eatonicysta? *mutabilireta* sp. nov.
(Pl. 4, figs 1–6)

1991 *Eatonicysta* sp. A Heine, pl. 23, figs 10, 11.

Derivation of name. From the latin *mutabilis* meaning changeable, variable, inconstant and *rete* meaning a net, referring to the variable nature of the ectophragm.



Explanation of Plate 4.

figs 1–6. *Eatonicysta*? *mutabilireta* sp. nov. (holotype), MPK 13895, e/f ref. R23/3: **1,** internal view (reversed); **6**, external view, the ventral and dorsal surfaces have not been distinguished. Scale bar 10 μm.

Diagnosis. A species questionably attributed to *Eatonicysta* possessing a distinctive ectophragm modified by sub-rounded perforations of variable size to an irregular meshwork defined by rounded to (more usually) polygonal lumina.

Holotype. MPK 13895; e/f ref: R23/3; Plate 4, figs 1–6; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 231.9–232.0 m, Burnham–Flamborough Chalk (undifferentiated), mid-*Gonioteuthis quadrata* Zone (high lower Campanian).

Description. Large chorate dinoflagellate cyst with an oblate spheroidal central body slightly dorso-ventrally compressed, but not lenticular. The body is two-layered and comprised of a smooth and thin endophragm and periphragm, the latter of which forms processes that support a thin and highly irregular ectophragm. The ectophragm completely surrounds the central body and is modified by sub-rounded to oval perforations of varying size to an irregular meshwork defined by rounded to (more usually) polygonal lumina. No indication of apical, lateral or antapical protuberances are observed in the cyst body. The processes are intratabular (but absent on the paracingulum and parasulcus) and solid, of consistent length, and near-constant width and unconnected at the base. The paratabulation is indicated by the position of the processes describing the formula: 4′?, 6″, 0c, 6‴, 1p, 1⁗, 0s. The archaeopyle is apical (Type tA, operculum detached) and formed by the loss of all apical paraplates.

Dimensions. Holotype, central body (w/l; excluding archaeopyle) 60 × 48 μm, processes' length (max.) 24 μm; range, central body (w/l; excluding archaeopyle) 51(62.2)76 × 44(50.4)67 μm, processes' length (max.) 10(20.9)26 μm. 10 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), low *Gonioteuthis quadrata* Zone (mid-lower Campanian) to the high *Gonioteuthis quadrata* Zone (high lower Campanian; Fig. 2).

Remarks. The species is questionably attributed to *Eatonicysta* on the interpretation of the presumed degree of dorso-ventral compression. Due to the thin nature of the central body, this species is frequently found damaged, folded or mechanically compressed. Few specimens, (including the holotype) indicate some dorso-ventral compression, but much less strongly than genera in the Family Areoligeraceae.

Comparison. Differs from *Eatonicysta exilis* sp. nov., *Membranilarnacia hapala* (Schiøler & Wilson, 1993: 346–347, pl. 2, figs 1–7, text-figs 12a–b) Lachkar & Masure in Fauconnier & Masure (2004) and *M. pterococcoides* (Wetzel, 1933b: 53, pl. 6, fig. 4) Eisenack, 1963b by possessing a distinctly perforate rather than entire ectophragm. *Eatonicysta*? *mutabilireta* sp. nov. closely resembles the type species *E. ursulae* (Morgenroth, 1966: 20, pl. 3, fig. 11–12) Stover & Evitt, 1978 but differs in the morphology of the ectophragm mesh. In *E. ursulae*, the mesh is usually uniform with usually polygonal lumina, while in *E*? *mutabilireta* sp. nov. the mesh is highly irregular and the lumina vary in size and shape (rounded to polygonal). *Glaphyrocysta* Stover & Evitt, 1978 differs by being lenticular, strongly dorso-ventrally flattened with an offset parasutural notch, and possessing annulate to arcuate penitabular process complexes. The ectophragm in *E*? *mutabilireta*, however, is very similar to that of *Glaphyrocysta semitectum* Bujak in Bujak *et al*., 1980 (46, 48, 50, pl. 14, figs 2–9; text-fig. 13) but differs by being completely developed. Species of *Riculacysta* Stover, 1977 also possess solid, normally isolated processes that support an ectophragm, but which differ by possessing ventrolateral processes that are longer than the lateral ones, and where the ectophragm is appressed or close to the autophragm dorsally.

Suborder **Ceratiineae** Fensome *et al*., 1993
Family **Ceratiaceae** Willey & Hickson, 1909
Genus *Odontochitina* Deflandre, 1937

Type species. According to Fensome *et al*. (2008), the nomenclatural type of the genus *Odontochitina* remains the holotype of *Odontochitina silicorum* Deflandre, 1937 (95, plate 18 (al. pl. 15), fig. 8).

Odontochitina diducta sp. nov.
(Pl. 6, fig. 1)

1967 *Odontochitina costata* Alberti, 1961; Clarke & Verdier, pl. 13, fig. 4 only.
1991 *Odontochitina operculata* (Wetzel, 1933a) Deflandre & Cookson, 1955; Heine: pl. 27, fig. 15.
1997 *Odontochitina operculata* (Wetzel, 1933a) Deflandre & Cookson, 1955; Roncaglia & Corradini: pl. 2, fig. 5.

