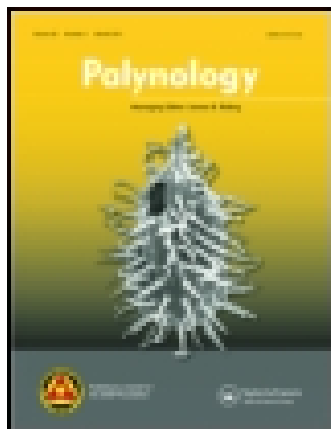


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## *Wetzeliella* and its allies – the ‘hole’ story: a taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae

Graham L. Williams<sup>a</sup>, Sarah P. Damassa<sup>b</sup>, Robert A. Fensome<sup>a\*</sup> and G. Raquel Guerstein<sup>c</sup>

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Fossil dinoflagellate cysts of the Paleogene peridiniacean subfamily Wetzelielloideae have a stable tabulation pattern similar to that of other fossil peridiniaceans, but distinguished by a four-sided (quadra) rather than a six-sided (hexa) 2a plate. Aside from tabulation, wetzelielloideans show great morphological variability, especially in ornamentation and horn development, but also in wall structure. This diversity has distracted attention from the morphological variation of the archeopyle, which, although always formed through loss of the 2a plate only, shows variations that we consider critical in unravelling the group's phylogeny. Important factors are the shape and relative dimensions of the archeopyle and whether the operculum is attached (adnate) or detached. These parameters allow us to define five archeopyle types: equiepeliform, hyperepeliform, hypersoleiform, latiepeliform and soleiform. Based primarily on archeopyle type and secondarily on wall morphology and ornamentation, we recognise six genera with an equiepeliform archeopyle, four with a hyperepeliform archeopyle, five with a latiepeliform archeopyle, five with a soleiform archeopyle and one with a hypersoleiform archeopyle. The earliest known wetzelielloideans, which occur around the Paleocene–Eocene boundary, have an equiepeliform archeopyle. Other archeopyle types evolved rapidly: taxa with hyperepeliform, latiepeliform and hypersoleiform types are known from the Ypresian. Latiepeliform and hyperepeliform types are restricted to the Ypresian and Lutetian. Forms with the soleiform archeopyle appeared in the late Lutetian, but were rare until the Bartonian, when they became the dominant type, and they were the only type in Priabonian and younger strata. Wetzelielloideans became extinct in the middle Oligocene. We make numerous taxonomic proposals, including the following new genera: *Castellodinium*, *Dolichodinium*, *Epelidinium*, *Kledodinium*, *Michouxdinium*, *Petalodinium*, *Piladinium*, *Rhadinodinium*, *Sagenodinium*, *Sophismatia*, *Stenodinium*, *Stichodinium* and *Vallodinium*. We emend the diagnoses of *Charlesdownia*, *Dracodinium* and *Wilsonidium*, and erect the species *Kledodinium filiosum*, *Petalodinium sheppeyense* and *Sagenodinium franciscanum*.

**Keywords:** biostratigraphy; dinoflagellate cysts; evolution; Paleogene; taxonomy; wetzelielloideans

### 1. Introduction

The genus *Wetzeliella* and related forms constitute an important group of Paleogene dinoflagellate cysts that have proven to be important biostratigraphic and paleoecological markers. However, debate and confusion over their taxonomy and classification have hampered their full utility in these applications, a situation that we aim to address herein.

When Alfred Eisenack (1938) erected *Wetzeliella*, he did not provide a detailed description for the genus. He remedied this situation in 1954 by specifying the presence of horns, spines (which, in current dinoflagellate-cyst terminology, we would refer to as processes) and a capsule (or endocyst) as diagnostic features. Once the morphology of *Wetzeliella* was clearly elucidated, the number of species assigned to the genus

rapidly increased, as did the number of allied genera. Those genera currently considered to be related to *Wetzeliella* are *Apectodinium*, *Axiodinium*, *Charlesdownia*, *Dracodinium*, *Kisselevia*, *Rhombodinium*, *Talladinium* and *Wilsonidium*.

The first suprageneric treatment of *Wetzeliella* and its allies was by Vozzhennikova (1965), who erected the family Wetzeliellaceae and included in it *Dracodinium*, *Palaeohystrichophora*, *Rhombodinium* and *Wetzeliella*. Bujak & Davies (1983) proposed the subfamily Wetzelielloideae, within the family Deflandreaceae. In the subfamily, Bujak & Davies included *Apectodinium*, *Dracodinium*, *Gochtodinium*, *Kisselevia*, *Rhombodinium*, *Wetzeliella* and *Wilsonidium*. In their diagnosis of the subfamily Wetzelielloideae, Bujak & Davies (1983, p. 135) stated that ‘a quadra second intercalary

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plate...forms the I (2a) archeopyle'. In an extensive revision of dinoflagellates in general, Fensome et al. (1993, p. 137) placed the subfamily Wetzelielloideae in the family Peridiniaceae, providing the following diagnosis: 'Peridiniaceans in which the mid-dorsal anterior intercalary plate is quadra (i.e. four-sided)'. Thus, as currently recognised, the subfamily Wetzelielloideae is characterised by a quadra 2a plate that touches the third apical plate (3') anteriorly, the first (1a) and third (3a) anterior intercalary plates laterally and the consistently six-sided fourth precingular plate (4'') posteriorly (Figure 1). Other fossil subfamilies of the Peridiniaceae,

such as the Deflandreioideae, are characterised by a six-sided (hexa) 2a plate.

Determining which features to use in diagnosing genera within the Wetzelielloideae has been a contentious issue, the result being that generic definitions have become blurred. In our view, this is in large part because of overemphasis on horn development and wall structure at both generic and specific levels. This situation has in turn led to the decreased utility of wetzelielloidean taxa as biostratigraphic markers: for example, based on current literature records, *Wetzeliella articulata* now spans most of the Eocene and

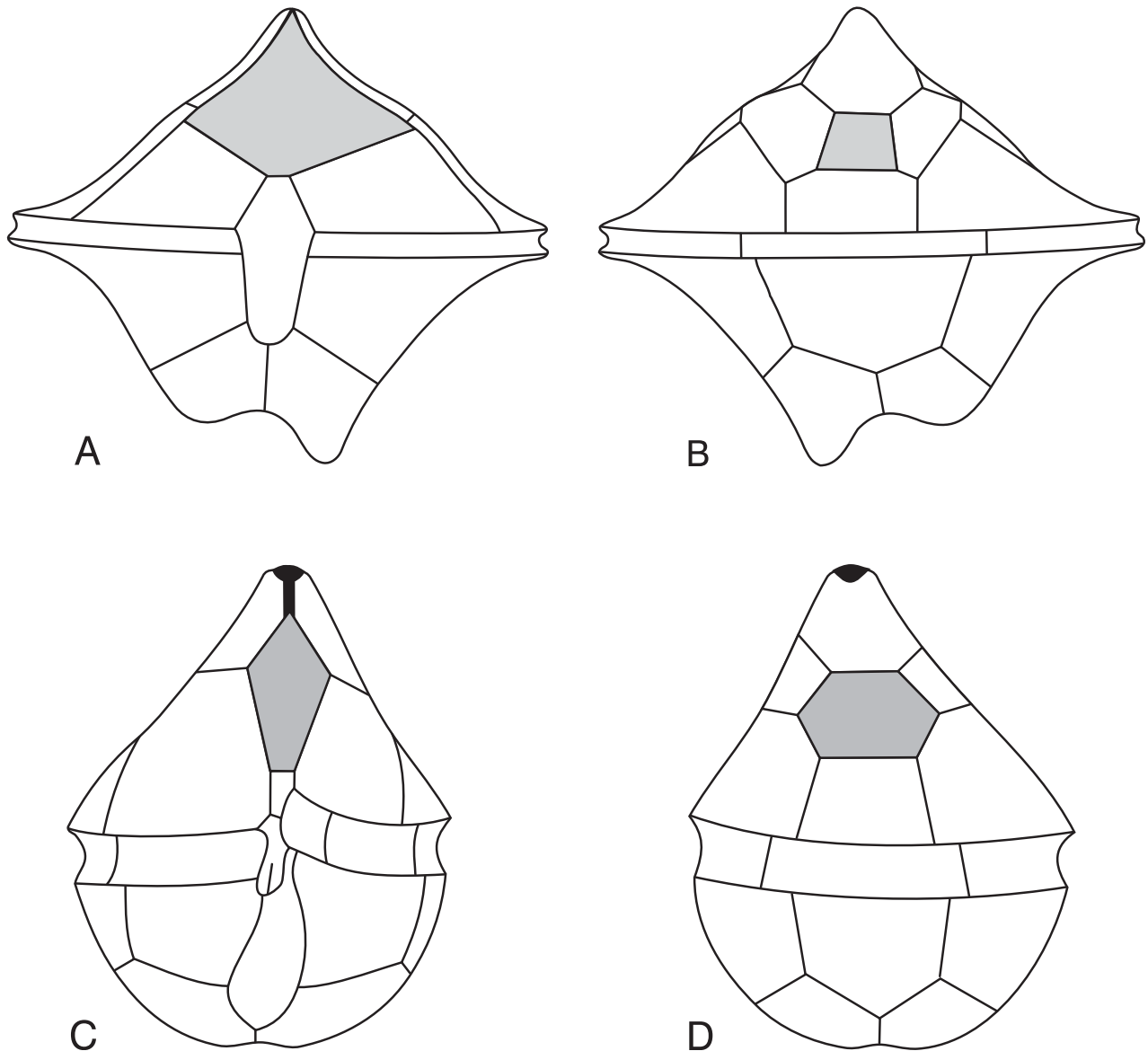


Figure 1. Comparison between the wetzelielloidean tabulation pattern and that of a calciodinelloidean, the latter being more typical of fossil peridiniaceans. A–B: wetzelielloidean tabulation, showing the ventral surface (A) and the dorsal surface (B); note especially the four-sided 2a plate (shaded) in B. C–D: tabulation of the modern calciodinelloid genus *Scrippsiella*, showing the ventral surface (C) and dorsal surface (D); note especially the six-sided 2a plate (shaded) in D. Stippling indicates the first apical plate (1') in A and C, and the second anterior intercalary plate (2a) in B and D. Adapted from Fensome et al. (1993).

Oligocene – an impressive but not very useful 32 million years. In this paper, we propose that the evolution and consequent morphological progression of wetzelielloideans can be better understood by focussing attention on the archeopyle, especially in the pericyst.

Differentiation of wetzelielloidean archeopyle types is not a new concept: several others, including Bujak (1979), Costa & Downie (1979) and Michoux (1988), have recognised differences in the quadra 2a archeopyle. However, no one has yet tried to define all genera in the subfamily using the archeopyle as the main criterion. Bujak (1979) erected the genus *Gochtodinium* to accommodate taxa with a distinctive soleiform archeopyle (see History of study) and proposed the restriction of *Rhombodinium* to forms with a soleiform archeopyle and lack of processes, but did not define any other wetzelielloidean genera according to their archeopyle type.

In this paper, we undertake a major review of all wetzelielloidean taxa and propose several new taxa. Our proposed hierarchy of morphologic features for distinguishing genera gives priority to archeopyle type, especially the periarcheopyle. Within groups united by having a distinctive archeopyle type, we use pericystal ornamentation as a secondary criterion in separating genera. The only deviation from these general principles is in the case of *Apectodinium* and *Axiodinium*; both genera have a similar style of archeopyle and pericystal ornament, but can be differentiated on the basis of pericoel development and wall thickness.

Although wetzelielloideans are an extinct cyst-based group to which ‘para’ terminology might be applied, we consider that their paratabulation is a direct reflection of the tabulation, and hence, for simplicity, we use thecal terminology.

## 2. History of study

In his paper erecting the genus *Wetzeliella*, Eisenack (1938) illustrated two specimens, one of *Wetzeliella articulata* and the other of *Wetzeliella clathrata*. He provided only minimal information on the morphology of the genus and the two species, noting that ‘The bristled integument and strengthened, almost limb-like protrusions of the body are characteristics of the species [*Wetzeliella articulata*]’ (Eisenack 1938, p. 187, translation).

Eisenack (1954) designated *Wetzeliella articulata* as the type of *Wetzeliella* and indicated that diagnostic features of the genus include the presence of horns (typically one apical, two lateral, two antapical), ornamentation in the form of ‘bristles or spines’ (i.e. processes) and a ‘capsule’ (i.e. endocyst). In his description of *Wetzeliella articulata*, Eisenack (1954) recognised the occasional presence of a ‘slip hole’ (i.e. archeopyle). In one specimen, he noted that the operculum

remained attached along the upper (anterior) margin of the archeopyle and was folded back. Eisenack also stated that the archeopyle (in the pericyst) had a quadratic outline. In other, more elongate specimens, archeopyles were relatively common. He stated:

I have studied over 100 specimens [of *Wetzeliella articulata*], of which very few show an opening, as illustrated in [Eisenack 1954] pl. 7, fig. 6. In a second specimen, the cover is still connected to the upper part of the opening, as a membranous fragment and is folded upward. . . . [T]he cover separates from the shell along a circular seam (sometimes this seam is quadrangular with rounded corners), but remains connected along its upper margin, i.e. closely below the apex and flaps upward in similar fashion to a tongue. [Eisenack 1954, p. 57, in translation]

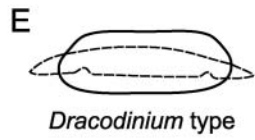
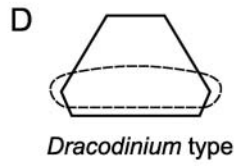
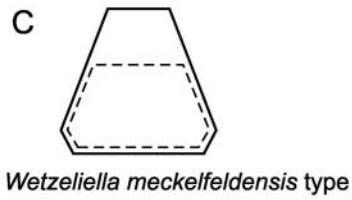
In today’s terminology, Eisenack was describing a classic soleiform archeopyle as described by Bujak (1979, p. 309). The attached and soleiform nature of the operculum was confirmed by one of us (RAF in 1993) in a re-examination of the holotype of *Wetzeliella articulata*.

Gocht (1955) used a lack of processes and horn development to distinguish *Rhombodinium* and *Dracodinium*, respectively, from *Wetzeliella*. Williams & Downie (1966, p. 195), by transferring the type of *Dracodinium* to *Wetzeliella*, subsequently synonymised *Dracodinium* with *Wetzeliella*, citing a continuum of horn development among specimens observed in the London Clay. Gocht (1969) presented a superbly illustrated review of the species then assigned to *Wetzeliella*, and preferred to redesignate *Rhombodinium* as a subgenus of *Wetzeliella*. He attempted to distinguish taxa on the presence or absence of horns and processes but admitted to having only limited success, invariably finding intermediate forms later.

The name *Kisselovia* was proposed by Vozzhennikova (1963) for forms that she described in part as follows: ‘Test smooth or has reticulate pattern with spinules in nodal positions, or without them’ (translation modified from Stover & Evitt 1978, p. 110). The generic name *Kisselovia*, however, was not validly published in 1963 due to lack of a validly published species name. Vozzhennikova (1967, p. 103) validated the name, as *Kisselevia*, by providing a description for the type. There has been confusion about the correct spelling of this generic name, compounded by the additional spelling *Kisseljovia*, used by Vozzhennikova (1961, p. 1462) – see Fensome & Williams 2004, p. 380–381. In the present paper, for consistency, we cite the correct name, *Kisselevia*, except in direct quotes and synonymy lists.

