A review of the areoligeracean dinoflagellate cyst *Cyclonephelium* and morphologically similar genera

Robert A. Fensome[a], Graham L. Williams[a], Stephanie E.L. Wood[b] and James B. Riding[b]

[a]Natural Resources Canada, Geological Survey of Canada (Atlantic), Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada; [b]British Geological Survey, Environmental Science Centre, Keyworth, Nottingham NG12 5GG, UK

CONTACT Robert A. Fensome rob.fensome@canada.ca.

Supplemental material for this article can be accessed here: http://doi.org/10.1080/xxxxxxx

ABSTRACT

A group of mainly Cretaceous areoligeracean dinoflagellate cyst genera, which we call the "*Cyclonephelium* group", has proved difficult to classify. The group comprises *Aptea*, *Canningia*, *Canninginopsis*, *Cassidium*, *Cauveridinium*, *Cerbia*, *Circulodinium*, *Cyclonephelium*, *Doidyx*, *Senoniasphaera* and *Tenua*. As a group, they also converge morphologically with ceratiaceans. *Cyclonephelium* group taxa show considerable morphological diversity and gradation. However, the most important criteria for discriminating dinoflagellate cyst-based genera — tabulation and archaeopyle type — are uniform among areoligeraceans and ceratiaceans and so are not useful in this case. Any subdivision of the *Cyclonephelium* group will break apparently natural continuities; nevertheless, any resolution must involve on a hierarchy of morphological criteria. In developing a "best-fit" hierarchy of morphological criteria for the *Cyclonephelium* group, and its separation from ceratiaceans, we consider historical concepts, morphological variation, illustrations in the literature (especially of types) and taxonomic stability. We conclude that the most pragmatic distinguishing feature of ceratiaceans in contrast to the *Cyclonephelium* group (and areoligeraceans in general) is that the former possess a lateral horn or distinct prominence on the inner body or wall. The hierarchy we favour within the *Cyclonephelium* group (in decreasing importance) is: 1) wall structure; 2) whether the ornament is linear or free standing; and 3) the distribution of the ornament. As a consequence, we propose one new genus (*Trimuridinium*), one new species (*Aptea cassis*), two new names (*Canningia glomerata* for *Senoniasphaera rotundata* and *Circulodinium vectensis* for *Pseudoceratium distinctum*), 49 new combinations and one new status. We emend the descriptions/diagnoses of *Aptea*, *Circulodinium*, *Cyclonephelium*, *Pseudoceratium, Senoniasphaera*, *Tenua* and *Tenua hystrix*. *Cyclonephelium* group taxa predominate in neritic marine palaeoenvironments, and their use in palaeocological analyses should be improved by a more cohesive and consistent taxonomy. The group may have been the root stock for ceratiaceans in the Late Jurassic, the two families becoming more clearly separate from the Late Cretaceous onwards. *Cyclonephelium* group areoligeraceans are sparse in the Palaeogene and confirmed species are absent in the Neogene.

KEYWORDS Areoligeraceae; biostratigraphy; Cretaceous; *Cyclonephelium* group; dinoflagellate cysts; evolution; taxonomy

1. Introduction

The Areoligeraceae is an extinct family of dinoflagellates known exclusively from cysts. Areoligeraceans appeared in the Late Jurassic and had mostly disappeared by the end of the Palaeogene. Common in many Cretaceous and Palaeogene assemblages, areoligeraceans exhibit a cyst body that is generally dorsoventrally flattened, an apical archaeopyle, an asymmetry involving the displacement of the parasulcus to the left, and commonly an asymmetrical antapical margin with the left side being more prominent. The displacement of the parasulcus is usually clearly seen by an offset parasulcal notch in the archaeopyle margin. Where discernible, the paratabulation is consistently sexiform gonyaulacalean (Evitt 1985, who referred to areoligeraceans as “Gv cysts”; Fensome et al. 1993). Aside from these common traits, however, areoligeracean morphology is very flexible. It includes variability in the nature and distribution of the ornament, in wall structure (including acavate, holocavate and circumcavate forms), and in shape, especially of the ambitus, which can vary from circular to triangular to lozenge-shaped.

The asymmetrical features of areoligeraceans distinguish them from gonyaulacaceans, which generally have symmetrical features including a mid-ventral parasulcus and a symmetrical antapical outline. Another family that shows similar asymmetry to the Areoligeraceae is the Cerateaceae, but its members are distinctive in generally having long horns, including one or more lateral horns or distinct prominences. Areoligeraceans lack lateral horns, although morphologically transitional forms exist between the Areoligeraceae and the Ceratiaceae that lead to problems in making clearcut distinctions.

Our focus is on a predominantly Cretaceous group of proximate to proximochorate areoligeracean genera that we refer to as the "*Cyclonephelium* group", whose generic differentiation has been a source of discussion and confusion for several decades, especially during the late twentieth century. The group comprises the following genera: *Aptea*, *Canningia*, *Canninginopsis*, *Cassidium*, *Cauveridinium*, *Cerbia*, *Circulodinium*, *Cyclonephelium*, *Doidyx*, *Senoniasphaera* and *Tenua*. We also consider the ceratiacean genus *Pseudoceratium* because of its morphological continuity with some *Cyclonephelium* group genera, especially *Aptea*. This apparent morphological continuum raises some interesting evolutionary questions. We consider that a review and rationalisation of the taxonomy of the above-listed genera (plus a few synonyms) and their species is essential in refining their biostratigraphical and palaeoecological applications.

As paratabulation and archaeopyle development in the Areoligeraceae (and Ceratiaceae) are strikingly consistent and stable, subdivision into genera must rely mostly on wall structure, shape and ornamentation. Unfortunately, broad intergradations exist in these features, such that a coherent scheme of genera that would not cut across at least some apparently natural boundaries is not possible (and thus will inevitably perturb the conventions of some researchers for separating genera). But the alternative of including the entire *Cyclonephelium* group in a single genus would be acceptable to few, if any. Hence, our aim is to develop a taxonomic scheme that is pragmatic, but respects previous work and, most of all, the morphology of the nomenclatural types of the genera in question.

2. Material and terminology

This paper was initially inspired by material rich in *Cyclonephelium* group taxa studied in middle Cretaceous strata of the Mackenzie Plain, Northwest Territories and Axel Heiberg Island, Nunavut, Canada (Fensome 2016). This has been augmented by material from offshore eastern Canada (Fensome et al. 2009). For locality and stratigraphical information for all specimens newly illustrated (excluding re-figured holotypes), see Appendix 3 and Supplemental data.

In this paper we have elected to use “paraterminology” for clarity, although recognise that it can sometimes be cumbersome. Note that paraterminology indicates that the cyst features referred to are “reflections” of features on the thecate cell, so “paratabulation” is synonymous with “reflected tabulation”. Ornament can be linear (involving rugulae, a reticulum or processes linked to various extents) or free-standing (involving processes, spines, bacula, granula etc.). We use the term “ambitus” to denote the outline in dorsoventral view.

The use of wall and cavity terminology used for areoligeracean cysts has been the source of confusion. This is largely because the use of conventional terminology may mean that homologous features bear different labels in what are clearly closely related taxa. Thus, for a form with two wall layers that are unconnected by intervening structural elements (although they may be partially appressed locally), it is generally conventional for the inner layer to be called the endophragm and the outer layer the periphragm; for a similar form that has interconnecting structures, the inner layer is conventionally called autophragm and the outer layer the ectophragm. These terminologies would be applied, for example, respectively to *Senoniasphaera microreticulata* (which does not have structures connecting wall layers) and *Canningia reticulata* (which does), even though the two species resemble one another in many ways and the wall layers are clearly homologous. We propose that for areoligeraceans and ceratiaceans, the inner and outer wall layers of the cyst wall be referred to consistently as endophragm and periphragm, whether or not connections exist. If only one undivided wall layer is present, we retain the conventional term autophragm. We continue to use the term holocavate for forms with two wall layers that are separated over some or all of the cyst but connected by intervening structures, such as pillars or muri. It is not always easy to determine if the holocavate condition is present over the entire cyst, marginally or locally, but we propose that the term be used regardless of its extent. We use the term circumcavate for forms in which the wall layers are seen to be separated around most of the ambitus in dorsoventral view, but lack supporting structures. We acknowledge that the cavation of circumcavate may or may not extend dorsoventrally, although, as with holocavation, the full extent of the cavation is usually very difficult to establish. However, we cannot conceive of a cyst in which the endocyst is totally detached from the pericyst, since in such a relationship the endocyst would be floating in space. As we unfold the taxonomic story below, we use quotes from the original literature freely, sometimes in translation. Our inserts in these quotes are indicated by square brackets.

3. History of study

3.1. Introduction

In this section, we develop an overview of the history of taxonomic concepts for *Cyclonephelium* group cysts from particular morphological perspectives. In the process, we review what earlier authors have reported and considered. In a later section, we propose a resolution to problems arising from shifting and collectively confusing historical treatments. We also provide a chronological listing of events in *Cyclonephelium* group taxonomy as Appendix 1.

3.2. Early development of core generic concepts (1955 to 1970)

The genus *Cyclonephelium* was introduced by Deflandre & Cookson (1955, p. 285) for Late Cretaceous aquatic palynomorphs comprising spheroidal, flattened shells "… with an equatorial ornamentation that extends for varying distances from the equator but never to the poles." What Deflandre & Cookson (1955) considered the equator, modern dinoflagellate workers would call the dorso-ventral outline, or ambitus; and what they called the poles we would now recognise as the mid-dorsal and mid-ventral areas. Deflandre & Cookson (1955) included *Cyclonephelium* in the zoological family Hystrichosphaeridae, not then recognised as being of dinoflagellate affinity but classified as *incertae sedis*. Also, as part of their description, Deflandre & Cookson (1955) recognised that the "shell" often had "a large ill-defined lateral opening". Thanks to the work of Evitt (1961, 1963a, 1963b) and later authors, we now recognise *Cyclonephelium* as a dinoflagellate cyst, with its “ill-defined lateral” opening now recognised as an apical archaeopyle, and with the distinctive areoligeracean asymmetry and plate equivalency (Fensome et al. 1993). Deflandre & Cookson (1955) designated their new species, *Cyclonephelium compactum*, as type; this species has an ornamentation consisting at least in large part of membranous crests. They also included the species *Cyclonephelium distinctum*, characterised by generally slender processes. Both *Cyclonephelium compactum* and *Cyclonephelium distinctum* exhibit dorsoventral areas devoid of ornament.

In a study of the Aptian of northern Germany, Eisenack (1958, p. 410) described a new hystrichosphere genus, *Tenua*, as consisting of “Thin-walled oval casings, without tabulation …, rather densely covered with short, solid, rod-like spines” (translation). His focus was very clearly on the nature of the spines, as would indeed befit a hystrichosphere. However, in an addendum to the diagnosis of the type, *Tenua hystrix*, Eisenack (1958, p. 410) mentioned that “Frequently, truncations are found … resulting in the absence of one polar cap” (translation). He noted that these seemed to be openings related to excystment and, with hindsight, we now know that *Tenua* is an areoligeracean dinoflagellate cyst and that the “openings” are apical archaeopyles. All specimens of *Tenua* illustrated by Eisenack (1958) have a rounded ambitus with little or no suggestion of horns or protuberances. Although not mentioned by Eisenack, *Tenua hystrix* differs from the type of *Cyclonephelium* (*Cyclonephelium compactum*) in having an ornament of processes rather than crests.

In the same publication, Eisenack (1958, p. 393) erected *Aptea*, with *Aptea polymorpha* as type, and provided the following diagnosis:

> Shell compressed oval in cross-section, in outline irregularly triangular with convex sides and 3 (or 4?) small protruding horns, which can be largely reduced, so that the outline is very variable and therefore tends to appear oval to circular. [Translation]

Eisenack compared *Aptea* only with *Pseudoceratium*, which he considered differed in having distinctly developed horns. *Pseudoceratium* had been established by Gocht (1957), with *Pseudoceratium pelliferum* as type — a form with three distinctive horns, including one in a lateral position.

Cookson & Eisenack (1960, p. 251) erected *Canningia*, describing it as follows: “Shell flattened, roughly five sided to almost circular with a slight apical prominence and a broadly indented base.” The generic description goes on to refine the shape, indicate a weakly defined paracingulum, and note an opening. The structure of the wall and the nature of the ornament was not mentioned, although the type (Cookson & Eisenack 1960, pl. 38, fig. 1, as *Canningia reticulata*) clearly shows a holocavate wall with a dense microreticulum formed by perforations in a delicate periphragm. It is clear that Cookson & Eisenack (1960) did not consider wall structure an important defining feature of the genus because they included other species in *Canningia* with various wall types; for example, *Canningia colliveri* has an autophragm with low ornament and *Canningia reticulata* is holocavate. This broader concept of *Canningia* was followed by subsequent authors; but we follow recent authors in restricting the genus to cavate forms, as further discussed below.

The genus *Circulodinium* was introduced by Alberti (1961, p. 28), with *Circulodinium hirtellum* as type, for forms that he diagnosed as follows:

> Shell compressed to flat, with almost circular to irregularly rounded outline. With a small apical process with a somewhat blunt tip. [Antapex concave, from] … which arise two antapical bulges, one of which may be reduced. Shell without … tabulation. Its surface, except for central ventral and dorsal areas and antapical concavity, with short, solid spines …. [Translation]

The description of *Cyclonephelium* was emended by Cookson & Eisenack (1962, p. 493–494) mainly to re-interpret the opening as apical. More significantly, though, for the present discussion, they confirmed the peripheral distribution of the ornament. They stated that their new specimens had “… demonstrated very clearly that the restriction of the ornament to the periphery of the shell is a constant and reliable generic feature.” Interestingly, Cookson & Eisenack (1962) also indicated that they had difficulty “… in deciding with which species an example [presumably meaning a specimen] should be identified, owing to the occurrence of … intermediate forms. For this reason we have allowed a rather wide margin of variation … [for] individual species, especially *C. compactum* and *C. distinctum*.” The presence of intergrading forms remains a continuing problematic theme in classifying *Cyclonephelium* group cysts.

Eisenack (1964, p. 322) stated that *Circulodinium* "… contains the two species, *C. hirtellum* [the type] and *C. deflandrei*. Their diagnoses and appearance would permit the assignment of *C. hirtellum* to … *Canningia* … and *C. deflandrei* to … *Cyclonephelium* …." He continued "Therefore I propose to eliminate the genus *Circulodinium* and from now on to call its two species *Canningia hirtella* … and *Cyclonephelium deflandrei* … " [translation]. Thus, Eisenack (1964) effectively considered *Circulodinium* to be a taxonomic junior synonym of *Canningia*. These considerations by Eisenack became confused in later work: Fensome & Williams (2004) indicated that Millioud (1969, p. 425) considered *Circulodinium* to be a taxonomic junior synonym of *Canningia*. However, Millioud included only a brief entry in his systematics section for *Canningia hirtella* (the type of *Circulodinium*) and lists '*Canningia hirtella* (Alberti) Eisenack … 1964 in synonymy, apparently simply following Eisenack's ideas.

Sarjeant (1966, p. 205–206) introduced the genus *Doidyx*, with *Doidyx anaphrissa* designated as type, and provided the following diagnosis:

> Proximate dinoflagellate cysts with flattened biconical shell, pronouncedly asymmetrical. Epitract in form of high cone which may be drawn out into an apical horn, giving a mammillate appearance: hypotract in form of flattened cone, with or without antapical prominence. Shell bulging out laterally to one side more than to the other: lateral horns lacking. Greater part of shell surface covered with short spines, simple or bifurcate: arrangement is in general random, but sometimes in rows, suggesting traces of tabulation. Equatorial zone, corresponding to cingulum, lacking spines: not hollowed. No pattern of sutures visible, no clear indication of sulcus. Apical archaeopyle formed by schism of shell on angular line of breakage.

Several features of the type material (as reflected in Sarjeant 1966, fig. 55) identify *Doidyx* as an areoligeracean, including the lozenge shape, symmetry and apical archeopyle with an offset parasulcal notch; the latter feature is partly obscured by debris but is still evident. Sarjeant (1966, p. 206) compared *Doidyx* mainly with genera that we would now consider peridiniaceans, but he did state that *Doidyx* "… differs from the superficially similar genus *Aptea* in the lack of an enclosing membrane." *Aptea* is more fully discussed below, but from our perspective, *Aptea* and *Doidyx*, although similar in having a lozenge-like ambitus, differ in that the former (based on its type) has an ornamentation consisting of muri arranged as a reticulum and the latter has predominantly free-standing ornament. Nevertheless, Sarjeant & Stover (1978) considered *Doidyx* to be a taxonomic junior synonym of *Aptea*. Clearly impressed by the strong asymmetry of their respective types, Bint (1986) subsequently considered both *Doidyx* and *Aptea* to be taxonomic junior synonyms of the ceratiacean genus *Pseudoceratium*, although the type of neither genus has a lateral horn formed by the endophragm.

Williams & Downie (1966, p. 223) presented an emended diagnosis for *Cyclonephelium*, essentially to include chorate species with longer spines and processes. These primarily Palaeogene chorate taxa were later re-assigned to *Glaphyrocysta* by Stover & Evitt (1978). Although a detailed evaluation of *Glaphyrocysta* is beyond the scope of the present study, some confusion remains in the differentiation of *Cyclonephelium* group genera from *Glaphyrocysta* and the similar genus *Areoligera* — an issue that we further address below.

The type of another genus proposed in the 1960s, *Cassidium*, was originally described as a pollen grain, *Ovoidites fragilis*, by Harris (1965). Drugg (1967, p. 22) originally described *Cassidium* as follows:

> Test crudely circular in outline. Wall thick, rugulate to imperfectly reticulate. Tabulation present consisting of apical and antapical plates plus several large equatorial plates. No girdle or longitudinal furrow present. The test opens by means of an apical archeopyle, the line of separation being zigzag.

The surface ridges that Drugg (1967) interpreted as parasutural may not actually reflect tabulation; for example, no paracingulum is evident. The ridges may represent a very coarse reticulation superimposed on a finer rugulate–reticulate pattern that covers the whole surface. The holotype of *Cassidium fragilis* clearly reflects tabulation in its archaeopyle outline, with a parasulcal notch appearing to be offset.

During the later 1960s, palynologists tried to constrain the concepts of *Cylonephelium*, *Circulododinium* and *Tenua*. Sarjeant (1968, p. 230–231) began by emending *Tenua*. He noted that he was enlarging “The diagnosis of the genus … to include reference to the [apical] archaeopyle and to permit … a wider range of ornamentation.” He included in *Tenua* several species that would now be placed in the gonyaulacacean genus *Sentusidinium* (see below). At that time, the differences between areoligeraceans and gonyaulacacean cysts based on asymmetry had not been recognised. Although *Tenua* is now accepted as an areoligeracean, the confusion was understandable because of the rounded symmetrical antapical outline of the specimens of *Tenua* illustrated by Eisenack (1958). Subsequently, following Sarjeant’s (1968) concepts, Davey (1978) tried to change the type of *Tenua* to one of Sarjeant’s species, *Tenua rioultii*. This was an illegitimate nomenclatural proposal, with Davey (1978) in effect creating a junior homonym, *Tenua* Davey, of *Tenua* Eisenack. Despite these issues, Sarjeant’s emendation of *Tenua* Eisenack, recognising the archaeopyle as apical and allowing a variety or ornamentation, is still applicable.

Thus, by 1970 several genera were available to accommodate *Cyclonephelium* group forms with single-layered walls and free-standing ornamentation: *Cyclonephelium* (if one considers *Cyclonephelium distinctum* to be assigned to *Cyclonephelium*), *Tenua*, *Circulodinium* and *Doidyx*. And others were available to accommodate forms with single-layered walls with linear ornamentation: *Cyclonephelium*, *Aptea* and *Cassidium*.

3.3. Development of core generic concepts from 1970

In his emended diagnosis of *Tenua*, Pocock (1972, p. 94) was first to recognise the offset parasulcal notch. Although this feature is not apparent on the type of *Tenua hystrix*, it is now accepted as a general feature of the Areoligeraceae, to which family *Tenua* clearly belongs. Pocock (1972) also expanded the generic concept to include forms with an ambitus that “… varies from more or less circular or oval … to rounded subtriangular with one apical and one or two antapical horns indicated by rounded lobes or angles.”

Norvick (1976) was among researchers who clearly and admittedly struggled with intergradation within and between species of what they considered to be *Cyclonephelium*. His fig. 14 shows a range of variation that we would consider belongs to several genera, as outlined in the systematics section below. Ioannides et al. (1977) proposed an emended diagnosis of *Cyclonephelium*, which however added nothing new and essentially followed the concept of

Williams & Downie (1966). Ioannides et al. (1977, p. 450) stated, somewhat cryptically, that "The genus … is here emended in order to clarify the types of cysts accommodated …. [It] … is believed to eliminate confusion regarding the taxonomy of these forms."

Davey (1978, p. 894) effectively synonymised both *Circulodinium* and *Tenua* Eisenack with *Cyclonephelium* by transferring their respective types to that genus, although he did not indicate the synonymy formally at generic rank. Davey (1978) noted that he had experienced:

> … some difficulty … allocating the rather variable group of dinocysts characterized by a spinose ornament and an angular apical archeopyle to described species. Variation is mainly in the shape of the antapex and the length, density and distribution of the spines. As so many specimens over a considerable stratigraphic interval were available for study, a re-evaluation of this group is attempted ….

Davey (1978) noted, in his entry for *Cyclonephelium* [al. *Circulodinium*] *hirtellum*, that

> The original diagnosis of this species clearly indicates that the spines … are restricted to the lateral margins of the shell. [Thus] … the affinities of *C. hirtellum* lie more with *Cyclonephelium* than *Canningia* ….

Under *Cyclonephelium* [al. *Tenua*] *hystrix*, Davey (1978) stated that "Eisenack's type material of this species possesses the characteristics … [of] *Cyclonephelium* — processes more or less restricted to a circumferential zone and an angular apical archeopyle." Davey (1978) went on to note that "… *Tenua* was originally defined as having an overall covering of short processes …. Hence … *T. hystrix*, possessing bald areas, never precisely complied with the generic diagnosis." Thus, Davey (1978) considered that he was removing *Tenua hystrix* from *Tenua* and hence tried, illegitimately, to redefine *Tenua* with a new type (as noted above). It is worth emphasising that Davey (1978) observed that *Tenua hystrix* had areas devoid of ornament, but considered that this was contrary to the original diagnosis of *Tenua* Eisenack.

In the same year as (and understandably unaware of) Davey (1978), Sarjeant & Stover (1978, p. 49) reviewed the morphology of *Tenua hystrix* on the basis of published and unpublished studies. They noted that a typical specimen of *Tenua hystrix* has:

1) a dorsoventrally flattened body.

2) a circular to subcircular outline (ambitus) with a tendency to have one or two low-rounded antapical bulges.

3) an apical archaeopyle with an offset parasulcal notch.

4) indications of paratabulation expressed by the archaeopyle margin and "… on some specimens, by faint alignment of features along paraplate boundaries …".

5) "a fairly dense covering of short, solid, generally simple processes that may be somewhat more widely spaced, as well as somewhat shorter, in the middorsal and midventral areas."

Sarjeant and Stover (1978) further noted that earlier revised diagnoses by Cookson & Eisenack (1962) and Ioannides et al. (1977) "permit the inclusion of forms [in *Cyclonephelium*] … in which the zone of ornament is broad rather than strictly circumferential." They thus concluded that *Tenua* is a taxonomic junior synonym of *Cyclonephelium* and reassigned what we would now regard as non-areoligeracean species such as *Tenua rioultii* to a new genus, *Sentusidinium*. The taxonomic concepts of Sarjeant & Stover (1978) thus paralleled those of Davey (1978) when he tried to establish *Tenua* Davey, with the illegitimate name *Tenua* Davey being a nomenclatural synonym of *Sentusidinium*, having the same type.

In their compendium of fossil dinoflagellate genera, Stover & Evitt (1978) accepted *Tenua* as a taxonomic junior synonym of *Cyclonephelium,* and established *Glaphyrocysta* for chorate forms, mainly of Palaeogene age, previously assigned to *Cyclonephelium*. In emending *Cyclonephelium*, Stover & Evitt (1978, p. 35) gave the following synopsis:

> Cysts proximochorate, lenticular; autophragm variously ornamented with numerous closely spaced features of low to moderate relief that may be spines or membranous septa; ornamentation generally reduced or lacking in midventral and middorsal areas; paratabulation rarely indicated by ornament; archeopyle apical … [with tetratabular simple operculum]; parasulcal notch offset.

In comparing *Cyclonephelium* to *Canningia*, Stover & Evitt (1978, p. 36) contended that "… the ornamentation on *Cyclonephelium* is typically more discrete (isolated) …. Processes on

Cyclonephelium … are short and rarely connected distally.” This is misleading as the type, *Cyclonephelium compactum*, is defined by its membranous ornament. Indeed, during the 1970s there seems to have been a tendency for the concept of *Cyclonephelium* to be based on *Cyclonephelium distinctum* rather than *Cyclonephelium compactum*, as evidenced by the contention of Stover & Evitt (1978).

Dörhöfer & Davies (1980, p. 41) also emended *Cyclonephelium*, restricting it “… to forms with an apteate ornament.” (Dörhöfer & Davies (1980) used the term apteate “… for ornament … developed on a proximate cyst, but does not reach any great length.” They attributed *Cyclonephelium* to the Areoligeraceae, and continued the acceptance of *Tenua* as a taxonomic junior synonym.

In a re-study of the material recorded by Pocock (1962, 1972), Jansonius (1986, p. 204) resurrected *Circulodinium* for forms ornamented with “… free elements of varying length and shape, usually spines with capitate or bifurcate tips … generally more strongly developed in peripheral regions, more or less strongly reduced in size and density in central ventral and dorsal regions.”

Helby (1987) did not directly address the generic definition of *Circulodinium,* and was apparently unaware of the paper by Jansonius (1986). However, from his generic designations of some species previously assigned to *Canningia*, it is clear that Helby (1987) had a concept for *Circulodinium* similar to that of Jansonius (1986), retaining it for areoligeraceans with relatively short ornamentation comprising free-standing elements (Helby 1987, table 3). Backhouse (1988) suggested that *Circulodinium* may be a taxonomic junior synonym of *Tenua*.

Thus, by the late 1980s, Backhouse’s (1988) suggestion notwithstanding, we had a situation in which *Cyclonephelium* and *Circulodinium* were generally accepted as correct generic names (in the sense of International Code of Nomenclature; Turland et al. 2018) and *Tenua* was considered by many to be a taxonomic junior synonym of *Cyclonephelium*. Such concepts ignored the facts that *Tenua* and *Circulodinium* were based on types with free-standing elements and *Cyclonephelium* was based on a type with ornament consisting of crests.

One further genus that can be included in the *Cyclonephelium* group was added by Khowaja-Ateequzzaman & Jain (1990). This is *Cauveridinium*, which the authors described as having “… autophragm ornamentation elaborate with processes along circumferential border zone but [essentially absent] on central dorsal and central ventral areas; processes … mostly connected proximally through ridges, rarely distally fused ….” *Cauveridinium* is clearly an areoligeracean; its relatively high crests make it intermediate between forms in the *Cyclonephelium* group and the *Glaphyrocysta*/*Areoligera* complex. Khowaja-Ateequzzaman & Jain (1990, table 1) differentiated *Cauveridinium* from *Cyclonephelium* in that the former has processes proximally interconnected and the latter has processes proximally unconnected. However, as further discussed below, based on the type of *Cyclonephelium* this difference does not withstand scrutiny.

From the historical progression of ideas discussed in this section, it is evident that by the 1990s no broad concensus in terms of generic distinctions within the *Cyclonephelium* group had emerged. We propose a resolution of this situation below, but for now we switch to a somewhat different focus.

3.4. Reflections of tabulation

The first indication that the expression of paratabulation might be important in defining some genera in the *Cyclonephelium* group was the erection of *Canninginopsis* by Cookson & Eisenack (1962, p. 488), with *Canninginopsis reticulata* as type. *Canninginopsis* is clearly an areoligeracean, but is distinguished by having tabulation reflected by parasutural features such as rows of nodules or low ridges, as well as generally (but not exclusively) a lack of ornament within paraplates. The specimens illustrated by Cookson & Eisenack (1962, pl. 1, figs 16–19) appear to show the paratabulation clearly, but the authors remarked that the “… small tooth-like projections … are sometimes only faintly indicated.”

Below (1981, p. 8) introduced *Cerbia* for forms similar to *Canninginopsis* but in which paratabulation is indicated by penitabular rather than parasutural elements. Below (1981) based *Cerbia* on the species *Cyclonephelium tabulatum*, described by Davey & Verdier (1974). However, *Cerbia* was synonymised with *Tenua* by Sarjeant (1985, p. 93–94). In his emended diagnosis for *Tenua*, Sarjeant (1985) noted: “Peniplates outlined by continuous or discontinuous lines of tubercles or short, solid processes; intratabular processes lacking.” He believed that the original description of *Tenua* by Eisenack (1958) was misleading in suggesting that the ornament was non-tabulate and marginate. However, the distribution of the ornament on the holotype of

Tenua hystrix as shown in Sarjeant's (1985, pl. 10, fig. 5) re-illustration is unclear. The elements seem to show some alignment, but this is not obvious. Moreover, the original illustration of Eisenack (1958) appears to show an overall cover of spines. From Sarjeant's (1985) re-illustration it appears that the mid-ventral ornament could be reduced, but the dorsoventral areas do not seem to be devoid of ornament altogether. Sarjeant (1985) referred to the illustrations of *Cerbia tabulata* in Duxbury (1983, pl. 1, figs 6, 9, 12) as clearly showing the penitabular nature of the ornament, as indeed they do; but this has no bearing on the interpretation of the morphology of the type of *Tenua hystrix*.

Following Sarjeant's (1985) synonymising of *Cerbia* with *Tenua*, disagreements developed over the synonymy of these two genera. Stover & Williams (1987, p. 55–56) and Lentin & Williams (1989, p. 53) retained *Cerbia* separately, the former authors considering that the ornament on *Tenua* is uniformly distributed. Sarjeant (1992, p. 678) re-instated the synonymy, but Duxbury (2002, p. 76, 78) again retaoined *Cerbia* as a separate genus.

In restating and emphasising the case for synonymy, Sarjeant (1992) re-illustrated the holotype of *Tenua hystrix*. He provided an interpretative line drawing of it, reproduced two photos of the type of *Cerbia* (the holotype of *Cerbia tabulata*), and reproduced several other illustrations of *Cerbia tabulata* from Below (1981) and Duxbury (1983). The holotype of *Cerbia tabulata* shows the penitabular nature of the ornament more clearly than the holotype of *Tenua hystrix*, but some of the spines on the latter seem to be aligned. This is not apparent in the interpretative drawings. The holotype of *Tenua hystrix* also appears to show spines within the paraplates (Sarjeant, 1992, figs 1–2). In retaining *Cerbia*, Duxbury (2002) considered that Sarjeant's images of the holotype of *Tenua hystrix* "show dense 'intratabular processes' … with apparently only minor evidence of 'lines of tubercles'". In our view, the evidence is not as clear as either Sarjeant (1992) or Duxbury (2002) contended, but we favour Duxbury's interpretation, retaining *Cerbia* for clearcut cases showing penitabular rows, as further discussed below. Duxbury (2002) also suggested that *Circulodinium* may be a taxonomic junior synonym of *Tenua*.

3.5. A bridge between the Areoligeraceae and the Ceratiaceae

As previously mentioned, the families Areoligeraceae and Ceratiaceae share many morphological features. This has led to confusion as to how to treat the genus *Aptea*, which has a morphology intermediate between the areoligeracean *Cyclonephelium* and the ceratiacean *Pseudoceratium*. Gocht (1957, p. 166) introduced *Pseudoceratium* for non-tabulate forms "… with a peridinian shape (produced by several … lengthy horns) …" (translation). In the diagnosis of *Pseudoceratium pelliferum*, the type of the genus, Gocht (1957) stated "Cyst flat, in outline asymmetrical-triangular, longer than wide, with strong apical horn and two shorter antapical horns of unequal length" (translation). From the protologue, it is clear that Gocht (1957) recognised *Pseudoceratium* as a dinoflagellate cyst, and that the often-dislodged apex was the result of excystment (i.e. an apical archaeopyle). It is also clear from the illustrations of Gocht (1957) and from subsequent studies (e.g. Fensome et al. 1993) that the "two shorter antapical horns of unequal length" are in fact an antapical horn and a lateral horn.

The morphological concept of *Aptea* was very confusing from the outset: Eisenack (1958, p. 393) referred to "not very conspicuous horns" and the tendency to adopt "an oval or circular" outline in the same sentence in his diagnosis. The type of *Aptea* (the holotype of *Aptea polymorpha*: Eisenack, 1958, pl. 22, fig. 5) has a rounded asymmetrical ambitus for its central body, but the ornament (of high crests) gives the overall ambitus a more pronounced angularity and a short right lateral protrusion. Many of the other specimens of *Aptea polymorpha* illustrated by Eisenack (1958) do not show a lateral prominence — indeed, in none of Eisenack's specimens is a lateral prominence expressed by the central body. Of the eight specimens figured in the protologue, five are completely rounded laterally; four show asymmetrical antapical bulges, but one (Eisenack 1958, pl. 22, fig. 12) has an essentially rounded outline laterally and antapically. Such variation is not unusual within (other) *Cyclonephelium* group species.

As already noted, the genus *Doidyx* was introduced by Sarjeant (1966) for spiny forms with an essentially identical autocyst shape to that of the type of *Aptea*, and was subsequently synonymised with it. However, *Doidyx* does not have a lateral prominence of any description, even one produced by ornament, as in the type of *Aptea*. *Doidyx* also differs from *Aptea* in having free-standing rather than linear ornament.

Dörhöfer & Davies (1980) developed a somewhat idiosyncratic interpretation of the paratabulation of a group of genera that they included in the family Pseudoceratiaceae, including *Aptea*, *Canningia* and *Pseudoceratium*, all three of which were emended accordingly. Dörhöfer

& Davies (1980) postulated the presence of two anterior intercalary paraplates in right lateral position, each of similar size to the apical paraplates. These two intercalary paraplates were, according to Dörhöfer & Davies (1980), incorporated into the operculum. However, subsequent authors have considered these genera to be lacking anterior intercalary paraplates. Paratabulation aside, Dörhöfer & Davies (1980, p. 39) considered that "… the sole difference between *Aptea* and *Pseudoceratium* is the length of the horns which are reduced in *Aptea*", a somewhat vague distinction.

In a review of fossil ceratiacean taxa, Bint (1986, p. 144–145) emended *Pseudoceratium* in part "… to include short-horned forms previously assigned to *Aptea* because a continuous range in horn length is now apparent." He further noted that *Cyclonephelium* differs from short-horned species of *Pseudoceratium* by having "no consistent indication of a right lateral horn". But neither does *Aptea*: based on its type material, the possession of a right-lateral horn is not just an inconsistent feature of *Aptea polymorpha*, but an atypical one — and moreover a superficial one formed by the ornament.

Helby (1987) reviewed *Muderongia* and related ceratiacean and similar areoligeracean genera. He considered *Endoceratium* to be a taxonomic junior synonym of *Pseudoceratium* on the basis that some forms of the latter genus have an incipient ectophragm (i.e. a connected periphragm in the terminology we are using here), and thus a generic separation is difficult to maintain (Helby 1987, p. 313–315). Despite this, *Endoceratium* was retained by Lentin & Williams (1989, p. 125). The retention seems justified to us because the type of *Endoceratium*, *Endoceratium ludbrookiae*, is circumcavate with no supports between the two wall layers (Cookson & Eisenack 1958, p. 52–54; pl. 5, figs 7–8). Species of *Pseudoceratium* with two wall layers are always holocavate. Helby (1987, p. 315) retained *Aptea* but noted that "*Pseudoceratium* is distinguished from *Aptea* … by reduced hypocystal horns of the latter, although the range of variation in *Aptea* … suggests that it will be difficult to maintain separation of these genera."

Like Helby (1987), Quattrocchio & Sarjeant (1992, p. 2-224) retained *Aptea*. They noted that Bint (1986) justified synonymising *Pseudoceratium* and *Aptea* because of a continuous range in morphology between long-horned and short-horned cysts (*Pseudoceratium* and *Aptea* respectively). Quattrocchio and Sarjeant (1992) argued that Bint did not "… satisfactorily demonstrate that this variation occurs at all stratigraphic horizons at which the two genera are present; and, in our view, the evidence … merely represents evolution from one [genus] to the other.” The problem with this argument is that the same case can be made for the gradation between *Aptea* and a clearly areoligeracean genus such as *Cyclonephelium*.

As with many aspects of the group of genera reviewed herein, it is difficult to decide where to draw the dividing line between genera. It is generally accepted that areoligeraceans lack lateral prominences and that ceratiaceans have distinct horns, but the gradational middle ground presents a conundrum. Two attempts have been made to avoid basing distinctions between areoligeraceans and ceratiaceans on horn length. Evitt (1985, fig. 10.6; Fig. 1) suggested that the distinction could be based on the position of hypocystal horns in relation to paratabulation. Thus, according to Evitt (1985), areoligeraceans (his “Gv cysts”) have antapical prominences, where present, completely within the single antapical paraplate (Fig. 1B); in contrast, hypocystal horns in ceratiaceans (his “Gc cysts”) straddle paraplate boundaries (Fig. 1D). Bint (1986) suggested that the difference is that the first precingular paraplate (1’’) in ceratiaceans has a straight (planate) anterior margin (Fig. 2A) whereas the equivalent paraplate in areoligeraceans is angular (camerate; Fig. 2B). The present authors have not been able to apply either of these suggestions as paratabulation is rarely clearly expressed in these groups, and the critical angle for viewing the anterior edge of the 1" paraplate usually coincides with the ambitus of the cyst and is thus indeterminable in the vast majority of specimens when viewed under transmitted light. Clearly a practical solution, insofar as possible, is needed and a proposal is discussed below.

(Please insert Figures 1 and 2 near here)

3.6. A question of wall layers: Canningia *and* Senoniasphaera

As noted above, in erecting *Canningia*, Cookson & Eisenack (1960) did not indicate wall structure to be an important distinguishing feature. However, the type (Cookson & Eisenack 1960, pl. 38, fig. 1, as *Canningia reticulata*) is clearly holocavate.

Senoniasphaera was introduced by Clarke & Verdier (1967), who recognised it as being cavate. They noted that the inner body is round or oval (i.e. has a round or oval ambitus) and that the outer membrane “… is extended … to form one apical, two antapical and often two lateral horns." They also stated in the diagnosis that paratabulation is present and that the archaeopyle is apical. A potential complication is that Clarke & Verdier (1967, p. 62) noted that "The outer membrane [periphragm] is attached to the inner body … by a series of perforated pillars which may be so short as to be hardly visible."

Below (1981, p. 30) provided the following emended diagnosis for *Canningia*.

> Spheroidal to lenticular cyst with round to pentagonal outline. Apex rounded or with a low apical knob. Antapex rounded, flattened or with a lobe. Cyst wall two-layered. Periphragm smooth or ornamented. Endocyst smooth toward the inside of the cyst. Between the two membranes is a variable structural infilling. The surface is usually nontabulate, only rarely divided into a gonyaulacoid paratabulation. Paracingulum and parasulcus indented or absent. Archaeopyle apical …. Operculum simple, attached and enlarged. [Translation]

Below (1981) considered that the difference between *Canningia* and *Senoniasphaera* is that the latter is (circum)cavate rather than holocavate, thus lacking structural supports or infilling between wall layers.