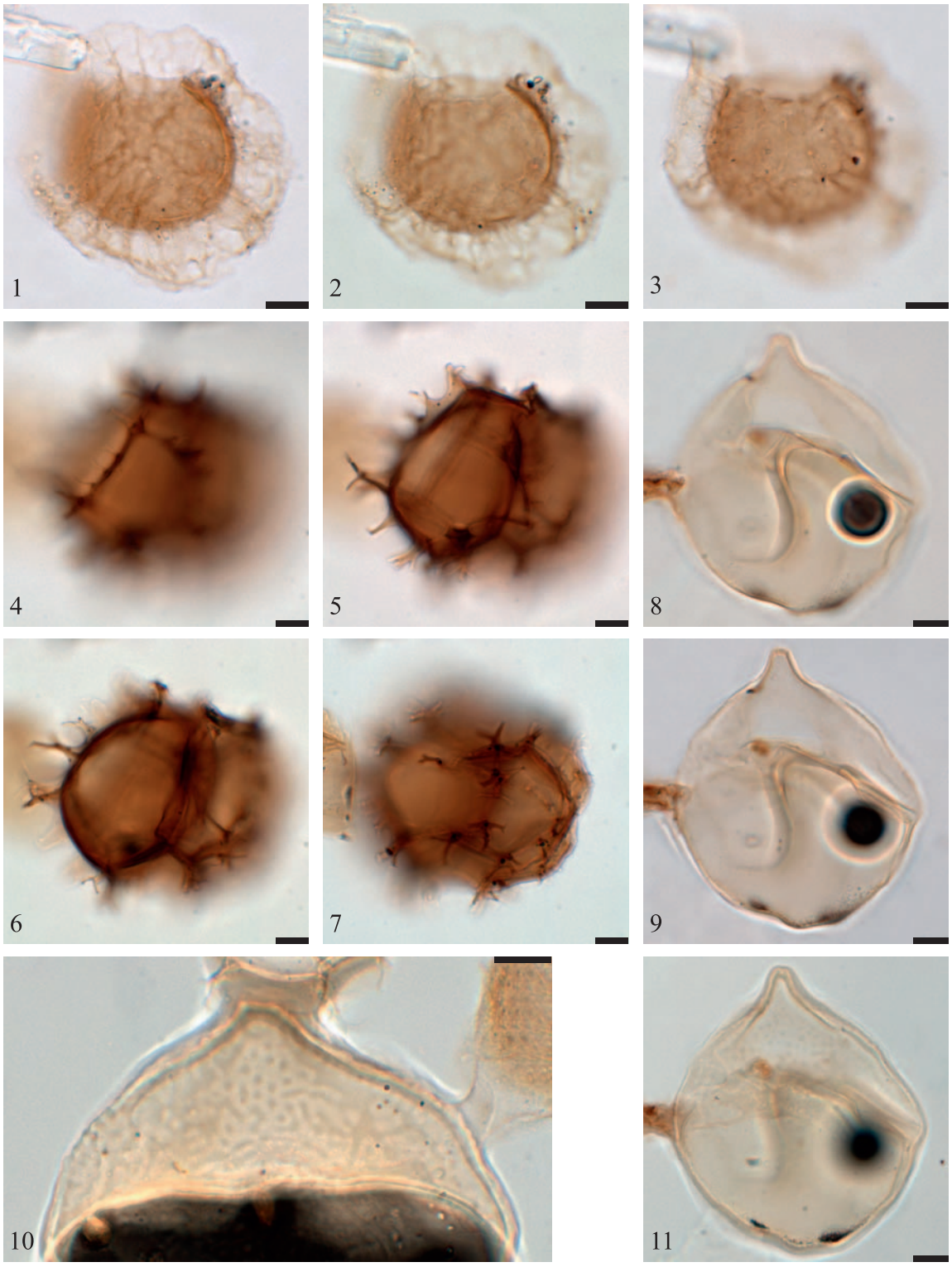
Derivation of name. From the latin *diducere*, meaning to physically separate, split, referring to the high angle between the antapical and lateral horns, which are also connected via an antapical pericoel.

Diagnosis. A species of *Odontochitina* with a widely divergent antapical and lateral horn separated by an angle equal to or greater than 80°.

Holotype. MPK 13896; e/f ref: O40/3; Plate 6, fig. 1; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

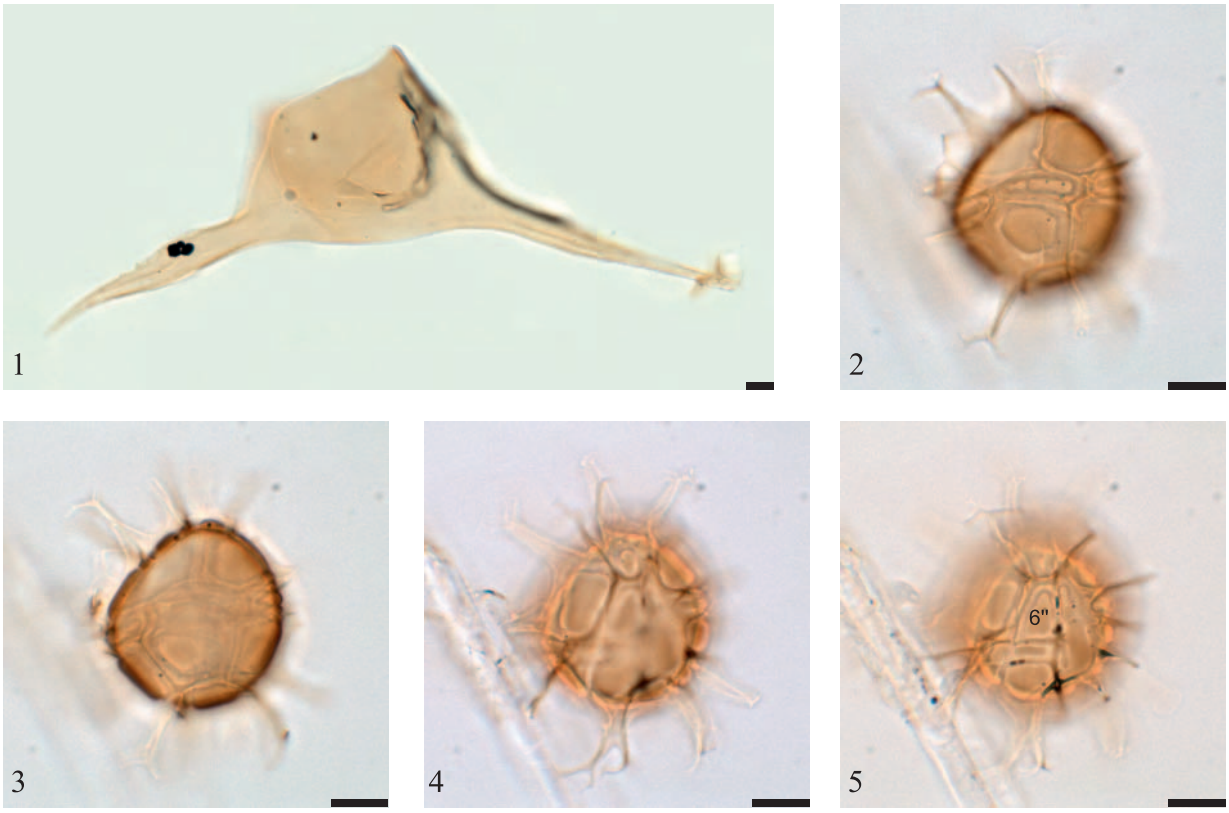
Type locality and horizon. Trunch borehole, Norfolk, UK; 279.9–280.0 m, Burnham–Flamborough Chalk (undifferentiated), high *Offaster pilula* Zone (mid-lower Campanian).