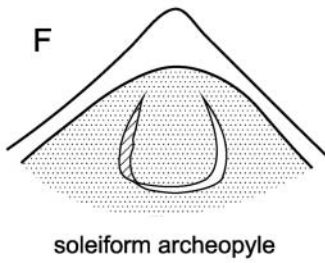
Lentin & Williams (1976) emended *Wetzeliella* and *Kisselevia*, and proposed a new genus, *Wilsonidium*, for

**COSTA &  
DOWNIE 1979**

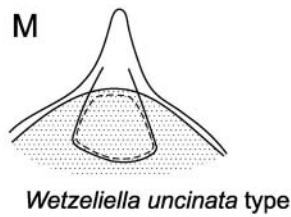
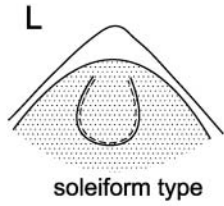
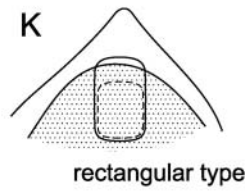
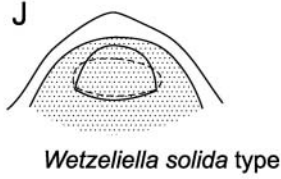
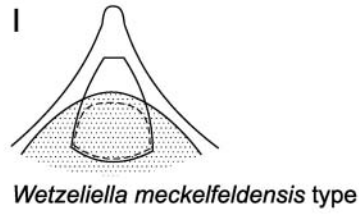
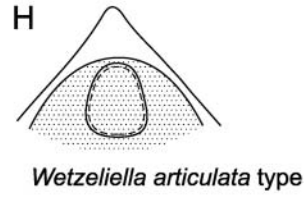


In A to E the 2a plate was assumed to be six-sided (hexa)

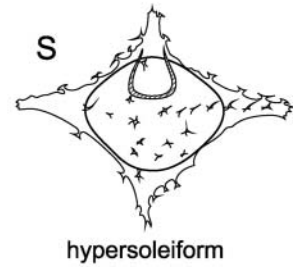
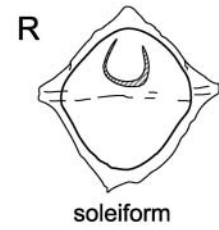
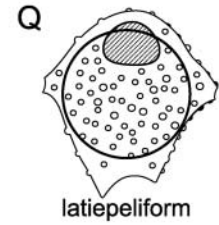
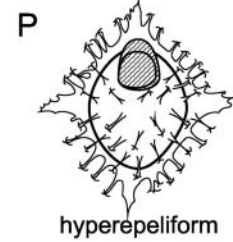
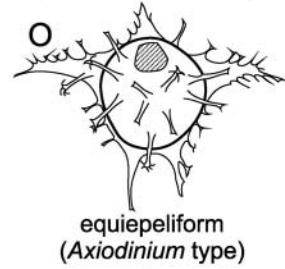
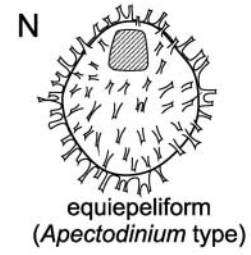
**BUJAK 1979**



**MICHOUX 1988**



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forms with predominantly sutural ornamentation on the pericyst. According to these authors, *Kisselevia* is distinguished from *Wetzeliiella* by its possession of distally interconnected processes. Lentin & Williams included in *Kisselevia* not only those species with cylindrical trabecula (e.g. *Kisselevia tenuivirgula*), but also those with a membranous ectophragm (e.g. *Kisselevia coleothrypta*).

Costa & Downie (1976) reviewed the stratigraphic distribution of *Wetzeliiella*, developed a zonation based on these fossils for northwestern Europe and proposed *Wetzeliiella* subgenus *Apectodinium*. The subgenus *Apectodinium* was raised to the generic rank by Lentin & Williams (1977).

The first comprehensive review of organic-walled fossil dinoflagellate genera, including wetzelielloideans, was by Stover & Evitt (1978). These authors accepted *Dracodinium* as a junior synonym of *Wetzeliiella*, and included in the group *Rhombodinium*, *Kisselevia* and *Wilsonidium*. In the following year, Bujak (1979) erected the genus *Gochtodinium* and emended *Rhombodinium*, both on the basis of the recognition of the soleiform archeopyle type (see Figure 2).

Although mistakenly describing the wetzelielloidean archeopyle as hexagonal, Costa & Downie (1979) made a significant contribution by recognising four archeopyle types. These were the *Apectodinium*, *Wetzeliiella meckelfeldensis*, *Wetzeliiella articulata* and *Dracodinium* types (see Archeopyle variability). However, they did not propose generic emendations based on their concepts. They also undertook an extensive morphometric analysis of wetzelielloidean taxa. Measurements included: pericyst length and breadth, endocyst length and breadth, lengths of apical, cingular and antapical horns, length and breadth of periarcheopyle, length from apex to anterior margin of periarcheopyle and length from tip of apical horn to cingulum. Although lengths and widths of pericysts and endocysts were surprisingly consistent, wide variations in horn length were observed within a single species.

Costa & Downie concluded that a few morphometric traits could be used to characterise taxa, such as the smaller size of *Apectodinium* and the greater width to length ratio in *Dracodinium*. But they admitted that 'the separation of a number of species was based on the arbitrary division of a continuum' (Costa & Downie 1979, p. 35).

In a phylogenetically oriented review of fossil peridinioids, Bujak & Davies (1983) emended the diagnosis for the subfamily to include reference to the quadra second anterior intercalary plate.

Evitt (1985, p. 195–198) included the *Wetzeliiella* and *Apectodinium* complexes in his 'Pq-cysts' (essentially wetzelielloideans). He noted that most Pq-cysts are over 100 µm long, with a peridinioid outline and cingular horns. Process development is variable, with common ectophragmal development. The endocyst, except in *Apectodinium*, is usually distinct. Archeopyle formation is exclusively through loss of the 2a plate, which may remain attached anteriorly. Evitt also noted that where ventral tabulation is discernible, it is of a 'para' type, with 1' contacting 2'' and 6''. He considered important features for identifying taxa in this group to be outline, number and prominence of horns, cavation, shape of endocyst, process type, presence of ectophragm, tabulation (as paratabulation), difference between peri- and endoarcheopyles and, whether the operculum is adnate.

Michoux (1988) expanded on the ideas of Costa & Downie (1979) by recognising seven distinctive archeopyle types (see Archeopyle variability). However, although his was an outstanding study in which six new species were recognised, Michoux proposed neither new genera nor emendations of generic diagnoses or descriptions.

In re-examining the type of *Kisselevia*, Lentin & Vozzhennikova (1989) restricted that genus to forms that they interpreted as having a reticulate periphragm. Therefore, they proposed a new genus, *Charlesdowniea*, for those species with trabecula supported by processes

Figure 2. Comparison of approaches to the categorisation of archeopyle types in the wetzelielloideans. A–E are from Costa & Downie (1979), who recognised the following categories: A. *Apectodinium* type; B. *Wetzeliiella articulata* type; C. *Wetzeliiella meckelfeldensis* type; D. *Dracodinium* type; E. a second *Dracodinium* type. Costa & Downie assumed the 2a plate to be six-sided (hexa). The generic names are as used by Costa & Downie. F is from Bujak (1979), who defined the soleiform archeopyle. G–M are from Michoux (1988), who recognised seven archeopyle types. These are: G. *Apectodinium* type; H. *Wetzeliiella articulata* type; I. *Wetzeliiella meckelfeldensis* type; J. *Wetzeliiella solida* type; K. Rectangular type, L. Soleiform type; and M. *Wetzeliiella uncinata* type. N–S represent the archeopyle types used in this paper. N. Equiepeliform type as shown in *Apectodinium homomorphum*; O. Equiepeliform type as shown in *Axioidinium augustum*. (Although both N and O represent the equiepeliform archeopyle type, they show considerable difference in archeopyle outline.) P. Hyperepeliform archeopyle type as shown in *Stenodinium meckelfeldense*. Q. Latiepeliform archeopyle type as shown in *Petalodinium condylos*. The specimen illustrated shows a distinctive characteristic of this archeopyle in that it commonly extends into the apical pericoel. R. Soleiform archeopyle as shown in *Rhombodinium draco*. S. Hypersoleiform archeopyle type as shown in *Dolichodinium uncinatum*.

arising from the periphragm as well as those with a membranous ectophragm (such as the type, *Charlesdowniea coleothrypta*). Lentin & Vozzhennikova (1989, p. 216) stated that:

Lentin & Williams (1976) emended the genus *Kisselovia* to include species from the genus *Wetzeliella* in which the processes are intratabular and connected distally by trabeculae or solid pieces of ectophragm. This emendation was based on an erroneous interpretation of the morphology of the holotype, complemented by the morphology of the species they chose to include in the genus.

Unfortunately, Lentin & Vozzhennikova (1989) were unable to re-illustrate the holotype of the type, which is lost, but they did propose a lectotype for *Kisselevia ornata*.

Since 1989, further progress has been made in our understanding of the wetzelielloideans, largely driven by the realisation that these taxa are ideal index fossils if the main criteria for distinguishing genera were primarily the archeopyle and secondarily the nature of the ornament. The present authors demonstrated this in Fensome et al. (2009), when they erected the genera *Axiodinium* and *Talladinium* and emended the diagnoses of *Apectodinium*, *Rhombodinium* and *Wetzeliella*.

The focus on using the archeopyle as the primary basis for generic differentiation further led us (in Fensome et al. 2009) to restrict *Wetzeliella* to forms with a soleiform archeopyle. Thus, many of the species formerly included in that genus were transferred to *Axiodinium*. Applying a similar reasoning to *Charlesdowniea*, Fensome et al. (2009) restricted that genus to forms with an equiepeliiform archeopyle, transferring those species with a soleiform archeopyle to the new genus *Talladinium*. But these authors did not emend the generic diagnosis for *Charlesdowniea*. Like *Charlesdowniea* (as emended here), *Talladinium* has intratabular processes connected distally by membranes.

In this paper, we expand on the concepts that we presented in Fensome et al. (2009) by proposing to differentiate all the wetzelielloidean genera, apart from *Apectodinium* and *Axiodinium*, primarily on archeopyle type and secondarily on ornamentation. (*Apectodinium* and *Axiodinium* both have an equiepeliiform archeopyle and distally free processes; however, they are distinguished by wall structure.) We believe that by adopting such an approach, we are developing a more natural classification based on evolutionary variations in the shape of the 2a plate and on how this influences other aspects of the morphology, such as horn length. And, by following this approach, we are also enhancing the stratigraphic utility of wetzelielloideans.

### 3. The wetzelielloidean 2a plate and archeopyle variability

*Wetzeliella* and its allies exhibit a distinctive variant of the standard peridinioid tabulation that clearly places it within the family Peridiniaceae (Fensome et al. 1993). Members of the subfamily Wetzelielloideae are distinguished by a unique combination of a bipesoid anterior dorsal tabulation and a four-sided ('quadra') 2a plate (Fensome et al. 1993; Figure 1). The term 'quadra' was first applied to the tabulation pattern of wetzelielloid dinoflagellates by Lentin & Williams (1976). The significance of the quadra archeopyle as a distinguishing characteristic of this group was also noted by Evitt (1978), who emphasised the need for careful interpretation of the archeopyle, given its relationship to tabulation. As Evitt so elegantly noted, to state that the 2a plate is hexa or quadra does not necessarily specify the precise shape of the archeopyle. Often, the only way to demonstrate whether the 2a is hexa or quadra is to compare the widths of the archeopyle with the width of the fourth precingular plate (4''). If 4'' is demonstrably wider, 2a is quadra. Where 4'' is demonstrably narrower, 2a is hexa. Perhaps there is some merit in following Evitt (1978), who proposed the descriptive phrases 'archeopyle formed by paraplate 2a in a hexa style paratabulation' (for hexa 2a archeopyle), or 'archeopyle intercalary in cyst with quadra style paratabulation' (for archeopyle quadra intercalary), but it makes for a cumbersome description.

The main features used to distinguish genera and species among the Wetzelielloideae have been surface ornamentation, wall relationships and structure, overall shape (including related horn and pericoel development) and process morphology and distribution. With few exceptions, the detailed morphology of the archeopyle has not been used to distinguish genera or species. However, the exceptions deserve comment here. In the description of one of his new species, *Wetzeliella lunaris*, Gocht (1969) noted and illustrated the difference in size between the endo- and periarcheopyle. Whereas the cingular margins of the two archeopyles coincided, there was a marked difference anteriorly. The rounding of the anterior margin of the endoarcheopyle was characteristic in *Wetzeliella lunaris* and some other species. Surprisingly, the two opercula detach as one and remain attached to each other.

Significantly, Gocht (1969) separated *Wetzeliella lunaris* and *Wetzeliella articulata* in part on their archeopyle shape. This was the first time that variations in archeopyle type had been proposed as a means of separating species of *Wetzeliella*. Gocht's insight was further demonstrated in his description of *Wetzeliella meckelfeldensis*. Based on archeopyle type, he allied *Wetzeliella meckelfeldensis* with *Wetzeliella lunaris* but

distinguished the former from *Wetzeliiella symmetrica*, which had a smaller archeopyle, with the periarchoepyle being approximately the same size as the endoarcheopyle. Gocht (1969) also noted that archeopyle openings are uncommon in *Wetzeliiella symmetrica*. We consider that this reflects a soleiform archeopyle, with the opercula often falling back in place, like a flap.

Bujak (1979) was first to name a distinctive quadra 2a archeopyle type: the soleiform archeopyle. In the soleiform type, the peri- and endoperculum remain attached along the anterior margin, usually have a distinctive tongue-like outline and tend to be of the same size. It is remarkable that the anterior attachment of the operculum was first noted by Eisenack (1954), yet its significance was overlooked for 25 years.

Another milestone paper on wetzelielloidean archeopyle variation was that by Costa & Downie (1979). These authors recognised four archeopyle types: the *Apectodinium* type, in which the peri- and endoperculum are attached to each other; the *Wetzeliiella meckelfeldensis* type, in which the periarchoepyle is longer than the endoarcheopyle; the *Wetzeliiella articulata* type, in which the periarchoepyle and endoarcheopyle are of equal length; and the *Dracodinium* type, in which the periarchoepyle is longer and narrower than the endoarcheopyle.

The idea that the archeopyle may be of fundamental importance to the classification of the wetzelielloideans was discussed by Goodman (1983) and Michoux (1988). Goodman (1983) recognised three basic 2a archeopyle types in the wetzelielloideans: the subcircular, the quadrate and the soleiform. The subcircular type is another term for the *Apectodinium* type of Costa & Downie (1979). Goodman (1983) subdivided the quadrate type into the quadrangular, the broad quadrangular and the trapezoidal. Separation of these three types is based on the variations in the height/width ratio of the archeopyle. Michoux (1988) considered the quadrangular to be equivalent to the *Wetzeliiella articulata* type of Costa & Downie (1979), the broad quadrangular to be equivalent to the *Dracodinium* archeopyle type of Costa & Downie (1979), and the trapezoidal to be equivalent to the *Wetzeliiella meckelfeldensis* type of Costa & Downie (1979). Goodman (1983) retained Bujak's (1979) concept for the soleiform archeopyle type.