Hedlund & Norris (1986, p. 295) considered Below's (1981) emendation of *Canningia* to be "not applicable" because "It is possible that the single wall layer in *C. colliveri* in … [their] material may be the result of weathering of samples." However, *Canningia colliveri* is not the type of the genus, and *Canningia* is now generally considered to be restricted to forms with the wall structure described by Below (1981).

Helby (1987, p. 321–322) emended *Canningia*, stating that "*Canningia* as used here embodies lenticular cysts that are subpentangular in outline, 2-layered [i.e., with a wall composed of two layers] and with or without indications of paratabulation …". Furthermore, "*Canningia* is distinguished from *Senoniasphaera* by the distinctive pericoel of the latter …". It is clear that Helby (1987) intended *Canningia* to be restricted to holocavate forms and *Senoniasphaera* to (circum)cavate forms, concepts that have been generally followed. However, Clarke & Verdier (1967, p. 62) noted that in the holotype of *Senoniasphaera protrusa*, "The outer membrane is attached to the inner body … by a series of perforated pillars which may be so short as to be hardly visible.” Even though they may be hard to see, the presence of “pillars” between wall layers in the type material of *Senoniasphaera* (Clarke & Verdier 1967, ig. 24, pl. 14, figs 7–8) undermines the generally accepted current distinction between *Canningia* and *Senoniasphaera* based on holocavate versus ccircumcavate wall structure, a problem we return to below.

4. The challenge of intergradation

4.1. Introduction

Many of the genera discussed in the present study exhibit internal variation and external intergradation with other genera. As demonstrated by the literature review above, these factors have caused extensive discussion and great confusion. Although few papers have addressed the taxonomy of the *Cyclonephelium* group in recent decades, we consider that the generic circumscriptions need to be further rationalised to enhance the practical utility of the group. A more concise delineation of the generic circumscriptions will improve communication and identification. However, any resolution must strictly respect the morphology of the nomenclatural types, although not necessarily the morphological concepts expressed by the original authors, not least because our understanding of dinoflagellate cyst morphology has evolved over the years. A resolution should respect existing taxonomic treatment and aspire to pragmatic application insofar as possible. Ideally, the morphological circumscriptions of related or similar genera should reflect a hierarchy of characters. We discuss the various features that could be used taxonomically, given that paratabulation and archaeopyle type do not vary in the *Cyclonephelium* group. The discussion that follows has been informed in part by observations on Canadian material, which includes some species with abundant specimens in which the apparent importance of the various morphological factors can be assessed — for example cyst ambitus within many of the species studied is very variable, in contrast to general ornament type.

4.2. Cyst ambitus

The presence of a lateral horn is a distinctive character of ceratiacean cysts. We prefer the term lateral horn to postcingular horn, since the position of such horns can impinge on the cingular area, sometimes substantially. Hence, the type of *Pseudoceratium*, *Pseudoceratium pelliferum*, with its single lateral horn, is unequivocally ceratiacean. However, the holotype of *Aptea polymorpha*, the type of *Aptea*, has a lateral prominence produced by the ornamentation.

Antapical margins of many areoligeracean species vary from being rounded to having one or two antapical bulges or, rarely, pointed prominences. Moreover, the degree of expression of the apical horn or prominence is also highly variable in what would generally be considered a single species. It might be useful to recognise some of these variations in ambitus outline at species level, but this has not been previously attempted and would probably be difficult to apply in an already taxonomically difficult group. In conclusion, cyst ambitus is critical in distinguishing areoligeracean from ceratiacean cysts, but seems to have low value in distinguishing genera within the *Cyclonephelium* group.

4.3. Wall structure

Most genera considered herein have an autophragm, usually covered with an ornament involving processes or crests of short to moderate height, the processes sometimes interconnected and/or arranged linearly. Exceptions to this general wall structure are the distinctly holocavate *Canningia*, the indistinctly holocavate to clearly circumcavate *Senoniasphaera*, and our new genus *Trimuridinium*, which has three separated wall layers. Wall structure tends to be intraspecifically stable, and hence of high hierarchical significance within the *Cyclonephelium* group.

4.4. Nature and distribution of the ornament

The ornament of the *Cyclonephelium* group may consist of linear elements, as in *Cyclonephelium compactum*, or free-standing elements such as spines, hairs or short processes, as in *Tenua hystrix*. In some cases, the ornament may contain a mixture of linear and free-standing elements, in which case we suggest that the generic assignment should be based on the predominant type.

Ornament in the *Cyclonephelium* group can vary from a general uniform covering to a concentration on the periphery, with the mid-dorsal and mid-ventral areas devoid of ornamentation. The peripheral concentration of ornament can be strongly to weakly developed.

Cauveridinium, *Circulodinium* and *Cyclonephelium* are based on types with a peripheral concentration of ornament. In *Aptea* and *Doidyx*, ornamentation is more or less uniform. The type of *Tenua* is more intermediate in coverage, as discussed further below. The ornamentation may or may not reflect tabulation. In *Cerbia*, paratabulation is indicated by penitabular rows of processes or other elements. *Canninginopsis* has rows of free-standing elements, typically tubercles, marking the parasutures.

5. A proposed resolution

In determining an appropriate hierarchy of morphological features for dinoflagellates, paratabulation is considered fundamental (Fensome et al. 1993). Even in cases where the group to be classified has a uniform paratabulation, some aspect of paraplate shape may be available: an example is the shape of the 2a paraplate in wetzelielloideans (Williams et al. 2015). However, among areoligeraceans the paratabulation is remarkably stable, as are features associated with the archaeopyle. Therefore, we must use other features, even though whatever we choose will tend to cut across what appear to be natural intergradations.

The separation of areoligeraceans from morphologically intergrading ceratiaceans is primarily focused on the genus *Aptea*. Because its type, the holotype of *Aptea polymorpha*, has a lateral prominence (not a horn) developed by ornament, and that other specimens in the protologue show no such feature, we propose that *Aptea* be considered an areoligeracean. We consider that the distinction between areoligeraceans and ceratiaceans be based on the development of a distinct right-lateral horn produced by the central body (autophragm/endophragm) of the cyst as in the ceratiaceans, not by ornament alone as in the areoligeraceans. On that basis, all specimens of *Aptea polymorpha* illustrated in the protologue can be considered areoligeraceans. We recognise that this is to some extent still arbitrary (as discussed in section 8), but it seems to us the most practical way to proceed.

Next, we need to consider how *Cyclonephelium* group areoligeraceans themselves are best subdivided into genera. Perhaps the clearest distinction within the group can be based on wall structure. Genera based on cavate cysts are *Canningia* and *Senoniasphaera*. The currently generally accepted distinction between these two taxa is that *Canningia* has structures connecting the two wall layers and *Senoniasphaera* lacks such structures. However our revisiting of the protologue of the type of *Senoniasphaera*, *Senoniasphaera protrusa*, reveals that Clarke and Verdier (1967) acknowledged the presence of perforated pillars between wall layers sometimes "hardly visible". We propose that *Canningia* be retained for holocavate forms with dense supporting structures and a generally narrow pericoel, and that *Senoniasphaera* be redefined to encompass cavate species with no or very sparse connecting structures and a generally wide pericoel. A third genus, *Trimuridinium*, is proposed to encompass a single species, *Senoniasphaera whitenessense*, with three separate wall layers.

In the early years of study of *Cyclonephelium* group taxa, emphasis was placed more on distribution of ornament, especially its commonly marginate nature, rather than whether the ornament was linear or free-standing. This is evidenced by the observation that *Cyclonephelium* itself became more closely identified with *Cyclonephelium distinctum*, with free-standing ornament, than the type, *Cylonephelium compactum*, which has linear ornament. An example is the generic synopsis of *Cyclonephelium* by Stover and Evitt (1978), as discussed above. In more recent studies the emphasis seems to have reversed, as witnessed by the increased use of the genus *Circulodinium* for forms with free-standing ornament for example by Jansonius (1986) and Helby (1987). We propose to retain the separation of forms with linear and free-standing ornament as a higher order distinction, and then use marginate versus uniform distribution of ornament as a lower order distinguishing feature (among non-cavate forms in which the ornament does not clearly define paratabulation). Neither of these distinctions is completely clearcut, but the alternative is to have unhelpfully large genera with excessively broad definitions. *Cyclonephelium* fills the need for a genus with marginate linear ornament, and *Aptea*, considered here as an areoligeracean, can accommodate forms with uniformly distributed linear ornament. We consider *Cauveridinium* and *Cassidium* to be taxonomic junior synonyms of *Cyclonephelium* and *Aptea* respectively. Of forms with free standing ornament, *Circulodinium* is based on a type with a marginate distribution of ornament and the type of *Doidyx* has uniformly distributed ornament. However, *Tenua* is senior to both *Circulodinium* and *Doidyx* and its ornament distribution has been long-debated (see subsection 3.4). We conclude from most published illustrations of the type of *Tenua* (the holotype of *Tenua hystrix*) that it does not show dorsal and ventral surfaces devoid of ornament, and hence we propose that *Tenua* be used for species with (more or less) uniformly distributed free-standing ornament. Hence, in this concept, *Tenua* becomes the senior taxonomic synonynm of *Doidyx*, and *Circulodinium* becomes the senior name for forms with marginate free-standing ornament. We propose that *Cerbia* be retained for forms with penitabular ornament, with little or no ornament in the central areas of paraplates; and *Canninginopsis* be retained for forms with parasutural ornament, free-standing or linear. These generic concepts are illustrated in Fig. 3.

One further issue needs to be resolved — how to distinguish forms in the *Cyclonephelium* group from those of the *Areoligera–Glaphyrocysta* complex. Both groups of dinoflagellate cysts have a variety of linear and free-standing ornament, but it is generally understood that the former has relatively low ornament and the latter relatively high ornament: to our knowledge, however, exactly how high and how low has never been defined. We suggest that the *Cyclonephelium* group be restricted to forms with ornament generally 25% or less in length compared to the maximum cyst width; and the *Areoligera–Glaphyrocysta* complex be restricted to forms in which the ornament is general greater than 25%. From our experience we consider that this will provide a practical distinction that will generally maintain existing usage. We add this feature to the diagnosis/synopsis of genera as appropriate.

(Please insert Figure 3 near here)

6. Systematic palaeontology

Appendix 2 provides a listing of genera and species in the *Cyclonephelium* group and *Pseudoceratium* accepted as correct (*sensu* ICN) in Williams et al. (2017) with their status according to the present work. We include two sets of figures illustrating *Cyclonephelium* group and *Pseudoceratium* species. The first is a batch illustrating our new material of selected species (Figs 4–11) and the second set presents reproductions of the holotypes of many of the species treated herein (Figs 12–20). Figs 4–20 are inserted throughout section 6.

All specimens newly illustrated herein are are curated in the National Collection of Type Invertebrate and Plant Fossils, Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario, Canada K1A 0E8. At the time of writing, these specimens are on long-term loan to GSC Atlantic, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2. In Appendix 3 these specimens are designated by GSC collection numbers.

Cyclonephelium **group taxa and** ***Pseudoceratium***

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 **Areoligeraceae** Evitt 1963b

Genus ***Aptea*** Eisenack 1958 emend. nov.

1958 *Aptea* Eisenack, p. 393.
1967 *Cassidium* Drugg, p. 22.

Type. Eisenack 1958, pl. 22, fig.5, as *Aptea polymorpha*.

Emended Diagnosis. Areoligeracean cysts that are proximate to proximochorate, with ornament height less than 25% of maximum cyst width. Central body dorsoventrally compressed, ambitus subcircular to lenticular, with a rounded to more commonly asymmetrical antapex and an apical horn; lateral horns or prominences formed by the central body are absent, although a lateral prominence may be formed by ornament. Acavate. Ornamentation consisting of linear elements such as crests or ridges, or free-standing elements that are in large part fused or connected to adjacent elements; ornament is more or less uniformly distributed over the cyst. Archaeopyle apical, with formula $A_{(1-4')}$, operculum free; parasulcal notch offset to the left.

Comments. As expressed above, *Aptea* is here considered an areoligeracean genus and not, as determined by some authors, a taxonomic junior synonym of *Pseudoceratium*. It is distinguished by ornament that is entirely or for the most part composed of linear elements, and this ornament is not absent dorsoventrally, although it may be reduced. *Cyclonephelium* also has predominantly linear sculptural elements but has dorsoventral areas devoid of ornament.

Eisenack (1958, p. 393) provided the following diagnosis for *Aptea*:

> Shell compressed oval in cross-section, in outline irregularly triangular with convex sides and 3 (or 4?) small protruding horns, which can be largely reduced, so that the outline is very variable and therefore tends to appear oval to circular. [Translation]

The “small protruding horns” mentioned by Eisenack (1958) are absent in most specimens illustrated in the protologue of the type and hence, as Eisenack (1958) also noted, specimens tend to be oval to circular. Among the specimens that do have a small protruding right-lateral horn, including the type, the protrusion is produced by the ornament, not the central body. Thus, *Aptea* can be distinguished from *Pseudoceratium* in lacking a lateral horn or prominence produced by the central body.

Cassidium is also an areoligeracean with more or less uniformly distributed linear ornament; and hence we consider it to be a taxonomic junior synonym of *Aptea*. Drugg (1967, p. 22) originally described *Cassidium* as follows:

> Test crudely circular in outline. Wall thick, rugulate to imperfectly reticulate. Tabulation present consisting of apical and antapical plates plus several large equatorial plates. No girdle or longitudinal furrow present. The test opens by means of an apical archeopyle, the line of separation being zigzag.

Accepted species.

Aptea cassis sp. nov.

(Figs 4 A–N)

Holotype. Fig. 5C, from the lowermost Slater River Formation (uppermost Albian or lower Cenomanian), Hume River section, Northwest Territories, Canada. Sample 07-Peel-43, 724.5 m from base of section, slide 5262-012C, coordinates 190x0909, England Finder T33-2; GSC type number 139874, curated in the National Collection of Type Invertebrate and Plant Fossils, Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario, Canada K1A 0E8. At the time of writing, this specimen was on long-term loan to GSC Atlantic, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2. See also Appendix 3 herein and Fensome (2016) for further details.

Derivation of name. From the Latin *cassis*, meaning hunting net or snare, in reference to the reticulate nature of the ornament. The epithet is a noun in apposition.

Diagnosis. A species of *Aptea* with a coarse reticulum formed of simple low membranous crests; there are no free-standing elements. The reticulum is distributed across the dorsal and ventral surfaces, although it may be somewhat more weakly developed in mid-ventral and mid-dorsal areas. The antapex is symmetrical or asymmetrical, with developments of two usually unequal antapical protuberances or horns.

Dimensions. Overall width 62 (71) 80 µm (range of 13 specimens); overall length (operculum in place) 77 (83) 90 µm (range of 4 specimens); overall length (operculum absent) 60 (70) 81 µm (range of 8 specimens). Holotype: Overall width 62 µm; overall length (operculum in place) 77 µm.

Comments. This species is characterised by a simple network of low crests; no additional convoluted or free-standing elements occur. The ornament of *Aptea polymorpha* tends to be higher and more convoluted. *Aptea cassis* also resembles *Cyclonephelium compactum*, but the latter has distinct dorsoventral areas devoid of ornament and higher and generally more convoluted muri. Extreme variants have a bulging lateral protuberance formed by the endophragm, but otherwise clearly belong to this species.

Stratigraphical occurrence. *Aptea cassis* occurs in the lowermost part of the Slater River Formation on the Mackenzie Plain, previously dated as early Cenomanian in age based on rare ammonites, fish scale and lithostratigraphical correlation, but dated by Fensome (2016) as latest Albian based on dinoflagellate cysts.

Aptea fragilis (Harris 1965) comb. nov.

(Fig. 12 A)

1965 *Ovoidites fragilis* Harris 1965, p. 97, pl. 27, figs 4–5

1967 *Cassidium fragile* (Harris) Drugg, p. 22.

Comments. Originally described as a pollen species by Harris (1965), Drugg (1967, p. 22) recognised the dinoflagellate affinity of the holotype and provided a revised diagnosis. He noted that it had a relatively thick wall (2–3 µm), and that its "… outer surface [is] rugulate to imperfectly reticulate, the rugulae being low, thick, and rounded." The cyst surface appears to have ridges that appear initially to be parasutural, but they may not actually reflect tabulation; for example, no paracingulum is evident. The ridges may represent a very coarse reticulation superimposed on a finer rugulate–reticulate pattern that covers the whole surface. The presence of apparent parasutures led Drugg (1967) to compare *Cassidium* (now *Aptea*) *fragile* with *Canninginopsis denticulata*, noting as differences the lack of a paracingulum and much thicker, rugulate wall in the former.

Although the coarser reticulum of *Aptea fragilis* may not reflect plate boundaries, the holotype clearly reflects tabulation in the archaeopyle outline and accessory archaeopyle sutures between precingular paraplates. The holotype is bowl shaped rather than lenticular, but the parasulcal notch appears to be offset; Drugg (1967) noted that antapical lobes are sometimes present. Therefore, it seems reasonable to consider this species to be an areoligeracean.

Stratigraphical occurrence. Harris (1965) recorded this species from the Lower Eocene of Victoria, Australia. According to Drugg (1967) it is abundant in the Maastrichtian–Danian interval of California, USA.

Aptea polymorpha Eisenack 1958

(Fig. 12 B)

1958 *Aptea polymorpha* Eisenack, p. 394, pl. 22, figs 5–12; pl. 24, fig. 5.

1986 *Pseudoceratium polymorphum* (Eisenack) Bint, p. 145.

Comments. Eisenack (1958, p. 394) provided the following diagnosis for *Aptea polymorpha*:

> Body … flat, irregularly triangular in outline with convex sides and distinctly prominent 'horns', standing out from a strongly rounded and dark inner body, surrounded by a more or less complete border. The surface is covered by a very irregular fully developed low network of ridges, which forms a more or less fine-meshed, but indistinct honeycomb pattern. The ridges spread in a somewhat radial trend onto the delicate, unevenly broad border, whose edges seldom form a smooth line, but commonly appear jagged and fragmented. Of the 3 (or 4?) [potentially] developed horns all but one may be more or less rudimentary. [Translation]

For further discussion of this species and the reason for retaining it as *Aptea polymorpha*, see under the genus *Aptea*.

Stratigraphical occurrence. Eisenack (1958) recorded *Aptea polymorpha* from the Aptian of northern Germany. Costa & Davey (1992) restricted the species to the Aptian. According to Stover et al. (1996), the stratigraphical range is late early Aptian to latest Albian.

Aptea? retirugosa (He Chengquan 1991) comb. nov.

(Fig. 12 C)

1991 *Canningia retirugosa* He Chengquan, p. 56; pl. 8, fig. 11.

2009 *Kallosphaeridium retirugosum* (He Chengquan) He Chengquan et al., p. 164.
2016 *Canningia*? *retirugosa* He Chengquan; Wood et al., p. 69–71.

Comments. This species was originally described in Chinese with a single illustration, which appears to show an areoligeracean with linear ornament. Thus, it does not belong in *Kallosphaeridium*, which is a gonyaulacacean with five climactal paraplates (Jan du Chêne & Adediran 1985, Wood et al. 2016). Wood et al. (2016) tentatively retained this species in *Canningia*, but as a cyst with a single wall layer and probably linear ornament (although possibly affected by corrosion), this species better fits the definition of *Aptea*. Hence, we questionably transfer it to *Aptea*, but recommend that the name be restricted to the holotype, pending further study.

Stratigraphical occurrence. He Chengquan (1991) recorded this species from the Upper Cretaceous of China

Aptea rotundata (Cookson & Eisenack 1961) comb. nov.

(Fig. 12 D)

1961 *Canningia rotundata* Cookson & Eisenack, p. 72, pl. 12, figs 1–5.
1962 *Cyclonephelium paucimarginatum* Cookson & Eisenack, p. 494, pl. 6, fig. 5–7.
1978 *Canningia*? *rotundata* Cookson & Eisenack: Stover & Evitt, p. 25.
1980 *Batiacasphaera rotundata* (Cookson & Eisenack) Dörhöfer & Davies, p. 41.
1987a *Circulodinium vermiculatum* Stover & Helby, p. 230, figs 4A–M.

Comments. Cookson & Eisenack (1961, p. 72) described this species as having a wall "…of variable thickness, *c* 2–5 μ, closely covered with a dense indistinctly vermiculate pattern." The wall is thus single layered, with ornament of linear elements, and so fits with *Aptea* rather than *Canningia*. Although the epithet implies a bowl-shaped body, the holotype is asymmetrical, attesting to its areoligeracean affinity.

In describing *Cyclonephelium paucimarginatum*, Cookson & Eisenack (1962) noted that the cyst has "… a narrow, continuous circumferential zone in which the sculptural elements, in the form of short, wavy ridges, are densely arranged and often intertwined. The general surface … is finely to coarsely granular to vermiculate, the individual elements coarser and more widely spaced on the central region of each side." Thus, the ornament is continuous, as is clear from the illustrations of the type material. We consider *Cyclonephelium paucimarginatum* to belong to *Aptea*, as a taxonomic junior synonym of *Aptea rotundata*, the type material of which also has vermiculate ornamentation.

Stover & Helby (1987a, p. 230) described *Circulodinium vermiculatum* as lenticular (although their illustrations show mainly specimens with a regularly bowl-shaped ambitus), with very irregular vermiculate ornamentation that varies considerably over the cyst. They did not compare *Circulodinium vermiculatum* with *Aptea rotundata*, although we consider the two as synonymous.

Stratigraphical occurrence. Cookson & Eisenack (1961) recorded *Aptea* (as *Canningia*) *rotundata* from the Senonian of Australia. The term "Senonian" is a former term for a Late Cretaceous epoch generally considered to encompass the Coniacean to Campanian interval but sometimes defined as including the Maastrichtian — we are uncertain as to the definition applied by Cookson and Eisenack (1961) Cookson & Eisenack (1962) described *Cyclonephelium paucimarginatum* from the ?late Albian to Cenomanian of Australia. The type material of *Circulodinium vermiculatum* is from the late Hauterivian to Barremian of offshore Western Australia.

Aptea? spongireticulata (Prössl 1990 ex Prössl 1992) comb. nov.

(Fig. 12 E)

1990 *Canningia spongireticulata* Prössl, p. 97, pl. 13, figs 2, 5, 13 (name not validly published; lodgement of holotype not specified).

1992 *Canningia spongireticulata* Prössl ex Prössl, p. 113–114.

Comments. Prössl (1990, p. 97) provided the following diagnosis and description for this species.

> Diagnosis: Spherical to polygonal cysts with a spongeous ectophragm, [formed] by a coarse-meshed reticulum. Description: The two-walled cyst exhibits a smooth or porous ectophragm. This is divided by spongeous … septa. The septal pattern shows a coarse-meshed, polygonal reticulum, which appears to follow the paratabulation formula 4’, 6’’, Xc, 6’’’, 1p, 1’’’’. The archaeopyle corresponds to type tA. [Translation; two paragraphs combined]

Although Prössl (1990) mentioned a “spongeous” ectophragm, it seems that the ornament consists of an autophragm bearing an extremely coarse reticulum with high septa. Prössl (1990) interpreted the reticulum as directly reflecting tabulation. Such a morphology fits better with *Aptea* than *Canningia* and hence we make the reassignment here. However, the material illustrated by Prössl (1990) seems more bowl shaped than lenticular and the characteristic areoligeracean asymmetry is at best weakly shown; thus, we question the assignment to *Aptea*.

Stratigraphical occurrence. Prössl (1990) recorded this species from the late Albian to middle Turonian of Saxony, Germany.

Aptea uncinata (Norvick 1976) comb. nov,

(Figs 4 Q–S, 12 F)

1976 *Adnatosphaeridium uncinatum* Norvick, p. 74–75, pl. 8, figs 11–12.
1978 *Cyclonephelium uncinatum* (Norvick) Stover & Evitt, p. 36.

Comments. In his diagnosis of *Adnatosphaeridium uncinatum*, Norvick (1976, p. 74) described the ornament as follows:

> Processes numerous, short, solid, narrow, and parallel-sided. Processes divide distally into narrow, flattened, smooth, unbranched aculei, which unite with those

> from adjacent processes. Processes similar or slightly longer at the antapex.

In the description, Norvick (1976, p. 75) expanded on the details as follows:

> The central body bears numerous straight, parallel-sided, solid processes with slightly expanded bases, about 3 to 5 µm apart. They are 0.5 to 1 µm in diameter (most are about 1 µm) and 5 to 10 µm in length. Distally they divide into ribbon-like aculei (0.5 to 1 µm wide), which become recurved and connect with those from adjacent processes. The aculei bear no spines and are seldom branched. The overall appearance of the processes is of a series of simple loops standing out from the central body wall. They are variably arranged but appear to be more closely set around the periphery. They are slightly longer at the antapex. The dorsal and ventral faces sometimes bear slightly smaller processes, arranged in soleate and linear complexes.

Thus, although some apparently paratabulation-related arrangement to the ornament exists, as does some differentiation between dorsoventral and lateral surfaces, the dorsoventral surfaces not entirely devoid of ornament. This distribution, together with the linked (i.e. linear) nature of the processes, prescribe an assignment to *Aptea*.

Cyclonephelium compactum has dorsoventral areas devoid of ornament, which is typically more complex than that of *Aptea uncinata*. *Aptea polymorpha* has distinct muri rather than linked processes. The arrangement of the processes into soleate complexes in *Aptea uncinata* is not readily apparent on the illustrations of the type material, although the ornament is clearly bunched, the bunches likely reflecting tabulation. This might be useful as a diagnostic criterion for the species, but was not apparent in the material newly illustrated herein.

Stratigraphical occurrence. Norvick (1976) recorded this species from the Cenomanian of northern Australia.

Aptea*? *vannophora (Davey 1969) comb. nov.

(Fig. 12 G)

1969 *Cyclonephelium vannophorum* Davey: 168, 170; pl. 9, fig. 3; pl. 11, figs 11–12; text-fig 16E.

Comments. This species, which has been used as a stratigraphical marker, was described by Davey (1969, p. 168) as follows:

> The processes vary greatly in size from mere enlarged granules (0.5 µ) to 8 µ in length. In the larger processes the stem is quite narrow, the distal third widening rapidly … and is sometimes bifurcate. The processes are often joined to form a short line on the shell surface. Rarely the cingulum is just discernible by a concentration of small processes along its borders.

The close-up of the holotype (Davey 1969, pl. 9, fig. 3) shows very fine hairs that may join, splay or thicken distally, forming a kind of filigree pattern, and in plan view commonly form linear clumps. However, subsequent photographs of the holotype by Iain Prince show that this "filigree" development is localised and the ornament over areas of the cysts appears free-standing (Martin Pearce, personal communication 2018). Thus, this species is intermediate between *Aptea* and *Tenua*, and hence we question its assignment to the former. *Aptea*? *vannophora* closely resembles *Tenua hystrix*, the difference (at least in theory) being that the former has predominantly interconnected (i.e. linear) ornament and the latter has predominantly free-standing ornament. However, it may be difficult in future to retain both species separately.

Although Davey (1969) did not specifically mention whether ornament is present or absent dorsoventrally, from the full illustration of the holotype of *Aptea vannophora* (Davey, 1969, pl. 11, fig. 11) the mid-ventral area appears to bear a less intense ornament cover than peripheral areas. Nevertheless, the dorsoventral areas do appear to bear ornament, which accords with an assignment to *Aptea*.

Davey (1969) noted that *Cyclonephelium vannophorum* "… is most closely comparable to ?*C. attadalicum* …. The processes are similar in form but the shell of ?*C. attadalicum* is more polygonal and the cingulum is always well defined." For us, the main difference between these two species is that *Cyclonephelium* (now *Tenua*) *attadalicum* appears to have isolated processes whereas *Aptea vannophora* (as represented in the holotype) has hair-like processes that tend to join and clump. However, the processes of the former are quite hair-like, so a re-examination of the type material of both species may reveal a closer resemblance.

Stratigraphical occurrence. Davey (1969) recorded *Aptea vannophora* (as *Cyclonephelium vannophorum*) from the Cenomanian of southern England.

Genus ***Canningia*** Cookson & Eisenack 1960

1960 *Canningia* Cookson & Eisenack, p. 251.
1980 *Canningia* Clarke & Verdier; emend. Dörhöfer & Davies, p. 36.
1980 *Hashenia* Yu Jingxian & Zhang Wangping, p. 107.
1981 *Canningia* Clarke & Verdier; emend. Below, p. 30 (however, see Hedlund & Norris 1986, p. 295).
1987 *Canningia* Clarke & Verdier; emend. Helby, p. 321–322.

Type. Cookson & Eisenack 1960, pl. 38, fig. 1, as *Canningia reticulata*.

Synopsis. Areoligeracean cysts that are proximate, dorsoventrally compressed, lenticular, with asymmetrical to rounded antapex and a generally short apical prominence. Holocavate with generally narrow pericoel; the connections between endophragm and periphragm generally densely distributed and may be in linear (muri) or isolated elements (pillars). Periphragm continuous or discontinuous, generally smooth or with ornamentation of low relief. Archaeopyle apical, with formula $\mathrm{A}_{(1\text{-}4')}$; operculum free or attached; parasulcal notch offset to the left.

Remarks. Cookson & Eisenack (1960, p. 251) provided the following description for *Canningia*:

> Shell flattened, roughly five-sided to almost circular with a slight apical prominence and a broadly indented base. The basal projections (corresponding to antapical horns) are either equal or unequal and frequently differ slightly in shape. An equatorial girdle is either absent or faintly indicated both on the surface or by re-entrant angles at the sides. The shell opens by a proximal break which results in the complete detachment of the apical region.

Wall structure was clearly not considered an important feature of this genus at the outset. In contrast, as discussed above, we regard the wall structure as a critical feature in distinguishing genera within the *Cyclonephelium* group, and define *Canningia* primarily on its holocavate wall structure.

Senoniasphaera is similar to *Canningia* in being cavate, but connecting structures are absent, sparse, or barely visible under the light microscope (see also discussion under *Senoniasphaera*). The pericoels are also generally broader in dorsoventral view in *Senoniasphaera*. In *Renidinium*, the walls are separated in mainly ventral marginal areas so that in apical view they project ventrally.

We consider the emendations of *Canningia* by Below (1981) and Helby (1987) as useful in developing our current concept of *Canningia*, but not that by Dörhöfer & Davies (1980); see the introductory sections for a full discussion of the contributions of these authors. At present, the genus contains species with an overall holocavate structure (as in the type) and species in which the holocavation is restricted to the ambital periphery of the cyst. Separation of the latter group of species into their own genus might merit future consideration.

Accepted species.

Canningia*? *clathromarginata (Cookson & Eisenack 1962) comb. nov.

(Fig. 12 H)

1962 *Cyclonephelium clathromarginatum* Cookson & Eisenack, p. 495, pl. 6, figs 1–4.

Comments. Cookson & Eisenack (1962, p. 495) described this species as follows:

> Shell flat, subcircular to approximately oval in plan aspect, with a circumferential border zone delimited by low and straight or fluted clathrate edges …. The edges are usually deepest in the antapical region and connected at wide intervals by short, narrow ridges …. The sculpture of the shell varies … from finely to coarsely granular or vermiculate.

The "circumferential border zone" appears to be a reflection of a distinctive peripheral holocavate structure. The type material consists of large cysts, all greater than 100 μm in length and width. We transfer this species to *Canningia* because it appears to be partially holocavate, but we do so questionably pending further clarification of the wall structure.

Stratigraphical occurrence. Cookson & Eisenack (1962) recorded this species from the Albian to Cenomanian of Australia.

Canningia crassimarginata (Cookson & Eisenack 1974) comb. nov.

(Fig. 12 I)

1974 *Cyclonephelium crassimarginatum* Cookson & Eisenack, p. 74–75, pl. 28, figs 1–4.

Comments. Cookson & Eisenack (1974, p. 74–75) provided the following diagnosis for this species.

> A species of *Cyclonephelium* with a more or less strongly rounded border, with perpendicular [?], strong, radial, but irregularly structured and arranged supports, which are covered and connected by a more or less wide, smooth bordering membrane. As usual with *Cyclonephelium* species, the base of the supports originate around the margin on both of the flat sides of the shell; the membrane is thus double, which of course is difficult to discern. The surface of the shell is distinctly granular.

The presence of an outer wall layer (periphragm) and relatively densely arranged supporting structures indicates that this species belongs in *Canningia* rather than *Cyclonephelium*, and we effect the transfer here. The periphragm and supporting processes appear to be restricted to peripheral areas.

Stratigraphical occurrence. Cookson & Eisenack (1974) described this species from the middle Cretaceous of Australia.

Canningia duxburyi Harding 1990 ex Williams et al. 1998

(Fig. 12 J)

1990 *Canningia duxburyi* Harding, p. 22–23, pl. 5, figs 1–13; text-fig. 8 (name not validly published — lodgement of holotype not specified).

1998 *Canningia duxburyi* Harding ex Williams et al., p. 88.

Comments. Harding (1990, p. 22–23) differentiated *Canningia duxburyi* from *Canningia reticulata* in that "it has an ectophragm [outer wall layer] which clearly breaks into paraplate related areas …". Harding illustrated *Canningia duxburyi* through scanning electron microscope (SEM) images. In our experience, some specimens of *Canningia reticulata* seen under the light microscope do show suggestions of tabulation, which might be more clearly seen in SEM images. Hence we question whether separation of the two species is justified, but retain *Canningia duxburyi* as it is considered a useful biostratigraphic marker (Martin Pearce, personal communication).

Stratigraphical occurrence. *Canningia duxburyi* was originally described from the upper Hauterivian to lower Barremian of Norfolk, England.

Canningia fairfieldensis Willumsen 2012

(Figs 12 K–L)

2012 *Canningia fairfieldensis* Willumsen, p. 59–60, pl. 2, figs 1–6.

Comments. Willumsen (2012, p. 59) indicated that the autophragm [i.e. endophragm in our terminology] in this species "… is covered by numerous short isolated clavate processes which are partly interconnected distally [by] an irregular perforate periphragm." The pericoel is typically narrow, bulging to form two antapical prominences, and the ornament and periphragm show no clear indication of paratabulation. This species is very similar to, and possibly a taxonomic junior synonym of, *Canningia areolata*, although the difference in age of the holotypes of the two species is considerable.

Stratigraphical occurrence. The species was originally described from the Early Paleocene of New Zealand.

Canningia? filosa (Wilson 1988) comb. nov.

(Figs 12 M–N)

1988 *Cassidium filosum* Wilson, p. 14–15, pl. 2, figs 8a–b, 9; pl. 3, figs 2a–b.

Comments. Wilson (1988, p. 14–15) described this species as having a "… relatively thick reticulate or rugulate autophragm [i.e. endophragm in our terminology], and bearing short irregular filamentous intratabular processes which are usually solitary but may occasionally be joined distally." This description is difficult to relate to the original illustrations, which appear to show a ragged membranous development arising from the reticulate autophragm, apparently connected by a discontinuous periphragm. Given the apparent presence of a periphragm, we questionably transfer this species to *Canningia*.

Stratigraphical occurrence. *Canningia*? *filosa* was originally described from the Paleocene of New Zealand.

Canningia glomerata nom. nov. subst. pro *Senoniasphaera rotundata* Clarke & Verdier 1967

(Fig. 12 O)

1967 *Senoniasphaera rotundata* Clarke & Verdier, p. 62–63, pl. 14, figs 1–3; text-fig. 25.

1999 *Senoniasphaera rotundata* Clarke & Verdier; emend. Prince et al., p. 162.

Derivation of name. From the Latin *glomeratus*, formed into a ball, in reference to the shape of the inner body, following the same intent of the original species epithet.

Comments. This species was proposed (as *Senoniasphaera rotundata*) by Clarke & Verdier (1967, p. 62–63) essentially for forms of *Senoniasphaera* in which the inner body "… seldom protrudes into the horns" and with ornament consisting of "a combination of perforations and an irregular reticulum". Clarke & Verdier (1967) noted that:

> In the ideal case the outer membrane is closely attached to the inner body [i.e. autocyst/autophragm] by short perforated pillars except where the membrane is detached and expanded to form the horns. In atypical forms … the outer membrane is detached over a larger and more irregular area and the attachment pillars become more visible.

This species is thus holocavate with a relatively dense arrangements of connecting structures between wall layers. Thus we transfer it to *Canningia* under the substitute name *Canningia glomerata*. The new epithet is necessary because the name *Canningia rotundata* is preoccupied (*Canningia rotundata* Cookson & Eisenack 1961).

Stratigraphical occurrence. Clarke & Verdier (1967) recorded *Canningia glomerata* (as *Senoniasphaera rotundata*) from the Senonian of the Isle of Wight, England. (Regarding "Senonian", see discussion under *Aptea rotundata*; we are uncertain as to exactly how Clarke & Verdier (1967) used this term.) Costa & Davey (1992) gave its stratigraphical range as earliest Coniacian to early Maastrichtian. Stover et al. (1996) considered the species to range from the

Coniacian to early Maastrichtian. Williams et al. (2004) placed its FAD within the early Turonian and its LAD within the late Campanian. Martin Pearce (personal communication) considers the range to be Coniacian to Campanian.

Canningia grandis Helby 1987

(Figs 12 Q–T)

1987 *Canningia grandis* Helby, p. 324–326, figs 29A–D, 30A–D.

Comments. Helby (1987, p. 324–326) noted that the "supports" of the outer wall layer are "… generally substantial, up to 9 µm long, up to 1.5 µm thick at base but thickening to 2.5 µm where [sic] they anastomose into the ectophragm." From Helby's illustrations, the structure seems to be a coarse reticulum with lumina of variable diameter supporting a reticulum. There is no obvious reflection of the tabulation other than the furrows (weakly) and archaeopyle. Although the name suggests large cysts, overlap exists between the size range of *Canningia grandis* and that of the type material of *Canningia reticulata*. Helby (1987, p.324–326) noted that *Canningia pistica* is "… usually smaller and shows a wider range of parasutural alignment of ectophragm supports …." And that *Canningia reticulata* has "… more delicate, densely packed, ectophragm supports … and a very finely reticulate to rugoreticulate ectophragm". Helby (1987) considered that *Canningia* cf. *reticulata* of Duxbury (1977) may be conspecific with *Canningia grandis*. Harding (1990) listed *Canningia* cf. *reticulata* of Duxbury (1977) in synonymy with his new species, *Canningia duxburyi.*

Stratigraphical occurrence. Helby (1987) recorded this species from the Hauterivian of offshore northwestern Australia.

Canningia*? *hulinensis He Chengquan et al. 1999

(Figs 13 A–C)

1999 *Canningia hulinensis* He Chengquan et al., p. 192,199–200, pl. 1, figs 1–6; text-fig. 3.

Comments. He Chengquan et al. (1999, p. 199) noted that the autophragm is "… covered by a great number of short processes which are slender, solid, unequal[ly] long, nontabular …." On the holotype the processes are "… arranged in many groups, each group … of 3 or 4 processes, some or all groups of processes connected distally by … pieces … of smooth ectophragm which is thickened, resulting in tuberous autophragm surface …." The illustrations appear to show short, irregular outgrowths from the endophragm, possibly resulting from corrosion. The species may be a taxonomic junior synonym of *Tenua scabrosa*; but given its unclear morphology, we retain it questionably in *Canningia* and suggest that it be restricted to the type material.