Description. Large ceratioid, cavate dinoflagellate cyst with one apical, antapical and lateral horn of comparable length. The wall is two-layered, comprising a smooth endophragm and smooth, incompletely and faintly striate or distally perforate (although this may be due to corrosion) periphragm. The periphragm and endophragm are attached in the precingular region such that the species has a well-developed cavation connecting the lateral and antapical horns. The endocyst is sub-spherical, lacking obvious projections into the pericoel. The antapical and lateral horns are separated by an angle of greater than 80°. The paracingulum may be indicated by faint ridges on



Explanation of Plate 5.

figs 1–3. *Membranilarnacia wilsonii* sp. nov. (holotype), MPK 13898; e/f ref. P69/1: **1,** internal view (reversed); **6,** external view, the ventral and dorsal surfaces have not been distinguished. **figs 4–7**. *Hystrichostrogylon robustum* sp. nov. (holotype), MPK 13890; e/f ref. P40/2: **4,** internal left lateral view (reversed) showing fine spines on the archaeopyle margin; **5–6,** ambital view showing the egg-shaped central body; **7,** external right lateral view showing the short, robust trifurcating gonal processes. **figs 8–9, 11**. *Nelsoniella incomposita* sp. nov. (holotype), MPK 13901, e/f ref. O38/4: **8,** internal dorsal view (reversed) showing the smooth periphragm; **9,** ambital view showing the well-developed apical horn; **11,** external ventral view showing the ornamentation on the ventral surface of the epi-periphragm; **fig. 10**. *Nelsoniella incomposita* sp. nov. (paratype), MPK 13902, e/f ref. R29/3, external ventral view showing the ornamentation on the ventral surface of the epi-periphragm. Scale bar 10 μm.



Explanation of Plate 6.

fig. 1. *Odontochitina diducta* sp. nov. (holotype), MPK 13896; e/f ref. O40/3, external ventral view showing the widely angle between right lateral and antapical horns and weak paracingulum. The perforations at the extremities of the horns are considered to be preservational. **figs 2–5**. *Spiniferites jarvisii* sp. nov. (holotype), MPK 13891; e/f ref. X25/2: **2,** oblique internal dorsal view (reversed) showing the distinctive thinning of the endophragm; **3,** ambital view showing the distinctive thinning of the endophragm; **4,** oblique external mid-ventral view; **5,** oblique external ventral view showing the sixth precingular paraplate. Scale bar 10 µm.

the periphragm. The archaeopyle is apical (Type tA, operculum detached), formed by the loss of all the apical paraplates.

Dimensions. Holotype, central body (w/l) 55 × 50 µm, angle subtending lateral and antapical horns 130°, distance of lateral horn tip to antapical horn tip 230 µm; range, central body (w/l) 39(47.5)62 × 30(44.5)58 µm, subtending lateral and antapical horns 80(122.7)180°, distance of lateral horn tip to antapical horn tip 93(174.3)230 µm. 20 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Micraster coranguinum* Zone (high middle Santonian) to the Sidestrand Chalk, high *Belemnitella mucronata* Zone (high upper Campanian; Fig. 2).

Remarks. The specimens figured by Cookson & Eisenack (1968: 112, pl. 2, fig. D) as *Odontochitina* sp. and Costa & Davey (1992, pl. 3.13, fig. 5) as *Odontochitina* sp. A also possess a conspicuous wide angle between the lateral and antapical horns but differ in being cornucavate, the periphragm and endophragm are appressed between.

Comparison. Differs from all other species of *Odontochitina* in the wide angle between the lateral and antapical horns that are also connected by the hypopericoel.

Suborder **Uncertain**
Family **Uncertain**
Genus *Cassiculosphaeridia* Davey, 1969

Type species. *Cassiculosphaeridia reticulata* Davey, 1969 (142, pl. 4, fig. 3).