In part, Michoux (1988) followed the classification of Costa & Downie (1979). He retained the *Apectodinium*, *Wetzeliiella articulata* and *Wetzeliiella meckelfeldensis* archeopyle types, changed the name of the *Dracodinium* type to the *Wetzeliiella solida* type (since he included that species in *Wetzeliiella*), and added the rectangular, soleiform and *uncinata* types. According to Michoux, the *Apectodinium* type has a subcircular

to ovoidal outline with the endo- and perioepulum being of similar size and shape, and free. In the *Wetzeliiella articulata* type, the endo- and periarchoepyle are of similar size and shape and both opercula are free: the outline is quadrangular with rounded corners, and narrows anteriorly. In *Wetzeliiella meckelfeldensis*, the periarchoepyle and endoarcheopyle are the same width, but the periarchoepyle extends further anteriorly and narrows considerably. Although Michoux renamed the *Dracodinium* type as the *Wetzeliiella solida* type, he did not change the concept. This archeopyle type has a laterally elongate endo- and periarchoepyle, with the former sometimes wider than the latter. The broad lateral dimension of the archeopyle tends to be present in forms with a relatively short and indistinct apical horn, a co-occurrence that is probably not coincidental. Both the peri- and endoperculum are free.

The three remaining archeopyle types defined in Michoux (1988) are the soleiform type, the rectangular type and the *Wetzeliiella uncinata* type. The soleiform type is as defined by Bujak (1979) and hinges (pun intended!) on the anterior attachment of the peri- and endoperculum. Although not mentioned by Michoux, this type is characteristic of the holotype of *Wetzeliiella articulata*. By naming another archeopyle type the *Wetzeliiella articulata* type, Michoux inadvertently created some ambiguity. However, his reasoning was understandable in the sense that, when one reviews the literature, many of the forms included in *Wetzeliiella articulata* do have a tapered rectangular 2a with a detached operculum. Uncertainty arises because the type of *Wetzeliiella articulata* does not have this morphology.

Michoux's rectangular archeopyle type, as in *Wilsonidium* (now *Castellodinium*) *compactum*, is characterised by 'subparallel opposite sides and rounded corners' (Michoux 1988, p. 21). Although Michoux noted that in this type, the archeopyle suture runs all the way around the periphery of the 2a plate, he found that in most specimens, the opercula remained adherent. In this paper, we consider the archeopyle of *Wilsonidium* (now *Castellodinium*) *compactum* an early example of the soleiform archeopyle.

One of the most distinctive 2a archeopyle types is encompassed by Michoux's *Wetzeliiella uncinata* type (Plate 4, figures 15–20). In this variant, the periarchoepyle tapers anteriorly and is elongate, the opening in part being in the apical pericoel. Thus, the periarchoepyle in this case is considerably longer than the endoarcheopyle. One notable feature is that the perioepulum is adnate along its anterior margin, but the endoperculum is free.

Although one of the pioneers in understanding the complexity and variability of the quadra 2a plate and the archeopyle that forms from it, Michoux considered



archeopyle variation to be an intrageneric feature. Based on observations of thousands of specimens over a number of years, we have concluded that the archeopyle is of fundamental importance to understanding the phylogeny and to refining the stratigraphic distribution of the wetzelielloideans, and hence should form the basis of the taxonomy of the group. That this has not been the case in the past has led to the extending of ranges of many species to the point where they are not useful stratigraphically. An example is *Wetzeliella articulata*. This name has been applied to all forms with five horns (one apical, two lateral and two antapical, usually of unequal length) and nontabular distribution of processes that are distally free, regardless of archeopyle type. Restriction of *Wetzeliella articulata* to forms with a soleiform archeopyle, as in the holotype, has the potential to constrain its range and thus make it far more useful stratigraphically.

The stratigraphic significance of an attached quadra 2a has been supported by the observations of other authors. For example, Lentin & Vozzhennikova (1989, p. 220) noted: 'There has been a great deal of discussion among palynologists regarding the relative significance of the soleiform archeopyle. . . . However, our experience suggests that the attachment of the 2a paraplate along its anterior margin is stratigraphically controlled – even within the same species'. These authors reported an increasing percentage of soleiform archeopyles from the Early to Late Eocene, citing *Rhombodinium longimanum* as an example. It would be helpful to know the Early Eocene records to which Lentin & Vozzhennikova (1989) referred. From our data, the oldest Eocene record of a taxon with a soleiform archeopyle is *Wilsonidium compactum*, which was recorded by Michoux (1988) from the early Lutetian nannoplankton zone NP 16.

Although acknowledging an increase in occurrence of the soleiform archeopyle in the late Eocene and early Oligocene, Lentin & Vozzhennikova (1989, p. 220) stated that they considered 'the presence or absence of a soleiform archeopyle to be an intraspecific variation, and do not accept its presence or absence as a basis for the separation of genera'. They thus considered *Gochtodinium* to be a junior synonym of *Wetzeliella*. It turns out that, in our view, Lentin & Vozzhennikova were correct in their synonymy but for the wrong reason. However, at that time, the nature of the archeopyle in the holotype of *Wetzeliella articulata* was not acknowledged to be soleiform.

The classification of wetzelielloideans is confused by the array of variable features and the lack of a consistently applied hierarchy among those features on which to base a phylogenetic framework. This situation led Goodman (1983, 1985) to advance ideas on character discordance. He noted (1985, unnumbered

page) that the 'solution to date in dealing with this variation has been fundamentally to propose a new genus for each new combination of characters. The result has been an overclassification of the complex at the generic level. . . .'. At the time, Goodman wrote that there were approximately 70 species in the '*Wetzeliella* complex' (i.e. what we would now call the Wetzelielloideae), distributed among seven genera. In our view, restricting the number of genera in a family or subfamily is valid only if the generic differentiations are unworkable.

#### 4. Proposed parameters for classification

Fensome et al. (1993, p. vii) stated that 'below the rank of class, amphiesmal structure, especially tabulation, is the most valuable and meaningful criterion in classifying dinoflagellates. . . .'. A major drawback in applying this principle to the wetzelielloideans is that the tabulation is so consistently quadra bipesioid. However, variations occur in the nature of the archeopyle in both the pericyst and the endocyst. Since these variations reflect differences in shape and relative dimensions of the 2a plate, and based on our studies of these dinoflagellate cysts, we feel that this aspect of tabulation can be used effectively and meaningfully to subdivide the subfamily Wetzelielloideae into genera. We consider that other approaches to classification of the wetzelielloideans, emphasising other morphological features at generic rank, have proven impractical and should no longer be used.

In this paper we recognise several archeopyle types and use these as diagnostic criteria for genera within the Wetzelielloideae (Figures 2 and 3). We define these archeopyle types on the basis of overall shape and attachment. Archeopyles with opercula that are attached at the anterior margin are termed 'soleiform', following Bujak (1979), or 'hypersoleiform'. These two terms are defined as follows:

soleiform: peri- and endoarcheopyle of approximately the same size and shape with distinctly rounded posterior margin. Both peri- and endoperculum are attached anteriorly. Periarcheopyle not opening into apical pericoel. Periarcheopyle length: breadth ratio approximately equal to 1.  
hypersoleiform: periarcheopyle longer than endoarcheopyle, elongated, opening in part into the apical pericoel; perioperculum attached anteriorly. Periarcheopyle length: breadth ratio >1.

We use the term 'epeliform' to denote an archeopyle with a detached operculum. We also apply epeliform as a suffix for more specific types defined on the basis of shape and relative proportions of the archeopyle margins, as follows:

| ORNAMENT<br>ARCHEOPYLE TYPE | smooth, or with features of low relief          | processes distally free   | processes trabeculate                              | membranous ectophragm                              | sutural-penitabular ornament quasi-tabular          |
|-----------------------------|---|---|--|--|---|
| EQUIEPELIFORM               | * <i>Epelidinium</i> ( <i>pechoricum</i> )<br>A | <i>Apectodinium</i> ( <i>homomorphum</i> )<br><i>Axiodinium</i> ( <i>prearticulatum</i> ) B | * <i>Sophismatia</i> ( <i>crassiramosa</i> )<br>C  | <i>Charlesdowniea</i> ( <i>coleothrypta</i> )<br>D | * <i>Vallodinium</i> ( <i>nigeriaense</i> )<br>E    |
| HYPEREPELIFORM              | * <i>Rhadinodinium</i> ( <i>glabrum</i> )<br>F  | * <i>Stenodinium</i> ( <i>meckelfeldense</i> )<br>G   | * <i>Sagenodinium</i> ( <i>franciscanum</i> )<br>H |  | <i>Wilsonidium</i> ( <i>tabulatum</i> )<br>I        |
| LATIEPELIFORM               | * <i>Petalodinium</i> ( <i>condylos</i> )<br>J  | <i>Dracodinium</i> ( <i>solidum</i> )<br>K  | * <i>Kledodinium</i> ( <i>filosum</i> )<br>L       | * <i>Piladinium</i> ( <i>columnum</i> )<br>M       | * <i>Stichodinium</i> ( <i>lineidentatum</i> )<br>N |
| SOLEIFORM                   | <i>Rhombodinium</i> ( <i>draco</i> )<br>O       | <i>Wetzelilla</i> ( <i>articulata</i> )<br>P  | * <i>Michouxdinium</i> ( <i>aculeatum</i> )<br>Q   | <i>Talladinium</i> ( <i>wulagenense</i> )<br>R     | * <i>Castellodinium</i> ( <i>compactum</i> )<br>S   |
| HYPERSOLEIFORM              |   |   |  |  | * <i>Dolichodinium</i> ( <i>uncinatum</i> )<br>T    |


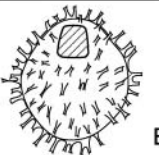



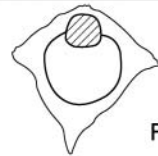

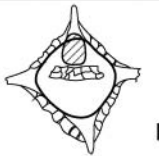
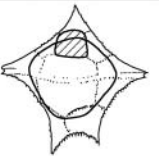
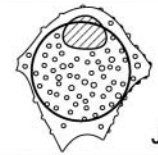
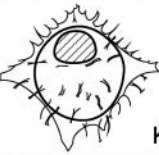

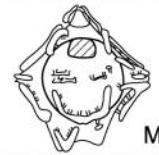
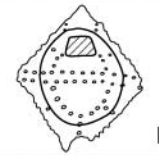
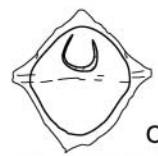




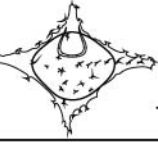
| ORNAMENT<br>ARCHEOPYLE TYPE | smooth, or with features of low relief  | processes distally free   | processes trabeculate  | membranous ectophragm   | sutural-penitabular ornament quasi-tabular  |
|-----------------------------|---|---|--|---|---|
| EQUIEPELIFORM               |  A  |  B  |  C  |  D  |  E  |
| HYPEREPELIFORM              |  F |  G |  H |   |  I |
| LATIEPELIFORM               |  J |  K |  L |  M |  N |
| SOLEIFORM                   |  O |  P |  Q |  R |  S |
| HYPERSOLEIFORM              |   |   |  |   |  T |

Figure 3. A. The scheme of genera proposed herein, as defined primarily by archeopyle type (see left column) and secondarily according to periphragm ornamentation (see top row). Generic names with an asterisk are those newly proposed herein. The epithet in parentheses beneath each generic name denotes the species whose type is also the type of the genus. B. Schematic illustrations of species in the genera listed in Figure 3A, presented on the same grid. Most of the line drawings are based on the type of the genus. The position of each line drawing represents the genus name in the equivalent position in Figure 3A, except that for forms with an equipeliform archeopyle and distally free processes we illustrate *Apectodinium* only, not *Axiodinium*.

equipeliform: peri- and endoarcheopyle of approximately the same size, the periarcheopyle not (or only minimally) opening into the apical pericoel. Periarcheopyle length: breadth ratio about 1.

hyperepeliform: periarcheopyle larger than endoarcheopyle, elongated, opening in part into the apical pericoel. Periarcheopyle length: breadth ratio from 1 to 1.2, generally closer to 1.2.

latiepeliform: periarcheopyle width exceeding length, often opening into apical pericoel, endoarcheopyle of approximately the same width as or wider than the periarcheopyle. Periarcheopyle length: breadth ratio < 1, generally about 0.8.

To use the archeopyle type alone in defining genera within the subfamily Wetzelielloideae would lead to some large genera that are diverse in ways other than archeopyle type. Therefore, we use the nature and distribution of ornamentation (primarily process development) and wall relationships (e.g. development of ectophragm) to distinguish genera with the same archeopyle type. For example, we have subdivided forms with a soleiform archeopyle on the basis of the following:

smooth, or with features of low relief: pericyst unornamented or granular, verrucate, tuberculate, perforate or reticulate (*Rhombodinium*).

processes distally free: pericyst processes well developed, bifid to aculeate, and not connected distally to other processes (*Wetzeliella*).

processes trabeculate: pericyst processes interconnected distally by trabeculae; connections typically restricted to those processes on an individual plate, so that trabeculum delineates tabulation (*Michouxidium*).

membranous ectophragm: pericyst processes interconnected distally to form an ectophragm (typically perforate). Development of ectophragm confined to intratabular areas, so that it delineates the tabulation (*Talladinium*).

sutural-penitabular ornament: pericyst processes with strong and conspicuous alignment along or parallel to and just within sutures, so as to delineate tabulation (*Castellodinium*).

Two variables in wetzelielloidians that are often overlooked because they are difficult to quantify are the development of the ambital pericoel and the thickness of the endophragm. Through the Eocene, there is a general trend for the ambital pericoel to be reduced and the endophragm to become thinner; for example, compare species of *Dracodinium* with species of *Wetzeliella*. The width of the ambital pericoel has a direct relationship to the categorisation of the archeopyle in some genera, particularly those with latiepeliform archeopyles. One such genus is *Dracodinium*, in which the periarcheopyle often markedly extends into the apical pericoel. Another is *Petalodinium*, in which the species *Petalodinium sheppeyense* commonly has an

archeopyle that opens primarily into the apical pericoel. We have not used the above criteria in generic differentiations, but such variations can provide clues to the age of species and assemblages.

A notable exception to the age-related variability in the features mentioned in the previous paragraph is the genus *Apectodinium*. Although *Apectodinium* first appears in the Selandian and does not occur in any great abundance above the Ypresian, it consistently has a thin endophragm and a pericyst and endocyst that are appressed. This distinctive feature is what distinguishes the genus from *Axiodinium*, which is characterised by an ambital pericoel and usually, but not always, a thicker endophragm.

We use horn development for species differentiation. However, determining which antapical horn is the longer can be difficult; indeed, Iakovleva & Heilmann-Clausen (2007) recently noted that in the species *Epelidinium* (as *Wilsonidium*) *pechoricum*, the right antapical horn is longer than the left. This situation can be seen also in scanning electron micrographs of specimens illustrated herein (Plate 5, figures 1 and 3). Variation in pericyst ornamentation is also a critical factor when speciating. However, in our view, the relative length and development of horns and pericyst ornamentation are secondary to archeopyle type for generic separation in wetzelielloideans. Thus, forms with a membranous or reticulate ectophragm that have been included within a single species or genus may now be separated from one another at the generic level on the basis of their archeopyle type. This approach makes the classification of the group more logical and increases its value in stratigraphic determinations, which is one of the primary considerations when erecting species.