Stratigraphical occurrence. *Canningia*? *hulinensis* was originally described from the upper Hauterivian to Barremian of Heilongjiang Province, China.

Canningia inconspicua (Duxbury 1983) comb. nov.

(Figs 5 H–O; 12 P)

1983 *Cyclonephelium inconspicuum* Duxbury, p. 32–33, pl. 3, fig. 6.

Comments. Duxbury (1983, p. 811) noted that this species has

> "… most distinctive [ornament] … around the dorsal and ventral periphery … [in the form of] a punctate/microreticulate layer which is attached to the cyst [sic] by very short rods (approximately 1 μm in height). Local increases in ornament height are apparent above the left antapical bulge and to the left of this [i.e. reflecting asymmetrical antapical prominences]."

Duxbury (1983) compared this species with *Cyclonephelium* (now *Aptea*) *vannophorum* and *Cyclonephelium intonsum*. However, neither of these species have a periphragm (Duxbury's "punctate/microreticulate layer"), the presence of which leads us to transfer this species to *Canningia*. The periphragm in *Canningia inconspicua* is far less continuous than in *Canningia* *reticulata* and the reticulum is relatively poorly and inconsistently developed.

Stratigraphical occurrence. Duxbury (1983) described *Canningia inconspicua* (as *Cyclonephelium inconspicuum*) from the upper Aptian of southern England.

Canningia keiemensis Louwye 1997

(Figs 13 E–H)

1997 *Canningia keiemensis* Louwye, p. 149, pl. 1, figs 1–6.

Comments. In erecting this species, Louwye (1997, p. 149) indicated that "The autophragm [i.e. endophragm in our terminology] is relatively thick (approx. 2 μm), scabrate and slightly granular." Further, "Solid, pillar-like protrusions [up to 6 μm high] and irregular septa cover the autophragm dorsally and laterally … [and] are fibrous and flare distally and proximally. They support a scabrate, perforate ectophragm [periphragm in our terminology]." The periphragm, which forms a small, distinct apical horn and one or two antapical protrusions, has its widest perforations in penitabular positions. Louwye (1997) noted that the periphragm is always absent from the ventral surface, "… where occasionally some isolated septa or pillarlike protrusions occur." This species is distinguished by its thick wall, distinctive ornament and wall structure, and the absence of the periphragm ventrally.

Stratigraphical occurrence. Louwye (1997) recorded this species from the uppermost Cenomanian to Santonian of western Belgium.

Canningia macroreticulata Lebedeva in Ilyina et al. 1994.

(Figs 13 I–J)

1994 *Canningia macroreticulata* Lebedeva in Ilyina et al., p. 71, pl. 30, figs 6–7; pl. 31, figs 1–6; text-fig. 10.

Comments. This species appears to be distinguished by its relatively coarse network of crests supporting a periphragm, the structure absent or reduced dorsoventrally. Paratabulation seems well developed, a feature especially clear on the scanning electron images (Ilyina et al. 1994).

Stratigraphical occurrence. *Canningia macroreticulata* was recorded from the upper Coniacian of Siberia.

Canningia pistica Helby 1987

(Figs 13 M–P)

1987 *Canningia pistica* Helby, p. 326–327, figs 29E–L, 30E–L.

Comments. This is a distinctive, well-illustrated species. Helby (1987, p. 326) noted that the two wall layers are "… separated by … supports up to 10 μm in length, 0.5–2 μm at base, often expanding distally to 3 μm at their junctions with ectophragm [i.e. periphragm] reticulum." He further noted that the supports are variably distributed, "generally concentrated in the vicinity of parasutural boundaries, but also as intratabular clusters …." He commented that the outer wall layer (periphragm) is thin, finely reticulate, and often incomplete in the parasulcal area. Although not tightly followed in detail by the ornament and outer wall layer, the general reflection of the tabulation is quite striking in a broad sense. Helby (1987, p. 327) indicated that *Canningia grandis* differs from *Canningia pistica* mainly in lack of clear reflection of the tabulation, and that *Canningia reticulata* has more densely packed autophragm supports and a finely reticulate to rugoreticulate periphragm.

Helby (1987, p.326) noted that "Distinct lateral protrusions [are] evident at [the] paracingulum." However, as these do not appear from the original illustrations to be pronounced, and seem to be formed by the periphragm only, we do not consider their presence to put into doubt the affinity of this species with *Canningia*, and with areoligeraceans in general.

Stratigraphical occurrence. Helby recorded *Canningia pistica* from the Hauterivian of Australia.

Canningia plera (Duxbury 1983) comb. nov.

(Fig. 13 D)

1983 *Aptea plera* Duxbury, p. 22, 25, pl. 1, figs 7–8, 11; pl. 10, fig. 3; text-figs 5–6).
1986 *Pseudoceratium plerum* (Duxbury 1983) Bint, p. 145.

Comments. Duxbury (1983, p. 22) noted that "Short, solid, distally and proximally flaring rods cover paraplate areas and these are distally united by a fine reticulum. Parasutural areas are free of such ornament." In ambital view, the reticulum appears as a more or less continuous periphragm similar to that in many species of *Canningia*, including the type, *Canningia reticulata*. Duxbury (1983) also stated that the species has well-developed right lateral and left antapical horns and more weakly developed left lateral and right antapical horns may be developed. However, especially in the holotype, the "horns" are actually prominences produced by the ornament. Because of the presence of an outer wall layer (periphragm) and lack of a right lateral horn produced by the inner wall layer (endophragm), we reassign this species to *Canningia*.

Duxbury (1983, p. 25) further commented that:

> Davey & Verdier (1974, p. 641) have stressed the 'typical and characteristic asymmetry' of *Aptea* which they consider distinguishes that genus from similar genera …. Such asymmetry has prompted the present author to include *Aptea plera* in that genus. However, that species termed *Canningia* cf. *reticulata* in Duxbury, 1977 has been re-examined … [and] the only relevant difference between *A. plera* and *C.* cf. *reticulata* is the absence in the latter of the 'typical and characteristic asymmetry' of *Aptea*, largely because of its lack of … or possession of … shorter horns …. The presence or absence of the *Aptea* asymmetry may prove a difficult criterion to maintain at generic level.

Thus Duxbury (1983) informally anticipated one of our major conclusions: that symmetry of the inner body is not a useful generic criterion within the *Cyclonephelium* group.

Stratigraphical occurrence. Duxbury (1983) recorded this species from the lower Aptian of southern England.

Canningia reticulata Cookson & Eisenack 1960

(Figs 5 A–G; 13 K–L)

1960 *Canningia reticulata* Cookson & Eisenack, p. 251, pl. 38, figs 1–2.
1960 *Cyclonephelium areolatum* Cookson & Eisenack, p. 253, pl. 38, fig. 8 (non fig. 7).
1977 *Canningia palliata* Brideaux, p. 11–12, pl. 3, figs 1–4.
1980 *Hashenia reticulata* Yu Jingxian & Zhang Wangping, p. 107, pl. 1, fig. 17; pl. 2, figs 1–2 (subsequently *Canningia xinjianensis*).
1980 *Yalkalpodinium areolatum* (Cookson & Eisenack) Morgan, p. 34.
1981 *Cyclonephelium chabaca* Below, p. 12–13, pl. 4, figs 9–11; pl. 9, figs 2–3; pl. 15, fig. 25.
1981 *Cyclonephelium palliatum* (Brideaux) Below, p. 10.
1981 *Canningia reticulata* Cookson & Eisenack; emend. Below, p. 32.
1987 *Canningia reticulata* Cookson & Eisenack; emend. Helby, p. 322–323.
1987 *Cyclonephelium areolatum* Cookson & Eisenack; Stover & Williams, p. 231.
1988 *Canningia xinjiangensis* Chen et al., p. 16 nom subst. pro *Hashenia reticulata* Yu Jingxian & Zhang Wangping 1980.

Comments. *Canningia reticulata* is distinguished by its finely reticulate periphragm and dense system of supports. We follow Helby (1987) in synonymising *Canningia palliata* with *Canningia reticulata*, and add the following taxonomic junior synonyms: *Cyclonephelium areolatum*, *Cyclonephelium chabaca*, *Cyclonephelium inconspicuum* and *Canningia xinjiangensis* (formerly *Hashenia reticulata*).

Cookson & Eisenack (1960, p. 253) described *Cyclonephelium areolatum* as comprising cysts that are circular to slightly oval in outline (i.e. ambitus), flat, and with "… a peripheral sculptured zone … in the form of a thin, finely vermiculate or areolate membrane …" with an "unsculptured portion", presumably mid-ventrally and/or mid-dorsally. Cookson & Eisenack's illustration of the holotype (their pl. 38, fig. 8) appears to show a form very similar to *Canningia reticulata* (the type of which is illustrated on the same plate) with a dark mid-dorsoventral area that these authors interpreted as unsculptured, and which presumably led them to assign this form to *Cyclonephelium* rather than *Canningia*. To us, the "areolation" described by Cookson & Eisenack (1960) reflects a holocavate wall very similar (if not identical) to that of *Canningia reticulata*, except for a dark, central "unsculptured" area. The latter feature we consider not sufficiently distinctive to justify retaining *Cyclonephelium areolatum* separately from *Canningia reticulata* and hence propose the synonymy.

Below (1981a, p. 12) provided the following diagnosis for *Cyclonephelium chabaca*.

> Proximate, nontabulate, lenticular central body of almost rounded outline, apically rounded or with a very low bulge. Low, broad apical horn frame-like, formed of periphragmal processes. Hypocyst asymmetrical with left antapical horn and marginally displaced bulge [?], or rarely rounded. Ornamentation of numerous thin, process-bearing, delicate, fine-meshed reticulum covering the whole cyst with the exception of a broad ventrally located surface corresponding to the parasulcal zone. Archaeopyle of type (A). The angular archaeopyle outline indicates six precingular paraplates and [paraplate] as [anterior sulcal]. Pandasutural bands are rarely partially developed. [Translation]

Below (1981a, p.13) appeared to suggest that *Cyclonephelium chabaca* differs from *Canningia reticulata* in that the periphragm in the former is mesh-like, whereas that of the latter is complete. However, in our view this difference does not accord with the original description and illustrations of *Canningia reticulata* (even with regard to the parasulcal hiatus in the outer wall layer), and so we consider *Cyclonephelium chabaca* to be a taxonomic junior synonym of *Canningia reticulata*. *Canningia xinjiangensis* (originally *Hashenia reticulata*) appears identical to *Canningia reticulata*.

Stratigraphical occurrence. *Canningia reticulata* was originally described from the Tithonian of Australasia. The type material of *Canningia areolata* is also from the Tithonian of Australia. Brideaux (1977) recorded *Canningia palliata* from the Barremian of northwestern Canada. *Canningia xinjiangensis* was originally described from the Turonian to Maastrichtian of China.

Below (1981a) recorded *Cyclonephelium chabaca* from the Aptian to Cenomanian of southwestern Morocco.

Canningia rugulosa (Clarke & Verdier 1967) Stover & Evitt 1978

(Fig. 13 Q)

1967 *Aptea rugulosa* Clarke & Verdier p. 57–58, pl. 12, figs 5–6; text-fig. 23.
1978 *Canningia rugulosa* (Clarke & Verdier) Stover & Evitt, p. 25.

Comments. From its original description and illustrations, this species is clearly holocavate. Clarke & Verdier (1967, p. 58) noted that the "… inner body is attached to the outer membrane except at the apex and antapex …." And that "The outer membrane is wavy in outline, and gives the appearance of a rugulation or an irregular reticulum." This wall structure and the apparent offset position of the parasulcal notch (Clarke & Verdier 1967, pl. 12, fig. 5) accords with an areoligeracean affinity, and with *Canningia* in particular. Although Clarke & Verdier (1967) emphasised the rugulate nature of the ornament, this may be difficult to distinguish from the ornament of *Canningia reticulata*, and thus the two species may be synonymous.

Stratigraphical occurrence. This species was originally recovered from the Santonian of the Isle of Wight, England.

Canningia senonica Clarke & Verdier 1967

(Fig. 13 R)

1967 *Canningia senonica* Clarke & Verdier, p. 20–21, pl. 1, figs 12–14; text-fig. 7.

Comments. Clarke & Verdier (1967, p. 21) noted that the "Sculpture [consists of] thin irregular processes up to 12 μ long which join distally to form an incomplete and irregular reticulum …". They distinguished *Canningia senonica* from *Canningia reticulata* by its higher reticulum.

Stratigraphical occurrence. Clarke & Verdier (1967) recorded *Canningia senonica* from the Santonian of the Isle of Wight, England.

Canningia transitoria Stover & Helby 1987b

(Figs 14 A–E)

1987b *Canningia transitoria* Stover & Helby, p. 262–263, figs 3A–P, 4A–B.
1990a *Canningia bassensis* Marshall, p. 13–14, figs 9F–G, 15A–K.

Comments. This species represents distinctive holocavate cysts with an apical archaeopyle and usually one to two antapical prominences asymmetrically disposed. The antapical prominences are formed primarily by the periphragm, although the endophragm does form a prominence on the more pronounced left side. Some specimens show weak lateral bulges, which would probably not bring areoligeracean affinity into question were it not for the stronger lateral bulges in the type material of *Canningia bassensis*, which we consider a taxonomic junior synonym of *Canningia transitoria*. The two species seem otherwise identical. Given all other morphological traits, however, we retain *Canningia transitoria* in *Canningia*. The pericoel is broad, 10–20% of the entire cyst width, and the overall ornament provides a penitabular reflection of the tabulation. Marshall (1990a) did not compare *Canningia bassensis* with *Canningia transitoria*.

Stratigraphical occurrence. The type material of *Canningia transitoria* is from the Barremian to lower Aptian of Western Australia. That of *Canningia bassensis* is from the Campanian of southeastern Australia.

Genus ***Canninginopsis*** Cookson & Eisenack 1962

1962 *Canninginopsis* Cookson & Eisenack, p. 488.
1990b *Canninginopsis* Cookson & Eisenack; emend. Marshall, p. 80–82.

Type: Cookson & Eisenack, 1962, pl.1, fig.16, as *Canninginopsis denticulata*.

Synopsis. Areoligeracean cysts with parasutures marked by low ridges or other elements of low relief. Autophragm otherwise typically smooth or inconspicuously ornamented.

Remarks. Cookson & Eisenack (1962, p. 488) provided the following description for *Canninginopsis*:

> Shell flat, roughly seven-sided in outline, with a slight apical prominence and an indented base. Girdle helicoid, approximately equatorial on the dorsal surface. Longitudinal furrow obliquely directed. Both surfaces of shell marked out into large fields that border both girdle and longitudinal furrow. Shell opening by the detachment of the proximal part of the epitheca.

Cookson & Eisenack (1962) differentiated *Canninginopsis* from *Canningia* by the presence of paratabulation of the former. In recent usage, *Canningia* has a holocavate wall and may or may not show evidence of paratabulation, usually through pandasutural zones when it does. *Canninginopsis* has an autophragm and paratabulation marked along parasutures; it is not cavate. *Canninginopsis* differs from *Cerbia* in having parasutural rather than penitabular features.

Accepted species.

Canninginopsis bretonica Marshall 1990b

(Figs 13 S–T)

1990b *Canninginopsis bretonica* Marshall, p. 84–86, figs 4L–T, 5F–H, 6L–U.

Comments. The critical feature of this species is the clearly outlined paratabulation on the dorsal and lateral surfaces, with the mid-ventral surface devoid of features. Marshall (1990b, p. 86) stated: “Paratabulation usually clearly indicated [except ventrally] … by parasutural septa up to 7 µm high …; fragments of parasutural boundaries occasionally outlined by 2 close-spaced rows of penitabular septa.” Thus, although the tabulation is reflected mostly by parasutural features, parts of it are reflected by penitabular features, and thus the species is transitional between *Canninginopsis* and *Cerbia*. However, as the paratabulation is mostly reflected by parasutural features, we retain this species in *Canninginopsis* without question. Aside from its dorsal and lateral crests, this species is also characterised by fine foveolation on its surface and crests, which may be developed to give the crests denticulate margins. Some specimens may show lateral bulges, but these are mostly subdued.

Stratigraphical occurrence. Marshall (1990b) recorded this species from the upper Campanian to middle Maastrichtian of Western Australia.

Canninginopsis denticulata Cookson & Eisenack 1962

(Fig. 14 F)

1962 *Canninginopsis denticulata* Cookson & Eisenack, p. 488, pl. 1, figs 16–19; text-fig. 2.

Comments. This species, the type of the genus, is characterised by distinct rows of denticles marking the parasutures.

Stratigraphical occurrence. Cookson & Eisenack (1962) recorded *Canninginopsis denticulata* from the Albian to Cenomanian of Australia.

Canninginopsis maastrichtiensis Slimani 1994

(Figs 14 I–K)

1994 *Canninginopsis verrucosa* Wilson in Slimani 1994, p. 97 (name not validly published).
1994 *Canninginopsis maastrichtiensis* Slimani, p. 97–98, pl. 16, figs 5–8, 13–14.

Comments. Slimani (1994) provided the following diagnosis.

> Cysts of *Canninginopsis*, lenticular to pentagonal with an apical protrusion and two unequal antapical protrusions of which that on the left is longer. The autophragm is typically ornamented by solid verrucae and/or granules (0.5 to 3 μm across), the smallest of which are always seen on the cingulum. The paratabulation is weakly indicated by low, solid, smooth or rarely undulating crests (up to 3 μm). It conforms to the following formula: 4', 5–6", ?c, 5–6"', 1p, 1"". The archaeopyle is apical, of

type (tA), with an attached or rarely free operculum. [Translation]

This species thus conforms to *Canninginopsis*.

Stratigraphical occurrence. *Canninginopsis maastrichtiensis* was originally described from the upper Maastrichtian of the Maastricht area, The Netherlands.

Canninginopsis monile (Duxbury 2002) comb. nov.

(Figs 14 G–H)

2002 *Cerbia monile* Duxbury, p. 78, pl. 1, figs 7–8, 10–12.

Comments. Duxbury (2002, p. 78) noted that "Short spines are aligned very largely along epicystal and hypocystal parasutures, although occasionally these also may occur along paracingular margins." Although from the illustrations, the alignment appears to be quite loose, we transfer the species to *Canninginopsis* on the basis that the ornament is parasutural rather than penitabular. The epithet is a noun in apposition.

Stratigraphical occurrence. Duxbury (2002) recorded this species from the Albian of the North Sea.

Genus ***Cerbia*** Below 1981

1981 *Cerbia* Below, p. 8.

Type. Davey & Verdier 1974, pl. 92, figs 1, 4, as *Cyclonephelium tabulatum*.

Synopsis. Areoligeracean cysts that are proximate to proximochorate, with ornament height less than 25% of maximum cyst width. Central body compressed, ambitus subcircular to lenticular, with a rounded to more commonly asymmetrical antapex and an apical horn. Acavate, with processes predominantly penitabular and thus reflecting tabulation. Archaeopyle apical, with formula $A_{(1-4')}$, operculum free; parasulcal notch offset to the left.

Comments. Below (1981) diagnosed *Cerbia* as follows:

> Proximate to proximochorate, single-layered lenticular cysts. Outline rounded, oval or rounded pentagonal. Apex rounded or with a weak bulge. Antapex rounded or with lobe [?] and two bulges. Membrane smooth or sculptured. Paratabulation 4', 6", Xc, 6"', 1p, 1"", Xs. Fields bordered by penitabular ornament, without intratabular processes. Archaeopyle apical, (A). [Translation]

Sarjeant (1985, p. 93–94) considered *Cerbia* to be a taxonomic junior synonym of *Tenua*; however, Duxbury (2002, p. 76, 78) retained *Cerbia*, an action that we support. *Cerbia* differs from *Tenua* in having processes that are clearly penitabular in arrangement. See further discussions above.

Accepted taxa.

Cerbia? aucda Below 1981

(Fig. 14 L)

1981 *Cerbia aucda* Below p. 8–9, pl. 4, fig. 3; pl. 12, fig. 20; text-figs 6a–c, g (non pl. 4, figs 5a–b).
1993 *Tenua aucda* (Below) Lentin & Williams, p. 638.

Comments. Below (1981, p. 8) diagnosed *Cerbia aucda* as follows:

> Proximate, dorsoventrally compressed, tabulate, one-layered cyst of elongate oval to pentagonal outline. Epicyst triangular or with rounded apex. Hypocyst trapezoidal. Antapex rounded, flattened or with a lobe, whereby two symmetrically disposed bulges are developed. The archaeopyle is expressed as type (A). Paracingulum spiral, undivided; parasulcus sigmoidally curved. From low penitabular rows, truncated [?]

> or conical, solid tubercles allow a paratabulation scheme of 4', 6'', Xc, 6''', pc, 1'''' to be recognised. The surface is verrucate to smooth. [Translation]

We retain this species in *Cerbia* as ornament on the holotype is penitabular. However, the specimen shown in Below (1981, pl. 4, figs 5a–b) does not clearly reflect the tabulation.

Stratigraphical occurrence. Below (1981) recorded *Cerbia aucda* from the Barremian of Morocco.

Cerbia*? *formosa Mao Shaozhi & Norris 1988

(Fig. 14 M)

1988 *Cerbia formosa* Mao Shaozhi & Norris, p. 31–32, pl. 1, figs 9–10; text-fig. 8, nos 1–2.
1991 *Cerbia suturispinosa* He Chengquan, p. 173, pl. 10, figs 1–3.
1993 *Tenua formosa* (Mao Shaozhi & Norris) Lentin & Williams, p. 639.
1993 *Tenua suturispinosa* (He Chengquan) Lentin & Williams, p. 640.

Comments. We retain this species in *Cerbia*, albeit questionably, because some of the process tips look dolabrate, and hence this species may be better assigned to *Cleistosphaeridium*, as is also suggested by the age (Eocene–Oligocene) of the type material. *Tenua suturispinosa* is also an Eocene species with similar morphology, and hence we consider it a taxonomic junior synonym of *Cerbia*? *formosa*.

Stratigraphical occurrence. *Cerbia formosa* was originally described from the Upper Eocene of China. He Chengquan (1991) recorded *Cerbia suturispinosa* from the Middle Eocene of China.

Cerbia*? *hexalobosa (Cookson & Eisenack 1974) comb. nov.

(Fig. 14 N)

1974 *Cassidium hexalobosum* Cookson & Eisenack, p. 76, pl. 26, fig. 7 (non 6).
1978 *Cyclonephelium hexalobosum* (Cookson & Eisenack) Stover & Evitt, p. 36.
2004 *Cyclonephelium*? *hexalobosum* (Cookson & Eisenack); Fauconnier & Londeix in

Fauconnier & Masure. p. 147.

Comments. In their diagnosis, Cookson & Eisenack (1974, p. 76) stated that "The type reveals a distinct but indecipherable paratabulation, and at its widest part a weakly discernible cingulum is recognisable." They further noted that "The surface is covered with shaggy spines, which in the type give the impression of a coarse granulation …" [both quotes translated from the German]. It is notable that the authors had to separate the type and paratype several times in their diagnosis. We consider that the paratype (Cookson & Eisenack 1974, pl. 26, fig. 6) is not conspecific with the holotype (Cookson & Eisenack 1974, pl. 26, fig. 5), and probably belongs to *Tenua hystrix*. As the type of this species appears to reflect the tabulation through penitabular lineation of the ornament, we tentatively transfer the species to *Cerbia*.

Stratigraphical occurrence. Cookson & Eisenack (1974) described *Cerbia*? *hexalobosa* from the middle Cretaceous to Senonian of Australia. (Regarding "Senonian", see discussion under *Aptea rotundata*.)

Cerbia intermedia (Morgan 1980) comb. nov.

(Figs 14 O–P)

1980 *Canninginopsis intermedia* Morgan, p. 18, pl. 3, figs 4–8.

Comments. Morgan (1980, p. 18) noted that the ornament consists of "… 0.5–1.0 μm diameter granules, larger, denser and more aligned in two paracingular rows and in peritabular [i.e. penitabular] position around dorsal paraplates …." Most of the rest of the cyst is evenly covered with granules. The morphology of this species thus accords better with *Cerbia* than *Canninginopsis*, and hence we propose the re-assignment here. Morgan used the epithet "*intermedia*" because he considered the species intermediate between *Canningia* (now *Tenua*) *colliveri* and *Canninginopsis denticulata*.

Stratigraphical occurrence. This species was originally described from the lower Albian of Australia.

Cerbia ordospinosa (Smith 1992) comb. nov.

(Fig. 14 Q)

1992 *Canninginopsis ordospinosa* Smith, p. 342, figs 5g–h, k–l, n, p; fig. 11i.

Comments. Smith (1992, p. 342) noted that "The cyst surface bears variably developed granulate … sculpture and pandasutural rows of spines." He further stated that:

> The autophragm is thin (<0.5 µm) and bears an ornament of intratabular grana and two to three pandasutural rows of spines and/or grana. These spines are up to 6 µm in length and may be furcate at their distal extremities.

The species thus accords with the morphology of *Cerbia* rather than of *Canninginopsis*, and we thus reassign it. Some specimens show development of a short postcingular prominence, which may be a reason to question the present assignment.

Stratigraphical occurrence. Smith (1992) recorded *Cerbia* (as *Canninginopsis*) *ordospinosa* from the upper Campanian to lower Maastrichtian of Vega Island, Antarctica.

Cerbia tabulata (Davey & Verdier 1974) Below 1981

(Figs 14 R–S)

1974 *Cyclonephelium tabulatum* Davey & Verdier, p. 630, 632, pl. 92, figs 1–4; pl. 93, fig. 6.
1977 *Canninginopsis tabulata* (Davey & Verdier) Duxbury, p. 27.
1981 *Cerbia tabulata* (Davey & Verdier) Below, p. 9.

Comments. For this species, Davey & Verdier (1974) stated that "The processes [actually short spines] are predominantly peritabular [i.e. penitabular] in position and clearly define the precingular and postcingular paraplates and the cingulum." The short, stout, capitate to rarely branched spines are essentially absent from paraplate centres and the parasulcus.

Stratigraphical occurrence. *Cerbia tabulata* (as *Cyclonephelium tabulatum*) was originally described from the Aptian of France. Costa & Davey (1992) gave the stratigraphical range of the species as earliest Barremian to late Aptian. Duxbury (2001) plotted the FAD of this species (as *Canninginopsis tabulata*) at the base of the middle Barremian and the LAD at the Aptian–Albian boundary.

Cerbia*? *wenquanensis (Cheng Jinhui & He Chengquan 2006) comb. nov.

(Figs 15 A–B)

2006 *Tenua wenquanensis* Cheng Jinhui & He Chengquan, p. 280–281, fig. 3s1–3s2; fig.5a–b.

Comments. We transfer this species to *Cerbia* because Cheng Jinhui & He Chengquan (2006) refer to "penitabular spines" in the protologue. As this is not clear from their illustrations, we question the assignment.

Stratigraphical occurrence. Cheng Jinhui & He Chengquan (2006) recorded *Cerbia*? (as *Tenua*) *wenquanensis* from the upper Kimmeridgian of China.

Genus ***Circulodinium*** Alberti 1961 emend. nov.

1961 *Circulodinium* Alberti, p. 28.

Type. Alberti 1961, pl. 4, fig. 20, as *Circulodinium hirtellum* (herein considered a taxonomic junior synonym of *Circulodinium distinctum*).

Emended diagnosis. Areoligeracean cysts that are proximate to proximochorate, with ornament height less than 25% of maximum cyst width. Central body dorsoventrally compressed with a subcircular, broadly subovoidal to asymmetrically lenticular ambitus, usually with an apical horn; posteriorly rounded to asymmetrical, with one or two weak to moderately developed antapical horns. Ornamentation consists of free-standing elements, some of which may be aligned to reflect aspects of tabulation; however, processes are marginately distributed, with mid-ventral and mid-dorsal areas devoid of, or with substantially reduced, ornament. Archaeopyle apical, type $A_{(1\text{-}4')}$, operculum free; parasulcal notch offset to the left.

Comments. As discussed extensively above, *Circulodinium* is herein retained for forms that, like the type, have a more or less marginate distribution of free-standing elements. *Cerbia* differs in having forms in which the ornament is clearly penitabular, and *Cyclonephelium* differs in having a marginately distributed ornamentation consisting at least in part of linear elements. *Tenua* differs in having more or less uniform, rather than marginate distribution of free-standing ornament.

Alberti (1961, p. 28) provided a diagnosis for *Circulodinium* as follows:

> Shell compressed to flat, its outline almost circular to irregularly rounded. With a small apical process, somewhat blunt at its tip. Hypotheca concave at the antapex. From this arise two antapical bulges, of which one may be more or less reduced. Shell without transverse furrow or tabulation. Its surface, with the exception of the central parts of ventral and dorsal surfaces and the antapical concavity, bears short, solid spines, in part broadening distally in paddle-like fashion, rarely branching. [Translation]

Accepted species.

Circulodinium almohadense (Below 1984) comb. nov.

(Figs 15 C–D)

1984 *Aptea almohadensis* Below, p. 635, pl. 1, figs 5A–B, 6–7.
1989 *Pseudoceratium almohadense* (Below) Lentin & Williams, p. 306.

Comments. Below (1984, p. 635) noted that this species "… occasionally [has] … a right lateral bulge in the region of the postcingular paraplate girdle [sic]", which he considered gave the species (as *Aptea almohadensis*) a "close connection" to *Pseudoceratium*. However, such a bulge is not evident in Below's illustrations of the holotype (his pl. 1, figs 5A–B). Below stated in his diagnosis that the cyst ornamentation is:

> … very sparse and in most cases without rules of orientation. Ornaments as low, solid, flattened, interconnected ledges, isolated short spines with distally acuminated or blunted ends, or simple cones forming tubercles. Sometimes these ornaments are arranged to pandasutural [i.e penitabular] lines.

However, in his description, Below (1984) noted that "The sparse distribution of low ornaments … makes any consideration of penitabular alignment along parasutures impossible." Below's illustrations (pl. 1, figs 5A–B, 6–7) clearly show sparse, low ornament with weak penitabular alignment; the dorsoventral areas appear essentially devoid of ornament, but Below (1984) did not comment on this. Although he mentioned "interconnected ledges", these may be flattened spines. On balance, we consider that the morphology of this species fits best with that of *Circulodinium*.

Stratigraphical occurrence. Below (1984) described this species from the middle to upper Aptian of offshore northwestern Africa.

Circulodinium circulatum (He Chengquan 1991) comb.nov.

(Fig. 14 T)

1991 *Cyclonephelium circulatum* He Chengquan, p. 135, pl. 10, figs 7–12.

Comments. The type material appears similar to *Circulodinium distinctum*, although there may be some connections between processes. The ornament, however, appears to be predominantly free-standing, so transfer this species to *Cyclonephelium*.

Stratigraphical occurrence. He Chengquan (1991) described this species from the Middle to Upper Eocene of China.

Circulodinium distinctum (Deflandre & Cookson 1955) Jansonius 1986

(Figs 6 A–D; 15 E)

1955 *Cyclonephelium distinctum* Deflandre & Cookson, p. 285–286, pl. 2, fig. 14; text-figs 47–48

1958 *Tenua hystricella* Eisenack, p. 411, pl. 23, figs 5–7.

1961 *Circulodinium hirtellum* Alberti, p. 28–29, pl. 4, fig. 20.

1961 *Circulodinium deflandrei* Alberti, p. 29, pl. 4, figs 7–13.

1969 *Canningia hirtella* (Alberti) Millioud, p. 425.

1969 *Cyclonephelium paucispinum* Davey, p. 170, pl. 9, figs 1–2.

1974 *Aptea securigera* Davey & Verdier, p. 642–643, pl. 91, fig. 3 (non pl. 91, fig. 2; text-fig. 5–vii).

1978 *Cyclonephelium hirtellum* (Alberti) Davey, p. 894.

1986 *Cyclonephelium distinctum* subsp. *laevigatum* Mehrotra & Sarjeant, p. 719–720, pl. 8, figs 1–2; pl. 9, fig. 2; text-fig. 7a.

1986 *Circulodinium distinctum* (Deflandre & Cookson) Jansonius, p. 204.

1986 *Pseudoceratium securigerum* (Davey & Verdier) Bint, p. 145.

1986 *Cyclonephelium distinctum* subsp. *laevigatum* Mehrotra & Sarjeant, p. 719–720, pl. 8, figs 1–2; pl. 9, fig. 2; text-fig. 7a.

1989 *Circulodinium distinctum* subsp. *laevigatum* (Mehrotra & Sarjeant), Lentin & Williams, p. 63.

1992 *Circulodinium formosum* Iosifova, p. 61; pl. 9, figs 3a–c; text-figs 1c–d.

2004 *Cyclonephelium formosum* (Iosifova) Fauconnier in Fauconnier & Masure, p. 146.

2004 *Circulodinium paucispinum* (Davey) Fauconnier in Fauconnier & Masure, p. 115.

Comments. This species differs from *Tenua hystrix* in generally having longer spines that have a clearly marginate distribution. The photograph of the type of *Circulodinium* (Alberti 1961, pl. 4, fig. 20 — the holotype of *Circulodinium hirtellum*) appears to have marginately distributed ornament, and processes similar to those of either *Circulodinium distinctum* or *Tenua hystrix*; since the processes of *Circulodinium hirtellum* appear to be marginately distributed, we consider that species to be a taxonomic junior synonym of *Circulodinium distinctum*. We note that the cysts comprising the type material of both *Circulodinium distinctum* and *Circulodinium hirtellum* are large, 64–97 µm for the former and a breadth of 97 µm for the latter. In our experience, most specimens assigned to *Circulodinium distinctum* are notably smaller than the larger dimensions cited here.

Deflandre & Cookson (1955, p. 285–286) described *Circulodinium* (as *Cyclonephelium*) *distinctum* as having "numerous short, solid appendages … the apices of which are bluntly pointed, capitate, enlarged or forked". Alberti (1961, p. 29) described *Circulodinium hirtellum* as follows:

> Shell compressed, its outline irregularly rounded, somewhat longer than wide. With a short apical projection whose end is truncated. Two unequally large antapical protrusions. Epitheca somewhat smaller than hypotheca. Except for the central parts of the ventral and dorsal surfaces, the shell surface bears short, mostly pointed, thorn-like processes. [Translation]

Thus, the spines described by Alberti (1961) for *Circulodinium hirtellum* appear to be more similar to those of *Circulodinium distinctum* than the very short, blunt spines of *Tenua hystrix*. The process distribution also suggests a synonymy with *Circulodinium distinctum*.

The same appears true for *Tenua hystricella*, a form that has previously been considered a taxonomic junior synonym of *Tenua hystrix*. Eisenack (1958, p. 411) stated that *Tenua hystricella* resembles *Tenua hystrix* but is smaller. He also remarked that the forking prongs of the spines in *Tenua hystricella* tend to coalesce, forming vermiculate lineations. If confirmed this might mean that *Tenua hystricella* would be better assigned to *Cyclonephelium*; but for now we consider it a taxonomic junior synonym of *Tenua distincta*.

Davey (1969, p. 170) described the wall of *Cyclonephelium paucispinum* as "… lightly to coarsely granular, bearing [a] small number of irregular processes confined to [the] peripheral region …." He noted that the processes of *Cyclonephelium paucispinum* "… most closely resemble those of *C. distinctum* but are fewer in number". We consider this morphology to be within the range of variation for *Circulodinium distinctum*.

Davey & Verdier (1974, p. 642) described the shape of the central body of their new species, *Aptea securigera*, as "… rounded triangular in shape [i.e. ambitus]. The left side is strongly, but evenly, convex; the right epitractal and hypotractal sides are slightly convex to straight and meet at approximately right angles in the cingular region." This is a good description for the paratype (their pl. 91, fig. 2), but does not at all fit the holotype (their pl. 91, fig. 3), which has a more or less circular ambitus, an apical horn, and a weakly developed antapical prominence offset, presumably, to the left. The paratype would be assignable to *Pseudoceratium*, but the holotype is clearly an areoligeracean. In describing the ornament for *Aptea securigera*, Davey & Verdier (1974) noted that:

> The cyst surface bears numerous short, flattened, solid processes which are concentrated in the circumferential region. A more or less circular area in the centre of the ventral and dorsal surfaces is devoid of, or possesses only rare, processes. The processes are of variable shape but are typically discrete, expanding both distally and proximally, and are flat-topped distally; their length is more than twice their medial width. The processes are longer and more variable at the cyst apices. Very rarely the cingulum and other tabulation is marked by narrow bands devoid of processes.

The combined possession of dorsoventral areas devoid of processes, the lack of clear paratabulation, and the discrete processes indicate that *Circulodinium* is the best generic fit for *Aptea securigera* (based on the morphology of its holotype). The processes are somewhat intermediate between those of *Tenua hystrix* and *Circulodinium distinctum*, but the presence of some longer processes and distinct dorsoventral areas devoid of processes inclines us to synonymise this species with *Circulodinium distinctum*. Unfortunately, *Pseudoceratium securigerum* (based on the morphology of the paratype) has been used as an important marker for the early Aptian, particularly in the Middle East (Martin Pearce, personal communication 2018). A resolution might be propose a new species based on the original paratype (Davey & Verdier 1974, pl. 91, fig. 2).

Alberti (1961, p. 29) diagnosed *Circulodinium deflandrei* as follows:

> Shell compressed to flat, its outline almost rounded. The free end of the small apical

> prominence is slightly truncated. At the antapex the hypotheca is weakly indented, thereby forming two antapical protrusions, of which one may be reduced. Shell surface, with the exception of the central parts of the ventral and dorsal sides and the antapical indentation, bearing numerous short, solid bristles, [which are] in part distally broadened in paddle-fashion, seldom furcate. [Translation]

Alberti (1961) further noted that some bristles, or processes, are joined proximally, sometimes arising from linear ridges; but these are not clearly evident on the illustrations of the type material. We thus consider *Circulodinium deflandrei* to be a taxonomic junior synonym of *Circulodinium distinctum*.

The holotype, and only specimen that Iosifova (1992) illustrated, of *Circulodinium formosum* has slightly longer than average processes for *Circulodinium distinctum*. But the overall morphology and the absence of processes on the dorsoventral areas of *Circulodinium formosum* indicate that Iosifova's species should be considered a taxonomic junior synonym of *Circulodinium distinctum*. We also consider *Cyclonephelium distinctum* subsp. *laevigatum* to be a taxonomic junior synonym of *Cyclonephelium distinctum.*

Stratigraphical occurrence. *Cyclonephelium distinctum* was originally recorded from the Senonian of Western Australia. (Regarding "Senonian", see discussion under *Aptea rotundata.*) Eisenack (1958) recorded *Tenua hystricella* from the Aptian of northern Germany. *Circulodinium hirtellum* and *Circulodinium deflandrei* were first described from the Valanginian–Hauterivian and upper Barremian respectively of Germany. The holotype of *Cyclonephelium paucispinum* is from the Cenomanian of France. The holotype of *Aptea securigera* is from the lower Aptian of southeastern France. Mehrotra & Sarjeant (1986) recovered *Cyclonephelium distinctum* subsp. *laevigatum* from the Valanginian of India. *Circulodinium formosum* was recovered originally from the Valanginian of Russia.