Cassiculosphaeridia alta sp. nov.
(Pl. 1, figs 7–9)

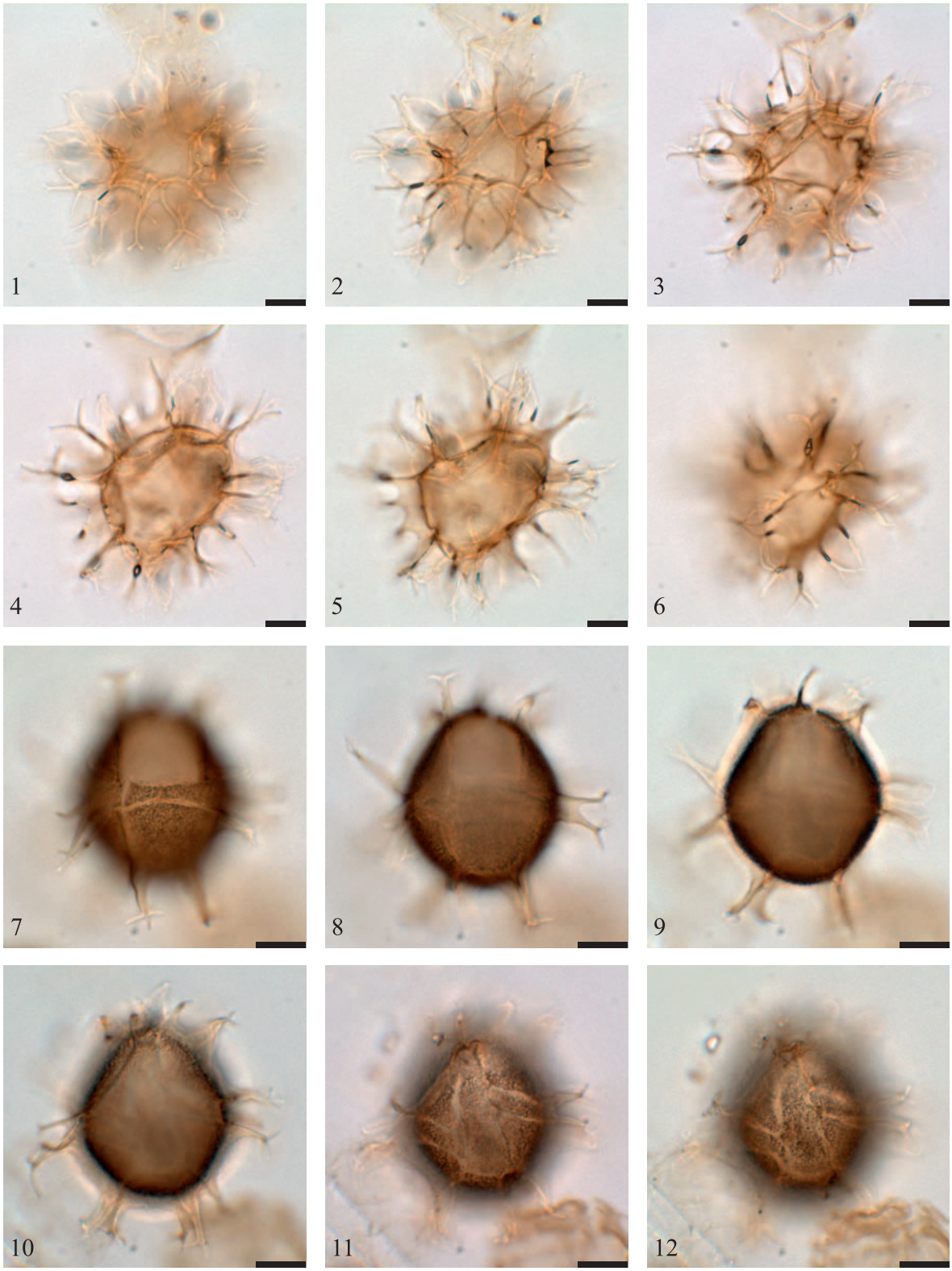
Derivation of name. From the latin *altus*, meaning high, referring to the high crests.

Diagnosis. A species of *Cassiculosphaeridia* with relatively high, non-tabular crests.

Holotype. MPK 13897; e/f ref: P65; Pl. 1, figs 7–9; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 455.9–456.0 m, Burnham–Flamborough Chalk (undifferentiated), mid-*Sternotaxis plana* Zone (mid-upper Turonian).

Description. Small, sub-spherical, proximate dinoflagellate cyst. The wall is single layered and composed of a smooth



Explanation of Plate 7.

figs 1–6. *Spiniferites multispinulus* sp. nov. (holotype), MPK 13892; e/f ref. P48: **1,** external dorsal view; **2–3,** external mid-dorsal views showing paired precingular intergonal processes; **4,** ambital; **5,** internal mid-ventral (reversed); **6,** internal ventral view (reversed), all showing paired postcingular intergonal processes. **figs 7–12**. *Spiniferites ramosus aquilus* sp. nov. (holotype), MPK 13893; e/f ref. M56/2: **7,** internal dorsal view (reversed) showing the micro-reticulate ornamentation; **8,** mid-dorsal view (reversed); **9–10**, ambital views showing the trifurcating gonal processes; **11,** external mid-ventral view; **12,** external ventral view showing the differentiated posterior sulcal paraplate. Scale bar 10 μm.

autophragm that forms crests. The crests are well-developed and relatively high (up to 7 μm, around one-fifth of the diameter of the central body) and form a complete and irregular, typically polygonal reticulum without traces of a paratabulation. The archaeopyle is apical (Type tA, operculum detached) and formed by the loss of all apical paraplates.

Dimensions. Holotype: central body (w/l): 36 × 36 μm, crest height: 6 μm; range: central body (w/l): 30(31.5)36 × 24(29.5)36 μm, crest height: 4(5.8)7 μm, 5 specimens measured.

Stratigraphic range. Ferriby Chalk, *Mantellioceras mantellii* Zone (lower Cenomanian) to Burnham–Flamborough Chalk (undifferentiated), low *Micraster coranguinum* Zone (mid-middle Coniacian; Fig. 2).