## 5. Systematic palaeontology

### 5.1. General remarks

In the systematics section that follows, genera are presented in alphabetical order. In contrast and to facilitate comparison, the plates are arranged so that all forms with the same archeopyle type are generally together. The diagnoses are intended to outline as briefly as possible the morphological features that distinguish each genus. The descriptions provide a detailed account of the degree of variability in all morphological features. The asterisk indicates the species containing the type of the genus ('type species'). In Appendices 1–3, we provide lists of taxa and affiliations relating the names used herein with those cited in Fensome & Williams (2004).

The plates include many images from the extensive slide collection of the senior author (GLW), and include his own photographs and those gleaned from

many colleagues over the decades, most notably Lew Stover. Unfortunately, details such as size and provenance have been lost for many of these specimens; but we have decided to use the images anyway because collectively they provide an excellent insight into the morphology of wetzelielloids, especially the archeopyle. To give a more specific idea of the sizes of taxa, we include some information available from the literature (from protologues of the appropriate species unless otherwise specified) as a final paragraph in the Discussion of each genus. For overall dimensions in generic descriptions, we follow Stover & Evitt (1978, p. 5) in using the terms 'small' (less than 50  $\mu\text{m}$ ), 'intermediate' (50–100  $\mu\text{m}$ ) and 'large' (greater than 100  $\mu\text{m}$ ). A 'thin' wall is interpreted as being about 1  $\mu\text{m}$ .

Note that in the plates the designation 'sp.' does not indicate that we recognise a specific informal taxon, but that we can assign the specimen illustrated only to generic rank. Thus, the labelling of multiple specimens within a genus as 'sp.' implies neither that they are conspecific nor that they are mutually separate forms.

The generic names *Axiodinium* and *Talladinium* were introduced by the present authors in Fensome et al. (2009) and so, technically, their authorship should be cited as "Williams, Damassa, Fensome & Guerstein in Fensome et al. 2009." However, for brevity, we cite the authorship as "Williams et al. in Fensome et al. 2009." Similar considerations apply also to some other taxonomic citations throughout the systematic section.

Division DINOFLAGELLATA (Bütschli 1885)

Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome et al.  
1993

Order PERIDINIALES Haeckel 1894

Family PERIDINIACEAE Ehrenberg 1831

Subfamily WETZELIELLOIDEAE (Vozzhennikova 1961) Bujak & Davies 1983

Genus *Apectodinium* (Costa & Downie 1976)

Lentin & Williams 1977 emend. Williams et al. in  
Fensome et al. 2009  
Plate 1, figures 6–9

1976 *Wetzeliella* subgenus *Apectodinium* Costa & Downie: 608.

1977 *Apectodinium* (Costa & Downie) Lentin & Williams: 8.

2009 *Apectodinium* (Costa & Downie): emend Williams et al. in Fensome et al.: 13–14.

**Type.** Deflandre & Cookson 1955, pl. 5, fig. 7, text-fig. 19, as *Wetzeliella homomorpha*.

**Diagnosis.** Wetzelielloidean cysts with an equiepiliform archeopyle; periphragm and endophragm conspicuously

thin and closely appressed except sometimes under horns; pericyst with processes that are distally free.

**Description.**

**Shape.** Dorso-ventral outline of pericyst ovoidal to rhomboidal to pentagonal, with variable development of horns. Dorso-ventral outline of endocyst conforms closely to shape of pericyst except below horns.

**Wall structure.** Periphragm is conspicuously thin, with slender, nontabular processes that are distally free; processes occasionally branching along the stem, with distal ends bifurcate to aculeate. Endophragm conspicuously thin, unornamented.

**Pericoels.** Usually restricted to horns.

**Tabulation.** Indicated by archeopyle when present.

**Archeopyle.** Commonly not formed or discernible. When developed, equiepiliform, typically ovoidal. Perioperculum and endoperculum appressed and of same size and shape.

**Furrows.** Cingulum may be expressed by alignment of processes; sulcus not clearly delineated.

**Size.** Predominantly intermediate.

**Stratigraphic occurrence.** Paleocene to Late Eocene (Selandian to Priabonian)

**Discussion.** *Apectodinium* and *Axiodinium* are similar in having an equiepiliform archeopyle and processes that are distally free. However, there are some significant differences in the nature of the archeopyles and the opercula. In *Apectodinium*, the endo- and periarcheopyle are essentially the same size and ovoidal, and the two opercular pieces are appressed, even after detachment from the rest of the cyst. This contrasts with *Axiodinium*, in which the periarcheopyle is generally larger than the endoarcheopyle and the peri- and endoperculum are separate. Morphologically, the archeopyle of *Axiodinium* could be thought of as intermediate between *Apectodinium* and *Stenodinium*.

Wall thickness and the development of pericoels are also different in *Apectodinium* and *Axiodinium*. *Apectodinium* invariably has an extremely thin periphragm and endophragm, whereas in *Axiodinium* both wall layers are relatively thick. And whereas *Axiodinium* is commonly circumcavate, *Apectodinium* is generally cornucavate. Thus, it is often difficult to distinguish the periphragm and endophragm in *Apectodinium* except in the vicinity of the horns.

Other genera with an equiepiliform archeopyle are *Charlesdowniea*, *Epelidinium*, *Sophismatia* and *Valloidinium*. *Charlesdowniea* is characterised by an ectophragm; *Epelidinium* has a pericyst surface that is smooth or ornamented with features of low relief;

*Sophismatia* is characterised by processes bearing trabeculae; and *Vallo-dinium* has sutural to penitabular processes on the pericyst. *Dracodinium*, *Stenodinium* and *Wetzeliella* also have distally free processes; however, *Stenodinium* has a hyperepeliform archeopyle, *Dracodinium* has a latiepeliform archeopyle and *Wetzeliella* has a soleiform archeopyle.

The overall diameter for *Apectodinium homomorphum*, excluding processes, is 44–60 µm; the overall diameter of the type, including processes, is 67 µm. The pericyst length for the type of *Apectodinium longispinosum* is 121 µm and the width is 83 µm. For the type of *Apectodinium quinquelatum*, the pericyst length is 94 µm, pericyst width is 105 µm and the endocyst length and breadth are both 69 µm.

#### Included species.

*Apectodinium africaense* (Jan du Chêne & Adediran 1985) comb. nov.

1985 *Wetzeliella africaensis* Jan du Chêne & Adediran: 30–31, pl. 6, figs. 5–6.

*Apectodinium capitulatum* He Chengquan 1991.

*Apectodinium cornufruticosum* Islam 1983c.

*Apectodinium geometricum* (Pastiels 1948 ex Downie & Sarjeant 1965) Fensome et al. 1990.

\**Apectodinium homomorphum* (Deflandre & Cookson 1955) Lentin & Williams 1977. (Plate 1, figures 8–9)

*Apectodinium hyperacanthum* (Cookson & Eisenack 1965) Lentin & Williams 1977.

*Apectodinium longispinosum* (Wilson 1968) Bujak & Davies 1983. (Plate 1, figure 6)

*Apectodinium paniculatum* (Costa & Downie 1976) Lentin & Williams 1977.

*Apectodinium paradoxum* He Chengquan 1991.

*Apectodinium parvum* (Alberti 1961) Lentin & Williams 1977.

*Apectodinium quinquelatum* (Williams & Downie 1966) Costa & Downie 1979. (Plate 1, figure 7)

*Apectodinium raritubiformium* Shaw Chenlong 1999.

*Apectodinium summissum* (Harland 1979) Lentin & Williams 1981.

*Apectodinium? williereae* (Boltenhagen 1977) Lentin & Williams 1981.

Genus *Axiodinium* Williams et al. in Fensome et al. 2009

Plate 1, figures 10–12; Plate 5, figure 11

2009 *Axiodinium* Williams et al. in Fensome et al.: 16.

**Type.** Williams & Downie 1966, pl. 18, fig. 1, as *Wetzeliella articulata*. Now *Axiodinium prearticulatum*.

**Diagnosis.** Wetzelielloidean cysts with an equiepeli-form archeopyle; periphragm and endophragm partially appressed or, more usually, with ambital pericoel; endophragm may be thicker than periphragm; processes are distally free.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal to rounded pentagonal, with apical, lateral and antapical horns usually well developed. Dorso-ventral outline of endocyst round to rhomboidal.

**Wall structure.** Periphragm thin to moderate, processes nontabular and distally free; process tips bifid to aculeate. Endophragm thin to thick, smooth to spongy to granular.

**Pericoels.** Cysts circumcavate to cornucavate.

**Tabulation.** Indicated by archeopyle only.

**Archeopyle.** Equiepeli-form. Periarcheopyle may extend a little into apical pericoel, operculum free. Endoarcheopyle may be same size but is commonly smaller and extends apically/antapically less than periarcheopyle; operculum also free.

**Furrows.** Not delineated.

**Size.** Intermediate to large.

**Stratigraphic occurrence.** Early to Middle Eocene (Ypresian–Lutetian).

**Discussion.** As noted previously, both *Axiodinium* and *Apectodinium* have an equiepeli-form archeopyle and processes that are distally free. However, the peri- and endoarcheopyle in *Apectodinium* is ovoidal, and the peri- and endopercula are appressed to each other even after detachment from the rest of the cyst. In *Axiodinium*, the periarcheopyle is often larger than the endoarcheopyle and the two opercular pieces are separate entities after detachment from the cyst. The endocyst of *Axiodinium* is frequently circular to ovoidal, with circumcavation being common. This contrasts with *Apectodinium*, which is generally acavate or cornucavate. *Apectodinium* invariably has extremely thin walls, whereas *Axiodinium* commonly has a relatively thick periphragm and, especially, endophragm.

Other genera with an equiepeli-form archeopyle are *Charlesdowniea*, *Epelidinium*, *Sophismatia* and *Vallo-dinium*. *Charlesdowniea* is characterised by an ectophragm. *Epelidinium* has a pericyst surface that is smooth or ornamented with features of low relief. *Sophismatia* is characterised by trabeculate processes. *Vallo-dinium* has sutural to penitabular ornamentation

on the pericyst. *Stenodinium*, *Dracodinium* and *Wetzeliiella* also have distally free processes; however, *Stenodinium* has a hyperepeliform archeopyle, *Dracodinium* has a latiepeliform archeopyle and *Wetzeliiella* has a soleiform archeopyle.

*Axioidinium prearticulatum* contains specimens formerly included in *Wetzeliiella articulata* but with an equiepeliform archeopyle.

For the holotype of *Axioidinium augustum*, the pericyst length (excluding horns) is 64  $\mu\text{m}$  and the width is 66  $\mu\text{m}$ . In specimens of *Axioidinium prearticulatum* (formerly assigned to *Wetzeliiella articulata*) described from the London Clay by Williams & Downie (1966), the overall pericyst length is 111–162  $\mu\text{m}$  and the overall width is 64–105  $\mu\text{m}$ .

#### Included species.

*Axioidinium abortivum* (Yu Jingxian 1989) comb. nov.  
1989 *Wetzeliiella abortiva* Yu Jingxian: 154–155, pl. 56, fig. 4; pl. 57, fig. 4.

*Axioidinium augustum* (Harland 1979) comb. nov.  
(Plate 1, figures 11–12)  
1979 *Wetzeliiella* (*Apectodinium*) *augustum* Harland: 63, pl. 2, figs. 13–15.

1981 *Apectodinium augustum* (Harland): Lentin & Williams: 14.

*Axioidinium degeneratum* (Yu Jingxian 1989) comb. nov.

1989 *Wetzeliiella degenerata* Yu Jingxian: 152, pl. 54, figs. 2–3.

*Axioidinium lunare* (Gocht 1969) comb. nov.  
1969 *Wetzeliiella lunaris* Gocht: 13–15, pl. 10, figs. 1–3; text-fig. 6.

\**Axioidinium prearticulatum* Williams et al. in Fensome et al. 2009.

*Axioidinium?* *tesselatum* (Châteauneuf & Gruas-Cavagnetto 1978) comb. nov.  
1978 *Apectodinium homomorphum* subsp. *tesselatum* Châteauneuf & Gruas-Cavagnetto p. 65–66, pl. 1, figs. 1–2.  
1983c *Wilsonidium tesselatum* (Châteauneuf & Gruas-Cavagnetto): Islam 1983c: 90.

We transfer this species to *Axioidinium* questionably because the archeopyle may be epeliform but, because of the apparent strong cavation, it is not assignable to *Apectodinium*.

Genus *Castellodinium* gen. nov.  
Plate 4, figure 14; Plate 5, figure 8

**Type.** Michoux 1988, pl. 1, figs. 1–3; text-figs. 13 A–B, as *Wilsonidium compactum*.

**Etymology.** From the Latin noun *castellum*, meaning fortress, castle, in reference to the enclosure of plates by sutural or penitabular features.

**Diagnosis.** Wetzeliielloidean cysts with a soleiform archeopyle and pericyst ornamentation that is conspicuously sutural to penitabular.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal to pentagonal in outline, horns moderately well developed. Dorso-ventral outline of endocyst rounded quadrangular.

**Wall structure.** Periphragm thin, with processes relatively short (for example, up to 6  $\mu\text{m}$  in the type; Michoux 1988) and sutural to penitabular in distribution; process tips blunt or capitate, distally free. Endophragm thin, with granular ornamentation.

**Pericoels.** Cysts circumcavate.

**Tabulation.** Fully delineated by processes on pericyst.

**Archeopyle.** Soleiform. Periarcheopyle operculum generally attached along anterior margin. Endoarcheopyle with operculum attached when observed.

**Furrows.** Cingulum variably expressed by one or two rows of sutural processes; sulcus also variably expressed.

**Size.** Intermediate to large.

**Stratigraphic occurrence.** The genus typically occurs in the Middle Eocene (Lutetian), but probably extends into the Late Eocene or even the Early Oligocene.

**Discussion.** Other genera with a soleiform archeopyle are *Michouxdinium*, *Rhombodinium*, *Talladinium* and *Wetzeliiella*. *Michouxdinium* has trabeculate processes; *Rhombodinium* is characterised by a pericyst that is smooth or is ornamented only with features of low relief; species of *Talladinium* have processes that are distally united by an ectophragm; and *Wetzeliiella* has processes that are distally free. Genera that also have sutural to penitabular ornamentation are *Dolichodinium*, *Stichodinium*, *Vallo-dinium* and *Wilsonidium*. *Dolichodinium* may be distinguished on the basis of its hypersoleiform archeopyle, while *Stichodinium*, *Vallo-dinium* and *Wilsonidium* have hypersoleiform, equiepeliform and hyperepeliform archeopyles, respectively.

The holotype of *Castellodinium compactum* has a pericyst length of 99  $\mu\text{m}$  and a width of 90  $\mu\text{m}$ .

#### Included species.

\**Castellodinium compactum* (Michoux 1988) comb. nov.

1988 *Wilsonidium compactum* Michoux: 38–39, pl. 9, figs. 1–9; pl. 10, figs. 1–9, text-figs. 13A–B, 14.

In a plate caption referring to this species, Michoux (1988, p. 34) stated that ‘The operculum remains adherent although completely surrounded by the archeopyle suture’.