Circulodinium*? *hughesii (Clarke & Verdier 1967) comb nov.

(Fig. 15 F)

1967 *Cyclonephelium hughesii* Clarke & Verdier, p. 21–22, pl. 2, fig. 6; text-fig. 8.

Comments. Clarke & Verdier (1967, p. 22) diagnosed this species as a *Cyclonephelium* with broad, short processes, and differentiated it from *Cyclonephelium* (now *Circulodinium*) *distinctum* and *Cyclonephelium densebarbatum* in having much broader processes. In their description they elaborated on the ornament a little, referring to "short broad appendages, closely spaced and with the distal part slightly expanded and indented." Their single photograph and their sketch suggest that the broad processes may be septa similar to those of *Cyclonephelium compactum*. However, for now we consider the ornament to consist of broad isolated elements distributed peripherally (more evident on the line drawing than on the photo) and re-assign this species tentatively to *Circulodinium*.

Stratigraphical occurrence. Clarke & Verdier (1967) recorded this species from the Cenomanian of southern England.

Circulodinium vectense nom. nov. subst. pro *Pseudoceratium distinctum* Duxbury 2001
(Fig. 15 G)

2001 *Pseudoceratium distinctum* Duxbury, p. 111–112, fig. 11, nos 1–4.

Derivation of name. From the Latin *Vectis*, Isle of Wight southern England, the type locality.

Comments. Duxbury (2001, p. 111) described *Pseudoceratium distinctum* as:

> A fairly large, ceratiacean dinocyst species whose ambitus may vary from being pronouncedly asymmetrical to more rounded. Distinct apical, left antapical and right lateral projections are observed; poorly-developed right antapical and left laterals may also be present. Ornament consists of slender spines of varying length, with those at horn tips often coalescing and extending horns considerably. Some distal connection of individual spines may be observed, otherwise spines are distally furcate, irregularly and variably.

From the illustrations in the protologue, the autocyst is asymmetrical and bulges in the right-lateral area, but in contrast to the original diagnosis there appears to be no distinct projection; it seems that the ornament/periphragm produces a projection, as in *Aptea polymorpha*. In none of the four figured specimens was there any hint of a left lateral projection, and in some of the specimens the right lateral projection is barely discernible. Hence, we transfer this species to the genus *Circulodinium*, as *Circulodinium vectense*, as the name *Circulodinium distinctum* is preoccupied.

Duxbury (2001) noted that *Pseudoceratium distinctum* differs from *Aptea polymorpha* "… in being generally more asymmetrical in outline and in having thickened mid-dorsal and mid-ventral areas devoid of ornament." He noted also that the ornament of *Pseudoceratium distinctum* tends to consist of individual, slender elements, whereas *Aptea polymorpha* has "… continuous, laterally connected, essentially reticulate ornament". Duxbury (2001) considered that *Pseudoceratium distinctum* differs from *Cyclonephelium compactum* "… in its asymmetrical ambitus and in having thickened areas devoid of ornament. We agree that *Circulodinium vectense* lacks the reticulate ornament of *Aptea polymorpha* and *Cyclonephelium compactum*. However, in terms of the additional criteria that Duxbury (2001) cited, in our view, degree of asymmetry is not a useful feature to use for taxonomic distinction in this group of cysts, as it is intraspecifically variable; and *Cyclonephelium compactum* does have dorsoventral areas devoid of ornament. The thickening of the cyst wall in dorsoventral areas may be an important criterion that has otherwise been overlooked.

Stratigraphical occurrence. Duxbury (2001) recovered this species from the uppermost lower to upper Aptian of the North Sea.

Circulodinium*? *wulaganense (He Chengquan 1991) He Chengquan et al. 2009

(Fig. 15 H)

1991 *Canningia wulagenensis* He Chengquan, p. 57; pl. 9, fig. 16.

2009 *Circulodinium wulagenensis* (He Chengquan) He Chengquan et al., p. 272.

Comments. This species was originally described in Chinese and accompanied by a single illustration, which appears to show an areoligeracean with free-standing ornament, possible secondary folds, and a central area with significantly reduced ornament, perhaps due to corrosion. The archaeopyle, with operculum attached, appears to be located to the right in the photograph (He Chengquan 1991, pl. 9, fig. 16). We questionably retain this species in *Circulodinium*, but recommend that the name be restricted to the holotype, pending further study.

Stratigraphical occurrence. He Chengquan (1991) originally described this species from the Upper Cretaceous of China.

Genus ***Cyclonephelium*** Deflandre & Cookson 1955 emend. nov.

1954 *Cyclonephelium* Deflandre & Cookson, p. 1237; not validly published — no description.
1955 *Cyclonephelium* Deflandre & Cookson, p. 285.
1962 *Cyclonephelium* Deflandre & Cookson; emend. Cookson & Eisenack, p. 493–494.
1966 *Cyclonephelium* Deflandre & Cookson; emend. Williams & Downie, p. 223.
1977 *Cyclonephelium* Deflandre & Cookson; emend. Ioannides et al., p. 450.
1978 *Cyclonephelium* Deflandre & Cookson; emend. Stover & Evitt, p. 35.
1978 *Cyclonephelium* Deflandre & Cookson; emend. Sarjeant & Stover, p. 51.
1980 *Cyclonephelium* Deflandre & Cookson; emend. Dörhöfer & Davies, p. 41.
1990 *Cauveridinium* Khowaja-Ateequzzaman & Jain, p. 172, 174.

Type. Deflandre & Cookson 1955, pl. 2, fig. 12, as *Cyclonephelium compactum*.

Emended diagnosis. Areoligeracean cysts that are proximate to proximochorate, with ornament height less than 25% of maximum cyst width. Cyst dorsoventrally compressed, ambitus subcircular to lenticular, with a rounded to more commonly asymmetrical antapex and an apex that is rounded or with a horn; lateral horns lacking. Acavate. Ornamentation marginate in distribution, consisting of predominantly linear elements such as crests or ridges, or short to moderately long free-standing elements that are in part fused or connected to adjacent elements. Archaeopyle apical, with formula $A_{(1-4')}$, operculum free; parasulcal notch offset to the left.

Comments. Deflandre & Cookson (1955, p. 285) provided the following description for *Cyclonephelium*:

> Shell spheroidal, flattened, with an equatorial ornamentation that extends for varying distances from the equator but never to the poles. The ornament is composed of processes that are either distinct or close and confluent and sometimes connected by more or less broad trabeculae. Shell often provided with a large ill-defined lateral opening. [Translation]

The diagnosis of *Cyclonephelium* is emended here to restrict the genus to forms with ornament consisting of, at least in part, linear elements; the ornament is marginately arranged, with cysts having mid-ventral and mid-dorsal areas devoid of, or with substantially reduced ornamentation. *Circulodinium* has ornamentation marginately arranged, but elements are consistently free standing. *Aptea* has ornament that is predominantly linear, like *Cyclonephelium*, but its distribution is continuous and more or less uniform over the cyst, including ventral and dorsal surfaces. The emended diagnosis above also specifies that ornament height is less that 25% of the maximum cyst width. Thus we consider *Cauveridinium*, which has marginately distributed linear ornament, a taxonomic junior synonym of *Cyclonephelium*.

We consider the emendation of Cookson & Eisenack (1962, p. 493–494) as useful in moving toward the concept of *Cyclonephelium* expressed here, but not those by Williams & Downie (1966), Ioannides et al. (1977), Sarjeant & Stover (1978), Stover & Evitt (1978) and Dörhöfer & Davies (1980).

Accepted species.

Cyclonephelium? barbiferum Cookson & Eisenack 1982

(Fig. 15 I)

1982 *Cyclonephelium*? *barbiferum* Cookson & Eisenack, p. 42, pl. 7, figs 8–9.

2004 *Circulodinium barbiferum* (Cookson & Eisenack) Fauconnier in Fauconnier & Masure, p. 113.

Comments. Cookson & Eisenack (1982, p. 42) provided the following diagnosis for this species.

> Shape somewhat circular to weakly elliptical, with a short border with tuft-like processes, which are developed mainly in lateral areas and large central, apical and antapical areas [are] free [of processes], but there are no sharp borders. The processes are simple, branched, or variously expanded at the ends. They often form a small tuft. [Part, translation]

From the illustrations, processes in the tufts appear to be connected distally, and the type has its ?mid-ventral area largely devoid of processes. Hence, we retain this as a species of *Cyclonephelium*, albeit questionably because the nature of the archaeopyle is not clear.

Stratigraphical occurrence. The type material is from the Albian to Cenomanian of Australia.

Cyclonephelium compactum Deflandre & Cookson 1955

(Figs 7 A–J; 15 J)

1955 *Cyclonephelium compactum* Deflandre & Cookson, p. 285, pl. 2, figs 11–13; text-figs 44–46.
1969 *Cyclonephelium eisenackii* Davey, p. 170, pl. 8, figs 3–4; pl. 9, fig. 4; text-figs 16a–b.
1974 *Aptea eisenackii* (Davey) Davey & Verdier, p. 643.
1986 *Pseudoceratium eisenackii* (Davey) Bint, p. 145.

Emended diagnosis. A species of *Cyclonephelium* with marginate ornament formed by relatively low lamella-like projections that are generally joined to form an irregular network. Elements may be joined by short trabeculae.

Comments. This species has not been emended since the protologue was published; hence we propose an emended diagnosis here that accords with the current status of the species as a dinoflagellate cyst. As the type of the genus *Cyclonephelium*, a clear understanding of the ornament is critical. Deflandre & Cookson (1955) commented that:

> The appendages forming the equatorial [i.e. peripheral or marginal in modern terminology] ornamentation are generally short and joined to one another, forming lamella-like projections arranged either parallel to the equator [i.e. periphery] of the shell or in the form of an irregular network. Sometimes a series of processes are joined by short trabeculae.

From this description and the illustrations of the type material, it is clear that *Cyclonephelium compactum* is characterised by projections that are variously joined proximally and/or distally to produce irregular but predominantly linear elements; they are generally peripherally distributed, areas on the mid-ventral and mid-dorsal surfaces being devoid of, or with substantially reduced, ornament.

We consider *Cyclonephelium* (al. *Pseudoceratium*) *eisenackii* to be a taxonomic junior synonym of *Cyclonephelium compactum*; given the morphological range of *Cyclonephelium compactum* (Fig. 7A–J herein), any distinction would be difficult. The type of *Cyclonephelium eisenackii* belongs in *Cyclonephelium* because it lacks lateral prominences. Davey (1969, p. 170) noted that the "Greater part of shell surface [is] ornamented by complex network of low crests and short, capitate processes. In centre of both dorsal and ventral sides there is a circular area devoid of ornamentation."

Cookson & Eisenack (1974, p. 74) considered *Cyclonephelium eisenackii* to be a taxonomic junior synonym of *Aptea polymorpha.* However, *Aptea polymorpha* has ornamentation over the entire cyst surface. Indeed, this is the main difference between *Aptea polymorpha* and *Cyclonephelium compactum*.

Stratigraphical occurrence. The type material of *Cyclonephelium compactum* is from the Albian to Santonian of Australia. Davey (1969) described *Cyclonephelium eisenackii* from the upper Albian of Saskatchewan, Canada. Duxbury (2001) considered the stratigraphical range of a form he termed *Cyclonephelium compactum* (extreme) and which has more pronounced ornament than the type to be uppermost lower Aptian to lowermost Albian.

Cyclonephelium deconinckii Boltenhagen 1977

(Figs 15 K–L)

1977 *Cyclonephelium deconinckii* Boltenhagen, p. 52–53, pl. 4, figs 5a–b, 6.

Comments. Boltenhagen (1977, p. 52) diagnosed this species as follows: “Shell subcircular to polygonal, characterised by apical and antapical protuberances [i.e. horns], ornamented around the periphery by rows of appendages forming a perforate jagged margin; archaeopyle apical, operculum pointed [presumably because of the apical horn] [translation]. The morphology is not clear from the original illustrations, and hence this species should be restricted to the type material pending further study.

Stratigraphical occurrence. Boltenhagen (1977) recorded *Cyclonephelium deconinckii* from the Campanian of Gabon, Africa.

Cyclonephelium indicum (Khowaja-Ateequzzaman & Jain 1990) comb. nov.

(Figs 15 M–Q)

1990 *Cauveridinium indicum* Khowaja-Ateequzzaman & Jain, p. 174, 176; pl. 1, figs 1–6; pl. 2, fig. 6; pl. 3, figs 5–6; text-figs 1 A–D.

1990 *Cauveridinium intermedium* Khowaja-Ateequzzaman & Jain, p. 178, pl. 2, figs 1–5; text-figs 2 A–B.

1990 *Cauveridinium longispinosum* Khowaja-Ateequzzaman & Jain, p. 178–179, pl. 3, figs 1–4; text-fig. 3.

Comments. Khowaja-Ateequzzaman & Jain (1990) described this species, in part, as follows: “processes restricted to circumferential border zone, absent on central dorsal and central ventral areas … proximally connected through thick ridges and a few mostly on dorsal surface also laterally connected through septa ….” From illustrations in the protologue it appears that the ornament height is less than 25% of the maximum cyst width: hence we consider this species to belong to *Cyclonephelium* and *Cauveridinium* (of which this species is type) to be a taxonomic junior synonym of *Cyclonephelium*. Khowaja-Ateequzzaman & Jain (1990) described two other species of *Cauveridinium*, but these appear to intergrade with the type and may be differentiated only with difficulty. Hence we consider *Cauveridinium intermedium* and *Cauveridinium longispinosum* to be taxonomic junior synonyms of *Cyclonephelium* (al. *Cauveridinium*) *indicum*.

Stratigraphical occurrence. Khowaja-Ateequzzaman & Jain (1990) recorded this species (including synonyms) from the Turonian to Santonian of the Cauvery Basin, India.

Cyclonephelium intonsum Duxbury 1983

(Figs 7 K–L; 15 R)

1983 *Cyclonephelium intonsum* Duxbury, p. 33–34, pl. 2, fig. 7; pl. 10, fig. 12; text-figs 13–14.

Comments. Duxbury (1983, p. 33–34) described the ornament of this species as follows:

> A dense, low ornament covers the ventral periphery and takes the form of irregular granules or short coni which may coalesce laterally to produce a crude microreticulum. Some interruption of ornament may be observed laterally in a position corresponding to the paracingulum.

The marginate distribution of the ornament is very distinct. *Cyclonephelium maugaad* has a similar ornament, but it consists of hair-like processes and process bundles.

Stratigraphical occurrence. This species was originally described from the upper Aptian to lower Albian of England.

Cyclonephelium maugaad Below 1981

(Fig. 15 S)

1981 *Cyclonephelium maugaad* Below, p. 15, pl. 11, figs 2, 3a–b; pl. 15, fig. 20.

Comments. Below (1981, p. 15) gave the following diagnosis and description for *Cyclonephelium maugaad*.

> Diagnosis: proximate, nontabulate cyst, central body round to oval in outline, dorsoventrally compressed. Archaeopyle apical (A). With the exception of the dorsal and ventral areas, surface always covered with crispae [?]. No indications of paracingulum, parasulcus or polar [apical?] process. Description: The cyst shows the features characteristic of the genus, dorso-ventral compression and areas on the central dorsal and ventral sides always without ornament. For me the conspicuous feature that marks and differentiates this from all other species of the genus … is the markedly crispate (Lat. *crispus* = curly) form of the appendages. The appendages are straight or curved, sinuous, [with] irregularly beaded thickenings, and bear in part lateral sprays. They are isolated or, especially marginally, appear concentrated, in which case they are joined basally. A variant of the species bears crispae only at the antapex. The autophragm between processes is smooth. [Translation]

Stratigraphical occurrence. Below (1981) recorded *Cyclonephelium maugaad* from the Hauterivian to Aptian of southwestern Morocco.

Cyclonephelium membraniphorum Cookson & Eisenack, 1962b

(Fig. 15 T)

1962b *Cyclonephelium membraniphorum* Cookson & Eisenack, p. 495, pl. 6, figs 8–14.
2004 *Cauveridinium membraniphorum* (Cookson & Eisenack) Masure in Fauconnier & Masure, p. 97.

Comments. This species is characterised by marginate membranes that (according to Cookson & Eisenack 1962b, p. 495) are:

> … supported by … widely spaced, equidistant, radial fibres. These fibres arise from the

> peripheral surfaces of the shell, and their bases are connected … tangentially. They are simple or capitate and relatively stout. …. Occasionally a union between … fibres [forms] wide funnel-like structures.

Masure in Fauconnier & Masure (2004) transferred this species to *Cauveridinium*. But since we now consider *Cauveridinium* to be a taxonomic junior synonym of *Cyclonephelium*, we retain this species in the latter genus.

Stratigraphical occurrence. Cookson & Eisenack (1962b) recorded this species from the Albian to Cenomanian of Australia.

Cyclonephelium*? *operculatum Yu Jingxian 1982

(Fig. 16 A)

1982 *Cyclonephelium operculatum* Yu Jingxian, p. 252–253, pl. 7, figs 20–22.

2004 *Cyclonephelium*? *operculatum* Yu Jingxian; Fauconnier & Londeix in Fauconnier & Masure, p. 147.

Comments. Fauconnier & Londeix in Fauconnier & Masure (2004) considered this a problematic species. We agree, and hence concur that its assignment to *Cyclonephelium* is questionable. We recommend that use of this name be restricted to the type material.

Stratigraphical occurrence. Yu Jingxian (1982) described this species from the Upper Jurassic–Lower Cretaceous of China.

Genus ***Senoniasphaera*** Clarke & Verdier 1967 emend. nov.

1967 *Senoniasphaera* Clarke & Verdier, p. 61.

Type. Clarke and Verdier, 1967, pl. 14, fig.8, as *Senoniasphaera protrusa*.

Emended diagnosis. Areoligeracean cysts that are proximate, dorsoventrally compressed; central body lenticular, with asymmetrical to rounded antapex and a generally short apical prominence. Holocavate with generally wide pericoel; the connections between endophragm and periphragm are absent or sparsely distributed and may be in linear (septa) or isolated elements (pillars). Periphragm generally continuous, but may be perforate, generally smooth or with ornamentation of low relief. Archaeopyle apical, with formula $A_{(1-4')}$, operculum free or attached; parasulcal notch offset to the left.

Comments. This genus has generally been used for cavate areoligeraceans without connections between wall layers, as implied in the original diagnosis by Clarke & Verdier (1967, p. 61), who wrote:

> Inner body round or oval. Outer membrane is extended from the inner body to form one apical, two antapical and often two lateral horns. The inner body frequently protrudes into the apical and antapical horns. Tabulation present. Girdle and longitudinal furrow present. Archaeopyle apical.

Clarke & Verdier (1967) did not mention connections between wall layers in the generic diagnosis. However, they described the type, *Senoniasphaera protrusa*, as having pillars connecting the two walls. Thus, separation of *Senoniasphaera* from *Canningia*, which is also a cavate areoligeracean with connections between wall layers, is somewhat problematic. The two genera have been used for broadly different morphologies, with *Senoniasphaera* tending to have broad pericoels and sparse supports between walls, whereas *Canningia* generally encompasses forms with a much narrower pericoel and dense supports. In order to maintain the current usage we have emended the diagnosis of *Senoniasphaera* to reflect these broad differences while adding the possible presence of structures between wall layers.

Senoniasphaera? clavellii Bailey et al. 1997

(Fig. 16 B)

1997 *Senoniasphaera clavellii* Bailey et al., p. 236, 239, figs 4d–h.

Comments. This species does not clearly show the asymmetry characteristics of an areoligeracean cyst. Because of this observation, we only questionably retain the species in *Senoniasphaera*.

Stratigraphical occurrence. Bailey et al. (1997) recorded *Senoniasphaera clavellii* from the upper Kimmeridgian of Dorset, England.

Senoniasphaera congrensa (Prince et al. 2008) stat. nov.

(Figs 16 C–D)

2008 *Senoniasphaera protrusa* subsp. *congrensa* Prince et al., p. 90, pl. 2, figs 1–3.

Comments. Prince et al. (2008, p. 90) defined this taxon as follows: "An elongate subspecies of *Senoniasphaera protrusa* in which the inner body is oval with a slight antapical protuberance on the centre line so that the inner body is vertically symmetrical." In their description, Prince et al. (2008) referred to the presence of a "small number of pillars" between wall layers. Prince et al. (2008) appeared to treat this taxon as a species rather than a subspecies, stating:

> The two most similar species [sic.] are [*Senoniasphaera*] *protrusa* and *Senoniasphaera macroreticulata*. *Senoniasphaera protrusa* has an inner body that has two antapical horns of unequal size, giving the inner body an asymmetrical shape. *Senoniasphaera macroreticulata* … has distinctive pillars that are elongate, slender or broad, perforate and fibrous. The cavities between these pillars have an irregular shape.

By raising this subspecies to species rank, the autonym, *Senoniasphaera protrusa* subsp. *protrusa* becomes redundant.

Stratigraphical occurrence. Prince et al. (2008) recorded this taxon from the uppermost Santonian of southeastern England.

Senoniasphaera? edenensis Marshall 1990a

(Figs 16 E–G)

1990a *Senoniasphaera edenensis* Marshall, p. 18, figs 9A–E, 15L–W.

Comments. Marshall (1990a, p. 18) noted that this species has “Scattered solid pillars [that] extend normally between wall layers around periphery of cyst ….” The presence of lateral prominences may indicate that *Senoniasphaera edenensis* is a ceratiacean rather than an areoligeracean, and thus we question its generic assignment. Marshall (1990a) provided additional information about the wall structure, noting that the pillars are:

> … tapering towards [their?] midlength where they are usually up to 1 µm thick. Additional finer pillars occur … around the edges of the middorsal and midventral surfaces where wall layers are in close proximity. Endophragm smooth …. Periphragm ... bearing numerous perforations and circular, shallow pits. …. Perforations close spaced and extremely fine … where layers are appressed, becoming larger and … [sparser] where separated.

Stratigraphical occurrence. Marshall (1990a) recorded this species from the Campanian of southeastern Australia.

Senoniasphaera filoreticulata (Slimani 1994) comb. nov.

(Figs 16 I–L)

1994 *Canningia filoreticulata* Slimani, p. 96–97, pl. 15, figs 1–6.

1999 *Cyclonephelium filoreticulatum* (Slimani) Prince et al., p. 164.

Comments. Slimani (1994, p. 96) diagnosed this species as follows:

> Cyst of *Canningia*, lenticular, with two antapical protrusions, of which the one on the left is often better developed. It is characterised by a reticulate ectophragm [i.e.

> periphragm in our terminology] supported by processes and fibroreticulate septa, well-spaced and reaching a height of about 1/5th of the total diameter. Except for the archaeopyle, paratabulation is apparently absent. [Translation]

This species thus appears to have a periphragm supported by septa and possibly processes, although it is unclear to us whether the processes described by Slimani (1994) are true projections or junctions of the septa. In transferring the species from *Canningia* to *Cyclonephelium*, Prince et al. (1999, p. 164) cited the absence of processes or septa in dorsoventral areas, the most similar species being *Cyclonephelium membraniphorum*, "… which differs by having pillars that are simple or acuminate, not expanded and anchor-shaped as in *C. filoreticulatum*." Prince et al. (1999) also referred to the wide wall [layer] separation in *Cyclonephelium filoreticulatum*, acknowledging the cavate nature of the species. Given its cavate nature of this species, the wide pericoels and relatively widely spaceds supporting structures, we reassign it to *Senoniasphaera*.

Stratigraphical occurrence. Slimani (1994) recorded this species from the Campanian of Belgium and southern Netherlands.

Senoniasphaera inornata (Drugg 1970) Stover & Evitt 1978

(Fig. 16 H)

1970 *Chiropteridium inornatum* Drugg, p. 811–812, figs 3C–F.
1978 *Senoniasphaera inornata* (Drugg) Stover & Evitt, p. 80.

Comments. Drugg (1970, p. 811–812) described this species as a double-walled cavate cyst. He noted that the endocyst was spherical to somewhat flattened, with weak antapical lobes possibly present. The periphragm is smooth and appressed to the endophragm dorsoventrally, but with a pericoel ambitally. He noted that "Sparse and faint supporting processes are sometimes present in a lateral position. The species is very similar to, and possibly a taxonomic junior synonym of, *Senoniasphaera lordii*.

Stratigraphical occurrence. Drugg (1970) recorded *Senoniasphaera inornata* (as *Chiropteridium inornatum*) from the Danian of Alabama, USA. Powell (1992) indicated that the FAD of the species is in the Cretaceous and that its LAD is within the Danian (NP4 Zone). Williams et al. (2004) placed its FAD immediately above the base of the Danian and its LAD in the middle Danian in Northern Hemisphere mid-palaeolatitudes.

Senoniasphaera jurassica (Gitmez & Sarjeant 1972) Lentin & Williams 1976

(Figs 16 M–N)

1972 *Hexagonifera jurassica* Gitmez & Sarjeant, p. 240–241, pl. 14, figs 5, 8.
1976 *Senoniasphaera jurassica* (Gitmez & Sarjeant) Lentin & Williams, p. 85.
1979 *Ambonosphaera jurassica* (Gitmez & Sarjeant) Fensome, p. 51.
1992 *Senoniasphaera jurassica* (Gitmez & Sarjeant); emend. Poulsen & Riding, p. 28.

Comments. This species was originally diagnosed in part by Gitmez & Sarjeant (1972, p. 240) as being cavate, with a delicate, smooth or minutely granular periphragm and a thick, densely granular endophragm with occasional tubercles. The emendation of Poulson & Riding (1992, p. 28) stressed the circumcavate wall structure, the lenticular shape, the occasional presence of an antapical claustrum, the partially developed paratabulation, and the markedly offset parasulcal notch.

Stratigraphical occurrence. Gitmez & Sarjeant (1972) recovered *Senoniasphaera* (as *Hexagonifera*) *jurassica* from the middle Kimmeridgian of England. Riding & Thomas (1992) placed the FAD of the species at the base of the Kimmeridgian and the LAD within the Portlandian (Tithonian). Stover et al. (2004) plotted its range as earliest Kimmeridgian to middle Portlandian (late Tithonian).

Senoniasphaera lordii (Cookson & Eisenack 1968) Lentin & Williams 1976

(Fig. 16 O)

1968 *Ascodinium lordii* Cookson & Eisenack, p. 112, figs 1I–K.
1976 *Senoniasphaera lordii* (Cookson & Eisenack) Lentin & Williams, p. 102.

Comments. Cookson & Eisenack (1968, p. 112) described the periphragm as "thin and more or less granular" and the endophragm as "… somewhat thicker and smooth, except near the margins where, in most specimens, a more or less coarse, somewhat finely reticulate pattern is evident." The species is very similar to, and possibly a taxonomic senior synonym of, *Senoniasphaera inornata*.

Stratigraphical occurrence. Cookson & Eisenack (1968) recovered this species from the Santonian to lower Campanian of Western Australia.

Senioniasphaera macroreticulata Prince et al. 2008

(Figs 16 Q–R)

2008 *Senoniasphaera macroreticulata* Prince et al., p. 90, pl. 1, figs 7–10.

Comments. Prince et al. (2008, p. 90) provided the following diagnosis for *Senoniasphaera macroreticulata*.

> A species of *Senoniasphaera* with a densely reticulate outer body connected to the inner body by fairly long fibrous pillars. The cavities between these pillars are rectangular to sub-rectangular in shape but never oval or rounded as in *Senoniasphaera protrusa*. Paratabulation may be indicated on the dorsal side by a concentration of ornamentation. However, this is often obscured by the densely reticulate outer body.

Although the paratype (Prince et al. 2008, figs 9–10) shows relatively dense interconnections between wall layers, in the holotype (Prince et al. 2008, figs 7–8) these structures appear to be sparse. Moreover, the pericoel in this species is wide. Hence we retain it in *Senoniasphaera*.

Stratigraphical occurrence. Prince et al. (2008) recorded this species from the upper Santonian to lower Campanian of England.

Senoniasphaera microciliata (Jain 1977) comb. nov.

(Fig. 16 P)

1977 *Canningia microciliata* Jain, p. 178, pl. 3, fig. 25; pl. 6, fig. 78.

1987 *Canningia*? *microciliata* Jain; Helby, p. 324–325.

Comments. Jain (1977, p. 178) noted that the periphragm "… is densely ornamented with fine cilia having bulbous base …" giving the cyst a "… coarsely granulate appearance." This species is clearly cavate, with no sign of connections between wall layers. Hence we transfer it to *Senoniasphaera*.

Stratigraphical occurrence. Jain (1977) described this species from the lower Albian of southern India.

Senoniasphaera microreticulata Brideaux & McIntyre 1975

(Figs 8 A–B, 17 A–C)

1975 *Senoniasphaera microreticulata* Brideaux & McIntyre, p. 35, pl. 11, figs 7–12; pl. 12, figs 1–8.

1981 *Canningia microreticulata* (Brideaux & McIntyre) Below, p. 31.

1981 *Senoniasphaera microreticulata* Brideaux & McIntyre; Lentin & Williams, p. 33.

Comments. This very distinctive species is circumcavate, "… the periphragm microreticulate and generally closely appressed to the thicker microreticulate endophragm" (Brideaux & McIntyre 1975, p. 35). It resembles forms of *Canningia* in having a narrow periocoel and a microreticulate periphragm. However, as the wall layers lack connections, we follow Lentin & Williams (1981) in retaining this species in *Senoniasphaera*.

Stratigraphical occurrence. Brideaux & McIntyre (1975) described *Senoniasphaera microreticulata* from the lower to middle Albian of the Northwest Territories (former District of Mackenzie), Canada.

Senoniasphaera palla Louwye 1997

(Figs 16 S–T)

1997 *Senoniasphaera palla* Louwye, p. 153, pl. 2, figs 3, 6.

Comments. In his diagnosis for this species Louwye (1997, p. 153) reported that “The endophragm forms low, solid and pillarlike protrusions which support the periphragm and mark subcircular thickenings on the periphragm.” However, connections between wall layers are sparse, so we retain this species in *Senoniasphaera*.

Stratigraphical occurrence. Louwye (1997) described this species from the Turonian of Belgium.

Senoniasphaera protrusa Clarke & Verdier 1967

(Fig. 17 D)

1967 *Senoniasphaera protrusa* Clarke & Verdier, p. 61–62, pl. 14, figs 7–9; text-fig. 24.
1999 *Senoniasphaera protrusa* Clarke & Verdier; emend. Prince et al., p. 161.

Comments. This species is the type of *Senoniasphaera* and was defined by Clarke & Verdier (1967, p. 61) as “A species of *Senoniasphaera* in which the inner body protrudes into the apical and antapical horns.” They noted that “The outer membrane is attached to the inner body mostly on the dorsal and ventral sides by a series of perforated pillars which may be so short as to be hardly visible.” Because of the lack of prominence of the interconnecting pillars and the broad pericoel, we retain this species.

Stratigraphical occurrence. Clarke & Verdier recorded *Senoniasphaera protrusa* from the Santonian of southern England. Costa & Davey (1992) gave its stratigraphical range as late Santonian to latest Campanian. Stover et al. (1996) considered it to be of Santonian to earliest Maastrichtian age. Williams et al. (2004) placed its FAD in the basal Santonian and its LAD in the early Campanian.

Senoniasphaera ptomatis Helby, May & Partridge in Helby 1987

(Figs 17 E–H)

1987 *Senoniasphaera ptomatis* Helby, May & Partridge in Helby, p. 319–321, figs 25A–S, 26.

Comments. Helby, May & Partridge in Helby (1987, p. 319–320) noted that the cyst wall is "… 2-layered, circumcavate; outlines of endophragm and periphragm essentially similar. Endophragm smooth, scabrate or granulate. Periphragm smooth, perforate or granulate in most regions, occasionally with low granular to rugoreticulate pandasutural ridges." No mention is made of elements connecting the wall layers, and none are apparent from most of the figures, including the holotype. Thus this species is readily accommodated in *Senoniasphaera*.

Stratigraphical occurrence. This species was described from the middle Berriasian of Australasia.

Senoniasphaera? reticulata (Khanna & Singh 1981) Lentin & Williams 1993

(Fig. 17 I)

1981 *Hexagonifera reticulata* Khanna & Singh, p. 391, fig. 1, nos 4, 6; text-fig. 3.
1993 *Senoniasphaera*? *reticulata* (Khanna & Singh) Lentin & Williams, p. 591.

Comments. Khanna & Singh (1981, p. 391) made the following statement in the diagnosis of this species regarding the wall structure: "… endophragm thick, broadly reticulate forming subcircular body; periphragm in the form of a thin, transparent membrane enclosing the body." They also remarked that "The periphragm … is detachable and occasionally … found separately in the form of a thin transparent sac. The lumina of the reticulum are narrow on the central part of the body whereas they widen out towards the periphery." As the wall layers are thus apparently unconnected, we retain this species in *Senoniasphaera*, although it closely resembles some reticulate species of *Canningia*. For that reason we follow Lentin & Williams (1993) in questioning the generic assignment.

The name *Hexagonifera reticulata* was not validly published in Singh et al. (1979, p. 35–

36), Khanna (1979, p. 216) and Khanna et al. (1981, p. 261) since no description was provided. This species is not synonymous with its invalid homonym *Senoniasphaera*? *reticulata* (see Wilson in Masure 1985, caption to fig.1b — p.202).

Stratigraphical occurrence. Khanna & Singh (1981) recovered this species from the Lower to Middle Eocene of northern India.

Senoniasphaera*? *turensis Vasilyeva in Andreeva-Grigorovich et al. 2011

(Fig. 17 J)

2011 *Senoniasphaera turensis* Vasilyeva in Andreeva-Grigorovich et al., p. 34, pl. 2, fig. 6.

Comments. Vasilyeva in Andreeva-Grigorovich et al. (2011, p. 34) provided the following description for this species:

> Pericyst almost round, with barely noticeable antapical horns. Pericyst outline seems to be jagged, slightly wavy. Endocyst is round, coinciding in shape with pericyst. Pericoel is very narrow, slightly expanded antapically. Periphragm is quite dense, transparent and forms wrinkles over the whole surface and, typical for this species, has small folds over the whole pericyst outline, which look like a range of open perforations in the pericoel. Periphragm is occasionally perforated. Endophragm is quite dense, single-layered, smooth. Periarchaeopyle is apical (type tA). Operculum is attached or absent. Archaeopyle outline is uneven. Paratabulation is expressed by the archaeopyle; small wrinkles of the periphragm indicate the paracingulum. [Translation courtesy Alina Iakovleva, personal communucation]

It is unclear whether connections exist between the wall layers, both from the description and illustration. For this reason, because the pericoel is narrower than is typical for *Senoniasphaera*, and because the single specimen illustrated shows no unequivocal features of areoligeracean affinity, we question the assignment of this species to *Senoniasphaera*.

Stratigraphical occurrence. This species was originally described from the Danian of the southern Ural Mountains, Russia.

Senoniasphaera turonica (Prössl 1990 ex Prössl 1992) Pearce et al. 2011

(Figs 17 K–L)

1990 *Craspedodinium turonicum* Prössl, p. 108–109, pl. 16, figs 1–2, 6–7 (name not validly published; holotype not designated).
1992 *Craspedodinium turonicum* Prössl ex Prössl, p. 114.
2003 *Senoniasphaera rotundata* subsp *alveolata* Pearce et al., p. 301–302, pl. 2, figs 6–7.
2011 *Senoniasphaera turonica* (Prössl ex Prössl) Pearce et al., p. 92.

Comments. In describing this species (as *Craspedodinium turonicum*), Prössl (1990) noted that "A rough to fine-mesh reticulum on the inside of the ectophragm [i.e. periphragm] is partially connected to the endophragm by round or elongate columns" (translation by Pearce et al. 2011, p. 91). Pearce et al. (2011) transferred this species to *Senoniasphaera* and considered *Senoniasphaera rotundata* subsp *alveolata* to be a taxonomic junior synonym.

Stratigraphical occurrence. Prössl (1990) recovered this species from the Turonian of northwestern Germany. Pearce et al. (2003) recorded *Senoniasphaera rotundata* subsp *alveolata* from the lower Turonian of England.

Genus ***Tenua*** Eisenack 1958 emend. nov.

1958 *Tenua* Eisenack, p. 410.
1966 *Doidyx* Sarjeant, p. 205–206.
1968 *Tenua* Eisenack; emend. Sarjeant, p. 230–231.
1972 *Tenua* Eisenack; emend. Pocock, p. 94.
1985 *Tenua* Eisenack; emend. Sarjeant, p. 94.
non 1978 *Tenua* Davey, p. 894.

Type. Eisenack 1958, pl. 23, fig. 1, as *Tenua hystrix*.

Emended diagnosis. Areoligeracean cysts that are proximate to proximochorate; central body dorsoventrally compressed, with a subcircular, broadly subovoidal to asymmetrically lenticular ambitus, usually with an apical horn; posteriorly rounded to asymmetrical, with one or two weak to moderately developed antapical horns. Ornamentation absent or consists of free-standing elements, some of which may be aligned to reflect aspects of tabulation; however, processes are more or less uniformly distributed or present but may be substantially reduced in density in dorsoventral areas. Archaeopyle apical, type $A_{(1-4')}$, operculum free; parasulcal notch offset to the left.

Comments. As we have noted, intergradation is a major problem in the *Cyclonephelium* group of genera. This problem is exacerbated when the type of a key genus has an unclear or "intermediate" morphology. Such is the case for the holotype of *Tenua hystrix*, the type of *Tenua* Eisenack 1958. *Tenua* is one of the earliest generic names in the group, but its morphology, especially process distribution, has been much debated, despite the fact that several authors have published new photographs of the type. After reviewing these images (referenced in the introductory sections), we conclude that the dorsoventral areas of the type are not devoid of ornament (as is the case in *Circulodinium*), although it is not uniformly distributed or distributed to clearly reflect tabulation (as in *Cerbia* and *Canningopsis*). Hence we propose the use *Tenua* for forms in which the ornament extends over the dorsovental areas, whether densely and uniformly or in a somewhat reduced and patchy manner, as in the type of *Tenua hystrix*. We consider that this retains to some extent the early intent and usage of the genus and will cause fewer taxonomic problems than would alternative interpretations. We emend the generic diagnosis accordingly.

Sarjeant (1966, p. 205–206) provided the following original diagnosis for *Doidyx*.

> Proximate dinoflagellate cysts with flattened biconical shell, pronouncedly asymmetrical. Epitract in form of high cone which may be drawn out into an apical horn, giving a mammillate appearance: hypotract in form of flattened cone, with or

> without antapical prominence. Shell bulging out to one side more than the other; lateral horns lacking. Greater part of shell covered with short spines, simple or bifurcate: arrangement is in general random, but sometimes in rows, suggesting traces of tabulation. Equatorial zone, corresponding to cingulum, lacking spines: not hollowed. No pattern of sutures visible, no clear indication of sulcus. Apical archaeopyle formed by schism of shell on angular line of breakage.

This diagnosis largely parallels our concept of *Tenua*, and hence we treat *Doidyx* as a junior synonym of the former genus; but the type of *Doidyx*, the holotype of *Doidyx anaphrissa*, better fits our concept of *Tenua*.