Comparison. Differs from species of *Valensiella* Eisenack, 1963b by lacking an ectophragm. Differs from *Cassiculosphaeridia reticulata* Davey, 1969 (142, pl. 3, fig. 7; pl. 4, fig. 3) as the most similar species by possessing distinctly higher crests that are stronger and consistently developed. *Cassiculosphaeridia magna* Davey, 1974 (46, pl. 1, figs 3–7) differs by being much larger (diameter 85–105 μm) with a particularly thick autophragm (up to 3 μm).

Genus *Membranilarnacia* Eisenack, 1963b

Type species. *Membranilarnacia leptoderma* (Cookson & Eisenack, 1958: 50–51, pl. 10, fig. 9) Eisenack, 1963b.

Membranilarnacia wilsonii sp. nov.
(Pl. 5, figs 1–3)

1974 *Membranilarnacia* '*multifibrata*' Wilson: 204, pl. 33, fig. 7.

Derivation of name. In honour of Dr Graeme Wilson who first described this species as *Membranilarnacia* '*multifibrata*' in his unpublished PhD thesis.

Diagnosis. A species of *Membranilarnacia* with a thin ectophragm supported by a large number of fine supporting processes.

Holotype. MPK 13898; e/f ref: P69/1; Plate 5, figs 1–3; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 419.9–420.0 m, Burnham–Flamborough Chalk (undifferentiated), mid-*Micraster cortestudinarium* Zone (mid-lower Coniacian).

Description. Small to medium-sized cavate dinoflagellate with a sub-spherical central body. The central body is comprised of a thin autophragm (~0.5 μm) that forms numerous thin, solid, non-tabular processes that support a thin, smooth to finely reticulate ectophragm. The processes are linked proximally forming an irregular polygonal reticulum of variable size and shape. Processes not obviously concentrated on the hypocyst but where they appear to be thicker. The archaeopyle is apical (Type tA, the operculum may be attached, but more usually detached), formed by the loss of all apical paraplates.

Dimensions. Holotype, central body (w/l) 41 × 38 μm, overall (w/l) 64 × 62; range, central body (w/l) 31(38.2)48 × 30(37.2)47 μm, overall (w/l) 50(55.9)64 × 44(54)64 μm. 14 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), mid-*Micraster coranguinum* Zone (mid-lower Coniacian) to the mid-*Gonioteuthis quadrata* Zone (high lower Campanian; Fig. 2). Extends to the upper Maastrichtian at Stevns Klint and Karlstrup, (Denmark) according to Wilson (1974).

Comparison. Many species of *Membranilarnacia* possess a particularly thin ectophragm but differ from *M. wilsonii* sp. nov. by possessing stronger, better developed processes. *Membranilarnacia*? *picena* Biffi & Manum, 1988 (190, 192, pl. 7, figs 1–3, 5–7, 9, 12) also possesses a thin veil-like ectophragm but differs in possessing a thicker spongy to externally pitted autophragm. *Membranilarnacia polycladiata* Cookson & Eisenack in Eisenack (1963b) (Cookson & Eisenack, 1958: 51, pl. 10, fig. 8) differs by possessing a thicker granular wall and processes that divide in such a way as to give a funnel-like appearance, which are more obviously concentrated on the hypocyst. *Membranilarnacia*? *tenella* Morgenroth, 1968 (554–555, pl. 48, figs 2–4) has 30–40 slender, stronger solid processes which may have tiny perforations. *Membranilarnacia* sp. of Kirsch (1991, pl. 26, figs 4–5) also possesses a thin ectophragm but it is supported by much shorter processes.

Order **Peridiniales** Haeckel, 1894
Suborder **Peridiniineae** (Autonym)
Family **Peridiniaceae** Ehrenberg, 1831
Subfamily **Deflandreoideae** Bujak & Davies, 1983
Genus *Alterbidinium* Lentin & Williams, 1985

Type species. According to Fensome *et al*. (2008), the nomenclatural type of the genus *Alterbidinium* remains the holotype of *Alterbidinium recticorne* (Vozzhennikova, 1967: 151–152, pl. 77, fig. 2) Harker & Sarjeant in Harker *et al*. (1990).

Alterbidinium ioannidesii sp. nov.
(Pl. 1, figs 1–6)

1986 Dinoflagellate type E Ioannides: 42, pl. 23, figs 13–16.

Derivation of name. In honour of Dr Nicos Ioannides who first recorded this species as Dinoflagellate type E.

Diagnosis. A species of *Alterbidinium* possessing a well-developed parasutural paratabulation on the periphragm.

Holotype. MPK 13899; e/f ref: K38/3; Plate 1, figs 1–6; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 298.9–299.0 m, Burnham–Flamborough Chalk (undifferentiated), low *Offaster pilula* Zone (low lower Campanian).

Description. Medium-sized peridinioid, cornucavate to circumcavate dinoflagellate cyst. The wall is two-layered composed of a smooth endophragm and a finely reticulate to striate periphragm that forms low parasutural ridges with no accessories. The pericyst is elongate ellipsoid to biconical and forms a well-developed apical and left antapical horn (right antapical horn much reduced or absent). The endocyst is sub-spherical to ovoidal and lacks horns, follows the general shape of the pericyst and lacks supporting processes. The paratabulation is indicated by well-developed parasutural crests indicating the formula: 4′, 3a, 7′, ?c, 5‴, 2‴″. The paracingulum is indicated by parallel horizontal crests, and undifferentiated, except perhaps by the most posterior paraplate in contact with the right sulcal boundary. The parasulcus is indicated by a deep longitudinal depression. The peri-archaeopyle is intercalary (Type I, operculum detached) and formed by the loss of a steno-deltaform 2a paraplate. The endo-archaeopyle type has not been identified.