*Castellodinium? intermedium* (Cookson & Eisenack 1961) comb. nov.

1961 *Wetzeliiella intermedia* Cookson & Eisenack: 40, pl. 1, figs. 5–6.

1973 *Rhombodinium intermedium* (Cookson & Eisenack): Lentin & Williams: 120.

1979 *Wilsonidium intermedium* (Cookson & Eisenack): Costa & Downie: 45.

We assign this species questionably to *Castellodinium* because of uncertainty over archeopyle type.

*Castellodinium? tuberosuturatum* (He Chengquan 1991) comb. nov.

1991 *Wilsonidium tuberosuturatum* He Chengquan: 103, pl. 37, figs. 7–8.

We assign this species questionably to *Castellodinium* because of uncertainty over archeopyle type.

Genus *Charlesdowniea* Lentin & Vozzhennikova  
1989 emend. nov.

Plate 1, figures 17, 20; Plate 5, figures 2, ?12

1989 *Charlesdowniea* Lentin & Vozzhennikova: 225, 227.

**Type.** Williams & Downie 1966, pl. 18, fig. 8; text-fig. 47, as *Wetzeliiella coleothrypta*.

**Emended diagnosis.** Wetzeliielloidean cysts with an equiepeliform archeopyle and pericyst with processes distally united by ectophragmal membranes.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal, horns moderately well developed. Dorso-ventral outline of endocyst rounded to quadrate.

**Wall structure.** Periphragm thin, with penitabular processes or clusters of intratabular processes; processes distally connected by an ectophragm. Endophragm thin, smooth to granular.

**Pericoels.** Cysts circumcavate to cornucavate.

**Tabulation.** Partially to completely delineated by processes and an ectophragm that is generally intratabular, but that can be restricted to penitabular areas.

**Archeopyle.** Equiepeliform. Periarcheopyle with no or minimal extension into apical pericoel, operculum free. Endoarcheopyle of same size or smaller than periarcheopyle, operculum free.

**Furrows.** Cingulum and sulcus variably to completely expressed by membranes supported by processes, or not delineated at all. Where developed, processes delineating cingulum are confined to a single row.

**Size.** Large.

**Stratigraphic occurrence.** Early to Middle Eocene (Ypresian–Lutetian).

**Discussion.** The membranous ectophragm uniting the processes distally is extremely variable in its distribution. In some species, such as *Charlesdowniea coleothrypta*, the membrane is clearly intratabular but mirrors plate boundaries. In others, such as *Charlesdowniea edwardsii*, the processes and the interconnected membranes are largely restricted to the ambital region. Other genera besides *Charlesdowniea* possessing an equiepeliform archeopyle are *Apectodinium*, *Axioidinium*, *Epelidinium*, *Sophismatia* and *Vallodinium*. *Apectodinium* and *Axioidinium* have processes that are distally free; *Epelidinium* has a pericyst surface that is smooth or ornamented with features of low relief; *Sophismatia* is characterised by processes joined by trabecula; and *Vallodinium* has sutural to penitabular ornamentation on the pericyst. *Piladinium* and *Talladinium* also have a membranous ectophragm, but have latiepeliform and soleiform archeopyles respectively.

The holotype of *Charlesdowniea coleothrypta* has a pericyst length of 122  $\mu\text{m}$  and a width of 110  $\mu\text{m}$ ; the endocyst length is 69  $\mu\text{m}$  and the width is 62  $\mu\text{m}$ .

#### Included species.

\**Charlesdowniea coleothrypta* (Williams & Downie 1966) Lentin & Vozzhennikova 1989 (Plate 1, figures 17, 20; Plate 5, figures 2, ?12).

*Charlesdowniea? fasciata* (Rozen 1965) Lentin & Vozzhennikova 1990.

We retain this species questionably in *Charlesdowniea* because of uncertainty over archeopyle type.

*Charlesdowniea? pengchiahsuensis* (Shaw Chenglong 1999) Fensome & Williams 2004.

We retain this species questionably in *Charlesdowniea* because of uncertainty over archeopyle type.

*Charlesdowniea? rotundata* (Châteauneuf and Gruas-Cavagnetto 1978) stat. nov.

1978 *Kisselevia coleothrypta* subsp. *rotundata* Châteauneuf & Gruas-Cavagnetto: 68–69, pl. 3, fig. 5.

1989 *Charlesdowniea coleothrypta* subsp. *rotundata* (Châteauneuf & Gruas-Cavagnetto): Lentin & Vozzhennikova: 227.

We assign this species questionably to *Charlesdowniea* because of uncertainty over archeopyle type.

*Charlesdowniea? taiwaniana* (Shaw Chenglong 1999) Fensome & Williams 2004.

We retain this species questionably in *Charlesdowniea* because of uncertainty over archeopyle type.

Genus *Dolichodinium* gen. nov.

Plate 4, figures 15–20; Plate 5, figure 9

**Type.** Michoux 1988, pl. 7, figs. 1–5, as *Wetzeliella uncinata*.

**Etymology.** From the Greek *dolichos*, meaning long, with reference to the elongate periarchoepyle and perioperculum.

**Diagnosis.** Wetzelielloidean cysts with a hypersoleiform periarchoepyle and pericyst ornamentation that is conspicuously sutural to penitabular.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal to pentagonal, horns well developed except for right antapical which is considerably shorter than the left antapical. Dorso-ventral outline of endocyst rounded to quadrangular to occasionally pentagonal.

**Wall structure.** Periphragm thin, with processes sutural or penitabular, relatively short (e.g. up to 3  $\mu\text{m}$  in *Dolichodinium uncinatum* and up to 7.5  $\mu\text{m}$  in *Dolichodinium conspicuum*), with tips blunt, capitate or aculeate distally and always free. Endophragm thin, usually smooth.

**Pericoels.** Cysts circumcavate, occasionally approaching cornucavate.

**Tabulation.** Delineated by sutural or penitabular processes on pericyst.

**Archeopyle.** Hypersoleiform. Periarchoepyle operculum generally attached along anterior margin and extending beyond anterior margin of endocyst in an apical direction. Endoarchoepyle with operculum attached anteriorly or free.

**Furrows.** Cingulum expressed by a single row of processes; sulcus delineated by processes.

**Size.** Large.

**Stratigraphic occurrence.** Early Eocene (Ypresian).

**Discussion.** *Dolichodinium* is the only known genus with a hypersoleiform archeopyle. Other wetzelielloidean genera with sutural and/or penitabular ornament are *Castellodinium*, *Stichodinium*, *Vallodinium* and *Wilsonidium*. *Castellodinium*, like *Dolichodinium*, has a perioperculum that is attached anteriorly, but the archeopyle is soleiform rather than hypersoleiform. *Stichodinium* has a latiepeliform archeopyle, *Vallodinium* has an equiepeliform archeopyle and *Wilsonidium* has a hyperepeliform archeopyle.

The holotype of *Dolichodinium uncinatum* has a pericyst length of 119  $\mu\text{m}$  and a width of 128  $\mu\text{m}$ .

#### Included species.

\**Dolichodinium uncinatum* (Michoux 1988) comb. nov. (Plate 4, figures 15–16, 18)

1988 *Wetzeliella uncinata* Michoux: 36, 38, pl. 7, figs. 1–6; pl. 8, figs. 1–7; text-fig. 12.

*Dolichodinium?* *unicaudale* (Caro 1973) comb. nov.

1973 *Wetzeliella unicaudalis* Caro: 366, 368, pl. 5, figs. 1, 9.

The basis for including this species in *Dolichodinium* is the presence of a hypersoleiform periarchoepyle in the specimen illustrated in Caro (1973, pl. 5, fig. 9). However, we assign this species questionably to *Dolichodinium* because of uncertainty over the archeopyle type in the holotype (Caro 1973, pl. 5, fig. 1).

Genus *Dracodinium* Gocht 1955 emend. nov.

Plate 3, figures 6–9

1955 *Dracodinium* Gocht: 87.

1980 *Dracodinium* Gocht: emend Bujak et al.: 28.

**Type.** Gocht 1955, text-fig. 3a, as *Dracodinium solidum*.

**Emended diagnosis.** Wetzelielloidean cysts with a latiepeliform periarchoepyle; endophragm typically much thicker than periphragm; with processes that are distally free.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rounded, rhomboidal to pentagonal, with variable development of horns; apical and right antapical horns are commonly reduced or absent. Dorso-ventral outline of endocyst round to rhomboidal.

**Wall structure.** Periphragm may be up to 3  $\mu\text{m}$  thick; processes nontabular and distally free; process tips bifid to aculeate. Endophragm up to 4  $\mu\text{m}$  thick, spongy to granular.

**Pericoels.** Cysts circumcavate to cornucavate.

**Tabulation.** Indicated by archeopyle.

**Archeopyle.** Latiepeliform. Periarchoepyle may extend into apical pericoel, operculum free but sometimes stays in place. Endoarchoepyle generally of same size as periarchoepyle but may be wider; operculum free, but sometimes stays in place.

**Furrows.** Not delineated.

**Size.** Intermediate to large.

**Stratigraphic occurrence.** Early Eocene (Ypresian).

**Discussion.** The holotype of *Dracodinium solidum* (Gocht 1955, text-figs. 3a–b) has a periarchoepyle



ratio of about 0.75 and an endoarcheopyle ratio of about 0.65. Thus the type of the genus *Dracodinium* has a latiepeliform archeopyle. The difference between the periarcheopyle and endoarcheopyle ratios is not unusual in the wetzelielloideans, but determining whether it has any value for specific differentiation is unclear.

Other genera with a latiepeliform archeopyle are *Petalodinium*, *Kledodinium*, *Piladinium* and *Stichodinium*. *Petalodinium* differs in not having processes, *Kledodinium* differs in having processes that are distally trabeculate, *Piladinium* differs in having a membranous ectophragm, and *Stichodinium* differs in having penitabular to sutural ornamentation. *Dracodinium* has processes that are more or less uniform in distribution and distally free. Other wetzelielloidean genera with processes are *Apectodinium*, *Axioidinium*, *Stenodinium* and *Wetzeliella*; however, none of these genera has a latiepeliform archeopyle. *Apectodinium* and *Axioidinium* have an equipeliform archeopyle, *Stenodinium* has a hyperepeliform archeopyle and *Wetzeliella* has a soleiform archeopyle.

For the holotype of *Dracodinium eocaenicum*, the pericyst length is 102  $\mu\text{m}$ , and the width is 80  $\mu\text{m}$ ; the endocyst length is 80  $\mu\text{m}$  and the width 67  $\mu\text{m}$ . The holotype of *Dracodinium samlandicum* has a pericyst measuring 114 by 93  $\mu\text{m}$  and an endocyst 69 by 67  $\mu\text{m}$ . The pericyst of the holotype of *Dracodinium simile* is 97 by 100  $\mu\text{m}$ , the endocyst is 67  $\mu\text{m}$  across. For the holotype of *Dracodinium solidum*, the pericyst length is 97  $\mu\text{m}$ , and the width is 113  $\mu\text{m}$ ; the endocyst length is 71  $\mu\text{m}$  and the width 69  $\mu\text{m}$ .

#### Included species.

*Dracodinium astra* (Dennison in Costa et al. 1978) comb. nov.

1978 *Wetzeliella astra* Dennison in Costa et al.: 263, text-fig. 2.

*Dracodinium? brevicornutum* (Heilmann-Clausen in Heilmann-Clausen & Costa 1989) comb. nov., stat. nov.

1989 *Wetzeliella articulata* subsp. *brevicornuta* Heilmann-Clausen in Heilmann-Clausen & Costa: 472, pl. 6, figs. 1, 6.

We assign this species questionably to *Dracodinium* because of uncertainty over archeopyle type.

*Dracodinium coronatum* (Vozzhennikova 1967) comb. nov.

1967 *Rhombodinium coronatum* Vozzhennikova: 170–171, pl. 89, figs. 1–3, 5; pl. 90, figs. 1–5.

1976 *Wetzeliella coronata* (Vozzhennikova) Lentin & Williams: 131.

According to Costa & Downie (1979, p. 43), this species is a taxonomic junior synonym of *Wetzeliella articulata*. However, Iakovleva & Heilmann-Clausen (2010, p. 211) retained the species as *Wetzeliella coronata*. Lentin & Vozzhennikova (1990, p. 80) stated that the

holotype (Vozzhennikova 1967, pl. 89, fig. 1 and pl. 90, fig. 4) was lost. Iakovleva & Heilmann-Clausen (2010, p. 211) designated a neotype (Iakovleva & Heilmann-Clausen 2010, pl. 12, fig. 4).

*Dracodinium crispum* (Agelopoulos 1967) comb. nov.

1967 *Wetzeliella crista* Agelopoulos: 21–22, pl. 3, fig. 8; pl. 4, figs. 5a–b.

*Dracodinium eocaenicum* (Agelopoulos 1967) comb. nov. (Plate 3, figure 7)

1967 *Wetzeliella eocaenicum* Agelopoulos: 16–17, pl. 2, figs. 6–7; pl. 3, figs. 1–7.

1973 *Wetzeliella pachyderma* Caro: 365, pl. 3, figs. 4–6.

1979 *Dracodinium pachydermum* (Caro): Costa & Downie: 44.

We consider *Dracodinium pachydermum* to be a taxonomic junior synonym of *Dracodinium eocaenicum*, both holotypes having a latiepeliform archeopyle.

*Dracodinium lobiscum* (Williams & Downie 1966) comb. nov.

1966 *Wetzeliella symmetrica* var. *lobisca* Williams & Downie: 196, pl. 20, fig. 3.

1973 *Wetzeliella symmetrica* subsp. *lobisca* (Williams & Downie) Lentin & Williams: 143.

1979 *Wetzeliella meckelfeldensis* subsp. *lobisca* (Williams & Downie) Costa & Downie: 43.

1989 *Wetzeliella lobisca* (Williams & Downie) Jolley & Spinner: 369.

*Dracodinium magnificum* (Iakovleva & Kulkova 2001) stat. nov., comb. nov.

2001 *Wetzeliella coronata* subsp. *magnifica* Iakovleva & Kulkova: 18; pl. 6, figs. 3–4; text-fig. 11.

2004 *Wetzeliella articulata* subsp. *magnifica* (Iakovleva & Kulkova) Fensome & Williams: 686.

Fensome & Williams (2004) transferred the subspecies to *Wetzeliella articulata* because *Wetzeliella coronata* was considered at the time to be a taxonomic junior synonym of that species. Because the type of this taxon has a latiepeliform archeopyle, we here transfer it to *Dracodinium* and raise it to specific rank.

*Dracodinium samlandicum* (Eisenack 1954) Costa & Downie 1979 (Plate 3, figures 8–9)

This species was retained in *Wetzeliella* by Neumann (1990, p. 163), but we retain it in *Dracodinium* because its archeopyle morphology accords with this genus.

*Dracodinium simile* (Eisenack 1954) Costa & Downie 1979. (Plate 3, figure 6)

\**Dracodinium solidum* Gocht 1955.

*Dracodinium varielongitudum* (Williams & Downie 1966) Costa & Downie 1979.

*Dracodinium wetzelii* (Agelopoulos 1967) comb. nov.

1967 *Wetzeliella wetzelii* Agelopoulos: 17–18, pl. 2, figs. 4, 5a–b.

Genus *Epelidinium* gen. nov.