Sarjeant & Stover (1978) and Bint (1986) considered *Doidyx* to be a taxonomic junior synonym of *Aptea* and *Pseudoceratium* respectively. However, *Pseudoceratium* has a distinct lateral horn and *Aptea* has linear ornament. Although the type of *Doidyx* has a lateral bulge, Sarjeant (1966) stated unequivocally that the species lacks a lateral horn, as is apparent from the type.

Accepted species.

Tenua anaphrissa (Sarjeant 1966) Benedek 1972

(Figs 9 D–H; 17 M)

1966 *Doidyx anaphrissa* Sarjeant, p. 206, pl. 22, fig. 8; pl. 23, fig. 6; text-fig. 55.
1972 *Tenua anaphrissa* (Sarjeant) Benedek, p. 9–10.
1978 *Aptea anaphrissa* (Sarjeant) Sarjeant & Stover, p. 51.
1978 *Cyclonephelium distinctum* subsp. *longispinatum* Davey, p. 894, pl. 3, figs 7–8 [non fig. 4].
1986 *Pseudoceratium anaphrissum* (Sarjeant) Bint, p. 145.
1989 *Circulodinium distinctum* subsp. *longispinatum* (Davey) Lentin & Williams, p. 63.
1990 *Pseudoceratium anaphrissum* (Sarjeant); emend. Harding, p. 17–18.
2004 *Cyclonephelium longispinatum* (Davey) Fauconnier in Fauconnier & Masure, p. 146.

Comments. Sarjeant (1966, p. 207) erected *Doidyx anaphrissa* and noted that it has:

> … a dense cover of short spines, most often capitate, less frequently evexate, oblate, bifid or bifurcate: these sometimes suggest arrangement into lines, but no coherent pattern was determined. An equatorial belt … corresponding to the cingulum, lacks spines.

The equatorial belt that, according to Sarjeant (1966), is devoid of spines is more apparent on his interpretative drawing than on his photographs, and we do not consider this constitutes a dorsoventral area devoid of ornament. We retain this species in *Tenua* as we consider *Doidyx* to be a taxonomic junior synonym of *Tenua*. This species accommodates forms of *Tenua* with slender, sometimes hair-like processes typically 4–10 µm long. *Tenua hystrix* has shorter, generally stubbier processes. The ambital outline of both species, as conceived herein, is variable.

In proposing *Cyclonephelium distinctum* subsp. *longispinatum* (subsequently *Cyclonephelium longispinatum*), Davey (1978, p. 894) noted that it was "… a subspecies … having a denser covering of long spines [presumably in comparison with the type subspecies?] which extend well on to the dorsal and ventral surfaces leaving only small areas devoid of processes". Because of its lack of dorsoventral areas clearly devoid of ornament and its hair-like processes, we consider this taxon to be a taxonomic junior synonym of from *Tenua anaphrissa*.

Stratigraphical occurrence. Sarjeant (1966) described *Doidyx anaphrissa* from the lower Barremian of Yorkshire, England. Costa & Davey (1992) plotted the FAD of this species near the base of the early Barremian and its LAD within the earliest late Barremian. The type material of *Cyclonephelium distinctum subsp. longispinatum* is from the Turonian of offshore southwestern Africa.

Tenua*? *apiculata (Jain & Garg in Jain et al. 1984) comb. nov.

(Fig. 17 N)

1984 *Canningia apiculata* Jain & Garg in Jain et al., p. 71–72, pl. 2, figs 27–29.

Comments. From the illustrations in Jain et al. (1984), this species appears to be an areoligeracean despite its early age, with the type having an asymmetrical antapex. It has a single wall layer and is thus not attributable to *Canningia* under the current concept of that genus. In the diagnosis, Jain & Garg in Jain et al. (1982, p. 71) noted the following: “processes short, distally truncate to bifid, distantly placed; crest well developed …”. In their remarks, the authors refer to ornamentation “with curved ridges”. Although the spines are evident on the illustrations and appear to be more or less uniform in distribution, but the nature of the “crest” and “curved ridges” are unclear, we tentatively transfer this species to *Tenua* and suggest that it be restricted to the type material until its morphology can be clarified.

Stratigraphical occurrence. The type material of *Tenua*? *apiculata* is from the Kimmeridgian to lower Tithonian of India.

Tenua*? *araneosa (Brideaux 1977) comb. nov.

(Figs 17 O–P)

1977 *Cleistosphaeridium araneosum* Brideaux, p. 22–23, pl. 9, figs 1–3.
1993 *Heterosphaeridium araneosum* (Brideaux) Islam, p. 84.
2004 *Circulodinium*? *araneosum* (Brideaux) Fauconnier in Fauconnier & Londeix in Fauconnier & Masure, p. 115.

Comments. Although we have transferred this species to *Tenua* based on its overall, albeit sparse, cover of ornament, we do so questionably because the species is not convincingly an areoligeracean. It has a rounded ambitus and the archaeopyle, at least from the illustrations, is not clearly apical.

Stratigraphical occurrence. Brideaux (1977) described this species from the Aptian and Albian of the Northwest Territories, former District of Mackenzie, Canada.

Tenua*? *asymmetrica (Burger 1980) comb. nov.

(Fig. 17 Q)

1980. *Cyclonephelium asymmetricum* Burger, p. 270, figs 6c, 7a–c.
2000 *Circulodinium asymmetricum* (Burger) He Chengquan & Sun Xuekun, p. 52.

Comments. Burger (1980) noted that:

> Tiny processes [i.e. spines] occur sparsely in equatorial region; mid-ventral and mid-dorsal areas largely free from ornament. Processes unevenly scattered and occasionally aligned, presumably along parasutures, usually more closely together and larger in antapical region.

From the illustrations of Burger (1980) of this species, the mid-dorsoventral areas devoid of spines are not readily apparent, but the holotype appears to show significant alignment of spines. Although we have transferred this species to *Tenua*, we do so provisionally because the distribution of ornament is not clear. The loose but occasionally aligned ornament is reminiscent of that of *Canninginopsis*? *monile*.

Stratigraphical occurrence. The type material of this species is from the Neocomian of Queensland, Australia.

Tenua*? *attadalica (Cookson & Eisenack 1962) comb. nov.

(Fig. 17 R)

1962 *Cyclonephelium*? *attadalicum* Cookson & Eisenack, p. 495, pl. 5, figs 12–15.
1974 *Aptea attadalica* (Cookson & Eisenack) Davey & Verdier, p. 643.
1978 *Canningia attadalica* (Cookson & Eisenack) Stover & Evitt, p. 24–25.
1987 *Circulodinium attadalicum* (Cookson & Eisenack) Helby, p. 324–325.

Comments. Cookson & Eisenack (1962, p. 495) commented:

> Surface ornamented with small, stiff, frequently capitate appendages which tend to

> be grouped at intervals around the shell, especially in the antapical region. The central portions of both surfaces are relatively free from appendages except in the equatorial region of one surface, which … is crossed by two rows of appendages that appear to delimit a girdle-like zone [i.e. the cingulum].

In terms of our generic criteria, this species is difficult to interpret, especially the holotype. As Cookson & Eisenack (1962) indicated, the spines seem to be clumped, and the dorsal and ventral surfaces have relatively sparse ornamentation. However, the holotype appears to have a clump of processes in the dorsoventral area. Given this uncertainty, we questionably transfer this species to *Tenua*.

Stratigraphical occurrence. The type material of this species is from the Aptian and Albian of Australia.

Tenua chinensis (He Chengquan 1991) comb. nov.

(Fig. 17 S)

1991 *Canningia chinensis* He Chengquan, p. 54–55, pl. 9, figs 17–18.
2009 *Circulodinium chinense* (He Chengquan) He Chengquan et al, p. 268.

Comments. We transfer this species to *Tenua* because it has an overall cover of isolated ornament. It closely resembles *Tenua hystrix*, but the Middle Eocene age of the type material of *Tenua chinensis* makes synonymy unlikely.

Stratigraphical occurrence. He Chengquan (1991) recovered this species from the Middle Eocene of Xinjiang, China.

Tenua colliveri (Cookson & Eisenack 1960) comb. nov.

(Figs 9 A–C; 17 T)

1960 *Canningia colliveri* Cookson & Eisenack, p. 251, pl. 38, figs 3–4.
1987 *Circulodinium colliveri* (Cookson & Eisenack) Helby, p. 324–325.

1988 *Canninginopsis colliveri* (Cookson & Eisenack) Backhouse, p. 77.

Comments. Cookson & Eisenack (1960, p. 251) noted that the thin autophragm is "… granular or closely to sparsely spinulate." The illustration of the holotype (Cookson & Eisenack 1960, pl. 38, fig. 4) appears to show a relatively thick wall with predominantly and evenly granular ornamentation. The other illustrated specimen (pl. 38, fig. 3) appears to have a partially vermiculate ornamentation and may not be conspecific with the holotype. We transfer this species to *Tenua* because it has an overall cover of unit ornament.

Stratigraphical occurrence. The type material is from the Aptian of Queensland, Australia.

Tenua compta (Davey 1982) comb. nov.

(Fig. 18 A)

1982 *Canningia compta* Davey, p. 268, pl. 8, figs 3–6.

1987 *Circulodinium comptum* (Davey) Helby, p. 324–325.

Comments. We transfer this species to *Tenua* because of its overall foveolate and verrucate ornamentation. Davey (1982, p. 268) noted that the ornament is "… less pronounced towards the centre of the dorsal postcingular paraplate and the parasulcal region." But from the illustrations of the type material, it is clear that the ornament continues across these areas, and there is no visibly defined area devoid of ornament.

Stratigraphical occurrence. This species was originally described from the lower Portlandian (Tithonian) to lowermost Valanginian of subsurface Denmark.

Tenua copei (Bailey et al. 1997) comb. nov.

(Fig. 18 B)

1997 *Circulodinium copei* Bailey et al. 1997, p. 235–236, figs 3a–f.

Comments. We transfer this species to *Tenua* because it has an overall cover of non-linear ornament. Bailey et al. (1997, p. 235) commented that "The wall is thick (1–2 µm) and variably structured, appearing intraperforate to spongiose …, sometimes with short spines." And that "The surface of the wall may appear microreticulate." The authors noted that the paracingulum and parasulcus may be indicated, but otherwise they saw no reflection of the tabulation. Bailey et al. (1997, p. 235) listed "*Chytroeisphaeridia mantellii* Ioannides et al." as a synonym of this species; however, this was presumably in reference only to specimens that Ioannides et al. (1977) had assigned to *Chytroeisphaeridia mantellii* Gitmez & Sarjeant 1972.

Stratigraphical occurrence. Bailey et al. (1997) recorded this species originally from the upper Kimmeridgian of England.

Tenua densebarbata (Cookson & Eisenack 1960) comb. nov.

(Fig. 18 C)

1960 *Cyclonephelium densebarbatum* Cookson & Eisenack, p. 253, pl. 38, figs 9–10.

2004 *Circulodinium densebarbatum* (Cookson & Eisenack) Fauconnier in Fauconnier & Masure, p. 114.

Comment. Cookson & Eisenack (1960, p. 253) described this species as having "… a broad … peripheral zone ornamented … with short, densely arranged, rod-shaped bristles ranging from c. 2–12 µm in length, with simple, usually capitate or sometimes bifurcate ends, and inner areas without bristles but with granular surfaces." They noted that *Cyclonephelium* (now *Tenua*) *densebarbatum* differs from *Cyclonephelium* (now *Circulodinium*) *distinctum* in the stouter nature of the shell and the much denser ornament; it is also significantly older. The two specimens of *Tenua densebarbata* illustrated by Cookson & Eisenack (1960) appear to have a thickened wall dorsoventrally.

Stratigraphical occurrence. Cookson & Eisenack (1960) described this species from the Oxfordian to lower Kimmeridgian of Western Australia.

Tenua dubia Jain & Millepied 1975

(Fig. 18 D)

1975 *Tenua dubia* Jain & Millepied, p. 152, pl. 5, figs 75–76.
1978 *Cyclonephelium dubium* (Jain & Millepied) Stover & Evitt, p. 52.
2004 *Cyclonephelium*? *dubium* (Jain & Millepied) Fauconnier & Londeix in Fauconnier & Masure, p. 147.

Comments. Jain & Millepied (1975, p. 152) described this species as being "… covered with long, bifurcate processes. As the species lacks dorsoventral areas devoid of ornament and the ornament is less that 25% of the maximum cyst width, we retain it in *Tenua*.

Stratigraphical occurrence. Jain & Millepied (1975) recovered this species from the Campanian–Maastrichtian of western Africa.

Tenua*? *elongata (He Chengquan 1991) comb nov.

(Fig. 18 E)

1991 *Canningia elongata* He Chengquan, p. 55, pl. 9, fig. 1.
2009 *Circulodinium elongatum* (He Chengquan) He Chengquan et al., p. 270.

Comments. We transfer this species to *Tenua* as its ornament appears to consist of an even covering of free-standing elements. However, the morphology of the holotype is unclear, and so we question the generic assignment and recommend that the name be restricted to the holotype.

Stratigraphical occurrence. He Chengquan (1991) recorded this species from the Turonian of Xinjiang, China.

Tenua hystrix Eisenack 1958 emend. nov.

(Fig. 9 I–L; 18 F)

1958 *Tenua hystrix* Eisenack, p. 410, pl. 23, figs 1, 3–4 (non fig. 2); text-fig. 10.
1962 *Palaeohystrichophora brevispinosa* Pocock, p. 81, pl. 14, figs 222–223.
1969 *Cyclonephelium distinctum* var. *brevispinatum* Millioud, p. 427–428; pl. 1, figs 8–9.

1973 *Cyclonephelium distinctum* subsp. *brevispinatum* (Millioud) Lentin & Williams, p. 36.
1977 *Tenua brevispinosa* (Pocock): emend. Brideaux, p. 15.
1978 *Canningia*? *brevispinosa* (Pocock): Stover & Evitt, p. 25.
1981 *Cyclonephelium brevispinosum* (Pocock): Lentin & Williams, p. 63.
1981 *Cyclonephelium brevispinatum* (Millioud) Below, p. 11.
1981 *Cyclonephelium brevispinatum* (Millioud) Yun Hyesu, p. 51.
1983 *Canningia americana* Pöthe de Baldis & Ramos, p. 432–433, pl. 1, figs 6, 9.
1986 *Circulodinium brevispinosum* (Pocock): Jansonius, p. 15–16.
1991 *Canningia insignis* He Chengquan, p. 55–56; pl. 9, figs 9–10.
1992 *Tenua americana* (Pöthe de Baldis & Ramos) Prössl, p. 116.
2004 *Circulodinium brevispinatum* (Millioud) Fauconnier in Fauconnier & Masure, p. 114.
2009 *Circulodinium insigne* (He Chengquan) He Chengquan et al., p. 271.

Emended description. A species of *Tenua* with very short isolated spines or projections, which are terminally acuminate to blunt or briefly bifid. The spines are present, but may be reduced in density and/or length, on the dorsal and ventral surfaces, and may show weak penitabular alignment. Cyst antapically rounded or asymmetrical with rounded protuberances.

Comments. Eisenack (1958, p. 410) gave the following diagnosis for *Tenua hystrix*.

> A species of *Tenua* 75–105 μ long and some 65–95 μm wide. In a single specimen, the spines are mostly of rather similar length, varying however from about 2–10 μ in length; they are either only slightly knobbed distally or weakly divided, only rarely do the short, thick prongs have secondary branches …. [Translation]

The species description is here emended to mention the possibility of weakly developed penitabular distribution of the spines. See under the genus *Tenua* and earlier sections of this paper for further discussion.

Pocock (1962, p. 81) provided the following description for *Palaeohystrichophora brevispinosa*:

> Theca more or less isodiametric, covered by short spines; transverse furrow equatorial, broad, marked by two rows of short spines; epitheca conical, terminated by a tuft of slightly longer spines than those covering the rest of the theca; epitheca terminated by two short blunt processes, one slightly longer and sharper than the other; the theca commonly encloses a spherical cyst about half the diameter of the theca; yellow green spherical organic bodies are also frequently present.

The inner body (“cyst”) described by Pocock (1962) is probably a misinterpretation of folds on the cyst wall, as the cyst is clearly an areoligeracean with a single wall layer and low ornamentation, as confirmed in a re-examination by Jansonius (1986). Isolated spines are the dominant form of ornament on the holotype, although, as Jansonius (1986) noted, occasional processes are connected. The line drawing of the holotype of *Circulodinium brevispinosum* by Jansonius (1986) appears to show a reduction of ornament mid-ventrally, but this is not evident in the re-illustration of the holotype by Fauconnier & Masure (2004, pl. 14, figs 7–8).

We consider *Canningia americana* to be indistinguishable from *Tenua hystrix*, as is *Circulodinium brevispinatum*, which was described as a subspecies of *Cyclonephelium distinctum* by Millioud (1969). Millioud (1969, p. 427) provided no details of the spines other than that they are less than 2 μm long.

This species accommodates forms of *Tenua* with short, usually blunt projections typically <4 μm long. *Tenua anaphrissa* has longer, generally hair-like processes. The ambital outline of both species, as conceived herein, is variable.

Stratigraphical occurrence. Eisenack (1958) described *Tenua hystrix* from the Aptian of northern Germany. Costa & Davey (1992) placed the LAD if this species in the latest Maastrichtian. He Chengquan (1991) recorded *Canningia insignis* from the Cenomanian of China. *Tenua* (as *Palaeohystrichophora*) *brevispinosa* was first described from the upper Barremian and Aptian of western Canada. Pöthe de Baldis & Ramos (1983) described the species *Canningia americana* from the lower Aptian of Argentina. The type material of *Cyclonephelium distinctum* var. *brevispinatum* is from the Berriasian to lower Aptian of France.

Tenua kukebaiensis (Mao Shaozhi & Norris 1988) comb. nov.

(Fig. 18 G)

1980 *Cyclonephelium distinctum* var. *psilatum* Yu Jingxian & Zhang Wangping, p. 115, pl. 6, figs 1–2.

1985 *Cyclonephelium distinctum* subsp. *psilatum* (Yu Jingxian & Zhang Wangping 1980) Lentin & Williams, p. 86.

1988 *Canningia kukebaiensis* Mao Shaozhi & Norris, p. 31, pl. 1, figs 6–8.

1989 *Circulodinium distinctum* subsp. *psilatum* (Yu Jingxian & Zhang Wangping) Lentin & Williams, p. 63.

2009 *Circulodinium kukebaiense* (Mao Shaozhi & Norris) He Chengquan et al., p. 271.

Comments. Cysts of this species are broadly ellipsoidal with an antapex that is rounded or with two “blunt lobations” (Mao Shaozi & Norris 1988, p. 31); the autophragm is granulate, with short, nontabular, isolated, acuminate spines, 1–5 μm long. This species thus conforms in morphology with *Tenua*, and so we re-assign it to that genus. The taxon described by Yu Jingxian & Zhang Wangping (1980) as *Cyclonephelium distinctum* var. *psilatum* appears to be conspecific with *Tenua kukebaiensis* and hence we propose the synonymy; *kukebaiense* is the senior epithet at specific rank. *Tenua kukebaiense* differs from *Tenua attadalica* primarily in its shape, the former having a rounded bowl-shaped central body, the latter having a more angular central body.

Stratigraphical occurrence. The type materials for both *Tenua* (as *Canningia*) *kukebaiensis* and *Cyclonephelium distinctum* subsp. *psilatum* are from the Turonian–Santonian of China.

Tenua magna (Duxbury 2001) comb. nov.

(Fig. 18 H)

2001 *Cerbia magna* Duxbury, p. 101–102, fig. 4, nos 1–4.

Comments. In erecting this species, Duxbury (2001, p. 101) stated:

> Low apical, lateral and antapical projections are present, and short spines are distributed over the surface of the cyst. These spines are variable in their distribution, often essentially penitabular, but sometimes more densely arranged.

Thus, penitabular features are not clearcut and ornament covers most or all of the surface: hence we transfer this species to *Tenua*.

Stratigraphical occurrence. Duxbury (2001) described this species from the upper Barremian of the North Sea.

Tenua*? *micibaculata (Jiabo 1978) comb. nov.

(Fig. 18 I)

1978 *Canningia micibaculata* Jiabo, p. 54, pl. 7, figs 1–2.
1987 *Canningia*? *micibaculata* (Jiabo); Helby, p. 324–325.
2009 *Circulodinium*? *micibaculatum* (Jiabo) He Chengquan et al., p. 271.

Comments. *Tenua? micibaculata* may be synonymous with *Tenua hystrix*. However, we refrain from proposing this synonymy because the morphology of *Tenua*? *micibaculata* is not clear, and hence the questionable assignment. We propose that this species be restricted to the holotype.

Stratigraphical occurrence. Jiabo (1978) recovered this species from the Lower Palaeogene of China.

Tenua*? *pentagona (He Chengquan 1991) comb. nov.

(Fig. 18 J)

1991 *Canningia pentagona* He Chengquan, p. 56, pl. 9, figs 13–14.
2009 *Circulodinium pentagonum* (He Chengquan) He Chengquan et al., p. 272.

Comments. Although the morphology of this species seems to fit *Tenua* better than *Canningia* or *Circulodinium*, we question the new attribution because the morphology of the holotype is not clear.

Stratigraphical occurrence. He Chengquan (1991) recorded this species from the Upper Cretaceous of Xinjiang, China.

Tenua reducta (Châteauneuf 1980) Courtinat in Fauconnier & Masure 2004

(Fig. 18 K)

1980 *Cyclonephelium reductum* Châteauneuf, p. 136, pl. 21, fig. 10.
2004 *Tenua reducta* (Châteauneuf) Courtinat in Fauconnier & Masure, p.557.

Comments. Châteauneuf (1980, p. 136) provided the following diagnosis for this species:

> [Cyst] lenticular and antapical protuberances bisymmetrical. Apical margin truncated, dorso-ventral flattening and median constriction of the cyst. Cyst surface composed of one thin layer or autophragm. Sutural features not discernible. In this type [species?] there is no cingular alignment of processes. Tabulation is expressed only by the truncated zigzag margin of the archaeopyle. Archaeopyle apical, with free operculum. Ornamentation dense, composed uniquely of spines of very variable length, with more or less expanded bases, with no ordered arrangement over the cyst surface. Ornamentation reduced in median dorso-ventral zones. The autophragm is ornamented between spines. …. [Translation]

The features of this species are not clearly shown on the single illustration that Châteauneuf (1980) provided. However they are clearer in the re-illustrations of the holotype in Fauconnier and Masure (2004, pl. 18, figs 11–15). These show the presence of short spines; the ventral surface may be devoid of spines in its centralmost area, but across the dorsal surface are sparse spines in a penitabular and nontabular arrangement. Châteauneuf (1980) did not mention the nature of the distal process endings and they are unclear in the original illustration; from the re-illustrations they appear to me mostly acuminate or slightly bulbous. This is an unusual morphology for Eocene areoligeraceans.

Stratigraphical occurrence. Châteauneuf (1980) recovered this species from the Upper Eocene of France.

Tenua scabrosa (Cookson & Eisenack 1970) comb nov.

(Figs 10 A–P; 18 L)

1970 *Canningia scabrosa* Cookson & Eisenack, p. 146, pl. 13, figs 6–7.
1971 *Canningia aspera* Singh, p. 322, pl. 50, fig. 1.
1978 *Canningia*? *aspera* Singh; Stover & Evitt, p. 25.
1980 *Epelidosphaeridia aspera* (Singh) Morgan, p. 23.
1981 *Cyclonephelium asperum* (Singh) Below, p. 10.
1987 *Circulodinium asperum* (Singh) Helby, p. 324–325.
1999 *Circulodinium cingulatum* He Chengquan et al., p. 193, pl. 2, figs 1–3.

Comments. Cookson & Eisenack (1970, p. 146) described the ornamentation of *Canningia scabrosa* (misspelled in the protologue as "*scabrose*") as consisting of "… densely arranged, irregularly outlined thickenings, some of which narrow to [form] short, hair-like appendages...". As the wall structure is clearly not holocavate and the ornamentation is apparently free-standing and covers the entire cyst surface, we transfer this species to *Tenua*. The ornament is so similar to that of *Canningia*? *aspera* that we consider the two species to be synonymous.

Canningia? *aspera* was erected by Singh (1971, p. 322) for large (average 97 x 100 µm) areoligeracean cysts. According to Singh, the 2.5 µm-thick wall is ornamented by "… thick, irregular-shaped elevations surmounted by 2–4-micron long, conical spines."

Specimens attributable to *Tenua scabrosa* are common in upper Lower Cretaceous material from Axel Heiberg Island, arctic Canada. In the arctic material, the wall is not as thick as Singh reported from Alberta, and the spines range from 2–8 µm in length. The dorsoventral area is darker than other parts of the cyst on some specimens, suggesting a wall thickening in that region.

He Chengquan et al. (1999) diagnosed *Circulodinium cingulatum* in part as follows:

"Autophragm … surface ornamented with rarely free processes of varying length and size, most of them shorter, verrucous to bluntly denticulate, 0.5 – 1.0 µm long, fewer processes shortly baculate (up to 3.5 µm long) with blunt unwidened tips." From the protologue illustrations, the processes appear to be short, isolated and broad based, as is the case for *Tenua scabrosa*. He Chengquan et al. (1999) differentiated *Circulodinium cingulatum* from *Tenua* (then *Circulodinium*) *attadalica* on the basis of the presence of paracingular ridges on the former. However, we consider the species of He Chengquan et al. (1999) to be akin to *Tenua scabrosa* rather than *Tenua attadalica*, and the presence or absence of a defined paracingulum to be an intraspecific variation.

Stratigraphical occurrence. Cookson & Eisenack (1970) recorded *Tenua* (as *Canningia*) *scabrosa* from the Albian to Cenomanian of Australia. Singh (1971) described *Tenua* (as *Canningia*) *aspera* from the Albian of Alberta, Canada. The type material of *Circulodinium cingulatum* is from the upper Hauterivian to Barremian of China.

Genus ***Trimuridinium*** gen. nov.

Type. Prince et al. 2008, pl. 1, figs 11–12, as *Senoniasphaera whitenessensis*.

Derivation of name. The name is derived from the Latin prefix "tri" for three, the Latin "murus" for wall, and "dinium", the common suffix for dinoflagellates. *Trimurodinium* is thus the "three-walled dinoflagellate cyst".

Diagnosis. Areoligeraceans in which the wall is constructed of three layers, the inner two of which are typically interconnected.

Comments. This genus is distinctive in having three wall layers. The presence of three wall layers is extremely unusual among dinoflagellate cysts, and, to our knowledge, previously unknown among areoligeraceans, even among gonyaulacineans. The best-known dinoflagellate cysts with three wall layers are perhaps the forms described by Evitt et al. (1998) and assigned to *Palaeoperidinium*. Evitt et al. (1998) referred to the outermost layer as the exophragm, a term that we favour here, retaining the terms endophragm and periphragm for the innermost and middle layers respectively. The two inner, interconnected, layers in *Trimuridinium* are clearly homologous with the endophragm and periphragm of *Canningia*. For *Palaeoperidinium*, Evitt et al. (1998) reasoned that the exophragm was formed outside the theca, and it would be of interest to examine *Trimuridinium whitecliffense* using the scanning electron microscope to see if any clues regarding the origin of the exophragm in this species might be revealed.

Trimuridinium differs from *Canningia* in the presence of a third wall layer. Duxbury (1983) erected the genus *Cepadinium*, which has four wall layers. However, *Cepadinium* is an ovoidinioidean peridinioid dinoflagellate cyst.

Accepted species.

Trimuridinium whitenessense (Prince et al. 2008) comb. nov.

(Figs 18 M–N)

2008 *Senoniasphaera whitenessii* Prince et al., p. 91, pl. 1, figs 11–12.

Comments. Prince et al. (2008, p. 91) diagnosed *Trimuridinium whitenessense* as “A globular *Senoniasphaera* with three wall layers, showing slight indications of both lateral and antapical horns on all wall layers. Rounded to rectangular cavities are located between the endo- and mesophragm.” Prince et al. (2008) referred to indications of lateral horns, these appear to be no more than bulges on the ectophragm in the single specimen illustrated. As the specific epithet was avowedly named after a place and not a person, Williams et al. (2017) revised the spelling to *whitenessensis*.

Stratigraphical occurrence. Prince et al. (2008) recovered this species from the upper Santonian of England.

Family **Ceratiaceae** Willey & Hickson 1909

Genus ***Pseudoceratium*** Gocht 1957 emend. nov.

1957 *Pseudoceratium* Gocht, p. 166.
1962 *Eopseudoceratium* Neale & Sarjeant, p. 446.
1980 *Pseudoceratium* Gocht; emend. Dörhöfer & Davies, p. 39.
1986 *Pseudoceratium* Gocht; emend. Bint, p. 144.
1987 *Pseudoceratium* Gocht; emend. Helby, p. 313–315.

Type: Gocht 1957, pl. 18, fig. 1, as *Pseudoceratium pelliferum*.

Emended diagnosis. Dorsoventrally compressed ceratiacean cysts with single apical, lateral (postcingular) and antapical horns or distinct prominences; the lateral horn or prominence is formed from the autophragm (or endophragm in cavate forms), not by the ornament alone. Proximate, wall formed of one or two layers. If two-layered, there are supports between the between the endophragm and periphragm. Paratabulation often indicated by ornamentation if present. Ornamentation may be granular or consist of short processes, which may be joined by trabecula or support a more extensive ectophragm. Archaeopyle apical, with formula $A_{(1–4')}$, operculum generally free; parasulcal notch offset to the left.

Comments. We emend *Pseudoceratium* to restrict it to forms in which the lateral horn or distinct prominence is formed by the autophragm or endophragm. Forms in which the lateral prominence is constructed solely from the ornament are referable to an areoligeracean genus, most commonly *Aptea*.

Gocht (1957, p. 166) provided the following original diagnosis for *Pseudoceratium*:

> Shell of organic material, of peridinioid shape (produced through several more or less long-drawn-out horns), untabulated, without girdle system, annular sutures [?] or ridge structures. Shell smooth or covered with short processes. Apical part commonly truncated by an irregular rupture line. [Translation]

We consider the emendation of Bint (1986) as useful in attaining the current concept of *Pseudoceratium*, but not those by Dörhöfer & Davies (1980) or Helby (1987). Areoligeracean genera lack a lateral projection. *Endoceratium* is circumcavate rather than holocavate, with no structures joining the two wall layers. *Muderongia*, *Nyktericysta* and *Vesperopsis* have more than three horns. *Odontochitina* has a distinct endocyst well separated from the pericyst.

Accepted species.

Pseudoceratium aulaeum Harding 1990 ex Harding in Williams et al. 1998

(Fig. 18 O)

1990 *Pseudoceratium aulaeum* Harding, p. 18, pl. 1, figs 1–6; name not validly published.
1998 *Pseudoceratium aulaeum* Harding ex Harding in Williams et al. 1998, p. 512.

Comments. This species is difficult to compare with other species of *Pseudoceratium* because the type material is illustrated by scanning electron micrographs (SEMs). Paratabulation is evident on the SEMs. Harding (1990, p. 18) noted that the "Intratabular sculptural elements consist of irregularly distributed processes supporting an ectophragmal trabecular reticulum."

Stratigraphical occurrence. Harding (1990, 1998) recorded this species from "presumed low-salinity" upper Barremian assemblages of England.

Pseudoceratium australiense Fensome & Williams 2004 nom. subst. pro *Pseudoceratium robustum* Riding & Helby 2001

(Figs 18 Q–R)

2001 Riding & Helby, p. 208, 210, 212, figs 15 A–L (illegitimate junior homonym of *Pseudoceratium robustum* Michael 1964).
2004 *Pseudoceratium australiense* Fensome & Williams, p. 554 (nom. subst. pro *Pseudoceratium robustum* Riding & Helby).

Comments. Riding & Helby (2001, p. 210) noted that their new species *Pseudoceratium* *robustum* (now *Pseudoceratium australiense*) "… is distinguished by its relatively large size [overall length 97–136 μm], the thick, robust autophragm and the distinctive processes which support a vacuolate ectophragm."

Stratigraphical occurrence. Riding & Helby (2001) recorded *Pseudoceratium australiense* (as *Pseudoceratium robustum*) from the Tithonian of northwestern Australia.

Pseudoceratium? brevicornutum Herngreen et al. 2000

(Fig. 18 P)

1994 *Pseudoceratium eopelliferum* Herngreen et al., p. 386 (name not validly published; synonym of *Pseudoceratium brevicornutum* according to Herngreen et al. 2000, p. 50).

2000 *Pseudoceratium brevicornutum* Herngreen et al., p. 50, pl. 9, figs 6–7.

Comments. This species differs from *Pseudoceratium pelliferum* in having distinctly shorter horns. In fact, the lateral horn on the holotype (Herngreen et al. 2000, pl. 9, fig. 6) is not clearly developed and so we questionably retain this species in *Pseudoceratium*. The other illustrated specimen (Herngreen et al. 2000, pl. 9, fig. 7) might be conspecific with *Pseudoceratium pelliferum*, albeit with a shorter than average horn.

Stratigraphical occurrence. Herngreen et al. (2000) recorded the range of this species from the North Sea and The Netherlands as upper Ryazanian (middle Berriasian) to lower Hauterivian.

Pseudoceratium expolitum Brideaux 1971

(Fig. 18 S)

1971 *Pseudoceratium expolitum* Brideaux, p. 102–103, pl. 30, figs 105–106, 108.

1971 *Pseudoceratium regium* Singh, p. 375–376, pl. 66, figs 2–4; pl. 67, figs 1–2.

Comments. Brideaux (1971, p. 102) noted that the "Wall appears thick and is smooth or occasionally scabrate to microreticulate, the latter probably due to corrosion." The material illustrated by Singh (1971) for his new species, *Pseudoceratium regium*, considered a taxonomic junior synonym of *Pseudoceratium expolitum* by Harker & Sarjeant (1975), is much better preserved than the material of Brideaux (1971). Singh (1971) described the cyst surface as "finely granulate and ornamented by a small-meshed network formed by faint, narrow, low muri."

Stratigraphical occurrence. Both Brideaux (1971) and Singh (1971) recorded their material from the middle to upper Albian of Alberta, Canada.

Pseudoceratium gochtii Neale & Sarjeant 1962

(Fig. 18 T)

1962 *Pseudoceratium* (*Eopseudoceratium*) *gochtii* Neale & Sarjeant, p. 446–448, pl. 20, figs 3–4; text-figs 5a–c (non *Pseudoceratium gochtii* Pocock).

1973 *Eopseudoceratium gochtii* (Neale & Sarjeant) Lentin & Williams, p. 54.

Comments. Lentin & Williams (1985, p. 297) retained this species in *Pseudoceratium*. It differs from *Pseudoceratium pelliferum* in that the arrangement of the ornament distinctly reflects the tabulation. Neale & Sarjeant (1962, p. 446) noted that "On its margins and on the boundaries of plates arise rows of spines, simple, bifurcate, or knobbed, sometimes rising from low ridges on the shell surface; elsewhere the shell has an irregular cover of very short spines of similar character." The interpretation of extra paraplates by Neale & Sarjeant (1962, fig. 5b–c) probably results from the fact that the ornament reflects penitabular rather than parasutural lines, and hence leaves areas been paraplate "boundaries".

Stratigraphical occurrence. Neale & Sarjeant (1962) recorded *Pseudoceratium gochtii*, as *Pseudoceratium* (*Eopseudoceratium*) *gochtii*, from the upper Hauterivian to middle Barremian of England.

Pseudoceratium? iehiense Helby & May in Helby 1987

(Figs 19 A–B)

1987 *Pseudoceratium iehiense* Helby & May in Helby, p. 315–316, figs 16A–K, 17.

Comments. Helby (1987, p. 315) noted that this distinctive species has a wall with closely spaced projections and short, discontinuous ridges between the endophragm and periphragm. The ectophragm is essentially continuous, with a coarsely reticulate, granulate or smooth surface. The ornament within the ectocoel is more closely packed and commonly higher in pandasutural regions. Helby (1987) stated that *Pseudoceratium weymouthensis* is larger and has "substantially longer horns".

Stratigraphical occurrence. Helby (1987) described *Pseudoceratium iehiense* from the upper Tithonian to lower Berriasian of subsurface Papua New Guinea.

Pseudoceratium interiorense Bint 1986

(Figs 19 C–D)

1986 *Pseudoceratium interiorense* Bint, p. 146, 148, pl. 3, figs 3–4, 9–15; pl. 7, figs 9–10.

Comments. Bint (1986, p. 146) described the wall structure for *Pseudoceratium interiorense* as follows:

> Cyst wall two-layered; ectophragm linked to autophragm by connecting structures over the cyst body, except at the horn tips where cornucavation develops. Autophragm extending almost to tips of hypocystal horns, but not as far into the apical so that the apical ectocoel is largest and quite obvious, whereas the hypocystal ectocoels are much smaller and usually difficult to discern. Autophragm smooth or scabrate, very finely perforate (0.5–1 μm) with occasional larger perforations. Perforations diminish in density towards the ends of horns and are rare in the terminal cavate portion. Structures linking autophragm and ectophragm appear to consist of the muri of an irregular, sometimes incomplete, reticulum with lumina about 3–8 μm across. This reticulation appears more closely connected with the ectophragm than the autophragm because remnants of it are preserved in at least part of the cavate portion of the apical horn.

The wall structure of *Pseudoceratium interiorense* closely resembles that of species of *Nyktericysta*, but the latter consistently have more than three horns. Bint (1986) recorded this species from the lowermost upper Albian of the US Western Interior, and thus its range overlaps that of species of *Nyktericysta*.

Stratigraphical occurrence. The type material is from the upper Albian of the USA.

Pseudoceratium iveri Nøhr-Hansen 1993

(Fig. 19 E)

1993 *Pseudoceratium iveri* Nøhr-Hansen, p. 100–102, pl. 19, figs 1–8; text-figs 13–15.

Comments. Nøhr-Hansen (1993, p.100) noted that *Pseudoceratium iveri*:

> … has two wall layers. The ectophragm consists of a complicated network, supported by processes. The network extends the horn terminations and is concentrated on the paraplates, leaving the pandasutural areas free of ornamentation.

Stratigraphical occurrence. Nøhr-Hansen (1993) recorded this species from the uppermost Barremian of eastern Greenland.

Pseudoceratium notiale (Quattrocchio & Sarjeant 1992) comb. nov.

(Fig. 19 F)

1992 *Aptea notialis* Quattrocchio & Sarjeant, p. 83 (al. p. 2-235), pl. 5, figs 1–4; pl. 7, figs 7–8.

Comments. We transfer this species to *Pseudoceratium* as it clearly has lateral prominences. Quattrocchio & Sarjeant (1992, p. 83) noted that:

> The ornament elements generally vary in height between 2 and 5 μm, but they are taller on the apical and antapical horns (9–20 μm). These elements are bifurcate,

> typically coalescing distally to support a delicate ectophragm. The pattern of the ornamentation forms an incomplete and irregular network, especially conspicuous on the three horns; the ornament is best developed around the cyst's periphery.

Stratigraphical occurrence. The type material is from the middle to upper Tithonian of Argentina.

Pseudoceratium*? *parvum Michael 1964

(Fig. 19 G)

1964 *Pseudoceratium parvum* Michael 1964, p. 28, pl. 2, fig. 1.
1986 *Pseudoceratium*? *parvum* Michael: Bint, p. 145.