Dimensions. Holotype, overall (w/l) 42 × 61 μm; range, overall (w/l) 40(54.3)62 × 54(64.6)74 μm. 15 specimens measured. As recorded by Ioannides (1986), overall (w/l) 50–64 × 70–98 μm, 14 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), low *Offaster pilula* Zone (low lower Campanian) to the low *Gonioteuthis quadrata* Zone (mid-lower Campanian; Fig. 2). Extends to the ?Maastrichtian at Bylot Island (Arctic Canada) according to Ioannides (1986).

Remarks. *Alterbidinium ioannidesii* is comparable in width to Dinoflagellate type E Ioannides, 1986 but shorter in overall length by 10–20 μm. Dinoflagellate type E has been recorded from Arctic Canada (questionably from the Maastrichtian, but no detailed occurrence data were provided) and extensively in the Norwegian Sea (pers. obs.) from the upper Santonian? to lower Campanian, often forming a common or even abundant component of the palynoflora. It is a feature of many peridinioid genera to reach a particularly large size in high (northern) latitudes (Lentin & Williams, 1980), which are otherwise smaller elsewhere, and this may account for the slightly smaller size at Trunch.

Comparison. Differs from other species of *Alterbidinium* by possessing clearly developed parasutural crests on the periphragm.

Genus *Chatangiella* Vozzhennikova, 1967

Type species. *Chatangiella niiga* Vozzhennikova, 1967 (129, pl. 56, fig. 1; pl. 57, fig. 1).

Chatangiella eminens sp. nov.
(Pl. 2, figs 1–6)

Derivation of name. From the latin *emineo*, to project, stand out, be conspicuous, remarkable, referring to the prominent paracingular spines.

Diagnosis. A species of *Chatangiella* possessing prominent spines on the paracingulum that are particularly well developed at the ambitus. Shorter spines are arranged in intratabular fields on the pre- and postcingular paraplates which may fuse on the margin of the pentapartite paracingulum and be randomly (but rarely) scattered elsewhere.

Holotype. MPK 13900; e/f ref: P60; Plate 2, figs 1–6; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type locality and horizon. Trunch borehole, Norfolk, UK; 331.9–332.0 m, Burnham–Flamborough Chalk (undifferentiated), low *Uintacrinus socialis* Zone (low upper Santonian).

Description. Medium-sized to large cornucavate peridinioid dinoflagellate cyst. The wall is two-layered composed of a smooth to finely granular (1 μm thick) endophragm and a smooth to finely granular (~0.5 μm thick) periphragm that forms solid penitabular spines. The spines are generally 2–4 μm in length, simple, evexate to capitate, longest when adjacent to paracingulum and are conspicuously long at the ambitus of the paracingulum. The spines are typically arranged in intratabular fields particularly on the pre- and postcingular paraplates and fuse on the paracingular margin where they demarcate a pentapartite paracingulum. Rare spines may also be randomly scattered over the pericyst. The pericyst is ventrodorsally compressed, longitudinally elongate, forming a short and blunt apical horn, two antapical horns (right antapical horn shorter), and a slight bulge around the paracingulum. Below the apical horn, the epicystal ambitus is convex with weakly to moderately well-developed rounded to sub-angular shoulders. From the paracingulum to the antapical horns, the ambitus of the hypocystal is concave to occasionally straight. The endocyst is sub-spherical to ovoidal, and follows the general shape of the pericyst. The left endo-antapical horn protrudes slightly into the antapical pericoel, the right endo-antapical horn is reduced. The paratabulation is incompletely indicated by the intratabular clustering of spines and the position of the archaeopyle: x′, 3a, 7″, ?c, 5‴, ?2″. The parasulcus is indicated by a deep longitudinal depression. The peri-archaeopyle is intercalary (Type I, operculum detached) and formed by the loss of an iso-thetaform to iso-deltaform 2a paraplate. The endo-archaeopyle type has not been determined.

Dimensions. Holotype, central body (w/l) 43 × 42 μm, overall (w/l) 47 × 95 μm, spine length (max.) 3 μm; range, central body (w/l) 30(39.5)44 × 30(39.7)50 μm, overall (w/l) 33(43.2)52 × 52(78.9)95 μm, spine length (max.) 2(2.9)4 μm. 20 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Micraster coranguinum* Zone (mid-middle Santonian) to the mid-*Uintacrinus socialis* Zone (low upper Santonian; Fig. 2).

Comparison. This species most closely resembles *Chatangiella madura* Lentin & Williams, 1976 (see Cookson & Eisenack, 1970, pl. 11, fig. 10) but differs by possessing longer and more strongly developed paracingular spines at the ambitus.

Genus *Nelsoniella* Cookson & Eisenack, 1960

Type species. *Nelsoniella aceras* Cookson & Eisenack, 1960 (4, pl. 1, fig. 12).

Nelsoniella incomposita sp. nov.
(Pl. 5, figs 8–11)

Derivation of name. From the latin *incompositus*, meaning irregular, disorderly, referring to the surface ornamentation.

Diagnosis. A species of *Nelsoniella* possessing verrucae on the ventral epitheca that may be isolated or coalesce into irregular ridges or patches.

Holotype. MPK 13901; e/f ref: O38/4; Plate 5, figs 8–9, 11; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Paratype. MPK 13902; e/f ref: R29/3; Plate 5, fig. 10; lodged at the British Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham, UK.

Type location and horizon. Trunch borehole, Norfolk, UK; 213.9–214.0 m, Burnham–Flamborough Chalk (undifferentiated), high *Gonioteuthis quadrata* Zone (high lower Campanian).