Plate 1, figures 1–5

**Type.** Iakovleva & Heilmann-Clausen 2007, fig. 2, nos. 4–5; fig. 3, no. 1, as *Wilsonidium pechoricum*.

**Etymology.** From the Greek noun *epelis*, meaning cover, lid, in reference to the free operculum.

**Diagnosis.** Wetzelielloidean cysts with an equiepeliiform archeopyle and pericyst unornamented or with features of low relief.

**Description.**

**Shape.** Dorso-ventral outline of pericyst rhomboidal, with variable development of apical horn. Right antapical horn reduced or denoted by a bulge. Dorso-ventral outline of endocyst rounded quadrate to ovoidal.

**Wall structure.** Periphragm thin, smooth or with features of low relief. Endophragm of variable thickness, typically unornamented.

**Pericoels.** Cavation is variable, circumcavate to cornucavate; may be epicavate.

**Tabulation.** Suggested by features of low relief on periphragm.

**Archeopyle.** Equiepeliiform. Periarcheopyle operculum free. Endoarcheopyle of same size or slightly smaller than periarcheopyle, operculum free.

**Furrows.** Cingulum incompletely delineated, typically suggested by folding or thickening of periphragm.

**Size.** Intermediate to large.

**Stratigraphic occurrence.** Early to Late Eocene (Ypresian to Priabonian). Some uncertainty exists as to the youngest occurrence of this genus.

**Discussion.** Other genera having an equiepeliiform archeopyle are *Apectodinium*, *Axioidinium*, *Charlesdownia*, *Sophismatia* and *Vallodinium*. *Apectodinium* and *Axioidinium* have processes that are distally free, *Charlesdownia* has an ectophragm, *Sophismatia* has trabeculate processes, and *Vallodinium* has sutural to penitabular ornamentation on the pericyst. Genera also having a pericyst that is unornamented or has only features of low relief include *Petalodinium*, *Rhadinodinium* and *Rhombodinium*. *Petalodinium* has a latiepeliiform archeopyle, *Rhadinodinium* has a hyperepeliiform archeopyle and *Rhombodinium* has a soleiform archeopyle.

The holotype of *Epelidinium pechoricum* has a pericyst 101  $\mu\text{m}$  long and 97  $\mu\text{m}$  wide. The respective dimensions for the holotype of *Epelidinium? translucidum* are 126  $\mu\text{m}$  and 135  $\mu\text{m}$ .

**Included species.**

*Epelidinium? granulatum* (Wilson 1967) comb. nov.

1967c *Wetzeliella glabra* var. *granulata* Wilson: 493, figs. 29–30.

1973 *Rhombodinium glabrum* subsp. *granulatum* (Wilson): Lentin & Williams: 120.

1981 *Dracodinium granulatum* (Wilson): Lentin and Williams: 92.

We assign this species questionably to *Epelidinium* because of uncertainty over archeopyle type.

\**Epelidinium pechoricum* (Iakovleva & Heilmann-Clausen 2007) comb. nov.

2007 *Wilsonidium pechoricum* Iakovleva & Heilmann-Clausen: 1021–1022, 1024, fig. 4, nos. 1–6; fig. 5, nos. 1–4; fig. 6, nos. 1–4.

Although some of the ornamentation in this species is sutural, much of it is intratabular; hence, we transfer it to *Epelidinium*.

*Epelidinium? translucidum* (Michoux 1988) comb. nov.

(Plate 1, figures 1–2)

1988 *Rhombodinium translucidum* Michoux: 31–32, pl. 4, figs. 1–5, 7–8; text-fig. 9.

The type material shows some variation in archeopyle configuration and, hence, we questionably assign this species to *Epelidinium*; however, the holotype has an equiepeliiform archeopyle.

*Epelidinium triangulatum* (Yu Jingxian 1989) comb. nov.

1989 *Gochtodinium triangulatum* Yu Jingxian: 155–156, pl. 58, figs. 2, 5, 8.

1993 *Wetzeliella triangulata* (Yu Jingxian): Lentin & Williams: 678.

Genus *Kledodinium* gen. nov.

Plate 3, figure 10

**Type.** Damassa 1979, pl. 7, figs. 4–7, as *Kisselovia stellata*. Now *Kledodinium filosum*.

**Etymology.** From the Greek *kledos*, meaning enclosure or hedge, in reference to how the processes ‘fence in’ the plates.

**Diagnosis.** Wetzelielloidean cysts with a latiepeliiform archeopyle and and pericyst with processes that are distally trabeculate.

**Description.**

**Shape.** Dorso-ventral outline of pericyst rhomboidal, horns moderately well developed. Dorso-ventral outline of endocyst rounded to rhomboidal. Horns, other than the right antapical, are generally of the same length.

**Wall structure.** Periphragm moderately thick, ornamented with penitabular processes or occasional

intratabular processes; processes distally connected by trabecula. Endophragm thin, smooth.

Pericoels. Cysts minimally circumcavate to cornucavate.

Tabulation. Delineated by the distally trabeculate processes, which are generally restricted to penitabular areas, forming simulate complexes.

Archeopyle. Latiepeliform, with no or minimal extension into apical pericoel, operculum free. Endoarcheopyle of same size or smaller than periarcheopyle, operculum free.

Furrows. Cingulum expressed by single row of trabeculate processes; sulcus devoid of processes.

Size. Large.

**Stratigraphic occurrence.** Early Eocene (Ypresian) to Middle Eocene (early? Lutetian).

**Discussion.** Other genera with latiepeliform archeopyles are *Dracodinium*, *Petalodinium*, *Piladinium* and *Stichodinium*. The periphragm of *Dracodinium* has processes that are more or less uniform in distribution and distally free. *Petalodinium* has a periphragm that is smooth or ornamented with features of low relief and that are usually nontabular. *Piladinium* has a membranous ectophragm and *Stichodinium* differs in having a periphragm with reduced ornamentation or free-standing processes, both of which may be sutural and/or penitabular. Other wetzelielloidean genera with trabeculate processes are *Michouxdinium*, *Sagenodinium* and *Sophismatia*, but none of these have a latiepeliform archeopyle. *Michouxdinium* has a soleate archeopyle; *Sagenodinium* has a hyperepeliform archeopyle and *Sophismatia* has an equiepeliform archeopyle.

This genus is typified by a new species, *Kledodinium filosum*, based on specimens that Damassa (1979) assigned to *Kisselovia stellata*. For her material, Damassa recorded an overall pericyst length of 132–170  $\mu\text{m}$ , an overall pericyst width of 121–157  $\mu\text{m}$ , an overall endocyst length of 92–119  $\mu\text{m}$ , and an overall endocyst width of 84–108  $\mu\text{m}$ .

*Kledodinium filosum* sp. nov.

Plate 3, figure 10

**Holotype.** Damassa 1979, pl. 7, figs. 4–7, as *Kisselovia stellata*. Repository: Stanford University Paleontological Type Collection at California Academy of Sciences, San Francisco; 10155, R10.4, +8.1 (fide Damassa 1979, p. 817, 834).

**Diagnosis.** A species of *Kledodinium* with slender trabecula that are narrower than the width of the processes.

**Description.** A wetzelielloidean species in which the pericyst has a rhomboidal outline with moderately well-developed horns. The endocyst is rounded to rhomboidal. The periphragm is ornamented with penitabular processes or occasional intratabular processes that are distally connected by slender trabecula narrower than the width of the processes. Cysts minimally circumcavate to cornucavate. The archeopyle is latiepeliform, with no or minimal extension into apical pericoel, operculum free. Endoarcheopyle of same size or smaller than periarcheopyle, operculum free.

**Discussion.** The specimen included in *Kisselevia stellata* by Damassa (1979, pl. 7, figs. 4–7) has a latiepeliform archeopyle. Therefore it cannot be included in *Vallodinium*, the genus to which we transfer *Kisselevia stellata*. Consequently, we are erecting the genus *Kledodinium* to which we assign the specimen illustrated in Damassa (1979, pl. 7, figs. 4–7).

Genus *Michouxdinium* gen. nov.

Plate 4, figures 10–11

**Type.** Michoux 1988, pl. 1, figs. 1, 4, 7, text-fig. 5A–B, as *Kisselovia aculeata*.

**Etymology.** Named for Daniel Michoux.

**Diagnosis.** Wetzelielloidean cysts with a soleiform archeopyle and processes that are distally trabeculate.

**Description.**

Shape. Dorso-ventral outline of pericyst rhomboidal, horns distinct but of limited development. Dorso-ventral outline of endocyst rhomboidal.

Wall structure. Periphragm thin, ornamented with penitabular processes or clusters of intratabular processes which are distally connected by trabecula; process tips may be distally aculeate. Endophragm thin, smooth to granular.

Pericoels. Cornucavate to narrowly circumcavate.

Tabulation. Partially to completely delineated by trabecular network which is supported by penitabular processes and forms simulate complexes.

Archeopyle. Soleiform. Endoarcheopyle of similar size to periarcheopyle.

Furrows. Delineated by processes and trabecula.

Size. Large.

**Stratigraphic occurrence.** Latest Early Eocene to Early Oligocene (Ypresian–Rupelian).

**Discussion.** Other genera with a soleiform archeopyle are *Castellodinium*, *Rhombodinium*, *Talladinium* and *Wetzeliella*. *Castellodinium* has sutural to penitabular processes. *Rhombodinium* has a pericyst that is smooth or is ornamented only with features of low relief. Species of *Talladinium* have processes that are distally united by an ectophragm. *Wetzeliella* has processes that are distally free. *Kledodinium*, *Sagenodinium* and *Sophismatia* also have trabeculate processes, but *Kledodinium* has a latiepeliform archeopyle, *Sagenodinium* has a hyperepeliform archeopyle and *Sophismatia* has an equiepeliform archeopyle.

The holotype of *Michouxdinium aculeatum* has a pericyst length of 124  $\mu\text{m}$  and width of 121  $\mu\text{m}$ . Bujak in Bujak et al. (1980) recorded the following range of dimensions for his specimens of *Michouxdinium variabile*: overall pericyst length 80–117  $\mu\text{m}$ , overall pericyst width 82–124  $\mu\text{m}$ ; overall endocyst length 65–92  $\mu\text{m}$ , overall endocyst width 66–100  $\mu\text{m}$ .

#### Included species.

- \**Michouxdinium aculeatum* (Michoux 1988) comb. nov.  
 1988 *Kisselevia aculeata* Michoux 1988, p. 24, 26, pl. 1, figs. 1, 4, 7–8; pl. 2, figs. 1–2; text-fig. 5A–B, 6A–B.  
 1990 *Charlesdownia aculeata* (Michoux): Lentin & Vozzhennikova: 74.

#### *Michouxdinium limitatum* (Stover & Hardenbol 1994) comb. nov.

- 1994 *Charlesdownia limitata* Stover & Hardenbol: 34–35, pl. 10, figs. 70a–c, 71a–c.

#### *Michouxdinium proserpina* (van Mourik et al. 2001) comb. nov.

- 2001 *Charlesdownia proserpina* van Mourik et al.: 239, 241, figs. 7a–e.

#### *Michouxdinium? rhomboidale* (He Chengquan 1991) comb. nov.

- 1991 *Kisselevia rhomboidalis* He Chengquan: 93, pl. 35, figs. 11–13.  
 1993 *Charlesdownia rhomboidalis* (He Chengquan): Lentin & Williams: 94.

We assign this species questionably to *Michouxdinium* because of uncertainty over archeopyle type.

#### *Michouxdinium variabile* (Bujak in Bujak et al. 1980) comb. nov. (Plate 4, figure 10)

- 1980 *Kisselevia variabilis* Bujak in Bujak et al.: 67, pl. 17, figs. 1–6; text-fig. 16.  
 1989 *Charlesdownia variabilis* (Bujak in Bujak et al.): 228.

#### Genus *Petalodinium* gen. nov.

Plate 3, figures 2–5

**Type.** Williams & Downie 1966, pl. 20, figs. 1–2, as *Wetzeliella condylos*.

**Etymology.** From the Greek *petalos*, meaning broad, flat, outspread, in reference to the latiepeliform nature of the archeopyle.

**Diagnosis.** Wetzelielloidean cysts with a latiepeliform archeopyle and a pericyst that is smooth or ornamented with features of low relief.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rounded quadrangular to ovoidal; apical horn reduced. Dorso-ventral outline of endocyst circular to ovoidal.

**Wall structure.** Periphragm thin, smooth or ornamented with features of low relief and that are usually nontabular. Endophragm of moderate thickness, smooth or ornamented with features of low relief.

**Pericoels.** Cysts cornucavate, occasionally circumcavate.

**Tabulation.** Faint suggestions of tabulation, shown by alignment of the ornamentation, may be observed.

**Archeopyle.** Latiepeliform. Periarcheopyle operculum free. Endoarcheopyle may be wider or smaller than periarcheopyle, operculum free.

**Furrows.** Cingulum may be indicated on lateral horns or on dorsal surface. Sulcus typically not indicated.

**Size.** Large.

**Stratigraphic occurrence.** Early to Middle Eocene (Ypresian–Lutetian).

**Discussion.** *Petalodinium* is one of five genera with a latiepeliform archeopyle. *Dracodinium* has processes that are distally free, *Kledodinium* has processes that are distally trabeculate, *Piladinium* has a membranous ectophragm, and *Stichodinium* has penitabular to sutural ornamentation. Other genera having pericysts that are smooth or have only features of low relief are *Epelidinium*, *Rhadinodinium* and *Rhombodinium*. *Epelidinium* has an equiepeliform archeopyle, *Rhadinodinium* has a hyperepeliform archeopyle and *Rhombodinium* has a soleiform archeopyle.

The holotype of *Petalodinium condylos* has a pericyst 122  $\mu\text{m}$  long and 113  $\mu\text{m}$  wide. The holotype of *Petalodinium waipawaense* has a pericyst 102  $\mu\text{m}$  long and 118  $\mu\text{m}$  wide and an endocyst for which both dimensions are 69  $\mu\text{m}$ .

#### *Petalodinium sheppeyense* sp. nov.

**Holotype.** Williams & Downie 1966, pl. 20, fig. 10, as *Wetzeliella (Rhombodinium) glabra*. Repository: Natural History Museum (formerly British Museum, Natural History), London; V51972 (fide Williams and Downie 1966, caption to pl. 20, fig 10).

**Etymology.** Named after the Isle of Sheppey, Kent, England, the locality from which the holotype was recovered.

**Diagnosis.** A species of *Petalodinium* with a rounded apex.

**Description.** Large cysts in which the pericyst outline is pentagonal, with a rounded apex and a strongly asymmetrical antapex; the left antapical horn strongly developed and the right antapical horn absent or only weakly developed; lateral horns well developed. Endocyst outline circular to ovoidal. Periphragm smooth; endophragm thicker than periphragm, smooth or ornamented with features of low relief. Circumcavate. Archeopyle latiepeliform; periarcheopyle operculum free; endoarcheopyle may be wider or smaller than periarcheopyle, operculum free.

**Discussion.** Bujak et al. (1980, p. 29) designated as the holotype of *Dracodinium politum* the specimen illustrated in Williams & Downie (1966, pl. 20, fig. 9), which has a hyperepeliform archeopyle. *Dracodinium politum* is now *Rhadinodinium politum*. Bujak et al. also included in *Dracodinium politum* the specimen illustrated in their pl. 11, fig. 1, which clearly has a latiepeliform archeopyle. This specimen has the same morphology as that illustrated by Williams & Downie (1966, pl. 20, fig. 10) and assigned by them to *Wetzeliiella glabra*; thus, we designate the latter specimen as the holotype of the new species *Petalodinium sheppeyense*.