Comments. We concur with Bint (1986) that, from the original illustration, the morphology of this species is problematic, and hence its attribution to *Pseudoceratium* is questionable. We recommend that use of the name be restricted to the type material.

Stratigraphical occurrence. Michael (1964) recovered this species from the early Barremian of northwestern Germany.

Pseudoceratium pelliferum Gocht 1957

(Figs 11 A–D; 19 I–K)

1957 *Pseudoceratium pelliferum* Gocht, p. 166–168, pl. 18, figs 1a–c, 2; text-figs 1–3.
1980 *Pseudoceratium pelliferum* Gocht; emend. Dörhöfer & Davies, p. 39.

Comments. Gocht (1957, p. 166) gave the following diagnosis for this species, which is the type of the genus.

> Shell compressed, asymmetrically triangular in outline, longer than wide, with a strong apical horn and two shorter antapical horns of unequal length. [The cyst] is more or less densely covered with short, roundly truncated bristle-like processes,

> which stand isolated or joined to one another at the bases. [Translation]

From the illustrations of Gocht (1957) of the type material, it appears that the spines (Gocht's "bristle-like processes") may also occasionally be connected distally.

Stratigraphical occurrence. Gocht (1957) recorded *Pseudoceratium pelliferum* from the upper Hauterivian of northwestern Germany. Costa & Davey (1992) plotted the FAD of this species within the early late Ryazanian (middle Berriasian), and the LAD in the latest Barremian. Stover et al. (1996) recorded its range as late Ryazanian (middle Berriasian) to late early Aptian for northern Europe, and Valanginian–Barremian for southern France.

Pseudoceratium retusum Brideaux 1977

(Figs 19 M–O)

1977 *Pseudoceratium retusum* Brideaux 1977, p. 14–15, pl. 4, figs 10–12; pl. 5, figs 1–2, 5–10.

Comments. Brideaux (1977, p. 14) described the wall structure of *Pseudoceratium retusum* as follows:

> [Periphragm] produced to form variously shaped sculpture elements which are discrete or linked basally and/or distally, which are nonparatabular or occasionally distinctly parasutural in position, the basal linkages persistent enough to form what may be termed parasutures; intertabular sculpture commonly linked basally to form an anastomosing network, or passing into a reticulate pattern; where the reticulum is reduced in the interior of the paraplate, commonly assuming a penesutural position; individual sculpture elements are generally bifid or bifurcate, but may be spatulate, fan-shaped or acicular; distal linkage of elements at the apices of the horns in places forming a canopy-like structure; reduction of the sculpture elements may occur ventrally and dorsally on the central parts of the hypotract; sculpture element length typically 3–5 μ but up to 8 μ at the apices.

From the illustrations of Brideaux (1977), the reflection of the tabulation appears a stronger feature than expressed in his text; and the dorsal and ventral areas devoid of ornament are strongly developed in most specimens and extend onto the epicyst as well as the hypocyst.

Stratigraphical occurrence. Brideaux (1977) recorded *Pseudoceratium retusum* from the Barremian–Aptian of the Northwest Territories, former District of Mackenzie, Canada.

Pseudoceratium? robustum (Michael 1964) Bint 1986

(Fig. 19 H)

1964 *Pseudoceratium robustum* Michael, p. 29, pl. 2, fig. 2. (non *Pseudoceratium robustum* Riding & Helby).
1986 *Pseudoceratium*? *robustum* Michael: Bint, p. 145.

Comments. We concur with Bint (1986) that from the original illustration the morphology of this species is problematic, and hence its attribution to *Pseudoceratium* is questionable. Accordingly, we recommend that use of the name be restricted to the type material.

Stratigraphical occurrence. Michael (1964) recovered this species from the upper Barremian of northwestern Germany.

Pseudoceratium solocispinum (Davey 1974) Harding 1990

(Fig. 19 L)

1974 *Pseudoceratium pelliferum* var. *solocispinum* Davey, p. 68, pl. 9, fig. 6.
1975 *Pseudoceratium pelliferum* subsp. *solocispinum* (Davey) Lentin & Williams, p. 2154.
1990 *Pseudoceratium solocispinum* (Davey); emend. Harding, p. 19.

Comments. This species was originally described as a variety of *Pseudoceratium pelliferum*. Davey (1974) did not clearly say how the variety differed from *Pseudoceratium pelliferum* var. *pelliferum* (and thus how *Pseudoceratium solicispinum* differs from *Pseudoceratium pelliferum*), but the epithet that he chose is partly based on the Latin *solox*, for coarse or rough. Certainly, the spines of *Pseudoceratium solicispinum* are longer than those of *Pseudoceratium pelliferum*. Harding (1990) raised this taxon to specific rank and provided an emended diagnosis, although he did not specifically state what his revised concept entailed. He provided some interesting SEMs, purportedly of *Pseudoceratium pelliferum* (his pl. 1, figs 7–8) and *Pseudoceratium solocispinum* (his pl. 1, figs 9–11) showing crispate ("curly") elements, somewhat more pronounced in the latter species. It is not easy to relate the SEMs of Harding (1990) with the original light micrograph of the holotype of *Pseudoceratium solocispinum*.

Stratigraphical occurrence. The type material is from the middle and upper Barremian of northeastern England. However, Costa & Davey (1992) reported that this species is confined to the late Barremian.

Pseudoceratium spitiens Jain & Garg in Jain et al. 1984

(Fig. 19 P)

1984 *Pseudoceratium spitiense* Jain & Garg in Jain et al., p. 72, pl. 3, figs 41–42.

Comments. The two specimens illustrated in the protologue appear to have an irregulary reticulate ornament, although this may reflect corrosion rather than original morphology.

Stratigraphical occurrence. Jain & Garg in Jain et al. (1984) described *Pseudoceratium spitiense* from the Kimmeridgian to lower Tithonian of the Malla Johar area, India.

Pseudoceratium toveae Nøhr-Hansen 1993

(Fig. 19 Q)

1993 *Pseudoceratium toveae* Nøhr-Hansen, p. 108, 110, pl. 21, fig. 11; pl. 22, figs 1–7.

Comments. In comparing *Pseudoceratium toveae* with *Pseudoceratium weymouthense*, Nøhr-Hansen (1993, p. 108, 110) noted that the latter species differs from *Pseudoceratium toveae*:

> … by its weak paratabulation, indicated by larger processes in the pandasutural areas

> which, according to Helby … are apparently covered by a continuous ectophragm, and by its rather pronounced extension of the cingulum onto the anterior part of the post-cingular horn.

Although the differences seem subtle, the apparent damage to some of the type material of both species makes detailed comparison difficult. Hence, although the two species are very similar, we retain both pending further study.

Stratigraphical occurrence. Nøhr-Hansen (1993) recovered *Pseudoceratium toveae* from the upper Barremian to ?lowermost Aptian of eastern Greenland.

Pseudoceratium turneri Cookson & Eisenack 1958

(Fig. 19 R)

1958 *Pseudoceratium turneri* Cookson & Eisenack, p. 55, pl. 5, figs 2–6.
1978 *Endoceratium turneri* (Cookson & Eisenack) Stover & Evitt, p. 45.

Comments. In their original description of this species, Cookson & Eisenack (1958, p. 55) noted that:

> The ornament usually takes the form of narrow lamella-like membranes with irregular, frequently curved outlines of variable lengths formed by the distal coalescence of short bifurcate processes, the lamellae either remaining free or uniting to form a more or less complete superficial network.

Although not easy to follow, this description and the accompanying illustrations, strongly indicate that this species has a complete or incomplete outer wall layer (“lamella-like membranes”, “superficial network”) and processes connecting it to the autophragm. We thus retain it in *Pseudoceratium*.

Stratigraphical occurrence. The holotype of *Pseudoceratium turneri* is from the Albian of

Western Australia. Costa & Davey (1992) placed the FAD of this species at the base of the late Aptian, and the LAD at the Albian–Cenomanian boundary.

Pseudoceratium weymouthense Helby 1987

(Figs 19 S–T)

1987 *Pseudoceratium weymouthense* Helby, p. 316–317, figs 19A–C, 20A–D.

Comments. This species is clearly distinguished by long apical, lateral, and antapical horns and an irregular "bubbly" reticulum, apparently formed by the periphragm. Helby (1987, p. 316) noted that the cyst wall is two-layered and composed of:

> … autophragm and ectophragm [i.e. endophragm and periphragm in our terminology], although in some areas ectocoel not apparent …. Ectophragm apparently continuous … [, its] surface … reticulate. Processes between wall layers … irregularly distributed although … slightly longer and more closely packed in pandasutural regions.

From the illustrations of Helby (1987), the pericoel is barely discernable and the wall surface resembles that typical of *Nyktericysta*, albeit with coarser ornament. See also comments under *Pseudoceratium toveae.*

Stratigraphical occurrence. Helby (1987) recorded *Pseudoceratium weymouthense* from the upper Tithonian to lower Berriasian of Queensland, Australia.

Other taxa.

The genera included in this section are not part of the *Cyclonephelium* group, but are included here because some forms previously included in genera within the *Cyclonephelium* group are reassigned to them, either as synonyms or new combinations. A re-evaluation of the content of each of the genera in this section is beyond the scope of the present work and we therefore include only selected species.

Other taxa

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 **Areoligeraceae** Evitt 1963b

Genus ***Cleistosphaeridium*** Davey et al. 1966

1966 *Cleistosphaeridium* Davey et al., p. 166.
2001 *Cleistosphaeridium* Davey et al.; emend. Eaton et al., p. 176.

Synopsis. Areoligeracean cysts that are proximochorate to chorate, with a subspheroidal to laterally subovoidal central body, sometimes with weak antapical asymmetry. Acavate. Solid, nontabular to penitabular processes or process complexes distributed over the central body, including the dorsoventral areas; some processes have process endings that are dolabrate (sickle-shaped) to incipiently licrate (sickle-shaped with a saw-toothed edge). Archeopyle apical, with formula $A_{(1\text{-}4')}$, operculum free.

Selected species

Cleistosphaeridium diversispinosum Davey et al. 1966

(Fig. 20 A)

1966 *Cleistosphaeridium diversispinosum* Davey et al., p. 167, pl. 10, fig. 7.
1987 *Cyclonephelium indicum* Mehrotra & Sarjeant, p. 163, pl. 2, fig. 2; pl. 7, fig. 1; name illegitimate.
1989 *Circulodinium indicum* Mehrotra & Sarjeant ex Lentin & Williams, p. 63.
1993 *Systematophora diversispinosa* (Davey et al.); Islam, p. 88.

2001 *Cleistosphaeridium diversispinosum* (Cookson & Eisenack); emend. Eaton et al., p. 177, 180, 183, 185, 187–188.

2004 *Circulodinium*? *indicum* Mehrotra & Sarjeant ex Lentin & Williams; Fauconnier & Londeix in Fauconnier & Masure, p. 116.

Comments. *Circulodinium*? *indicum* has slender processes, some of which appear to have dolabrate endings. As such, it is indistinguishable from *Cleistosphaeridium diversispinosum*, and hence we consider it a taxonomic junior synonym of that species.

The name *Cyclonephelium indicum* was illegitimate in Mehrotra & Sarjeant (1987) because it was a junior homonym of *Cyclonephelium indicum* Khanna & Singh 1981. By "transferring" the species to *Circulodinium*, Lentin & Williams (1989, p. 63) effectively created a new name. According to Mehrotra & Sarjeant (1987, p. 163), the autophragm is "covered with numerous (usually exceeding 100) …" spines 6–10 µm long, which cover the cyst uniformly.

Stratigraphical occurrence. Davey et al. (1966) described *Cleistosphaeridium diversispinosum* from the Lower Eocene of southern England. Fensome et al. (2008) gave the LAD of this species as early Messinian (latest Miocene). Mehrotra & Sarjeant (1987) recovered *Cyclonephelium indicum* from the Paleocene of southern India.

Cleistosphaeridium latoaculeum (Yun Hyesu 1981) comb. nov.

(Fig. 20 B)

1981 *Cleistosphaeridium multifurcatum* subsp. *latoaculeum* Yun Hyesu, p. 42–43; pl. 11, figs 17–19.

1993 *Heterosphaeridium latoaculeum* (Yun Hyesu) Islam, p. 84.

1999 *Circulodinium latoaculeum* (Yun Hyesu) Prince et al., p. 160.

Comments. Yun Hyesu (1981, p. 43) provided the following for this species:

> Diagnosis: a subspecies of [*Cleistosphaeridium*] *multifurcatum* with broad, compressed spines, which are proximally and distally broadened. Description: The

> cyst has in places a granular layer, from which the solid spines are constructed. They are distally broadened and truncated, the distal margin [is] sometimes notched and split. In contrast to the relatively constant length of the spines, the width varies considerably. Wide spines can thus appear together with narrow ones. The narrow ones are narrowest at their distal ends, whereas wide spines are broadest medially [?]. Relatively larger or longer spines are developed at the poles. [Translation; paragraphs joined]

The relatively long spines of this species and the dolabrate endings of some spines (observed on the illustrations of Yun Hyesu (1981), although not specifically described by him) suggest that this species accords better with *Cleistosphaeridium* than with *Circulodinium* or *Tenua*.

Stratigraphical occurrence. Yun Hyesu (1981) described this taxon from the Santonian of Germany. Prince et al. (1999) recorded it from the lower Santonian of the Isle of Wight, England.

Cleistosphaeridium*? *longispinosum (He Chengquan 1991) comb. nov.

(Fig. 20 C)

1991 *Cyclonephelium longispinosum* He Chengquan, p. 136, pl. 9, fig. 19; pl. 60, fig. 5.

Comments. The process endings appear to be dolabrate. For this reason, we questionably transfer this species to *Cleistosphaeridium*. We recommend that the name be restricted to the holotype.

Stratigraphical occurrence. He Chengquan (1991) recorded this species from the Middle Eocene of China.

Family **Gonyaulacaceae** Lindemann 1928

Subfamily **Gonyaulacoideae** (autonym)

Genus ***Spiniferites*** Mantell 1850

1850 *Spiniferites* Mantell, p. 191.
1933 *Hystrichosphaera* Wetzel, p. 33 (name not validly published).
1937 *Hystrichosphaera* Wetzel ex Deflandre, p. 61.
1953 *Hystrichokibotium* Klumpp, p. 387.
1970 *Spiniferites* Mantell; emend. Sarjeant, p. 75.
2002 *Pseudospiniferites* Lund, p. 87.

Synopsis. Gonyaulacacean (gonyaulacoidean) cysts that are proximochorate to chorate, with a subspheroidal to subovoidal central body. Acavate. Surface paratabular, processes generally solid but can be hollow and open; parasutural and gonal in position, distally bifid and trifid respectively. Archeopyle precingular, with formula $P_{3''}$, operculum free.

Selected species.

Spiniferites? ambiguus (He Chengquan 1991) comb. nov.

(Fig. 20 D)

1991 *Cyclonephelium*? *ambiguum* He Chengquan, p. 135, pl. 28, figs 7–8.
1991 *Cyclonephelium*? *tarimense* He Chengquan, p. 136–137, pl. 28, fig. 9.

Comments. Although the morphologies of *Cyclonephelium*? *ambiguum* and *Cyclonephelium*? *tarimense* are unclear, they appear to us to be similar and questionably assignable to *Spiniferites*. We recommend that both names be restricted to their respective holotypes.

Stratigraphical occurrence. The type materials of both *Spiniferites*? *ambiguus* (as *Cyclonephelium ambiguum*) and *Cyclonephelium*? *tarimense* are from the Paleocene of China.

Subfamily **Cribroperidinioideae** Fensome et al. 1993

Genus ***Turbiosphaera*** Archangelsky 1969

1969 *Turbiosphaera* Archangelsky, p. 408.

Synopsis. Gonyaulacacean (cribroperidinioid) cysts that are chorate, with subspheroidal to subovoidal central body. Acavate. One process per paraplate, processes hollow, open or closed, more or less cylindrical, and generally uniform in size, except that paracingular processes are taeniate — strongly elongate transversely. Wall fibrous, especially that of processes. Archaeopyle precingular, with formula $P_{3''}$, operculum free.

Selected species

Turbiosphaera*? *sarrisii (Archangelsky 1969) comb. nov.

(Figs 20 E–F)

1969 *Polystephanephorus*? *sarrisii* Archangelsky, p. 411, pl. 2, figs 5–7.
1978 *Senoniasphaera*? *sarrisii* (Archangelsky) Stover & Evitt, p. 80.

Comments. Archangelsky (1969) considered that this species has an apical archaeopyle. However, G. R. Guerstein (personal communication 2017) noted that a restudy of the type material confirmed that this species has a precingular archaeopyle. Following suggestions by Archangelsky (1969), Gonzalez Estebenet et al. (2015, 2016) considered *Senoniasphaera sarrisii* to be an extreme member of the *Turbiosphaera filosa* complex (their morphotype 1). These authors considered the morphological variation within the *Turbiosphaera filosa* complex to parallel the variation described by Benedek & Gocht (1981 and references therein) and Pross (2001) for *Thalassiphora pelagica*. However, Gonzalez Estebenet et al. (2015, 2016) made no formal taxonomic proposals, so for now we questionably transfer *Senoniasphaera*? *sarrisii* to *Turbiosphaera*.

Stratigraphical occurrence. The type material is from the Eocene of Argentina.

Subfamily **Uncertain**

Genus ***Batiacasphaera*** Drugg 1970

1970 *Batiacasphaera* Drugg, p. 813.

2016 *Batiacasphaera* Drugg; emend. Wood et al., p. 62.

Synopsis. Proximate, acavate gonyaulacalean dinoflagellate cysts with subspherical to ovoidal central body in dorso-ventral view. The autophragm bears nontabular ornament that is rugulate to reticulate or isolated elements that align. The archaeopyle is apical, with a free operculum (see the emended diagnosis of Wood et al. 2016, p. 62).

Selected species.

Batiacasphaera*? *bulbosa (Smith & Harding 2004) comb. nov.

(Figs 20 I–K)

2004 *Cyclonephelium*? *bulbosum* Smith & Harding, p. 375–376, pl. 4, figs 6–10; pl. 5, figs 4–6; text-fig. 7.

Comments. Smith & Harding (2004, p. 375–376) described the archaeopyle of this species as complex, involving "… all of the apical plate homologues as a simple … operculum which remains adnate via plates 6", as, and 1', and also plate 3" which remains adnate via its boundary with the cingulum." No known areoligeracean has any archaeopyle type other than apical, and its shape, involving a flat antapex with somewhat angular corners and a dome-shaped apex, would also be highly unusual for an areoligeracean. Although Smith & Harding (2004) acknowledged the problematic nature of the generic assignment, they were influenced by the marginate distribution of the ornament, which they noted consisted of "… short solid rod-like projections with expanded terminations, which may be discrete or branching/anastomosing/fused, and are concentrated in marginal and apical regions." As this species is clearly not an areoligeracean, we transfer it provisionally to the gonyaulacacean genus *Batiacasphaera*.

Stratigraphical occurrence. The type material is from the middle Volgian (upper Tithonian) of the Volga Basin, western Russia.

Genus ***Trichodinium*** Eisenack & Cookson 1960.

1960 *Trichodinium* Eisenack & Cookson, p. 5.
1967 *Trichodinium* Eisenack & Cookson; emend. Clarke & Verdier, p. 18–19.

Synopsis. Gonyaulacacean cysts that are proximate to proximochorate, subspheroidal, usually surmounted by an apical horn or an apical tuft of longer spines. Acavate. Autophragm atabular to weakly paratabular, moderately to densely covered with short spines or short bifid to capitate processes that may show alignment. Archaeopyle precingular, with formula $P_{3''}$, operculum free.

Selected species.

Trichodinium*? *granulatum (Horowitz 1975) comb. nov.

(Fig. 20 G)

1975 *Doidyx granulata* Horowitz, p. 25, pl. 1, fig. 4.
1978 *Cyclonephelium*? *granulatum* (Horowitz) Stover & Evitt, p. 36.

Comments. This species is clearly a gonyaulacacean with a precingular archaeopyle, and it possesses short spines (referred to in the original description and contrasting with the granulation suggested by the epithet), and thus seems to fit the circumscription of *Trichodinium*. Hence, we tentatively assign it to that genus. Although the holotype was recorded from supposedly Triassic strata, it was most probably caved from younger horizons (Conway & Cousminer 1983, p. 35). Given the questions surrounding its generic assignment and its problematic provenance, we recommend that the name be restricted to the holotype.

Stratigraphical occurrence. Horowitz (1975) considered this species to be from the Upper Triassic of Israel. However, the specimens are from uncased wells and so probably represent material caved fron higher in the section.

Suborder **Goniodomineae** Fensome et al. 1993
Family **Goniodomaceae** Lindemann 1928
Subfamily **Pyrodinioideae** Fensome et al. 1993
Genus ***Polysphaeridium*** Davey & Williams 1966

1966 *Polysphaeridium* Davey & Williams, p. 91–92.
1967 *Hemicystodinium* Wall, p. 110.
1980 *Polysphaeridium* Davey & Williams; emend. Bujak et al., p. 32, 34.

Synopsis. Goniodomacean (pyrodinioid) cysts that are proximochorate to (typically) chorate with a subspheroidal central body. Acavate. Processes usually hollow and open, numerous, arranged in paraplate-related groups or (typically) apparently nontabular. Archaeopyle epicystal, with formula $(\mathrm{A}_{1\text{-}4'}\ \mathrm{P}_{1\text{-}6''})$; operculum simple.

Selected species.

Polysphaeridium*? *combibaculum (Song Zhichen in Song Zhichen et al. 1985) comb nov.

(Fig. 20 H)

1985 *Cyclonephelium combibaculum* Song Zhichen in Song Zhichen et al., p. 29–30, pl. 6, figs 10–11.

Comments. This species appears to have the morphology of *Polysphaeridium* rather than *Cyclonephelium*, and its Pleistocene age supports that observation. We thus tentatively transfer the species to *Polysphaeridium*.

Stratigraphical occurrence. The type material is from the Pleistocene of the East China Sea.

Order **Peridiniales** Haeckel 1894
Suborder **Peridiniineae** Autonym
Family **Peridiniaceae** Ehrenberg 1831

Subfamily **Deflandreoideae** Bujak & Davies 1983

Genus ***Deflandrea*** Eisenack 1938

1938 *Deflandrea* Eisenack, p. 187.
1966 *Deflandrea* Eisenack; emend. Williams & Downie, p. 231.
1974 *Deflandrea* Eisenack; emend. Stover, p. 169–170 (as a revised description).
1976 *Deflandrea* Eisenack; emend. Lentin & Williams, p. 35–36.

Synopsis. Peridiniacean (deflandreoid) cysts that are proximate, peridinioid in shape, and more or less symmetrical antapically. Circumcavate to bicavate. Archeopyle intercalary, with formula I_{2a}, operculum free, occasionally attached; paraplate 2a is latideltaform hexa.

Selected species.

Deflandrea*? *stagonoides (Benedek 1972) Lentin & Williams 1976

(Fig. 20 L)

1972 *Ascodinium stagonoides* Benedek, p. 10, pl. 2, fig. 12; text-fig. 5.
1976 *Deflandrea stagonoides* (Benedek) Lentin & Williams, p. 44.
1981 *Ascodinium stagonoides* Benedek; emend. Benedek & Sarjeant, p. 324.
1983 *Senoniasphaera stagonoides* (Benedek) Helenes, p. 262.

Comments. On the basis that its archaeopyle may be latideltaform, we retain this species questionably in *Deflandrea*.

Stratigraphical occurrence. The type material is from the Upper Oligocene of Germany.

Subfamily **Ovoidinioideae** (Norris 1978) Bujak & Davies 1983

Genus ***Epelidosphaeridia*** Davey 1969

1969 *Epelidosphaeridia* Davey, p. 142.

Synopsis. Peridiniacean (ovoidinioid) cysts that are proximate to proximochorate; central body subspheroidal to subovoidal with offset antapical prominence and/or spine. Acavate. Archaeopyle combination apical-intercalary, with formula ($A_{1'-4'}$ + I_{1a-3a}), operculum simple and free.

Comments. In his original description of this genus, Davey (1969) described the archaeopyle simply as apical, and in their overview of dinoflagellate cyst genera, Stover & Evitt (1978, p. 46) accepted this interpretation, writing "archeopyle apical, type uncertain". No formal revisions of the genus have been made subsequently, but in a conference abstract, Costa (1985, unnumbered page) stated "*Epelidosphaeridia* is represented (in material from offshore arctic Norway) by *E. spinosa* and three new species. Their morphology demonstrates that this genus is a [p]eridinioid dinoflagellate with a tAtI archeopyle." Fensome et al. (1993) concurred with this interpretation and assigned *Epelidosphaeridia* to the subfamily Ovoidinioideae. It differs from *Ovoidinium* in being acavate. *Arcticacysta* Sangiorgi et al. 2009 may be a taxonomic junior synonym of *Epelidosphaeridia*, having a combination apical-intercalary archaeopyle and being acavate.

Selected species.

Epelidosphaeridia*? *turrita (Brideaux 1977) comb. nov.

(Figs 20 M–O)

1977 *Canningia*? *turrita* Brideaux, p. 13, pl. 4, figs 1–9.
1981 *Ovoidinium*? *turritum* (Brideaux) Below, p. 125.

Comments. In his original description for this species, Brideaux (1977, p. 13) noted that "the two [wall] layers [are] closely appressed … without pericoel development …." It seems that Brideaux (1977) assumed that two layers were present based on comparison with similar species, but probably saw no actual evidence for separate layers. On proposing a new genus, *Arcticacysta*, from the Miocene of the Arctic, Sangiorgi et al. (2009, p. 252) stated:

> The only other dinosporin cyst having a 3A(?)3I archeopyle is '*Canningia*' *turrita*

> Brideaux 1977 …. The assignment to the genus '*Canningia*' by Brideaux (1977) was … provisional, since the archeopyle of *Canningia* sensu stricto is formed by the loss of four apical plates only. The description of '*Canningia*' *turrita* seems to closely resemble that of *Arcticacysta*, except for the mentioning of a pericyst and an endocyst, which have never been observed in *Arcticacysta*.

Sangiorgi et al. (2009) did not consider *Epelidosphaeridia* for their new material, probably because *Epelidosphaeridia* has never been formally emended. As mentioned above, *Arcticacysta* might be a taxonomic junior synonym of *Epelidosphaeridia*, although the age difference mitigates against a close relationship. One of several putatively (non-marine?) ovoidinioidean genera from the Palaeogene of China might also prove senior to *Arcticacysta* (see Fensome et al. 1993, p. 136), but further investigation of this possibility is beyond the scope of the present work.

Here we agree with Below (1981) that this species appears more like an ovoidinioidean than an areoligeracean, but provisionally assign it to the acavate genus *Epelidosphaeridia* rather than follow him in including it in the cavate genus *Ovoidinium*.

Stratigraphical occurrence. Brideaux (1977) recorded *Epelidosphaeridia*? (as *Canningia*) *turrita* from a sidewall core in the Barremian of the Northwest Territories, former District of Mackenzie, Canada.

Subfamily **Wetzelielloideae** (Vozzhennikova 1961) Bujak & Davies 1983

Genus ***Petalodinium*** Williams et al. 2015

2015 *Petalodinium* Williams et al., p. 307.

Synopsis. Wetzelielloidean cysts with a latiepeliform archaeopyle and a pericyst that is smooth or ornamented with features of low relief.

Selected species.

Petalodinium*? *granulatum (Morgenroth 1966) comb. nov.

(Fig. 20 P)

1966 *Canningia granulata* Morgenroth, p. 12, pl. 2, fig. 10.
1978 *Canningia*? *granulata* Morgenroth; Stover & Evitt, p. 25.

Comments. Morgenroth (1966, p. 12) provided the following diagnosis and description.

> Diagnosis: A species of the genus *Canningia* with a thick-walled, strongly granulate shell. Description: The dorsoventrally compressed, thick, dark brown shell has a rounded-pentagonal outline. The apical pole is distinguished by a very short, more or less truncated horn. The two short, broad antapical horns are of unequal length. The whole shell has a strong granulation. The girdle furrow [paracingulum] is not present. The holotype has a broad ellipse-like pylome [archaeopyle] below the apical horn. [Translation; paragraphs joined]

Although the detailed morphology of the holotype is unclear from the single image of Morgenroth (1966), the shape and probable intercalary nature of the archaeopyle (as Morgenroth noted, it is “below the apical horn”) and the suggestion of an endophragm in one of the antapical horns suggest that it is a wetzelielloidean. If wetzelielloidean affinity is confirmed, the archaeopyle would be lati-epeliform, and hence we provisionally transfer this species to *Petalodinium*. We recommend that the name be restricted to the holotype.

Stratigraphical occurrence. Morgenroth (1966) recovered this species from the Lower Eocene of northern Germany.

Family **Protoperidiniaceae** Balech 1988

Genus ***Selenopemphix*** Benedek 1972 nom. cons.

1965 *Margosphaera* Nagy: p. 208.

1972 *Selenopemphix* Benedek: p. 47.
1975 *Multispinula* Bradford: p. 3067.
1975 *Omanodinium* Bradford: p. 3070.
1980 *Selenopemphix* Benedek; emend. Bujak in Bujak et al., p. 82.
1972 *Protoperidinium* subgenus *Protoperidinium* section *Selenopemphix* (Benedek) Harland: p. 396 (combination not validly published).
1993 *Selenopemphix* Benedek; emend. Head: p. 32.
2016a *Selenopemphix* Benedek nom. cons. prop; Fensome et al., p. 636.
2016a *Margosphaera* Nagy nom. rej. prop.; Fensome et al. p. 636.

Synopsis. Protoperidiniacean cysts that are proximate to chorate, antero-posteriorly compressed, with low crests, spines or processes marking the paracingulum. Acavate. Archeopyle intercalary, with formula I_{2a}, commonly offset from a mid-ventral position.

Selected species.

Selenopemphix? _baculatum_ (Song Zhichen in Song Zhichen et al. 1985) comb. nov.
(Fig. 20 Q–R)

1985 *Cyclonephelium baculatum* Song Zhichen in Song Zhichen et al., p. 30, pl. 6, figs 1–3.

Comments. The morphology of this species, consisting of apparently antero-poteriorly flattened central body with a rim of processes discontinuous at what may be the parasulcus, suggests an attribution to the protoperidiniacean genus *Selenopemphix*; hence we questionably transfer the species to that genus. The age of this species conforms with its assignment to a protoperidiniacean genus rather than a *Cyclonephelium* group genus.

Stratigraphical occurrence. The age of the type material is early? Pleistocene.

(Please insert Figures 4–20 [in order], throughout the previous section - #6)

7. Palaeoecology and palaeogeography

In our studies of Cretaceous dinoflagellate cysts, we have found that the most species-rich assemblages are neritic, but marginal marine or open ocean occurrences are known. (By "open ocean", we mean a setting beyond the shelf edge and thus, by implication, deeper water.) In the Late Cretaceous and Cenozoic, non-*Cyclonephelium* group areoligeraceans — such as *Areoligera*, *Glaphyrocysta* and *Cleistosphaeridium* — proliferated and tended to prefer inner neritic settings (Nøhr-Hansen et al. 2017, table 1). However, we have insufficient data on *Cyclonephelium* group taxa to determine if they follow a similar trend, especially during the Early Cretaceous when these taxa were at their most diverse and abundant.

Generally, palaeoecological studies of fossil dinoflagellate cysts have primarily focused on Cenozoic taxa. But several authors — including Lister & Batten (1988), Cornu & Monteil in Monteil (1990), Harker et al. (1990), Kirsch (1991), Marheinecke (1992), Masure & Vrielynck (2009), Masure et al. (2013) and Pearce et al. (2003) — have published on Mesozoic palaeoenvironments and palaeogeography. Based on R-mode cluster analysis, Harker et al. (1990) recognised 14 species groups and several subgroups of organic-walled microplankton that defined specific palaeoenvironments in the Campanian of Canada, Wyoming and Texas. Their subgroup B1, which included *Circulodinium* (as *Cyclonephelium*) *distinctum*, was considered to characterise a marine environment with varying degrees of reduced salinity. *Senoniasphaera protrusa* was included in group F, which they considered indicative of relatively normal marine conditions. Our conclusions from the above is that subgroup B1 and group F are probably indicative of inner neritic palaeoenvironments. Harker et al. (1990) also used Q-mode analysis to define 14 groups and several subgroups, of which subgroup 9B contained *Circulodinium* (as *Cyclonephelium*) *distinctum*. The subgroup was considered representative of an offshore setting, which was supported by lithology (McLean 1971). The Q-mode analysis is thus at variance with the conclusion drawn from the R-mode analysis. The other possibility, which would explain the discrepancy, is that the assemblage primarily represents taxa redeposited in deeper water.

Pearce et al. (2003) recognised two dinoflagellate cyst assmblages based on species numbers and taxonomic compositions that are characteristic of the Turonian–Coniacian in the

North Sea, southern England and northern France. The *Spiniferites–Palaeohystrichophora* (S–P) assemblage was considered to represent more open-marine paleoenvironments. In contrast, the *Circulodinium–Heterosphaeridium* (C–H) assemblage, of low-diversity and dominated by species of the two genera after which it was named, was indicative of shallower-water settings. Samples from an uppermost Cenomanian to upper Coniacian succession of the Chalk Group in the Banterwick Barn borehole in Berkshire, England, analysed by these authors, were dominated by taxa of the C–H assemblage. Although not believed to be geographically close to a shoreline during the Turonian–Coniacian, Banterwick Barn was situated in a relatively high topographical position with water depths only of decametres. The above findings provide convincing evidence that at least some Cretaceous areoligeraceans were indicators of shallower-water palaeoenvironments.

Major advances in our knowledge of the palaeogeography of Cretaceous dinoflagellate cysts resulted from Masure & Vrielynck (2009) and Masure et al. (2013). In a study of worldwide distribution patterns of late Albian dinoflagellate cysts, Masure & Vrielynck (2009) considered two species — *Cyclonephelium chabaca* (which we treat as a taxonomic junior synonym of *Canningia reticulata*) and *Cyclonephelium* (now *Aptea*) *vannophorum*, to be indicative of warmer waters. The assemblages in which these two species occurred were predominantly restricted to a palaeolatitudinal belt extending from 25° north to 40° south, representing “a tropical-subtropical oceanic–neritic species group”. Masure & Vrielynck (2009, p.131) designated the two species as specialised tropical–subtropical taxa that “should be more tolerant to temperature variations”. They considered the occurrence of the two species at higher southern palaeolatitudes than northern palaeolatitudes to reflect warmer sea-surface temperatures in the Southern Hemisphere.

Masure et al. (2013) found that one of the marker species in the Aptian was *Cerbia tabulata*, which they recorded as extending from palaeolatitudes 5° to 60° north; the species did not occur in the Southern Hemisphere. The palaeoclimatic zones spanned by the assemblages were northern mid-low to southern mid-high palaeolatitudinal belts. Although the extent of the interval within the Aptian was not specified, we assume that the records of species occurrences span all of that stage. In the Albian, Masure et al. (2013) noted that *Canningia reticulata* (as *Cyclonephelium chabaca*) and *Cyclonephelium vannophorum* (now *Aptea*? *vannophora*) were thermophilic species and restricted to south of 30° in the Northern Hemisphere. In the Southern Hemisphere these two species occurred as high as 70° south and formed part of their Tethyan assemblage. Late Albian dinoflagellate cysts defined a northern low-palaeolatitude belt between 10° and 30° north and a southern low-palaeolatitude belt, extending to 35° south. Masure et al. (2013) postulated that the assemblages, including *Canningia reticulata* (as *Cyclonephelium chabaca*) and *Cyclonephelium* (now *Aptea*) *vannophorum*, were restricted to regions where sea-surface temperatures were warmer than 22–24° C. The results of the studies by Masure et al. (2013) and Masure & Vrielynck (2009) demonstrate the potential, as well as the problems (including stability of taxonomy) of dinoflagellate cysts in evaluating Cretaceous palaeoclimates.

8. Evolution

It is clear that the gonyaulacalean families Areoligeraceae and Ceratiaceae are closely related, as witnessed by the striking similarity of some of their morphological features. Most notably, both have sexiform gonyaulacalean paratabulation, a usually asymmetrical outline in ambital view with usually a more pronounced left side, a parasulcus (and parasulcal notch) offset to the left, and invariably an apical archaeopyle. The difference between the two families, as stressed herein, is the presence of one or two distinct lateral horns in the Ceratiaceae and their absence in the Areoligeraceae. This difference unequivocally places most genera in one or other of the two families, and there is generally no doubt that the two are morphologically and phylogenetically separable. But, especially in the Early Cretaceous, there is a gradation of morphologies between certain genera that makes any means of separation somewhat arbitrary. The presence of lateral prominences formed solely by ornamention also demonstrates the sometimes gradational interface between the two families. For example, the holotype of *Aptea polymorpha* has a lateral prominence produced solely by ornament, whereas most other specimens of the type material of that species show no such prominence.

The earliest confirmed occurrence of an areoligeracean, *Senoniasphaera jurassica*, is in the early Kimmeridgian (~156 Ma), and that of ceratiaceans (*Muderongia* spp.) is in the middle Tithonian (~150 Ma; e.g., Woollam & Riding 1983; Riding & Thomas 1992). The fossil evidence alone, therefore, suggests that areoligeraceans appeared first and gave rise to the

Ceratiaceae. However, these two dates are so close that this is a tentative conclusion, especially given the cyst-based nature of the fossil record. Nonetheless, that the Ceratiaceae evolved from the Areoligeraceae is a logical conclusion if the long horns of most ceratiaceans are considered to reflect a specialised morphology, in contrast to the more conservative shapes of areoligeraceans.

During the Late Cretaceous and Cenozoic, the distinction between the two families is more consistently clearcut, with ceratiaceans from this interval showing clear development of horns, and areoligeraceans tending less to have incipient lateral prominences formed from the ornamentation. *Cyclonephelium* group genera are rare in the Cenozoic. However, areoligeraceans are well represented during the Palaeogene by commonly abundant species of genera such as *Areoligera*, *Cleistosphaeridium* and *Glaphyrocysta*. The Ceratiaceae virtually disappear from the fossil record in the Cenozoic, with only one genus, *Taurodinium*, known (Fensome et al. 2016). Oddly, ceratiaceans are well represented among living dinoflagellates, but areoligeraceans (including *Cyclonephelium* and its allies) are unknown, the family apparently becoming extinct during the Late Miocene.

9. Conclusions

Following decades of confusion (the 1960s through early 2000s) and an interval of relative quiescence in taxonomic work on the *Cyclonephelium* group of areoligeracean cysts, the time is opportune to attempt to reduce the taxonomic problems that continue to hamper the applicability of this group. How to distinguish some *Cyclonephelium* group genera from the ceratiacean genus *Pseudoceratium* also remained a problem, given the morphological gradation involving “intermediate” genera such as *Aptea* and *Doidyx*. Indeed, intergradation of morphological features such as ambital shape and ornament distribution has plagued the taxonomy of the *Cyclonephelium* group genera. The fact that, whatever generic definitions are agreed upon, some apparent natural continuities will be broken is probably an unresolvable problem in this group.