Description. Large compressed sub-spherical epicavate dinoflagellate cyst with a short apical horn. The wall is two-layered, comprised of a thin (usually less than 0.5 μm but up to 1 μm) and smooth to finely granular endophragm and a periphragm of variable thickness (1–2 μm) being thickest at the antapex and often the apex. The periphragm is ornamented by verrucae that are either isolated or fused into discontinuous and wavy ridges with no clear or consistent pattern, generally restricted to the ventral surface of the epicyst. The endocyst is confined to the hypocyst, appressed to the periphragm in the hypocystal region and comprises one-half to two-thirds the dinocyst length, and resulting in a wide epi-pericoel. The pericyst forms a short apical horn of variable length that is often concave at the apex and may possess ridges that pass from the edge of the apical horn onto the dorsal epicyst. The peri-archaeopyle is isodeltaform with a transverse archaeopyle index of 0.4–0.5 (as typical of genus, operculum detached). The endo-archaeopyle type has not been determined.

Dimensions. Holotype, overall (w/l) 84 × 88 μm, central body (w/l) 82 × 53 μm, apical horn length 6 μm; range, overall (w/l) 70(77.5)86 × 70(84.9)101 μm, central body (w/l) 68(75.1)83 × 31(47.9)64 μm, apical horn length 3(7.8)13 μm. 20 specimens measured.

Stratigraphic range. Burnham–Flamborough Chalk (undifferentiated), high *Gonioteuthis quadrata* Zone (high lower Campanian) to the low *Belemnitella mucronata* Zone (low upper Campanian; Fig. 2).

Comparison. *Nelsoniella aceras* Cookson & Eisenack (1960: 4, pl. 1, figs 12–13) lacks a prominent apical horn and is deeply concave at the extreme apex, *Nelsoniella oviformis* Cookson & Eisenack (1982: 33, pl. 3, fig. 2) possesses a strong apical horn but the cyst is clearly longer than broad with a weakly smooth to clearly granulated periphragm. *Nelsoniella semireticulata* Cookson & Eisenack (1960: 4–5, pl. 1, fig. 15) is ornamented on the epicyst ventral surface with a low, thin-walled reticulum. *Nelsoniella tuberculata* Cookson & Eisenack (1960: 4, pl. 1, fig. 14) has an epitheca ornamented with small tubercles or large granules, but which do not coalesce as frequently or as randomly as in *N. incomposita* sp. nov.

Other dinocyst taxa
Genus *Whitecliffia* gen. nov.

Type species. *Thalassiphora*? *spinosa* (Clarke & Verdier, 1967: 77–78, pl. 17, figs 1–2; text-fig. 31) Foucher, 1975.

Derivation of name. Named after the locality, Whitecliff (Isle of Wight, UK) where the type species was described.

Diagnosis. Laterally cavate dinoflagellate cyst formed by the separation of the periphragm and endophragm that become appressed towards the polar regions. Distinctive apical and antapical processes are developed.

Description. Medium-sized to large, laterally bicavate dinoflagellate cyst. The wall is two-layered, comprised of a thin endophragm and periphragm, which are in contact towards the apex and antapex and widely separated elsewhere. The endocyst is sub-spherical, the pericyst is sub-circular to ovoidal in plan view and broadly ovoidal in lateral view. The pericoel expands medially, prior to terminating in a rounded margin. A separation in wall layers is also apparent at the apex and antapex with the formation of processes. Four? processes conforming to paraplates 1′–4′ occur at the apex and a single, wide and tubular processes conforming to paraplate 1″″ occurs at the antapex. Archaeopyle type has not been determined.

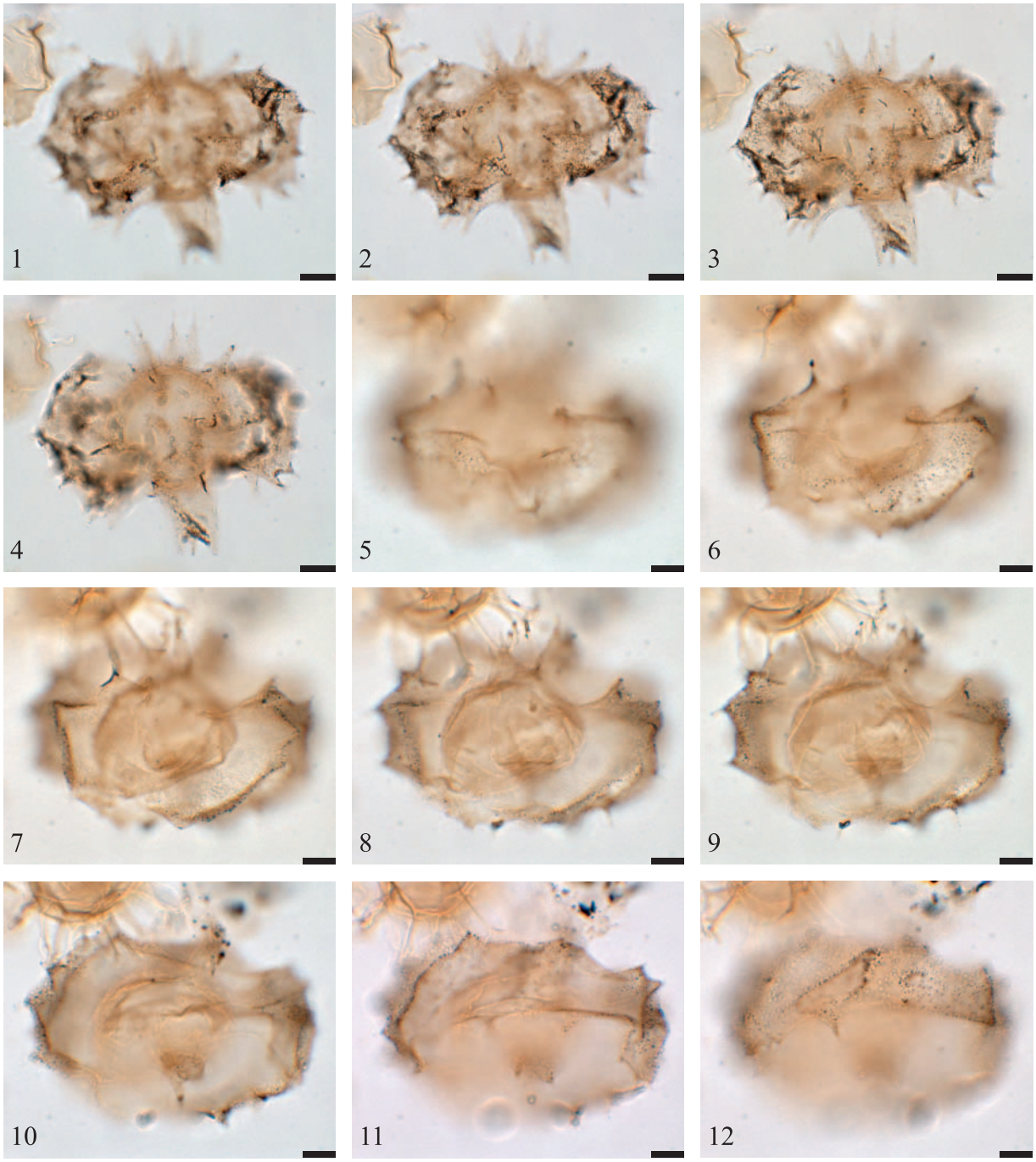
Comparison. Differs from *Flandrecysta* Slimani, 1994, *Invertocysta* Edwards, 1984, *Lophocysta* Manum, 1979, *Thalassiphora* Eisenack & Gocht, 1960 and *Turnhosphaera* Slimani, 1994 in displaying polar, rather than dorsal-ventral, appression of the wall layers. Differs from *Saturnodinium* Brinkhuis *et al*., 1992 by possessing apical and antapical structures.