#### Included species.

\**Petalodinium condylos* (Williams & Downie 1966) comb. nov. (Plate 3, figure 3)

1966 *Wetzeliiella condylos* Williams & Downie: 193–194, pl. 20, figs. 1–2.

1976 *Rhombodinium condylos* (Williams & Downie): Lentin & Williams: 128.

1979 *Dracodinium condylos* (Williams & Downie): Costa & Downie: 43.

*Petalodinium crassithecum* (Vozzhennikova 1967)

comb. nov., stat. nov.

1967 *Rhombodinium glabrum* forma *crassithecum* Vozzhennikova: 170, pl. 91, figs. 1–2, 4–6.

1973 *Rhombodinium glabrum* subsp. *crassithecum* (Vozzhennikova): Lentin & Williams: 120.

*Petalodinium laszczynskii* (Gedl 1995) comb. nov.

1995 *Dracodinium laszczynskii* Gedl: 205, pl. 7, figs. 11, 13.

*Petalodinium rhomboideum* (Alberti 1961) comb. nov.

1961 *Wetzeliiella rhomboidea* Alberti: 10, pl. 1, figs. 1–5; pl. 12, fig. 9.

1973 *Rhombodinium rhomboideum* (Alberti): Lentin & Williams: 121.

1979 *Dracodinium rhomboideum* (Alberti): Costa & Downie: 44.

*Petalodinium rhomboideum?* subsp. *ovale* (Andreeva-Grigorovich & Savitskaya 1993) comb. nov.

1993 *Dracodinium rhomboideum* subsp. *ovale* Andreeva-Grigorovich & Savitskaya: 44–45, pl. 1, figs. 5, 7–8.

We transfer this subspecies to *Petalodinium* to follow the transfer of the species, but the morphology of the holotype is unclear; we therefore question its assignment to *Petalodinium rhomboideum*.

*Petalodinium rhomboideum* subsp. *rhomboideum* (autonym)

*Petalodinium rugosum* (Michoux 1988) comb. nov.

1988 *Rhombodinium rugosum* Michoux: 30–31, pl. 3, figs. 1–9; text-figs. 8A, B.

*Petalodinium sheppeyense* sp. nov. herein (see above)

*Petalodinium spinula* (Islam 1983a) comb. nov., stat. nov.

1983a *Dracodinium politum* subsp. *spinula* Islam: 236, pl. 2, fig. 4.

*Petalodinium waipawaense* (Wilson 1967) comb. nov.

(Plate 3, figure 5)

1967 *Wetzeliiella waipawaensis* Wilson 1967, p. 493–494, figs. 18, 20.

1973 *Rhombodinium waipawaense* (Wilson): Lentin & Williams: 121.

1979 *Dracodinium waipawaense* (Wilson): Costa & Downie: 44.

Genus *Piladinium* gen. nov.

Plate 3, figures 11–14

**Type.** Michoux 1988, pl. 1, figs. 2–3, as *Kisselovia columna*.

**Etymology.** From the Latin *pila*, meaning column, pier, in reference to the process supports of the membranes that characterise this genus.

**Diagnosis.** Wetzeliielloidean cysts with a latiepeliform archeopyle and pericyst with processes distally united by membranes (ectophragm).

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal, horns weakly to moderately well developed. Dorso-ventral outline of endocyst rounded to rhomboidal.

**Wall structure.** Periphragm moderately thick, ornamented with processes that tend to show alignment to sutures or may be marginally distributed; processes distally connected by membranes. Endophragm thin, smooth.

**Pericoels.** Cysts circumcavate to cornucavate.

**Tabulation.** Weakly to moderately delineated by the processes and possibly by ectophragmal membranes.

**Archeopyle.** Latiepeliform, with no or minimal extension into apical pericoel, operculum free.

Endoarcheopyle of same size or smaller than periarcheopyle, operculum free.

Furrows. Cingulum may be expressed by single row of processes; sulcus devoid of processes.

Size. Intermediate to large.

**Stratigraphic occurrence.** Early Eocene (Ypresian) to Middle Eocene (?early Lutetian).

**Discussion.** Other genera with latiepeliform archeopyles are *Dracodinium*, *Petalodinium*, *Stichodinium* and *Kledodinium*. The periphragm of *Dracodinium* has processes that are more or less uniform in distribution and distally free. *Stichodinium* also has distally free processes, but having a sutural or penitabular distribution. *Petalodinium* has a periphragm that is smooth or ornamented with features of low relief and more or less uniform distribution. *Kledodinium* has processes distally linked by trabeculae rather than membranes. Other wetzelielloidean genera with processes distally connected by membranes are *Charlesdowniea* and *Talladinium*, but these have equiepeliform and soleiform archeopyles, respectively.

The holotype of *Piladinium columna* has a pericyst 121  $\mu\text{m}$  long and 124  $\mu\text{m}$  wide. The holotype of *Piladinium edwardsii* has a pericyst 96  $\mu\text{m}$  long and 107  $\mu\text{m}$  wide and an endocyst 50  $\mu\text{m}$  long and 58  $\mu\text{m}$  wide.

#### Included species.

\**Piladinium columna* (Michoux 1988) comb. nov. (Plate 3, figures 11–12)

1988 *Kisselevia columna* Michoux: 28, 30, pl. 1, figs. 2–3, 5–6; pl. 2, figs. 3–5; text-figs. 7A–B.

1990 *Charlesdowniea columna* (Michoux): Lentin & Vozzhennikova: 74.

*Piladinium edwardsii* (Wilson 1967) comb. nov. (Plate 3, figure 14)

1967 *Wetzeliella edwardsii* Wilson: 477, figs. 8–9.

1978 *Kisselevia edwardsii* (Wilson): Stover & Evitt: 111.

1989 *Charlesdowniea edwardsii* (Wilson): Lentin & Vozzhennikova: 227.

Genus *Rhadinodinium* gen. nov.  
Plate 2, figures 7–12

**Type.** Williams & Downie 1966, pl. 20, fig. 9, as *Wetzeliella* (*Rhombodinium*) *glabra*.

**Etymology.** From the Greek *rhadinos*, meaning slender, tapering, in reference to the hyperepeliform nature of the archeopyle.

**Diagnosis.** Wetzelielloidean cysts with a hyperepeliform archeopyle and pericyst unornamented or with features of low relief.

#### Description.

Shape. Dorso-ventral outline of pericyst rhomboidal, horn development variable. Dorso-ventral outline of endocyst rounded to ovoidal.

Wall structure. Periphragm thin to moderate, surface smooth or with features of low relief.

Endophragm thicker than periphragm, smooth to granular.

Pericoels. Cysts circumcavate.

Tabulation. Expressed by the archeopyle and by the cingulum.

Archeopyle. Hyperepeliform. Perioperculum free. Endoarcheopyle equal in width, but shorter than periarcheopyle; endoperculum free.

Furrows. Cingulum indicated by slight folding or thickening of pericyst along sutures. Sulcus not clearly delineated.

Size. Large.

**Stratigraphic occurrence.** Early Eocene (Ypresian).

**Discussion.** *Rhadinodinium* may be distinguished from *Sagenodinium*, *Stenodinium* and *Wilsonidium*, all of which have hyperepeliform archeopyles, by its pericyst-al ornamentation, i.e. smooth or with features of low relief. Other genera with ornamentation like that of *Rhadinodinium* are *Epelidinium*, *Petalodinium* and *Rhombodinium*. *Epelidinium* has an equiepeliform archeopyle, *Petalodinium* has a latiepeliform archeopyle and *Rhombodinium* has a soleiform archeopyle.

In specimens of *Wetzeliella glabra* (now *Rhadinodinium glabrum*) from the London Clay described by Williams & Downie (1966), the overall pericyst length had a range of 140–151  $\mu\text{m}$ , with an overall width of 147–168  $\mu\text{m}$ , an overall endocyst length of 66–80  $\mu\text{m}$  and an overall endocyst width of 69–76  $\mu\text{m}$ .

#### Included species.

\**Rhadinodinium glabrum* (Cookson 1956) comb. nov.

1956 *Wetzeliella glabra* Cookson: 186, pl. 2, figs. 1–5.

1967 *Rhombodinium glabrum* (Cookson): Vozzhennikova: 169.

1979 *Wilsonidium glabrum* (Cookson): Costa & Downie: 45.

1989 *Rhombodinium?* *glabrum* (Cookson): Head & Norris: 532.

*Rhadinodinium politum* (Bujak et al. 1980) comb. nov.

1980 *Dracodinium politum* Bujak et al.: 29.

The holotype of this species is the specimen illustrated in pl. 20, fig. 9 of the re-issue of Williams & Downie (1966). See Fensome et al. (2005, entry for *Dracodinium politum*) for further discussion.

Genus *Rhombodinium* Gocht 1955 emend.  
Williams et al. in Fensome et al. 2009

Plate 3, figures 18–20; Plate 4, figure 1

- 1955 *Rhombodinium* Gocht: 85.  
 1961 *Wetzelietta* subgenus *Rhombodinium* (Gocht); Alberti: 9.  
 1963 *Kisselevia* Vozzhennikova: 183; name not validly published.  
 1967 *Kisselevia* Vozzhennikova ex Vozzhennikova: 103.  
 1976 *Kisselevia* Vozzhennikova ex Vozzhennikova; emend Lentin & Williams: 134–137.  
 1977 *Rhombodinium* Gocht: Lentin & Williams: 139.  
 1979 *Rhombodinium* Gocht; emend Bujak: 313–314 (however, see Lentin & Vozzhennikova 1989, p.218–219).  
 1989 *Kisselevia* Vozzhennikova ex Vozzhennikova: emend Lentin & Vozzhennikova: 221.  
 2009 *Rhombodinium* Gocht; emend. Williams et al. in Fensome et al.: 57.

**Type.** Gocht 1955, text-fig. 1c, as *Rhombodinium draco*.

**Diagnosis.** Wetzeliielloidean cysts with a soleiform archeopyle and a pericyst that is smooth or with features of low relief.

**Description.** Shape. Dorso-ventral outline of pericyst rhomboidal, horns variably developed. Dorso-ventral outline of endocyst ovoidal to quadrate.

Wall structure. Periphragm typically thin, smooth or ornamented with features of low relief. Endophragm of variable thickness, smooth to granular.

Pericoels. Cornucavate to narrowly circumcavate.

Tabulation. Generally not expressed except by the archeopyle and the cingulum.

Archeopyle. Soleiform. Periarcheopyle operculum attached at anterior margin, posterior margin of operculum with rounded corners. Endoarcheopyle operculum attached at anterior margin, of same size as perioperculum.

Furrows. Cingulum delineated by folds or thickening in pericyst. Sulcus not clearly delineated.

Size. Typically large.

**Stratigraphic occurrence.** Middle Eocene to Early Oligocene (Bartonian–Rupelian).

**Discussion.** *Rhombodinium* may be distinguished from other genera having a soleiform archeopyle as follows: *Castellodinium* has sutural to penitabular processes, *Michouxdinium* has trabeculate processes, *Talladinium* has an ectophragm and *Wetzelietta* has distally free processes. Other genera with ornamentation similar to that of *Rhombodinium* are *Epelidinium*, *Petalodinium* and *Rhadinodinium*. However, *Epelidinium* has an equi-epeliform archeopyle, *Petalodinium* has a latiepeliform archeopyle and *Rhadinodinium* has a hyperepeliform archeopyle.

In their emended diagnosis for *Kisselevia* (as *Kisselevia* – see Fensome et al. (2005, entry for *Kisselevia*) for a discussion of the correct spelling of this generic name), Lentin & Vozzhennikova (1989, p. 221) stated: ‘Periphragm externally ornamented by a low reticulum, which may be absent over the pandasutural areas. Low pore-like hollow tubes or delicate spinules may be present at the junctions of the reticulum’. In their comparisons, Lentin and Vozzhennikova differentiated *Kisselevia* from *Charlesdowniea* on the absence of processes and an ectophragm. The specimen designated by Lentin & Vozzhennikova (1989, pl. 1, figs. 1–2) as the lectotype also has a periphragm with a surface reticulum, as stated clearly in the emended diagnosis of Lentin & Vozzhennikova (1989, p. 223) and evident from the illustration (their pl. 1, figs. 1–2).

Lentin & Vozzhennikova (1989, p. 221) interpreted the archeopyle of *Kisselevia* as ‘type I/I quadra, [with the operculum] free or attached’. In the illustrations of the lectotype, an archeopyle is not visible; however, two other specimens (pl. 1, figs. 3–4 and pl. 2, fig. 2) strongly suggest the presence of a soleiform archeopyle with the operculum still attached along the anterior margin. Given the evidence that the type and lectotype appear to have a reticulum on the periphragm rather than a trabecular network, and that soleiform archeopyles are evident in the type material, we consider *Kisselevia* to be a junior synonym of *Rhombodinium*.

Some specimens assigned to *Kisselevia ornata* by recent authors (for example, Iakovleva & Heilmann-Clausen 2010, pl. 7, figs. 11, 19, 22) appear to have a true trabecular network supported by processes arising from the periphragm. Such specimens are assignable to *Michouxdinium*.

The holotype of *Rhombodinium draco* measures 150 µm long by 158 µm wide. The pericyst of the holotype of *Rhombodinium? longimanum* measures 156 by 161 µm and the endocyst 101 by 97 µm. Specimens recorded by Bujak (1979) in the protologue of *Rhombodinium porosum* had the following dimensions: overall length of pericyst 105–150 µm, overall width of pericyst 115–175 µm, endocyst length 75–115 µm and endocyst width 75–120 µm. Specimens recorded by Bujak (1979) in the protologue of *Wetzelietta spinula* (now *Rhombodinium spinulum*) had the following dimensions: overall length of pericyst 90–120 µm, overall width of pericyst 95–130 µm, endocyst length 75–95 µm and endocyst width 75–100 µm.

**Included species.**

*Rhombodinium cerciatum* He Chengquan 1991

*Rhombodinium denticulatum* He Chengquan 1991

\**Rhombodinium draco* Gocht 1955 (Plate 3, figure 18)

subsp. *draco* (autonym)  
subsp. *quadratum* He Chengquan 1991

*Rhombodinium elegans* He Changquan 1991

*Rhombodinium elongatum* He Chengquan 1991  
subsp. *elongatum* (autonym)  
subsp. *spinale* He Chengquan 1991

*Rhombodinium?* *fornicale* (Yu Jingxian 1989) comb. nov.

1989 *Gochtodinium fornicale* Yu Jingxian: 155, pl. 58, figs. 1, 3.  
1993 *Wetzeliella fornicale* (Yu Jingxian): Lentin & Williams: 673.

We assign this species questionably to *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium?* *freienwaldense* (Gocht 1955) Costa & Downie 1979

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium irtyschense* (Alberti 1961) comb. nov.  
1961 *Wetzeliella irtyschensis* Alberti: 8, pl. 1, figs. 11–12; pl. 12, fig. 8.