The best resolution in any taxonomic imbroglio generally involves deciding on a hierarchy of morphological criteria. Among dinoflagellate cysts, tabulation is generally the most important consideration, with archaeopyle type also commonly very important. However among areoligeraceans and ceratiaceans, tabulation and archeopyle type cannot be used because these features are effectively the same across the two families (at least among fossils). In developing a "best-fit" hierarchy of morphological criteria for the *Cyclonephelium* group internally, and its separation from ceratiacean cysts, we considered the history of concepts (Appendix 1), morphological variation in our own material, and illustrations in the literature, especially of types.

The first issue to resolve was how to distinguish the family Areoligeraceae from the family Ceratiaceae. Although few if any dinoflagellate cyst researchers would doubt that there are two distinct high taxonomic level entities, first clearly expressed by Evitt (1985) as his Gv and Gc cysts, intergradational forms exist. Whatever criterion is used to separate the two families, selecting the diagnostic features within the intergrading taxa will inevitably be somewhat arbitrary. Possession of one or more lateral horns is a consistent feature among ceratiaceans, and lateral horns are generally absent among areoligeraceans. But when does a prominence become a horn? And how should we treat forms in which a prominence, even a "horn", is a product of the ornament, whereas the central/main body of the cyst lacks a horn or prominence? From consideration of the options, we have concluded that the most pragmatic and consistent route is to define ceratiaceans on the presence of a lateral horn on the central body (endophragm/autophragm) of the cyst. Conversely, areoligerations by this definition lack a lateral horn on the central body/inner wall layer. We acknowledge that this is somewhat arbitrary, but no better option is in our view available.

Within the Areoligeraceae, aside from the lack of a lateral horn, shape seems to be a low-level, usually intraspecific, variable. All factors considered, including our own experience and the desire to keep the taxonomy as stable as possible, we have determined the following hierarchy of features:

1) wall structure — whether a cyst is acavate, holocavate or circumcavate.
2) whether the ornament is linear or free standing.
4) whether the ornament is distributed all over the cyst (albeit sometimes somewhat reduced dorsoventrally) or whether the dorsoventral areas are devoid of ornament.
5) whether the ornament is non-aligned or shows alignment

Other features, such as ambital shape, degree of asymmetry, and finer details of the ornament are, in our view, not useful taxonomically or are used to define taxa at the species level.

Within the *Cyclonephelium* group, cavate forms are placed in *Canningia* (if densely holocavate and with a narrow perocoel) or *Senoniasphaera* (with complete wall-layer separation or sparse supporting structures, plus usually a broad periocoel). *Trimuridinium* gen. nov. contains species with three wall layers. Forms with linear ornament are assigned to *Aptea* (if over all the cyst surface, albeit possibly somewhat reduced dorsoventrally; including *Cassidium* as a taxonomic junior synonym) or *Cyclonephelium* (if dorsoventral areas devoid of ornament are present; including *Cauveridinium* as a taxonomic junior synonym). Forms with free-standing ornament are assigned to *Tenua* (if dorsoventral areas have ornament, albeit sometimes reduced or sparse; including *Doidyx* as a taxonomic junior synonym) or *Circulodinium* (if dorsoventral areas are devoid of ornament). Two special cases of acavate genera are *Canninginopsis*, which has parasutural ornament, and *Cerbia*, which has penitabular ornament. Forms with horns or distinct prominences formed by the endophragm or autophragm, such as *Pseudoceratium* are assigned to the Ceratiaceae. We consider that our refinement of the taxonomy of the *Cyclonephelium* group of areoligeracean dinoflagellate cysts will lead to their significantly improved use in biostratigraphical and palaeoenvironmental analyses.

Acknowledgements

We are greatly indebted to Ian Harding and Martin Pearce for their detailed and insightful reviews of this paper, which led to significant improvements; and also Peta Mudie for her review on behalf of the Geological Survey of Canada, which led to important refinements. Bill MacMillan assisted with drafting. Susanne Feist-Burkhardt, Uli Heimhofer and an unnamed librarian at Hannover University, Germany provided literature. Jennifer Galloway, Thomas Hadlari and Andrew MacRae provided graphics on which some of the diagrams in the Supplemental data are based. Thomas Hadlari, Danielle Thomson and Claudia Schröder-Adams collected samples from the Hume River section, Thomas Hadlari collected samples from the Imperial River section, and Jennifer Galloway collected samples from the Glacier Fiord section. We are grateful to all these individuals. The publication of this paper was entirely financed by the British Geological Survey and the Geological Survey of Canada (Natural Resources Canada).

SELW and JBR publish with the permission of the Executive Director, British Geological Survey (NERC). This is NRCan Contribution number 20180002.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

ROBERT A. FENSOME works for the Geological Survey of Canada (GSC) in their Atlantic Division at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia. During his 31-year tenure at the GSC, Rob has focussed mainly on the Mesozoic and Cenozoic dinoflagellate cysts from off Canada's east coast, but is now venturing into projects involving assemblages from northwestern and Arctic Canada. While biostratigraphical and paleoenvironmental studies justify his paycheck, he also has a strong interest in dinoflagellate evolution.

GRAHAM L. WILLIAMS's main field of interest is the Mesozoic-Cenozoic palynostratigraphy of offshore eastern Canada, including the arctic. His long-standing interest in dinoflagellate cysts has led to studies of these palynomorphs in both hemispheres, including the deep ocean basins. After seven years at Pan American Petroleum Corporation (for anyone who remembers that far back), Graham joined the Geological Survey of Canada in 1971. He has spent the last 43 years at the Bedford Institute of Oceanography in Nova Scotia, where he has the good fortune to work with some outstanding colleagues.

JAMES B. RIDING is a geologist/palynologist with the British Geological Survey (BGS) in Nottingham, UK. He undertook the MSc in palynology at the University of Sheffield and, several years later, Jim was awarded a PhD by the same institution. During 2004, Jim gained a DSc from the University of Leicester, where he did his Bachelor's degree in geology. His interests include the Mesozoic–Cenozoic palynology of the world, palaeoenvironmental palynology, palynomorph floral provinces, forensic palynology, preparation techniques, the history of palynology, and the morphology, systematics and taxonomy of dinoflagellate cysts.

Jim is a past President of AASP – The Palynological Society, and became Managing Editor in 2004.

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Appendix 1

Significant milestones in the conceptual evolution of the *Cyclonephelium* group of areoligeraceans and *Pseudoceratium*. The name *Tenua* refers to *Tenua* Eisenack 1958, not *Tenua* Davey 1978, unless otherwise specified.

1955	Deflandre & Cookson (1955) erected the genus *Cyclonephelium*, with *Cyclonephelium compactum* as type, with the genus also including *Cyclonephelium distinctum*.
1957	Gocht (1957) erected the genus *Pseudoceratium*, with *Pseudoceratium pelliferum* as type.
1958	Eisenack (1958a) erected the genus *Tenua*, with *Tenua hystrix* as type. In the same publication, Eisenack (1958a) erected *Aptea*, with *Aptea polymorpha* as type.
1960	Cookson & Eisenack (1960b) erected the genus *Canningia*, with *Canningia reticulata* as type.
1961	Alberti (1961) erected *Circulodinium*, with *Circulodinium hirtellum* as type.
1961/1963	Evitt (1961c, 1963a, 1963b) recognised the nature of archaeopyles, allowing the assignment of forms now attributed to the Areoligeraceae as dinoflagellate cysts.
1962	Cookson & Eisenack (1962b) erected *Canninginopsis*, with *Canninginopsis denticulata* as type.

1964	Eisenack (1964) considered *Circulodinium* to be a taxonomic junior synonym of *Canningia*.
1966	Sarjeant (1966c) erected *Doidyx*, with *Doidyx anaphrissa* as type.
	Williams & Downie (1966c) emended *Cyclonephelium* to include chorate species.
1967	Drugg (1967) erected *Cassidium*, with *Cassidium fragilis* as type.
	Clarke & Verdier (1967) erected the genus *Senoniasphaera*, with *Senoniasphaera protrusa* as type.
1968	Sarjeant (1968) emended *Tenua* to include some forms now considered to belong to the non-areoligeracean genus *Sentusidinium*.
1972	Pocock (1972) emended *Tenua*, recognising for the first time the offset parasulcal notch.
1974	Norvick & Burger (1974) presented an overview of *Cyclonephelium,* but made no taxonomic proposals.
1977	Ioannides et al. (1977) emended *Cyclonephelium* to "clarify the types of cysts accommodated in the genus."
1978	Sarjeant & Stover (1978) considered *Doidyx* to be a taxonomic junior synonym of *Aptea*. They also considered *Tenua* to be a taxonomic junior synonym of *Cyclonephelium,* and erected the genus *Sentusidinium* to accommodate non-areoligeracean species previously assigned to *Tenua*.
	Stover & Evitt (1978) emended *Cyclonephelium* and removed chorate species from it, assigning them to their new genus *Glaphyrocysta*. They accepted *Tenua* as a taxonomic junior synonym of *Cyclonephelium*.
	Davey (1978) proposed illegitimately to change the type of *Tenua*, inadvertently creating the homonym *Tenua* Davey. *Tenua* Davey is a taxonomic junior synonym of *Sentusidinium* (as well as an illegitimate junior homonym of *Tenua* Eisenack. Davey (1978) also effectively considered *Circulodinium* and *Tenua* Eisenack to be taxonomic junior synonyms of *Cyclonephelium*.
1980	Dörhöfer & Davies (1980) emended *Cyclonephelium*, restricting it to forms with and "apteate" ornament. They accepted *Tenua* as a taxonomic junior synonym of *Cyclonephelium*. They also emended *Aptea, Canningia* and *Pseudoceratium* to

	accord with a re-interpretation of paratabulation no longer accepted.
1981	Below (1981a) erected *Cerbia* for forms similar to *Canninginopsis* but with penitabular rather than parasutural ornament. He also emended *Canningia*, considering that is differed from *Senoniasphaera* in being holocavate rather than cavate.
1985	Sarjeant (1985a) considered *Cerbia* to be a taxonomic junior synonym of *Tenua*.
1986	Bint (1986) considered *Doidyx* and *Aptea* to be taxonomic junior synonyms of *Pseudoceratium*, which he also emended.
	In a restudy of material described by Pocock (1962, 1972), Jansonius (1986) resurrected *Circulodinium* for areoligeraceans with short, free-standing elements.
1987	Helby (1987) independently retained *Circulodinium* with a similar concept to that of Jansonius (1986). He retained *Aptea* and *Pseudoceratium* separately but suggested that this separation would be difficult to maintain. He also emended *Canningia*, re-emphasising that it is holocavate rather than cavate, like *Senoniasphaera*.
	Stover & Williams (1987) retained *Cerbia* separately from *Tenua*.
1988	Backhouse (1988) suggested that *Circulodinium* may be a taxonomic junior synonym of *Tenua*, but did not make a formal proposal to that effect.
1992	Sarjeant (1992b) re-instated the synonymy of *Cerbia* with *Tenua*.
	Quattrocchio & Sarjeant (1992) retained *Aptea* separately from *Pseudoceratium*.
2002	Duxbury (2002) retained *Cerbia* as a separate genus.

Appendix 2

The current status of taxa of *Aptea*, *Canningia*, *Canninginopsis*, *Cassidium*, *Cerbia*, *Circulodinium*, *Cyclonephelium*, *Pseudoceratium*, *Senoniasphaera* and *Tenua* considered “correct” in Williams et al. (2017). TJS = taxonomic junior synonym. An asterisk denotes the type of the genus.

***APTEA* Eisenack 1958 emend. nov.**
Aptea notialis Quattrocchio & Sarjeant 1992
Now *Pseudoceratium notialis*
**Aptea polymorpha* Eisenack 1958
Still *Aptea polymorpha*

***CANNINGIA* Cookson & Eisenack 1960**
Canningia apiculata Jain & Garg in Jain et al. 1984
Now *Tenua*? *apiculata*
Canningia bassensis Marshall 1990a
TJS of *Canningia transitoria*
Canningia duxburyi Harding 1990
Still *Canningia duxburyi*
Canningia fairfieldensis Willumsen 2012
Still *Canningia fairfieldensis*
Canningia grandis Helby 1987
Still *Canningia grandis*
Canningia? *granulata* Morgenroth 1966
Now *Petalodinium*? *granulatum*
Canningia hulinensis He Chengquan et al. 1999
Now *Canningia*? *hulinensis*
Canningia keiemensis Louwye 1997
Still *Canningia keiemensis*
Canningia macroreticulata Lebedeva in Ilyina et al. 1994
Still *Canningia macroreticulata*
Canningia? *microciliata* Jain 1977
Now *Senoniasphaera microciliata*
Canningia pistica Helby 1987
Still *Canningia pistica*
**Canningia reticulata* Cookson & Eisenack 1960

Still *Canningia reticulata*
Canningia retirugosa He Chengquan (al. *Kallosphaeridium retirugosum*)
Now *Aptea*? *retirugosa*
Canningia? *rotundata* Cookson & Eisenack 1961
Now *Aptea rotundata*
Canningia rugulosa (Clarke & Verdier 1967) Stover & Evitt 1978
Still *Canningia rugulosa*
Canningia scabrosa Cookson & Eisenack 1970
Now *Tenua scabrosa*
Canningia senonica Clarke & Verdier 1967
Still *Canningia senonica*
Canningia spongireticulata Prössl 1990
Now *Aptea*? *spongireticulata*
Canningia torulosa Davey & Verdier 1973
Now *Sindridinium torulosum* (see Nøhr-Hansen et al. 2017)
Canningia transitoria Stover & Helby 1987b
Still *Canningia transitoria*
Canningia? *turrita* Brideaux 1977
Now *Epelidosphaeridia*? *turrita*
Canningia xinjiangensis Chen et al. 1988
TJS of *Canningia reticulata*

***CANNINGINOPSIS* Cookson & Eisenack 1962**
Canninginopsis bretonica Marshall 1990b
Still *Canninginopsis bretonica*
**Canninginopsis denticulata* Cookson & Eisenack 1962
Still *Canninginopsis denticulata*
Canninginopsis intermedia Morgan 1980
Now *Cerbia intermedia*
Canninginopsis maastrichtiensis Slimani 1994

Still *Canninginopsis maastrichtiensis*
Canninginopsis ordospinosa Smith 1992
Now *Cerbia ordospinosa*

CASSIDIUM Drugg 1967 (TJS of *Aptea*)
Cassidium filosum Wilson 1988
Now *Canningia*? *filosa*
**Cassidium fragile* (Harris 1965) Drugg 1967
Now *Aptea fragilis*

CAUVERIDINIUM Khowaja-Ateequzzaman & Jain 1990 (TJS of *Cyclonephelium*)
Cauveridinium indicum
Now *Cyclonephelium indicum*
Cauveridinium intermedium
TJS of *Cyclonephelium indicum*
Cauveridinium longispinosum
TJS of *Cyclonephelium indicum*
Cauveridinium membraniphorum
Now *Cyclonephelium membraniphorum*

***CERBIA* Below 1981**
Cerbia magna Duxbury 2001
Now *Tenua magna*
Cerbia monile Duxbury 2002
Now *Canninginopsis monile*
**Cerbia tabulata* (Davey & Verdier 1974) Below 1981
Still *Cerbia tabulata*

***CIRCULODINIUM* Alberti 1961 emend. nov.**
Circulodinium? *araneosum* (Brideaux 1977) Fauconnier in Fauconnier & Masure 2004

Now *Tenua*? *araneosa*

Circulodinium asperum (Singh 1971) Helby 1987

TJS of *Tenua scabrosa*

Circulodinium asymmetricum (Burger 1980) He Chengquan & Sun Xuekun 2000

Now *Tenua*? *asymmetrica*

Circulodinium attadalicum (Cookson & Eisenack 1962) Helby 1987

Now *Tenua*? *attadalica*

Circulodinium barbiferum (Cookson & Eisenack 1982) Fauconnier in Fauconnier & Masure 2004

Now *Cyclonephelium*? *barbiferum*

Circulodinium brevispinatum (Millioud 1969) Fauconnier in Fauconnier & Masure 2004

TJS of *Tenua hystrix*

Circulodinium brevispinosum (Pocock 1962) Jansonius 1986

TJS of *Tenua hystrix*

Circulodinium chinense (He Chengquan 1991) He Chengquan et al. 2009

Now *Tenua chinensis*

Circulodinium cingulatum He Chengquan et al. 1999

TJS of *Tenua scabrosa*

Circulodinium colliveri (Cookson & Eisenack 1960) Helby 1987

Now *Tenua colliveri*

Circulodinium comptum (Davey 1982) Helby 1987

Now *Tenua compta*

Circulodinium copei Bailey et al. 1997

Now *Tenua copei*

Circulodinium deflandrei Alberti 1961

TJS of *Circulodinium distinctum*

Circulodinium densebarbatum (Cookson & Eisenack 1960) Fauconnier in Fauconnier & Masure 2004

Now *Tenua densebarbata*

Circulodinium distinctum (Deflandre & Cookson 1955) Jansonius 1986

Still *Circulodinium distinctum*

Circulodinium distinctum subsp. *distinctum*

Now redundant

Circulodinium distinctum subsp. *laevigatum* (Mehrotra & Sarjeant 1986) Lentin & Williams 1989

TJS of *Circulodinium distinctum*

Circulodinium distinctum subsp. *psilatum* (Yu Jingxian & Zhang Wangping 1980) Lentin & Williams 1989

TJS of *Tenua kukebaiensis*

Circulodinium elongatum (He Chengquan 1991) He Chengquan et al. 2009

Now *Tenua*? *elongata*

**Circulodinium hirtellum* Alberti 1961

TJS of *Circulodinium distinctum*

Circulodinium? *indicum* Mehrotra & Sarjeant 1987 ex Lentin & Williams 1989

TJS *Cleistosphaeridium diversispinosum*

Circulodinium insigne (He Chengquan 1991) He Chengquan et al. 2009

TJS of *Tenua hystrix*

Circulodinium kukebaiense (Mao Shaozhi & Norris 1988) He Chengquan et al. 2009

Now *Tenua kukebaiensis*

Circulodinium latoaculeum (Yun Hyesu 1981) Prince et al. 1999

Now *Cleistosphaeridium latoaculeum*

Circulodinium? *micibaculatum* (Jiabo 1978) He Chengquan et al. 2009

Now *Tenua*? *micibaculata*

Circulodinium paucispinum (Davey 1969) Fauconnier in Fauconnier & Masure 2004

TJS of *Circulodinium distinctum*

Circulodinium pentagonum (He Chengquan 1991) He Chengquan et al. 2009

Now *Tenua*? *pentagona*

Circulodinium vermiculatum Stover & Helby 1987a

TJS of *Aptea rotundata*

Circulodinium wulagenense (He Chengquan 1991) He Chengquan et al. 2009

Now *Circulodinium*? *wulagenensis*

***CYCLONEPHELIUM* Deflandre & Cookson 1955 emend. nov.**
Cyclonephelium? *ambiguum* He Chengquan 1991
Now *Spiniferites*? *ambiguus*
Cyclonephelium areolatum Cookson & Eisenack 1960
TJS of *Canningia reticulata*
Cyclonephelium? *baculatum* Song Zhichen in Song Zhichen et al. 1985
Now *Selenopemphix*? *baculatum*
Cyclonephelium? *bulbosum* Smith & Harding 2004
Now *Bataiacasphaera*? *bulbosa*
Cyclonephelium chabaca Below 1981
TJS of *Canningia reticulata*
Cyclonephelium circulatum He Chengquan 1991
Now *Circulodinium circulatum*
Cyclonephelium clathromarginatum Cookson & Eisenack 1962
Now *Canningia*? *clathromarginata*
Cyclonephelium combibaculum Song Zhichen in Song Zhichen et al. 1985
Now *Polysphaeridium*? *combibaculum*
**Cyclonephelium compactum* Deflandre & Cookson 1955
Still *Cyclonephelium compactum*
Cyclonephelium crassimarginatum Cookson & Eisenack 1974
Now *Canningia crassimarginata*
Cyclonephelium deconinckii Boltenhagen 1977
Still *Cyclonephelium deconinckii*
Cyclonephelium? *dubium* (Jain & Millepied 1975) Sarjeant & Stover 1978
Now *Tenua dubia*
Cyclonephelium filoreticulatum (Slimani 1994) Prince et al. 1999
Now *Senoniasphaera filoreticulata*
Cyclonephelium formosum (Iosifova 1992) Fauconnier in Fauconnier & Masure 2004

TJS of *Circulodinium distinctum*

Cyclonephelium? *granulatum* (Horowitz 1975) Stover & Evitt 1978

Now *Trichodinium*? *granulatum*

Cyclonephelium? *hexalobosum* (Cookson & Eisenack 1974) Stover & Evitt 1978

Now *Cerbia*? *hexalobosa*

Cyclonephelium hughesii Clarke & Verdier 1967

Now *Circulodinium*? *hughesii*

Cyclonephelium inconspicuum Duxbury 1983

Now *Canningia inconspicua*

Cyclonephelium intonsum Duxbury 1983

Still *Cyclonephelium intonsum*

Cyclonephelium longispinatum (Davey 1978) Fauconnier in Fauconnier & Masure 2004

TJS of *Tenua anaphrissa*

Cyclonephelium longispinosum He Chengquan 1991

Now *Cleistosphaeridium*? *longispinosum*

Cyclonephelium maugaad Below 1981

Still *Cyclonephelium maugaad*

Cyclonephelium? *operculatum* Yu Jingxian 1982

Still *Cyclonephelium*? *operculatum*

Cyclonephelium paucimarginatum Cookson & Eisenack 1962

TJS of *Aptea rotundata*

Cyclonephelium? *tarimense* He Chengquan 1991

TJS of *Spiniferites*? *ambiguus*

Cyclonephelium uncinatum (Norvick 1976) Stover & Evitt 1978

Now *Aptea uncinata*

Cyclonephelium vannophorum Davey 1969

Now *Aptea*? *vannophora*

***PSEUDOCERATIUM* Gocht 1957 emend. nov.**

Pseudoceratium almohadense (Below 1984) Lentin & Williams 1989

Now *Circulodinium almohadense*

Pseudoceratium anaphrissum (Sarjeant 1966) Bint 1986

Now *Tenua anaphrissa*

Pseudoceratium aulaeum Harding 1990 ex Harding in Williams et al. 1998

Still *Pseudoceratium aulaeum*

Pseudoceratium australiense Fensome & Williams 2004

Still *Pseudoceratium australiense*

Pseudoceratium brevicornutum Herngreen et al. 2000

Now *Pseudoceratium*? *brevicornutum*

Pseudoceratium distinctum Duxbury 2001

Now *Circulodinium vectensis* (substitute name)

Pseudoceratium eisenackii (Davey 1969) Bint 1986

TJS of *Cyclonephelium compactum*

Pseudoceratium expolitum Brideaux 1971

Still *Pseudoceratium expolitum*

Pseudoceratium gochtii Neale & Sarjeant 1962

Still *Pseudoceratium gochtii*

Pseudoceratium iehiense Helby & May in Helby 1987

Now *Pseudoceratium*? *iehiense*

Pseudoceratium interiorense Bint 1986

Still *Pseudoceratium interiorense*

Pseudoceratium iveri Nøhr-Hansen 1993

Still *Pseudoceratium iveri*

Pseudoceratium? *parvum* Michael 1964

Still *Pseudoceratium*? *parvum*

**Pseudoceratium pelliferum* Gocht 1957

Still *Pseudoceratium pelliferum*

Pseudoceratium plerum (Duxbury 1983) Bint 1986

Now *Canningia plera*

Pseudoceratium retusum Brideaux 1977

Still *Pseudoceratium retusum*

Pseudoceratium? *robustum* Michael 1964

Still *Pseudoceratium*? *robustum*

Pseudoceratium securigerum (Davey & Verdier 1974) Bint 1986

TJS of *Circulodinium distinctum*

Pseudoceratium solocispinum (Davey 1974) Harding 1990

Still *Pseudoceratium solocispinum*

Pseudoceratium spitiense Jain & Garg in Jain et al. 1984

Still *Pseudoceratium spitiensis*

Pseudoceratium toveae Nøhr-Hansen 1993

Still *Pseudoceratium toveae*

Pseudoceratium weymouthense Helby 1987

Still *Pseudoceratium weymouthense*

SENONIASPHAERA **Clarke & Verdier 1967 emend. nov.**

Senoniasphaera clavellii Bailey et al. 1997

Now *Senoniasphaera*? *clavellii*

Senoniasphaera edenensis Marshall 1990a

Still *Senoniasphaera edenensis*

Senoniasphaera inornata (Drugg 1970) Stover & Evitt 1978

Still *Senoniasphaera inornata*

Senoniasphaera jurassica (Gitmez & Sarjeant 1972) Lentin & Williams 1976

Still *Senoniasphaera jurassica*

Senoniasphaera lordii (Cookson & Eisenack 1968) Lentin & Williams 1976

Still *Senoniasphaera lordii*

Senoniasphaera macroreticulata Prince et al. 2008

Still *Senoniasphaera macroreticulata*

Senoniasphaera microreticulata Brideaux & McIntyre 1975

Still *Senoniasphaera microreticulatum*

Senoniasphaera palla Louwye 1997

Still *Senoniasphaera palla*
**Senoniasphaera protrusa* Clarke & Verdier 1967
Still *Senoniasphaera protrusa*
Senoniasphaera protrusa subsp. *congrensa* Prince et al. 2008
Now *Senoniasphaera congrensa*
Senoniasphaera protrusa subsp. *protrusa*
Now redundant
Senoniasphaera ptomatis Helby et al. in Helby 1987
Still *Senoniasphaera ptomatis*
Senoniasphaera? *reticulata* (Khanna & Singh 1981) Lentin & Williams 1993
Still *Senoniasphaera*? *reticulatum*
Senoniasphaera rotundata Clarke & Verdier 1967
Now *Canningia glomerata* (substitute name)
Senoniasphaera rotundata subsp. *alveolata*
TJS of *Senoniasphaera turonica*
Senoniasphaera? *sarrisii* (Archangelsky 1969) Stover & Evitt 1978
Now *Turbiosphaera*? *sarrisii*
Senoniasphaera stagonoides (Benedek 1972) Helenes 1983
Now *Deflandrea*? *stagonoides*
Senoniasphaera turensis Vasilyeva in Andreeva-Grigorovich et al. 2011
Now *Senoniasphaera*? *turensis*
Senoniasphaera turonica (Prössl 1990) Pearce et al. 2011
Still *Senoniasphaera turonica*
Senoniasphaera whitenessensis Prince et al. 2008.
Now *Trimuridinium whitenessense*

TENUA Eisenack 1958 emend. nov.

Tenua? *americana* (Pöthe de Baldis & Ramos 1983) Prössl 1992
TJS of *Tenua hystrix*
Tenua aucda (Below 1981) Lentin & Williams 1993

Now *Cerbia*? *aucda*

Tenua formosa (Mao Shaozhi & Norris 1988) Lentin & Williams 1993

Now *Cerbia*? *formosa*

**Tenua hystrix* Eisenack 1958

Still *Tenua hystrix*

Tenua reducta (Châteauneuf 1980) Courtinat in Fauconnier & Masure 2004

Still *Tenua reducta*

Tenua suturispinosa (He Chengquan 1991) Lentin & Williams 1993

TJS of *Cerbia*? *formosa*

Tenua wenquanensis Cheng Jinhui & He Chengquan 2006

Now *Cerbia*? *wenquanensis*

Appendix 3.

A table illustrating the details of the provenance of the specimens newly illustrated in this study. Column A gives the relevant figure number in the present paper. Column B gives the taxon name. Column C gives the Geological Survey of Canada (GSC) type number. Columns D and E give the region and locality name respectively. Column F gives the processing number (GSC Calgary system). Column G gives the sample and slide number. Column H gives height from base of section or formation for surface section (ss) samples (the prefix C = Christopher Formation; the prefix I = Isachsen Formation); or depth in the well for ditch cuttings (dc) and conventional core (CC) samples; for further information, see Supplemental data. Column I gives the microscope coordinates on Zeiss Axioplan microscope serial no. 310243 at GSC (Atlantic). Column J gives England Finder (EF) coordinates (the asterisk indicating that the England Finder was inserted upside down and parentheses indicate that the EF coordinates were derived from the microscope coordinates, not relocation of the specimen). Column K gives provides specifics of the lens used for the photograph (pc = phase contrast; ic = interference contrast; bf = bright field).

Figure Captions:

Figure 1. The position of the main antapical/lateral horns according to Evitt (1985). A, C: the position of main antapical/lateral horns (dotted circles) in the Areoligeraceae (including the *Cyclonephelium* group). B, D: the position of main antapical/lateral horns (dotted circles) in the Ceratiaceae (including *Pseudoceratium*). Redrawn after Evitt (1985, fig. 10.6).

Figure 2. Configuration of the anterior margin of the first precingular paraplate (1''; indicated by the arrow) in the Areoligeraceae (including the *Cyclonephelium* group) (A) and Ceratiaceae (including *Pseudoceratium*) (B) according to Bint (1986). Redrawn after Bint (1986, fig. 11).

Figure 3. Flow chart showing how the genera reviewed in this study are related. The top row illustrates the difference between areoligeraceans and the ceratiacean genus *Pseudoceratium*. In the lower two rows, each genus is represented by an idealised line drawing showing the principal characteristics. The one genus accepted as a member of the *Cyclonephelium* group herein but not illustrated in this figure is *Trimuridinium*, which is characterised by three wall layers.

Figure 4. New specimens of *Aptea* and *Canninginopsis*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–N**, *Aptea cassis* sp. nov.: C is the holotype; A–D, G–H, L–M show ventral views of mostly the ventral surface; E–F show the ventral and dorsal surfaces respectively of a ventral view of a single specimen; I, K and possibly J and N show dorsal views of mostly the ventral surface. **O–P**, *Aptea* sp., a thick-walled microreticulate form, dorsal view of dorsal (O) and ventral (P) surfaces. **Q–S**, *Aptea uncinata*: Q shows a ventral view; Q shows an oblique dorsoventral view; and S shows a dorsoventral view. **T**, *Canninginopsis* sp., ventral view.

Figure 5. New specimens of *Canningia* and *Cerbia*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–G**, *Canningia reticulata*: A shows a ventral view of the ventral surface; B shows a ventral view of the dorsal surface; C shows a dorsal view of the dorsal surface; D shows a dorsal view of the ventral surface; E–G are dorsoventral views. **H–O**, *Canningia inconspicua*:

H shows a ventral view; I shows a ventral view of the ventral surface; J shows a ventral view of the dorsal surface; K–M show dorsal views; N–O show ventral views. **P**, *Cerbia* sp., probably a ventral view.

Figure 6. New specimens of *Circulodinium*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–D,** *Circulodinium distinctum*: A, C show dorsoventral views; B shows a dorsal view; D shows a ventral view.

Figure 7. New specimens of *Cyclonephelium*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–J**, *Cyclonephelium compactum*: A, D, I–J show dorsal views; B–C show dorsal view of dorsal (B) and ventral (C); E shows a ventral view; F–H shows a dorsoventral (probably dorsal) view at high (F), medium (G) and low (H) foci. **K–L,** *Cyclonephelium intonsum*, dorsoventral views.

Figure 8. New specimens of *Senoniasphaera*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–B**, *Senoniasphaera microreticulata*, ventral views. **C–D**, *Senoniasphaera* sp., dorsoventral views.

Figure 9. New specimens of *Tenua* (1); complete details are shown in Appendix 3. Scale bars = 20 µm. **A–C,** *Tenua colliveri*: A shows a dorsal view of the ventral surface; B–C show ventral views. **D–H,** *Tenua anaphrissa*; D–E show dorsal views; H shows a ventral view; F–G show dorsoventral views. **I–L,** *Tenua hystrix*: I shows a ventral view; J–K show dorsal views; L shows a dorsoventral view.

Figure 10. New specimens of *Tenua* (2); complete details are shown in Appendix 3. Scale bars = 20 µm. **A–P,** *Tenua scabrosa*: A shows a dorsoventral (?dorsal) view; B–C, G–H show ventral views; D, M–P show dorsal views; E–F show dorsal views of ventral (E) and dorsal (F) surfaces; I–J show dorsal views of dorsal (I) and ventral (J) surfaces; K–L show ventral views of ventral (K) and dorsal (L) surfaces.

Figure 11. New specimens of *Pseudoceratium*; complete details are shown in Appendix 3. Scale bars = 20 µm. **A–D,** *Pseudoceratium pelliferum*: A–B, D show dorsal views; C shows a ventral view.

Figure 12. Reproduced illustrations of holotypes of species treated in the present work — 1.

A. *Aptea fragilis*. Holotype from Harris (1965, pl. 27, fig. 5, as *Ovoidites fragilis*); Lower Eocene; Princetown Member, Dilwyn Clay; Princetown area, Victoria, Australia. The specimen appears to be in ventral view; length 60 µm, breadth 70 µm, derived from magnification (x630) given in publication.

B. *Aptea polymorpha*. Holotype from Eisenack (1958, pl. 22, fig. 5, as *Aptea polymorpha*); Aptian; northern Germany. The specimen is in ventral view; length 114 µm, breadth 81 µm.

C. *Aptea*? *retirugosa*. Holotype from He Chengquan (1991, pl. 8, fig. 11, as *Canningia retirugosa*); Upper Cretaceous; western Tarim Basin, southern Xinjiang Province, China. The specimen appears to be in dorsoventral view; dimensions unknown.

D. *Aptea rotundata*. Holotype from Cookson & Eisenack (1961, pl. 12, fig.1, as *Canningia rotundata*); Senonian (Upper Cretaceous); Belfast No. 4 bore, southwestern Victoria, Australia. The specimen appears to be in dorsal view; length 87µm, breadth 90 µm.

E. *Aptea*? *spongireticulata*. Holotype from Prössl (1990, pl. 13, fig. 5, as *Canningia spongireticulata*); upper Albian – middle Turonian; Konrad 101 core, Lower Saxony Basin, northwestern Germany. The specimen is in dorsoventral view; length 55 µm, breadth 61 µm.

F. *Aptea unicinata*. Holotype from Norvick (1976, pl. 8, fig. 11, as *Adnatosphaeridium uncinatum*); Cenomanian; Bathurst Island No. 2 well, core 9, Northern Territory, Australia. The specimen is in dorsoventral (possibly ventral) view; length 58 µm, breadth 65 µm.

G. *Aptea*? *vannophora*. Holotype from Davey (1969, pl. 11, fig.11, as *Cyclonephelium vannophorum*); Cenomanian; Lower Chalk Group; Compton Bay, Isle of Wight, England. The specimen is in dorsoventral view; length 65 µm, breadth 62 µm.

H. *Canningia clathromarginata*. Holotype from Cookson & Eisenack (1962, pl. 6, fig. 2, as *Cyclonephelium clathromarginatum*); upper Albian – Cenomanian; Wapet's seismic shot hole B1, north of Gingin, Australia. The specimen is in dorsoventral view; breadth 136 µm.

I. *Canningia crassimarginata*. Holotype from Cookson & Eisenack (1974, pl. 28, fig. 3, as

Cyclonephelium crassimarginatum); middle Cretaceous; Gingin Brook bore, Australia. The specimen is in dorsoventral view; breadth 94 µm.

J. *Canningia duxburyi* Holotype from Harding (1990b, pl.5, fig.1, ex Harding in Williams et al., 1998 as *Canningia duxburyi*); upper Hauterivian – lower Barremian; Norfolk, England. The specimen is in dorsal view; scale bar is 10 µm.

K–L. *Canningia fairfieldensis*. Holotype from Willumsen (2012, pl. 2, figs 1–2, as *Canningia fairfieldensis*); Lower Paleocene; Fairfield Quarry, South Island, New Zealand. The specimen is in ventral view according to Willumsen (2012); other details of focal levels not given; scale bar in Q is 10 µm.

M–N. *Canningia*? *filosa*. Holotype from Wilson (1988, pl. 2, figs 8a–b, as *Cassidium filosum*); Paleocene; Waipawa section, Hawkes Bay, New Zealand. The figures show a dorsoventral view of the dorsal (M) and ventral (N) surfaces; scale bar in M is 20 µm.

O. *Canningia glomerata*. Holotype from Clarke and Verdier (1967, pl.14, fig.2, as *Senoniasphaera rotundata*); Senonian; Isle of Wight, England. The specimen is in dorsoventral view; overall length 92 µm, overall breadth 67 µm.

P. *Canningia inconspicua*. Holotype from Duxbury (1983, pl. 3, fig. 6, as *Cyclonephelium inconspicuum*); upper Aptian; Lower Greensand; Isle of Wight, southern England. The specimen is in dorsal view; length 58 µm, breadth 64 µm.

Q–T. *Canningia grandis*. Holotype from Helby (1987, figs 30A–D, as *Canningia grandis*); Hauterivian; Plover-2 well, Australia. The specimen appears to be in ventral view, the figures ranging (from Q to T) from low to high focus; length 105 µm, breadth 123 µm, derived from magnification (x400) given in publication.

Figure 13. Reproduced illustrations of holotypes of species treated in the present work — 2.

A–C. *Canningia*? *hulinensis*. Holotype from He Chengquan et al. (1999, pl. 1, figs 1–3, as *Canningia hulinensis*); upper Hauterivian – Barremian; H87-3 well, Hulin Basin, eastern Heilongjiang, northeastern China. The specimen is in dorsoventral view, ranging from low to high focus; length 110 µm, breadth 104 µm.

D. *Canningia plera*. Holotype from Duxbury (1983, pl.1, fig.7, as *Aptea plera*); lower Aptian; Lower Greensand; Isle of Wight; England. The specimen is in dorsal view; length 82 µm, breadth 102 µm.

E–H. *Canningia keiemensis*. Holotype from Louwye (1997, pl., figs 1–3, 6, as *Canningia keiemensis*); Turonian; well 36E135, West Flanders, Belgium. The specimen appears to be in ventral view, with E–F of the ventral surface and G–H of the dorsal surface; length 91 µm, breadth 84 µm.

I–J. *Canningia macroreticulata*. Holotype from Ilyina et al. (1994, pl. 30, figs 6–7, as *Canningia macroreticulata*); upper Coniacian; Siberia. The specimen is in dorsoventral view; length 65 µm, breadth 72 µm, derived from magnification (x900) given in publication.

K–L. *Canningia reticulata*. Holotype (K) and other specimen (L) from Cookson & Eisenack (1960, pl. 38, figs 1–2 respectively, as *Canningia reticulata*); Tithonian; of Broome No. 1 bore, Western Australia. Both specimens show dorsal views; holotype length 100 µm, breadth 86 µm.

M–P. *Canningia pistica*. Holotype from Helby (1987, figs 30I–L, as. *Canningia pistica*); Hauterivian; Plover-2 well, Australia. The specimen appears to be in ventral view, the figures ranging (from M to P) from low to high focus; length 94 µm, breadth 108 µm, derived from magnification (x400) given in publication.

Q. *Canningia rugulosa*. Holotype from Clarke & Verdier (1967, pl. 12, fig. 6, as *Aptea rugulosa*); Santonian; Chalk Group; Culver Cliff, Isle of Wight, England. The specimen is in (possibly oblique) dorsoventral view; length 74 µm, breadth 50 µm.

R. *Canningia senonica*. Holotype from Clarke & Verdier (1967, pl. 1, fig. 12, as *Canningia senonica*); Santonian; Chalk Group; Culver Cliff, Isle of Wight, England. The specimen is possibly in dorsal view; length 69 µm, breadth 57 µm.