Whitecliffia spinosa (Clarke & Verdier, 1967) gen. et comb. nov.
(Pl. 8, figs 1–12)

1967 *Pterospermopsis spinosa* Clarke & Verdier: 77–78, pl. 17, figs 1–2.
1973 *Pterospermella spinosa* (Clarke & Verdier) Eisenack *et al*.: 1011–1012.
1974 *Hexagonifera* "*perforata*" sp. nov. Wilson: 279–280.
1975 *Thalassiphora*? *spinosa* (Clarke & Verdier) Foucher: 9.

Type species. As for the genus.

Holotype. *Pterospermopsis spinosa* Clarke & Verdier, 1967, pl. 17, fig. 1.



Explanation of Plate 8.

figs 1–4. *Whitecliffia spinosa* gen. et comb. nov.: **1,** internal view (reversed); **4,** external view, the ventral and dorsal surfaces have not been distinguished, showing the spines on the inflated periphragm, four apical processes and the tubular antapical process; **figs 5–12**. *Whitecliffia spinosa* gen. et comb. nov., the ventral and dorsal surfaces have not been distinguished: **5–6,** internal oblique apical views showing the microreticulate to microperforate periphragm; **7,** internal oblique apical view showing a possible single plate precingular archaeopyle; **8,** ambital view; **9–10,** external oblique antapical views showing the paracingulum; **11–12**, external oblique antapical views showing the details of the antapical process. Scale bar 10 μm.

Locality and horizon. Culver Cliff, Isle of Wight, UK; Sample CV28, *Marsupites testudinarius* Zone (upper Santonian).

Supplementary description. Medium-sized to large, laterally bicavate dinoflagellate cyst. The wall is two-layered comprising a smooth and thin (0.5 μm) endophragm and a smooth to microreticulate or microperforate and thin (0.5 μm) periphragm. The periphragm is in contact towards the apex and antapex and widely separated elsewhere and is ornamented by non-tabular short, thorn-like acuminate spines or rarely by short processes

with expanded tops. The endocyst is sub-spherical; the pericyst is sub-circular to ovoidal in plan view and broadly ovoidal in lateral view. The pericoel expands medially, prior to terminating in a rounded margin. A separation in wall layers is also apparent at the apex with the formation of four (or possible more) long, hollow, acuminate processes resembling a crown, and at the antapex with the formation of a wide (~20 μm wide), hollow, distally tapering, tubular process. Spines are also developed on the distal margin of the antapical process. The paracingulum is poorly expressed by two weakly developed ridges, no expression of a parasulcus has been observed. The archaeopyle type is uncertain, possibly remains attached, but may involve the one or more precingular paraplates.

Dimensions. Type material of Clarke & Verdier (1967), holotype: overall diameter (polar view) 93 μm; inner body diameter 38 μm; length of spines 5–12 μm; range: overall diameter (polar view) 85–100 μm; inner body diameter 35–50 μm; length of spines 3–18 μm (may therefore include the antapical process).

Trunch borehole material, range: inner body (max. Ø) 32(41.5)74 μm, outer body (max. Ø) 63(79.6)90 μm, spine length 3(4.1)6 μm, 1 specimen enabled the measurement of the apical spines (21 μm) and antapical process (23 μm), 11 specimens measured.

Stratigraphic range. Type section, as restudied by Prince *et al*. (1999): Newhaven Chalk, high *Uintacrinus socialis* Zone (middle Santonian) to the *Offaster pilula* Zone (lower Campanian).

Trunch borehole material: Burnham–Flamborough Chalk (undifferentiated), mid-*Offaster pilula* Zone (low lower Campanian) to the Eaton–Weybourne Chalk (undifferentiated), low *Belemnitella mucronata* Zone (low upper Campanian; Fig. 2).

Comparison. See those for the genus.

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