S–T. *Canninginopsis bretonica*. Holotype from Marshall (1990b, figs 6N–O, as *Canninginopsis bretonica*); upper Campanian – middle Maastrichtian; Western Australia. The specimen appears to be in ventral view, showing dorsal (S) and ventral (T) surfaces; length 71 µm, breadth 81 µm.

Figure 14. Reproduced illustrations of holotypes of species treated in the present work — 3.

A–E. *Canningia transitoria*. Holotype from Stover & Helby (1987b, figs 3A–E, as *Canningia transitoria*); Barremian – lower Aptian; Houtman-1 well, Western Australia. The specimen is in dorsoventral view; A–C are in interference contrast, from high to low focus; D–E are in bright field illumination, high focus and optical section respectively; length 114 µm, breadth 122 µm, derived from magnification (x340) given in publication.

F. *Canninginopsis denticulata*. Holotype from Cookson & Eisenack (1962, pl., fig. 16, as *Canninginopsis denticulata*); Albian – Cenomanian; Australia. The specimen is ventral view, showing the dorsal surface; length 120 µm, breadth 111 µm.

G–H. *Canninginopsis monile*. Holotype from Duxbury (2002, pl. 1, figs 7–8, as *Cerbia monile*); upper Aptian – lower Albian; well 13/30a-4, Central North Sea Basin. The specimen appears to be in dorsal view, in dorsal (G) and ventral (H) foci; length 83 µm, breadth 85 µm.

I–K. *Canninginopsis maastrichtiensis*. Holotype from Slimani (1994, pl. 16, figs 5–7, as *Canninginopis maastrichtiensis*); upper Maastrichtian; Halembaye, Turnhout, Belgium. The specimen is apparently in dorsoventral view, in dorsal (I) and ventral (J–K) foci; length 64 µm, breadth 52 µm.

L. *Cerbia*? *aucda*. Holotype from Below (1981, pl. 4, fig. 3, as *Cerbia aucda*); Barremian; Chichaoua bore, southwestern Morocco. The specimen is in dorsal view; length 88 µm, breadth 83 µm.

M. *Cerbia*? *formosa*. Holotype from Mao Shaozhi & Norris (1988, pl. 1, fig. 9, as *Cerbia formosa*); Upper Eocene – Lower Oligocene; Wulagen Formation; Qimugen section, Kashi area, Tarim Basin, Xinjiang Province, China. The specimen is probably in ventral view; length 65 µm, breadth 63 µm.

N. *Cerbia*? *hexalobosa*. Holotype from Cookson & Eisenack (1974, pl. 26, fig. 7, as *Cassidium hexalobosum*); middle to Upper Cretaceous; Balcatta bore, Australia. The specimen is possibly in ventral view; length 90 µm, breadth 76 µm.

O–P. *Cerbia intermedia*. Holotype from Morgan (1980, pl. 3, figs 7–8, as *Canninginopsis intermedia*); lower Albian; Australia. The specimen is in ventral view, showing dorsal (O) and ventral (P) surfaces; length 97 µm, breadth 102 µm.

Q. *Cerbia ordospinosa*. Holotype from Smith (1992, fig. 5i, as *Canninginopsis ordospinosa*); upper Campanian – lower Maastrichtian; Cape Lamb Member, López de Bertodano Formation; Cape Lamb, Vega Island, Antarctica. The specimen is upright and is in dorsal view; length 112 µm, breadth 88 µm, derived from magnification (x600) given in publication.

R–S. *Cerbia tabulata*. Holotype from Davey & Verdier (1974, pl. 92, figs 1, 4, as *Cyclonephelium tabulatum*); Aptian; La Bédoule, southeastern France. The specimen is in dorsoventral view, in dorsal (R) and ventral (S) foci; length 57 µm, breadth 72 µm.

T. *Circulodinium circulatum.* Holotype from He Chengquan (1991, pl. 10, fig. 7, as *Cyclonephelium circulatum*); Middle to Upper Eocene; Tarim Basin, southern Xinjiang Province, China. The specimen is obliquely oriented, probably with apex to upper right and in dorsoventral view; dimensions are unknown.

Figure 15. Reproduced illustrations of holotypes of species treated in the present work — 4.

A–B. *Cerbia*? *wenquanensis.* Holotype from Cheng Jinhui & He Chengquan (2006, fig. 3s1–3s2, as *Tenua wenquanensis*); upper Kimmeridgian; Xueshan Formation; Wenquan, Tanggulashan Town, Golmud City, Qinghai Province, China. The specimen is in dorsoventral view, apparently in dorsal (A) and ventral (B) foci; length 31 µm, breadth 42 µm.

C–D. *Circulodinium almohadensis.* Holotype from Below (1984, pl. 1, figs 5A–B, as *Aptea almohadensis*); middle–upper Aptian; Mazagan Plateau, northwestern Africa. The specimen is ventral view, optical section? (C), ventral surface (D); length 58 µm, breadth 60 µm; scale bar is 10 µm.

E. *Circulodinium distinctum.* Holotype from Deflandre & Cookson (1955, pl. 2, fig. 14, as *Cyclonephelium distinctum*); Senonian (Upper Cretaceous); Gingin, Western Australia. The specimen is apparently in dorsoventral view; length 80 µm, breadth 120 µm, derived from magnification (x400) given in publication.

F. *Circulodinium*? *hughesii.* Holotype from Clarke & Verdier (1967, pl. 2, fig. 6, as *Cyclonephelium hughesii*); Cenomanian – lower Turonian; Southern Cliff, Isle of Wight, England. The specimen is in uncertain orientation; length 66 µm, breadth 63 µm.

G. *Circulodinium vectensis.* Holotype from Duxbury (2001, fig. 11, no. 1, as *Pseudoceratium distinctum*); upper Aptian; central North Sea; offshore UK. The specimen is in ventral view; length 88 µm, breadth 94 µm; scale bar is 10 µm.

H. *Circulodinium*? *wulaganensis.* Holotype from He Chengquan (1991, pl. 9, fig. 16, as *Canningia wulagenensis*); Upper Cretaceous; western Tarim Basin, southern Xinjiang Province, China. The specimen is rotated by -90° and is possibly in dorsoventral view; dimensions unknown.

I. *Cyclonephelium*? *barbiferum.* Holotype from Cookson & Eisenack (1982, pl. 7, fig. 9, as

Cyclonephelium? *barbiferum*); Albian – Cenomanian; Balcatta bore, Australia. The specimen is possibly in dorsoventral view; length 95 µm, breadth 88 µm.

J. *Cyclonephelium compactum*. Holotype from Deflandre & Cookson (1955, pl. 2, fig. 12, as *Cyclonephelium compactum*); Albian – Santonian; Onepah Station, New South Wales, Australia. The specimen is in ventral view, showing the ventral surface; length 78 µm, breadth 82 µm, derived from magnification (x420) given in publication.

K–L. *Cyclonephelium deconinckii*. Holotype from Boltenhagen (1977, pl. 4, figs 5a–b, as *Cyclonephelium deconinckii*); Campanian; Port Gentil, Gabon, Africa. The specimen is in dorsoventral view, general view (K), optical section showing structure of processes (L); length 64 µm, breadth 67 µm.

M–Q. *Cyclonephelium indicum*. Holotype from Khowaja-Ateequzzaman & Jain (1990, pl.1, figs 1–5; text-figs 1A–C as *Cauveridinium indicum*); Turonian – Santonian of the Cauvery Basin, India. The specimen is in dorsal high to dorsal low views (M–O) respectively and ventral low and ventral high views (P–Q) respectively; length of body 70 µm, breadth of body 80 µm, length of processes 6–12 µm.

R. *Cyclonephelium intonsum*. Holotype from Duxbury (1983, pl. 2, fig. 7, as *Cyclonephelium intonsum*); upper Aptian – lower Albian; Sandrock Series; Atherfield section, Isle of Wight, England. The specimen is in dorsal view; length 75 µm, breadth 81 µm.

S. *Cyclonephelium maugaad*. Holotype from Below (1981, pl. 11, fig. 2, as *Cyclonephelium maugaad*); Hauterivian – Aptian; southwestern Morocco. The specimen is in dorsoventral view; length 54 µm.

T. *Cyclonephelium membraniphorum*. Holotype from Cookson & Eisenack (1962b, pl.6, fig.9, as *Cyclonephelium membraniphorum*); upper Albian – Cenomanian; Wapet's seismic shot hole B1, north of Gingin, Australia. The specimen is in dorsoventral view; length 127 µm, breadth 108 µm.

Figure 16. Reproduced illustrations of holotypes of species treated in the present work — 5.

A. *Cyclonephelium*? *operculatum*. Holotype from Yu Jingxian (1982, pl. 7, fig. 21, as *Cyclonephelium operculatum*); Upper Jurassic – Lower Cretaceous; eastern Heilongjiang Province, China. The specimen is possibly in dorsoventral view; dimensions unknown.

B. *Senoniasphaera clavellii*. Holotype from Bailey et al. (1997, fig. 4d, as *Senoniasphaera clavellii*); upper Kimmeridgian; Kimmeridge Clay Formation, Bed 75; Hen Cliff, near Kimmeridge Bay, England. The specimen appears to be in dorsoventral view; length 85 µm, breadth 55 µm.

C–D. *Senoniasphaera congrensa*. Holotype from Prince et al. (2008, pl. 2, figs 1, 2, as *Senoniasphaera protrusa* subsp. *congrensa*); middle Santonian – lower Campanian; Chalk Group, England. The figures show a ventral view of the ventral (C) and dorsal (D) surfaces; length 62 µm, breadth 54 µm.

E–G. *Senoniasphaera*? *edenensis*. Holotype from Marshall (1990a, figs 15R–T, as *Senoniasphaera edenensis*); Campanian; Gippsland Basin, southeastern Australia. The specimen is in dorsal view — high focus (E), mid focus (F) and low focus (G); length 69 µm, breadth 84 µm.

H. *Senoniasphaera inornata*. Holotype from Drugg (1970, fig. 3C, as *Chiropteridium inornatum*); Danian; McBryde Limestone Member, Clayton Formation; Alabama, U.S.A. The specimen is in dorsal view; length 121 µm, breadth 102 µm, derived from magnification (x384) given in publication.

I–L. *Senoniasphaera filoreticulata*. Holotype from Slimani (1994, pl. 15, figs 1–4, as *Canningia filoreticulata*); Campanian; Beutenaken, The Netherlands. The specimen is in dorsal view, showing progressively lower foci from I to L; length 80 µm, breadth 100 µm.

M. *Senoniasphaera jurassica*. Holotype from Gitmez & Sarjeant (1972, pl. 14, fig. 5, as *Hexagonifera jurassica*); middle Kimmeridgian *wheatleyensis* zone; BGS Warlingham Borehole, Surrey, England. The specimen is apparently in ventral view; length 126 µm, derived from magnification (x350) given in publication.

N. *Senoniasphaera jurassica*. Specimen (BGS figured specimen MPK 1265) from Davey (1979, pl. 1, fig. 3, as *Hexagonifera jurassica*); Tithonian; Upper Kimmeridge Clay Formation; BGS Warlingham Borehole, Surrey, England at 696.65 m. The specimen is in ventral view; overall length 89 µm; breadth at paracingulum 75 µm.

O. *Senoniasphaera lordii*. Holotype from Cookson & Eisenack (1968, fig. 1J, as *Ascodinium lordii*); Santonian – lower Campanian; Gingin Brook Silty Limestone; No. 4 borehole, Western Australia. The specimen is in dorsoventral (possibly dorsal) view; length 90 µm, breadth 77 µm.

P. *Senoniasphaera microciliata.* Holotype from Jain (1977, pl. 3, fig. 25, as *Canningia microciliata*); lower Albian; Kallakkudi Limestone Quarry, Dalmiapuram, southern India. The specimen is is possibly in dorsoventral view; length 60 µm, breadth 56 µm.

Q–R. *Senoniasphaera macroreticulata.* Holotype from Prince et al. (2008, pl. 1, figs 7–8, as *Senoniasphaera macroreticulata*); upper Santonian – lower Campanian; Chalk Group; England. The specimen is in dorsoventral view; Q is in general view; R is focused on supporting pillars; length 70 µm, breadth 69 µm.

S–T. *Senoniasphaera palla.* Holotype from Louwye (1997, pl. 2, figs 3, 6, as *Senoniasphaera palla*); Turonian; well 95W153, Nieuwkerke, West Flanders, Belgium. The specimen is in dorsoventral view; S is a general view; T is an optical section; length 71 µm, breadth 65 µm.

Figure 17. Reproduced illustrations of holotypes of species treated in the present work — 6.

A–C. *Senoniasphaera microreticulata.* Holotype from Brideaux & McIntyre (1975, pl. 11, figs 7–9, as *Senoniasphaera microreticulata*); middle Albian; Horton River Formation; Northwest Territories, Canada. The figures show the specimen in ventral view, ventral surface at high focus (A), ventral surface at mid-focus (B) and dorsal surface at low focus (C); length 123 µm, breadth 118 µm.

D. *Senoniasphaera protrusa.* Holotype from Clarke & Verdier (1967, pl. 14, fig. 8; as *Senoniasphaera protrusa*); Santonian; Culver Cliff, Isle of Wight, England. The specimen is in ventral view; length 92 µm, breadth 67 µm.

E–H. *Senoniasphaera ptomatis.* Holotype from Helby (1987, figs 25A–D, as *Senoniasphaera ptomatis*); middle Berriasian; Lacepede-1A well, Australia. The figures show the specimen in ventral view, dorsal surface (E), mid-foci (F–G) and ventral surface (H); length 82 µm, breadth 80 µm, derived from magnification (x400) given in publication.

I. *Senoniasphaera*? *reticulata.* Holotype from Khanna & Singh (1981, fig. 1, no. 4, as *Hexagonifera reticulata*); Lower to Middle Eocene; Subathu Formation; Dharmpur, Simla Hills, India. The specimen is apparently in dorsoventral view; length 79 µm, breadth 66 µm.

J. *Senoniasphaera*? *turensis.* Holotype from Vasilyeva in Andreeva-Grigorovich et al. (2011, pl. 2, fig. 6, as *Senoniasphaera turensis*); Danian; Lithuania. The specimen is apparently in dorsoventral view; length 69 µm, breadth 66 µm.

K–L. *Senoniasphaera turonica*. Holotype from Prössl 1990, pl. 16, figs 1–2, as *Craspedodinium turonicum*); middle Cenomanian – upper Turonian; Konrad 101 core, Lower Saxon Basin, northwestern Germany. The specimen is possibly in dorsoventral view; length 78 µm, breadth 79 µm.

M. *Tenua anaphrissa*. Holotype from Sarjeant (1966, pl. 22, fig. 8, as *Doidyx anaphrissa*); lower Barremian; Speeton Clay; Shell West Heslerton borehole, Yorkshire, England. The specimen is apparently in ventral view; length 105 µm, breadth 118 µm.

N. *Tenua*? *apiculata*. Holotype from Jain et al. (1984, pl. 2, fig. 27, as *Canningia apiculata*); Kimmeridgian – lower Tithonian; Spiti Shale; Malla Johar area, Himalaya, India. The specimen appears to be in dorsal view; length 80 µm, breadth 66 µm.

O–P. *Tenua*? *araneosum*. Holotype from Brideaux (1977, pl. 9, figs 1–2, as *Cleistosphaeridium araneosum*); Aptian – Albian; Horton River Formation, Richardson Mountains, Northwest Territories, Canada. The specimen is in dorsoventral view, high focus apparently on dorsal surface (O) and low focus apparently on ventral surface (P); length 55 µm, breadth 52 µm, derived from magnification (x1000) given in publication.

Q. *Tenua*? *asymmetrica*. Holotype from Burger (1980, fig. 7a, as *Cyclonephelium asymmetricum*); Neocomian (Lower Cretaceous); Rolling Downs Group; seismic shot hole, Carpentaria Basin, northern Queensland, Australia. The specimen is in dorsoventral view; length 90 µm, breadth 77 µm, derived from magnification (x600) given in publication.

R. *Tenua*? *attadalica*. Holotype from Cookson & Eisenack (1962, pl. 5, fig. 13, as *Cyclonephelium*? *attadalicum*); Aptian – Albian; Osbourne Formation; Attadale borehole, Australia. The specimen is in dorsal view; length 82 µm, breadth 72 µm.

S. *Tenua chinensis*. Holotype from He Chengquan (1991, pl. 9, fig. 17, as *Canningia chinensis*); Middle Eocene; western Tarim Basin, southern Xinjiang Province, China. The specimen is appears to be in ventral view; dimensions unknown.

T. *Tenua colliveri*. Holotype from Cookson & Eisenack (1960, pl. 38, fig. 4, as *Canningia colliveri*); Aptian; Roma Formation; Balmoral No. 1 well, northern Queensland, Australia. The specimen appears to be in dorsal view; length 107 µm, breadth 100 µm.

Figure 18. Reproduced illustrations of holotypes of species treated in the present work — 7.

A. *Tenua compta.* Holotype from Davey (1982, pl. 8, fig. 3, as *Canningia compta*); Portlandian (Tithonian) – lowermost Valanginian; Sandringham Sands; Brook Farm, North Runcton, Norfolk, England. The specimen is in dorsal view; length 54 µm, breadth 52 µm.

B. *Tenua copei.* Holotype from Bailey et al. (1997 fig. 3a, as *Circulodinium copei*); upper Kimmeridgian; Golden Hill Quarry, Marton, North Yorkshire, England. The specimen is in dorsoventral view; length 70 µm, breadth 75 µm.

C. *Tenua densebarbata.* Holotype from Cookson & Eisenack (1960, pl. 38, fig. 10, as *Cyclonephelium densebarbatum*); Tithonian; Alexander Formation, Western Australia. The specimen is possibly in ventral view; length 95 µm, breadth 92 µm.

D. *Tenua dubia.* Holotype from Jain & Millepied (1975, pl. 5, fig. 76, as *Tenua dubia*); Campanian – Maastrichtian; Borehole No. CM-4, Senegal Basin, west Africa. The specimen is in dorsoventral view; length 78 µm, breadth 70 µm.

E. *Tenua elongata.* Holotype from He Chengquan (1991, pl. 9, fig. 1, as *Canningia elongata*); Turonian; western Tarim Basin, southern Xinjiang Province, China. The specimen is in dorsoventral view; dimensions unknown.

F. *Tenua hystrix.* Holotype from Eisenack (1958, pl. 23, fig. 1, as *Tenua hystrix*); Aptian; northern Germany. The specimen appears to be in ventral view; length 97 µm, breadth 86 µm.

G. *Tenua kukubaiensis.* Holotype from Mao Shaohi & Norris (1988, pl. 1, fig. 7, as *Circulodinium kukebaiensis*); Turonian – Santonian; Kukebai Formation; Wuluokeqiate section, Tarim Basin, Xinjiang Province, China. The specimen appears to be in dorsoventral view; length 48 µm, breadth 58 µm.

H. *Tenua magna.* Holotype from Duxbury (2001, fig. 4, no. 3, as *Cerbia magma*); upper Barremian; central North Sea, offshore U.K. The specimen appears to be in dorsal view; length 117 µm, breadth 127 µm; scale bar is 10 µm.

I. *Tenua*? *micibaculata.* Holotype from Jiabo (1978, pl. 7, fig. 1, as *Canningia micibaculata*); Palaeogene, coastal region of Bohai, China. The specimen is possibly in dorsoventral view; dimensions unknown.

J. *Tenua*? *pentagona.* Holotype from He Chengquan (1991, pl. 9, fig. 13, as *Canningia pentagona*); Upper Cretaceous; western Tarim Basin, southern Xinjiang Province, China. The specimen is in ventral view; dimensions unknown.

K. *Tenua reducta*. Holotype from Châteauneuf (1980, pl. 21, fig. 10, as *Cyclonephelium reductum*); Upper Eocene; Calcaire de St-Ouen; Paris Basin, France. The specimen is rotated by -66° with apex facing upper left. possibly in ventral view; length 70 µm, breadth 60 µm, derived from magnification (x1000) given in publication.

L. *Tenua scabrosa*. Holotype from Cookson & Eisenack (1970, pl. 13, fig. 6, as *Canningia scabrosa*); Albian – Cenomanian; Madura No. 1 Bore, Eucla Basin, Western Australia. The specimen is possibly in ventral view; length 102 µm, breadth 90 µm.

M–N. *Trimuridinium whitenessensis*. Holotype from Prince et al. (2008, pl. 1, figs 11–12, as *Senoniasphaera whitenessense*); upper Santonian; White Ness, Isle of Thanet, England. The specimen is in dorsoventral view, ventral (M) and dorsal (N) sides; note the three wall layers; length 58 µm, breadth 72.5 µm, derived from magnification (x430) given in publication.

O. *Pseudoceratium aulaeum*. Holotype from Harding (1990, pl. 1, fig. 1, as *Pseudoceratium aulaeum*); upper Barremian; Warlingham borehole, Surrey, England. The specimen is rotated by -15 ° and is in dorsal view; scale bar is 10 µm.

P. *Pseudoceratium brevicornutum*. Holotype from Herngreen et al. (2000, pl. 9, fig. 6, as *Pseudoceratium brevicornutum*); upper Ryazanian (middle Berriasian) – lower Hauterivian; Vlieland Claystone Formation; well L02-03, The Netherlands. The specimen is in ventral view; length 114 µm, breadth 60 µm.

Q–R. *Pseudoceratium australiense*. Holotype from Riding & Helby (2001, figs 15J–K, as *Pseudoceratium robustum*); Tithonian; Mindil-1 well, northwestern Australia. The specimen is in ventral view, high focus (Q) and median focus (R); scale bar is 25 µm.

S. *Pseudoceratium exploitum*. Holotype from Brideaux (1971, pl. 30, fig. 106, as *Pseudoceratium exploitum*); middle – upper Albian; Lower Colorado Group; central Alberta, Canada. The specimen is in ventral view; length 158 µm, breadth 66 µm.

T. *Pseudoceratium gochtii*. Holotype from Neale & Sarjeant (1962, pl. 20, fig. 3, as *Pseudoceratium* (*Eopseudoceratium*) *gochtii*); upper Hauterivian – middle Barremian; Speeton Clay; West Heslerton, Yorkshire, England. The specimen is in ventral view; length 187 µm, breadth 93 µm.

Figure 19. Reproduced illustrations of holotypes of species treated in the present work — 8.

A–B. *Pseudoceratium*? *iehiense.* Holotype from Helby (1987, figs 16I–J, as *Pseudoceratium iehiense*); upper Tithonian – lower Berriasian; Zeewulf-1 well, Exmouth Plateau, Western Australia. The specimen is in ventral view, foci on dorsal (A) and ventral (B) surfaces; x400.

C–D. *Pseudoceratium interiorense.* Holotype from Bint (1986, pl. 3, figs 3, 9, as *Pseudoceratium interiorense*); upper Albian; Kiowa Formation; Western Interior, U.S.A. Enlargement (x640) of operculum (C) — note two wall layers and reticulate connections; dorsal view (D); length with operculum detached 82 µm, breadth 40 µm, derived from magnification (x800) given in publication.

E. *Pseudoceratium iveri.* Holotype from Nøhr Hansen (1993, pl. 19, fig. 1, as *Pseudoceratium iveri*); uppermost Barremian; Wollaston Formation; Aucella Bjerg, East Greenland. The specimen is upright and is in dorsal view; length 170 µm, breadth 85 µm.

F. *Pseudoceratium notiale.* Holotype from Quattrocchio & Sarjeant (1992, pl. 5, fig. 1, as *Aptea notialis*); middle – upper Tithonian; Puente del Arroyo Picún Leufú, Neuquén Basin, Argentina. The specimen is in dorsal view; length 75 µm, breadth 55 µm; scale bar is 10 µm.

G. *Pseudoceratium*? *parvum.* Holotype from Michael (1964, pl. 2, fig. 1, as *Pseudoceratium parvum*); lower Barremian; Ziegeleigrube Roklum, northwestern Germany. The specimen is of indeterminate orientation; length 25 µm.

H. *Pseudoceratium robustum.* Holotype from Michael (1964, pl. 2, fig. 2, as *Pseudoceratium robustum*); lower Barremian; Ziegeleigrube Roklum, northwestern Germany. The specimen is in dorsoventral view; length 154 µm.

I–K. *Pseudoceratium pelliferum.* Holotype from Gocht (1957, pl. 18, figs 1a–c, as *Pseudoceratium pelliferum*); Valanginian – upper Hauterivian; Rühlertwist-3 borehole, Emsland, northwestern Germany. The specimen is in ventral view — ventral surface (I), apical horn (J), left antapical horn (K); length 132 µm, breadth 59 µm.

L. *Pseudoceratium solocispinum.* Holotype from Davey (1974, pl. 9, fig. 6, as *Pseudoceratium pelliferum* var. *solocispinum*); middle – upper Barremian; Speeton Clay, Yorkshire, England. The specimen is in dorsal view; length 103 µm, breadth 67 µm; phase contrast.

M–O. *Pseudoceratium retusum.* Holotype from Brideaux (1977, pl. 4, figs 10–12, as *Pseudoceratium retusum*); Barremian – Aptian; Richardson Mountains, Northwest Territories, Canada. The specimen is in dorsal view; length 100 µm, breadth 82 µm — dorsal (M) and ventral (N) surfaces and detail of periphragm in left paracingular area (re-oriented with apex to left); M–N x500, O x1200.

P. *Pseudoceratium spitiensis*. Holotype from Jain et al. (1984, pl. 3, fig. 42, as *Pseudoceratium spitiense*); Kimmeridgian – lower Tithonian; Spiti Shale; Malla Johar area, India. The specimen is in dorsal view; length 114 µm, breadth 70 µm.

Q. *Pseudoceratium toveae*. Holotype from Nøhr-Hansen (1993, pl.22, fig.1, as *Pseudoceratium toveae*); upper Barremian – lowermost Aptian; Greenland. Overall length 190 µm.

R. *Pseudoceratium turneri*. Holotype from Cookson & Eisenack (1958, pl.5, figs 2–6 as *Pseudoceratium turneri*); Albian; Gearle Siltstone; Rough Range No. 1, Western Australia. The specimen is in dorsal view; length 171 µm, breadth 122 µm, derived from magnification (x420) given in publication.

S–T. *Pseudoceratium weymouthense.* Holotype from Helby (1987, figs 19A–B, as *Pseudoceratium weymouthense*); upper Tithonian – lower Berriasian; Cape Weymouth-2 well, northern Queensland, Australia. The specimen is in ventral view — dorsal (S) and ventral (T) surfaces; length 130.5 µm, breadth 73 µm, derived from magnification (x400) given in publication.

Figure 20. Reproduced illustrations of holotypes of species treated in the present work — 9.

A. *"Circulodinium indicum"* (herein considered a taxonomic junior synonym of *Cleistosphaeridium diversispinosum*). Holotype from Mehrotra & Sarjeant (1987, pl. 2, fig. 2, as *Cyclonephelium indicum*, an illegitimate name); Paleocene of Andhra Pradesh, India; length 55 µm, breadth 65 µm.

B. *Cleistosphaeridium latoaculeum.* Holotype from Yun Hyesu (1981, pl. 11, fig. 18, as *Cleistosphaeridium multifurcatum* subsp. *latoaculeum*); lower Santonian; Westphalia, Germany. The specimen is in dorsoventral view; length 72 µm, breadth 88 µm, derived from magnification (x550) given in publication.

C. *Cleistosphareidium*? *longispinosum.* Holotype from He Chengquan (1991, pl. 9, fig. 19, as *Cyclonephelium longispinosum*); Middle Eocene; western Tarim Basin, southern Xinjiang Province, China. The specimen appears to be in dorsoventral view; dimensions unknown.

D. *Spiniferities*? *ambiguus.* Holotype from He Chegquan (1991, pl. 28, fig. 7, as *Cyclonephelium* *ambiguum*); Paleocene; western Tarim Basin, southern Xinjiang Province, China. The specimen is in uncertain orientation; dimensions unknown.

E–F. *Turbiosphaera*? *sarrisii*. Holotype from Archangelsky (1969, pl. 2, figs 6–7, as *Polystephanephorus*? *sarrisii*); Eocene; Río Turbio Formation, Santa Cruz Province, Argentina. The specimen is in uncertain orientation; length 43 µm, breadth 40 µm.

G. *Trichodinium*? *granulatum*. Holotype from Horowitz (1975, pl.1, fig.4, as *Doidyx granulata*); originally considered to be from the Upper Triassic, but see text; southern Israel. The specimen is in ventral view; length 75 µm, breadth 67 µm.

H. *Polysphaeridium*? *combibaculum*. Holotype from Song Zhichen et al. (1985, pl. 6, fig 10, as *Cyclonephelium combibaculum*); ?Lower Pleistocene; Longjing structural area, Shelf Basin, Donghai region, East China Sea. The specimen is in uncertain orientation; dimensions unknown.

I–K. *Batiacasphera*? *bulbosa*. Holotype from Smith & Harding (2004, pl. 4, figs 6–8, as *Cyclonephelium bulbosum*); middle Volgian (upper Tithonian); Kashpir section, Volga Basin, Russia. The specimen is possibly in dorsoventral view; ventral focus (I), median focus (J) and dorsal focus (K); scale bar is 10 µm.

L. *Deflandrea*? *stagonoides*. Holotype from Benedek (1972, pl. 2, fig. 12, as *Ascodinium stagonoides*); Upper Oligocene; Tönisberg, Lower Rhine region, Germany. The specimen is in dorsoventral view; dimensions unknown.

M–O. *Epelidosphaeridia*? *turrita*. Holotype from Brideaux (1977, pl. 4, figs 1–3, as *Canningia turrita*); Barremian; Stoney Core Hole F-42, Richardson Mountains, Northwest Territories, Canada. The specimen is possibly in ventral view, high focus on ventral surface (M), mid-focus on ventral surface (N), low focus on dorsal surface (O); length 42 µm, breadth 50 µm.

P. *Petalodinium*? *granulata*. Holotype from Morgenroth (1966, pl. 2, fig. 10, as *Canningia granulata*); Lower Eocene; of the Fehmarn, Katharinenhof, Germany. The specimen is in dorsoventral view; length 90 µm, breadth 78 µm.

Q–R. *Selenopemphix? baculatum*. Holotype from Song Zhichen et al. (1985, pl. 6, figs 1–2, as *Cyclonephelium baculatum*); ?Lower Pleistocene; Longjing structural area, Shelf Basin, Donghai region, East China Sea. The specimen is presumably in dorsoventral view; dimensions unknown.

Supplemental data

The new material used in this study was drawn from the following sources: the Hume River and Imperial River outcrop sections in the Mackenzie Plain – Peel Plateau area of the Northwest Territories, Canada; the Glacier Fiord surface section, Axel Heiberg Island, Nunavut, Canada; exploration wells in offshore southeastern Canada (Argo F-38, Demascota G-32, Onondaga E-84 and Wenonah J-75); and exploration wells in the Labrador–Baffin Seaway (Roberval K-92 and Skolp E-07). Sections on each of these four areas follow.

Mackenzie Plain – Peel Plateau area

Material from this area is from two surface sections, the Hume River and Imperial River (Supplemental data Fig. 1). Samples from the Hume River section were collected by Thomas Hadlari of the Geological Survey of Canada (Calgary), and Danielle Thomson and Claudia Schröder-Adams of Carleton University, Ottawa, Canada; samples from the Imperial River section were collected by Thomas Hadlari. Information on the samples and specimens from this section used in this study is presented in Supplemental data Table 1. The basic stratigraphy is shown in Supplemental data Fig. 2 after Thomson et al. (2011), and a commentary to possible variation on this can be found in Fensome (2016). Details of sample occurrence in the Hume River section is shown in Supplemental data Figs 3–4. Details of sample occurrence in the Imperial River section is shown in Supplemental data Fig. 5.

Glacier Fiord section, Axel Heiberg Island

This is a single section collected by Jennifer Galloway of Geological Survey of Canada (Calgary). The location of the section is shown in Supplemental data Fig. 6. Information on the samples and specimens from this section used in this study is presented in Supplemental data Table 2. Details of sample occurrence in the Isachsen Formation in the Glacier Fiord section are shown in Supplemental data Fig 7. A similar chart for samples from the younger Christopher Formation is not available, but details of this part of the section can be found in Schröder-Adams et al. (2014).

Scotian Margin

Material from four Scotian Margin wells was used in this study (Supplementary data Fig. 8). Information on the samples and specimens from this section used in this study is presented in Supplemental data Table 3. Biostratigraphical analyses of Demascota G-32, Onondaga E-84 and Wenonah J-75 were recorded in detail by Fensome et al. (2008, 2009). Charts for each of these wells are reproduced here as Supplemental data Figs 9–11, with samples used in the present study indicated by red boxes. The material from Argo F-38 used in the present study is based on new reconnaissance analyses, although no new stratigraphy has been developed; a chart for this well is provided here as Supplemental data Figs 9–12.

Labrador Margin

Material from two Labrador Margin wells was used in this study (Supplementary data Fig. 13). Information on the samples and specimens from this section used in this study is presented in Supplemental data Table 4. Biostratigraphical analyses of Roberval K-92 were recorded in detail by Williams (2017). Biostratigraphical scheme for Skolp E-07 has been provided by one of us (GLW) and L. Dafoe (unpublished data). Charts for each of these wells are reproduced here as Supplemental data Figs 14–15, with samples used in the present study indicated by red boxes.

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Figure and table captions:

Figures:

Supplemental data Figure 1. Map of the Mackenzie Plain – Peel area showing the locations of the Hume River and Imperial River surface sections. Adapted from Hadlari et al. (2014, figs 1–2).

Supplemental data Figure 2. Chronostratigraphy and formations according to Thomson et al. (2011). Adapted from Thomson et al. (2011, fig. 3).

Supplemental data Figure 3. Sample locations in the Hume River section — Martin House and Arctic Red formations. Samples with specimens illustrated in this study are framed by a red box. Adapted from Thomson et al. (2011, figs 6–7).

Supplemental data Figure 4. Sample locations in the Hume River section — Slater River and

Trevor formations. Samples with specimens illustrated in this study are framed by a red box. Adapted from Thomson et al. (2011, figs 6, 8–9).

Supplemental data Figure 5. Sample locations in the Imperial River section. Samples with specimens illustrated in this study are indicated in the inset red box. Adapted from a figure provided by Thomas Hadlari.

Supplemental data Figure 6. Map of part of the Canadian Arctic Archipelago showing the location and general geological setting of the Glacier Fiord section on Axel Heiberg Island. Adapted from a figure provided by Jennifer Galloway (Galloway et al. 2013).

Supplemental data Figure 7. Sample locations in the Galcier Fiord section — Isachesen Formation. Samples with specimens illustrated in this study are framed by a red box. Adapted from a figure provided by Jennifer Galloway.

Supplemental data Figure 8. Map of the Scotian Margin, offshore eastern Canada, showing the location of the wells from which specimens illustrated in the present paper derive. Adapted from a figure provided by Andrew MacRae; see also Fensome et al. (2008) and Weston et al. (2012).

Supplemental data Figure 9. Chart showing biostratigraphical, chronostratigraphical, lithostratigraphical, sample and well-log data from the Demascota G-32 well. For location, see Supplemental data Figure 8. Samples with specimens illustrated in this study are framed by a red box. Adapted from Fensome et al. (2008).

Supplemental data Figure 10. Chart showing biostratigraphical, chronostratigraphical, lithostratigraphical, sample and well-log data from the Onondaga E-84 well. For location, see Supplemental data Figure 8. Samples with specimens illustrated in this study are framed by a red box. Adapted from Fensome et al. (2008).

Supplemental data Figure 11. Chart showing biostratigraphical, chronostratigraphical, lithostratigraphical, sample and well-log data from the Wenonah J-75 well. For location, see Supplemental data Figure 8. Samples with specimens illustrated in this study are framed by a red box. Adapted from Fensome et al. (2008).

Supplemental data Figure 12. Chart showing biostratigraphical, chronostratigraphical, lithostratigraphical and sample data from the Argo F-38 well. For location, see Supplemental data Figure 8. Samples with specimens illustrated in this study are those shown. Adapted from a figure provided by Andrew MacRae; lithostratigraphy from McLean and Wade (1993); biostratigraphy adapted from Bujak in Barss et al. (1979).

Supplemental data Figure 13. Map of the Labrador Margin, offshore eastern Canada, showing the location of the wells from which specimens illustrated in the present paper derive. Adapted from Nøhr-Hansen et al. (2017).

Supplemental data Figure 14. Chart showing biostratigraphical, lithology and lithostratigraphical data from the Roberval K-92 well, and the location of the single sample used in this study from this well. For location, see Supplemental data Figure 13. Lithostratigraphy from Canada–Newfoundland-Labrador Offshore Petroleum Board (2008); biostratigraphy from Williams (2017).

Supplemental data Figure 15. Chart showing biostratigraphical, lithology and lithostratigraphical data from the Skolp E-07 well, and the location of the single sample used in this study from this well. For location, see Supplemental data Figure 13. Lithostratigraphy from Canada–Newfoundland-Labrador Offshore Petroleum Board (2008); biostratigraphy from L. Dafoe and G.L. Williams (personal communication March 2018).

Tables:

Supplemental data Table 1. Table showing the details of Mackenzie Plain – Peel Plateau area samples and specimens used for this publication. Column A gives the relevant Figure number from the present paper. Column B gives the taxon name. Column C gives the locality name. Column D gives the GSC Calgary locality (P) number. Column E gives the palynology slide number. Column F gives the GCS Calgary laboratory sample number. Column G gives the field-sample collection number. Column H gives the measurement above the base of the section. Column I gives the GSC Type Collection number. Column J give the coordinates on the slide. England finder coordinates and optical details can be found through cross-referencing with Appendix 3 in the paper.

Supplemental data Table 2. Table showing the details of Glacier Fiord samples and specimens used for this publication. Column A gives the relevant Figure number from the present paper. Column B gives the taxon name. Column C gives the GSC Calgary locality (P) number. Column D gives the palynology slide number. Column E gives the GCS Calgary laboratory sample (C) number. Column F gives the field-sample collection number. Column G gives the measurement in metres above the base of the formation: I = Isachsen Formation; C = Christopher Formation. Column H gives the GSC Type Collection number. Column I give the coordinates on the slide. England finder coordinates and optical details can be found through cross-referencing with Appendix 3 in the paper.

Supplemental data Table 3. Table showing the details of Scotian Margin samples and specimens used for this publication. Column A gives the relevant Figure number from the present paper. Column B gives the taxon name. Column C gives the well name. Column D gives the palynology (P) preparation sample number. Column E gives the slide number. Column F gives the depth in the well in metres (m) or feet (ft) and the type of sample (dc = ditch cutting, swc = sidewall core). Column G give the coordinates on the slide. Column H gives the GSC type number. England finder coordinates and optical details can be found through cross-referencing with Appendix 3 in the paper.

Supplemental data Table 4. Table showing the details of Labrador Margin samples and specimens used for this publication. Column A gives the relevant Figure number from the present paper. Column B gives the taxon name. Column C gives the well name. Column D gives the GSC type number. Column E gives the conventional-core number (Roberval K-92). Column F gives the depth in the well in metres. Column G give the coordinates on the slide. England finder coordinates and optical details can be found through cross-referencing with Appendix 3 in the paper.