*Rhombodinium?* *kunlunene* He Chengquan 1991

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium?* *longimanum* Vozzhennikova 1967  
(Plate 3, figure 20)

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium?* *majus* Xu Jingxian 1982

The morphology of this species is problematic. We follow Lentin & Williams (1985) in questionably retaining this species in *Rhombodinium* and recommend that the name be restricted to the holotype.

*Rhombodinium?* *minus* He Chengquan 1991

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium mirabile* He Chengquan 1991

*Rhombodinium?* *oravense* Grigorovich 1971

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium ornatum* (Vozzhennikova 1967) comb. nov.  
1963 *Kisselevia ornata* Vozzhennikova: 183, figs. 16 a–b (name not validly published; no description).

1967 *Kisselevia ornata* Vozzhennikova: 103–104, pl. 42, figs. 1–3; pl. 43, figs. 1–4; pl. 44, figs. 1–12; pl. 45, figs. 1–3.

1989 *Kisselevia ornata* Vozzhennikova: emend. Lentin & Vozzhennikova: 223.

This is the type of the genus *Kisselevia*, which we synonymise herein with *Rhombodinium*.

*Rhombodinium pentagonum* Vozzhennikova 1967

*Rhombodinium perforatum* (Jan du Chêne & Château-neuf 1975) Lentin & Williams 1977

*Rhombodinium porosum* Bujak 1979 (Plate 3, figure 19)

*Rhombodinium?* *pustulosum* Châteauneuf 1980

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium?* *rotundatum* Balteş 1969

We retain this species questionably in *Rhombodinium* because of uncertainty over archeopyle type.

*Rhombodinium sinense* He Chengquan 1991

*Rhombodinium spinula* (Bujak 1979) comb. nov. (Plate 4, figure 1)

1979 *Gochtodinium spinula* Bujak: 313, pl. 2, figs. 3–9; text-fig. 8E.  
1989 *Wetzeliella spinula* (Bujak): Lentin & Vozzhennikova: 228.

*Rhombodinium tuberculatum* He Chengquan 1991

*Rhombodinium variabile* (He Chengquan 1991) comb. nov.

1991 *Dracodinium variabile* He Chengquan: 92, pl. 35, fig. 1; text-fig. 12.

*Rhombodinium vialovii* Oleinik 1976

*Rhombodinium?* *vozhennikovae* nom. subst. pro *Kisselevia major* Vozzhennikova 1967.

1963 *Kisselevia major* Vozzhennikova: fig. 15 (name not validly published; no description).

1967 *Kisselevia major* Vozzhennikova: 104–105.

We assign this species to *Rhombodinium* because its morphology appears similar to that of the lectotype of *Rhombodinium* (formerly *Kisselevia*) *ornata*, albeit questionably because of uncertainty over archeopyle type. A new name is necessary because a new combination based on the original epithet would create a junior homonym to *Rhombodinium?* *majus* Yu Jingxian, which is herein questionably transferred to *Endoscrinium*.

*Rhombodinium wuqaiense* He Chengquan 1991

Genus *Sagenodinium* gen. nov.

Plate 2, figures 15–17

**Type.** Damassa 1979, pl. 8, fig. 8, as *Kisselevia cras-soramosa*. Now *Sagenodinium franciscanum*.

**Etymology.** From the Latin noun *sagena*, meaning fishnet, snare, with reference to the distal connections of the processes.



**Diagnosis.** Wetzelielloidean cysts with a hyperepeli-form archeopyle and a periphragm with processes that are distally trabeculate.

**Description.** Shape. Dorso-ventral outline of pericyst rhomboidal, with well-developed apical horn; right antapical horn reduced or absent. Dorso-ventral outline of endocyst ovoidal to quadrate.

Wall structure. Periphragm moderately thick, ornamented with penitabular processes that support a trabecular network. Endophragm moderately thick, smooth to granular.

Pericoels. Cysts cornucavate.

Tabulation. Delineated by trabecular network, which is supported by penitabular processes, and forms simulate complexes.

Archeopyle. Hyperepeli-form. Perioperculum free. Endoarcheopyle smaller in size than periarcheopyle, endoperculum free.

Furrows. Both delineated by penitabular processes and trabeculum. The cingulum has a single row of processes.

Size. Large.

**Discussion.** *Sagenodinium* may be distinguished from other genera with hyperepeli-form archeopyles as follows: *Rhadinodinium* has a pericyst that is smooth or ornamented with features of low relief, *Stenodinium* has processes that are distally free, and *Wilsonidium* has conspicuously penitabular to sutural ornamentation. Other genera with trabeculate processes, *Michouxdinium*, *Kledodinium* and *Sophismatia*, may be distinguished on the basis of their archeopyle types: *Michouxdinium* has a soleiform archeopyle, *Kledodinium* has a latiepeli-form archeopyle and *Sophismatia* has an equiepeli-form archeopyle.

This genus is based on a new species, *Sagenodinium franciscanum*, based on specimens that Damassa (1979) assigned to *Kisselevia crassoramosa*. For her material, Damassa recorded an overall pericyst length of 121–154  $\mu\text{m}$ , an overall pericyst width of 110–148  $\mu\text{m}$ , an overall endocyst length of 64–105  $\mu\text{m}$  and an overall endocyst width of 62–100  $\mu\text{m}$ .

**Stratigraphic occurrence.** Early Eocene.

\**Sagenodinium franciscanum* sp. nov.  
(Plate 2, figures 15–16)

**Holotype.** Damassa 1979, pl. 8, fig. 8, as *Kisselevia crassoramosa*. Repository: University of California, Los Angeles, Department of Earth and Space Sciences,

Paleontological Collection; UCLA 57909, R4.9, +8.8 (fide Damassa 1979, p. 817, 837).

**Diagnosis.** A species of *Sagenodinium* with trabecula and processes of uniform thickness.

**Description.** A wetzelielloidean species in which the pericyst has a rhomboidal outline with a well-developed apical horns; right antapical horn reduced or absent. The endocyst is ovoidal to quadrate in outline. The periphragm is ornamented with penitabular processes that support a trabecular network; the trabecula and processes are of uniform thickness. Cysts cornucavate. The archeopyle is hyperepeli-form; perioperculum free; endoarcheopyle smaller in size than periarcheopyle, endoperculum free.

Genus *Sophismatia* gen. nov.

Plate 1, figures 13–16; Plate 5, figure 1

**Type.** Williams & Downie 1966, pl. 20, figs. 2, 4; text-fig. 49, as *Wetzeliella tenuivirgula*.

**Etymology.** From the Greek noun *sophisma*, meaning clever device, trickery, in reference to the similarity of *Sophismatia* to the genus *Charlesdowniea*.

**Diagnosis.** Wetzelielloidean cysts with an equiepeli-form archeopyle and pericyst with processes that are distally trabeculate.

**Description.**

Shape. Dorso-ventral outline of pericyst rhomboidal, with variable horn development. Dorso-ventral outline of endocyst ovoidal to quadrate. Horns, other than the right antapical, are generally of the same length.

Wall structure. Periphragm moderately thick, ornamented with penitabular processes or clusters of intratabular processes which are distally connected by trabecula. Endophragm moderately thick, surface smooth to granular, or with features of low relief.

Pericoels. Cysts typically cornucavate.

Tabulation. Delineated by trabecular network, which is supported by penitabular processes and forms simulate complexes.

Archeopyle. Equiepeli-form. Perioperculum free. Endoperculum of approximately equal size to that of perioperculum; endoperculum free.

Furrows. Delineated by trabecular network, as above.

Size. Large.

**Stratigraphic occurrence.** Early to Middle Eocene (Ypresian–Lutetian).

**Discussion.** *Sophismatia* may be distinguished from other genera having an equiepeliform archeopyle on the basis of its trabeculate processes. *Apectodinium* and *Axioidinium* have processes that are distally free. *Charlesdowniea* has an ectophragm. *Epelidinium* has a pericyst that is smooth or has features of low relief. *Valloodium* has penitabular to sutural ornamentation. *Kledodinium*, *Michouxdinium* and *Sagenodinium* also have trabeculate processes. However, *Kledodinium* has a latiepeliform archeopyle, *Michouxdinium* has a soleiform archeopyle and *Sagenodinium* has a hyperepeliform archeopyle.

Williams & Downie (1966) provided the following dimensions for the type material of *Wetzeliella* (now *Sophismatia*) *tenuivirgula*: overall pericyst length 125–175  $\mu\text{m}$ , pericyst width 120–158  $\mu\text{m}$ , endocyst length 72–113  $\mu\text{m}$  and endocyst breadth 70–104  $\mu\text{m}$ . For the holotype of *Sophismatia crassiramosa*, the measurements are overall length 125  $\mu\text{m}$ , overall width 122  $\mu\text{m}$ , endocyst length 80  $\mu\text{m}$  and endocyst width 71  $\mu\text{m}$ .

**Included species.**

*Sophismatia conopia* (Williams & Downie 1966) comb. nov., stat. nov.

- 1966 *Wetzeliella articulata* var. *conopia* Williams & Downie: 184, pl. 18, fig. 5.  
 1973 *Wetzeliella articulata* subsp. *conopia* (Williams & Downie): Lentin & Williams: 141.  
 1979 *Kisselevia tenuivirgula* subsp. *conopia* (Williams & Downie): Costa & Downie: 44.  
 1989 *Charlesdowniea tenuivirgula* subsp. *conopia* (Williams & Downie): Lentin & Vozzhennikova: 227.

*Sophismatia crassiramosa* (Williams & Downie 1966) comb. nov. (Plate 1, figures 13, ?16)

- 1966 *Wetzeliella tenuivirgula* var. *crassiramosa* Williams & Downie: 189–190, pl. 19, figs. 1, 5, 7; text-fig. 50.  
 1973 *Wetzeliella tenuivirgula* subsp. *crassiramosa* (Williams & Downie): Lentin & Williams: 143.  
 1976 *Kisselevia tenuivirgula* subsp. *crassiramosa* (Williams & Downie): Lentin & Williams: 137.  
 1979 *Kisselevia crassiramosa* (Williams & Downie): Damassa: 837.  
 1989 *Charlesdowniea crassiramosa* (Williams & Downie): Lentin & Vozzhennikova: 227.

*Sophismatia? exouros* (Islam 1983c) comb. nov., stat. nov.

- 1983c *Kisselevia tenuivirgula* subsp. *exouros* Islam: 88, pl. 3, figs. 3–4.  
 1989 *Charlesdowniea tenuivirgula* subsp. *exouros* (Islam): Lentin & Vozzhennikova: 228.

We assign this species questionably to *Sophismatia* because of uncertainty over archeopyle type.

*Sophismatia? insolens* (Eaton 1976) comb. nov.

- 1976 *Kisselevia insolens* Eaton: 292–293, pl. 18, figs. 1–2.  
 1989 *Kisselevia? insolens* Eaton: Lentin & Vozzhennikova: 221.

Although all other features of this species accord with *Sophismatia*, we make this assignment provisionally because the nature of the archeopyle on the holotype is unclear.

*Sophismatia reticulata* (Williams & Downie 1966) comb. nov.

- 1966 *Wetzeliella reticulata* Williams & Downie: 187–188, pl. 19, figs. 3, 6; text-fig. 48.  
 1976 *Kisselevia reticulata* (Williams & Downie): Lentin & Williams: 136.  
 1989 *Charlesdowniea reticulata* (Williams & Downie): Lentin & Vozzhennikova: 227.

\**Sophismatia tenuivirgula* (Williams & Downie 1966) comb. nov. (Plate 1, figure 14; Plate 5, figure 1)

- 1966 *Wetzeliella tenuivirgula* Williams & Downie: 188–189, pl. 19, figs. 1–2, 4–5, 7, text-figs. 49–50.  
 1976 *Kisselevia tenuivirgula* (Williams & Downie): Lentin & Williams: 136.  
 1989 *Charlesdowniea tenuivirgula* (Williams & Downie): Lentin & Vozzhennikova: 227.

Genus *Stenodinium* gen. nov.

Plate 2, figures 13–14; Plate 5, figures 3–4

**Type.** Gocht, 1969, pl. 10, fig. 13, as *Wetzeliella meckelfeldensis*.

**Etymology.** From the Greek *stenos*, meaning narrow, tight, in reference to the hyperepeliform nature of the archeopyle.

**Diagnosis.** Wetzelielloidean cysts with a hyperepeliform archeopyle and processes that are distally free.

**Description.**

**Shape.** Dorso-ventral outline of pericyst rhomboidal, with long horns, especially the apical horn; right antapical horn commonly reduced. Dorso-ventral outline of pericyst ovoidal to quadrate.

**Wall structure.** Periphragm thin, ornamented with nontabular, distally free processes; process tips bifid to aculeate. Endophragm 1–2  $\mu\text{m}$  thick; may be granular.

**Pericoels.** Cyst cornucavate.

**Tabulation.** Not apparent other than the archeopyle.

**Archeopyle.** Hyperepeliform. Perioepiculum and endopericulum free.

**Furrows.** May be faintly indicated by alignment of processes.

**Size.** Large.

**Stratigraphic occurrence.** Early Eocene.

**Discussion.** *Stenodinium* may be distinguished from *Rhadinodinium*, *Sagenodinium* and *Wilsonidium*, other genera with a hyperepeliform archeopyle, on the basis of its distally free, nontabulate processes. *Rhadinodinium* has a pericyst that is smooth or ornamented with features of low relief; *Sagenodinium* has trabeculate processes, and *Wilsonidium* has penitabular to sutural ornamentation. Other genera with distally free processes are *Apectodinium*, *Axioidinium*, *Dracodinium* and *Wetzeliella*. *Apectodinium* and *Axioidinium* both have an equiepeliform archeopyle, *Dracodinium* has a latiepeliform archeopyle and *Wetzeliella* has a soleiform archeopyle.

The holotype of *Stenodinium meckelfeldense* is 151  $\mu\text{m}$  long and 140  $\mu\text{m}$  wide, and the endocyst is 84  $\mu\text{m}$  across.

#### Included species.

\**Stenodinium meckelfeldense* (Gocht 1969) comb. nov. (Plate 2, figures 13–14)

1969 *Wetzeliella meckelfeldensis* Gocht: 15–16, pl. 10, figs. 12–15.

Genus *Stichodinium* gen. nov.

Plate 3, figures 15–17; Plate 5, figure 10

**Type.** He Chengquan & Wang Kede 1990, pl. 2, fig. 3, as *Wilsonidium subtile*.

**Etymology.** From the Greek noun *stichos*, meaning row, line, rank, in reference to the alignment of the ornamentation.

**Diagnosis.** Wetzelielloidean cysts with a latiepeliform archeopyle and sutural or penitabular ornamentation that consists of features of low relief or processes that are distally free.

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal, with reduced horns. Dorso-ventral outline of endocyst rounded.

**Wall structure.** Periphragm, bearing granules, verrucae, spines or free-standing processes that are distally bifid, trabeculate, or connected by a membranous endophragm.

**Ornamentation.** Endophragm granular to rugose. Periphragm and endophragm moderately thick.

**Pericoels.** Cysts cornucavate to circumcavate.

**Tabulation.** Denoted by sutural or possibly penitabular granules, verrucae, spines or processes and the archeopyle.

**Archeopyle.** Latiepeliform. Periarcheopyle length/breadth ratio about 0.8, operculum free but may stay

in place. Endoarcheopyle smaller than periarcheopyle, operculum free but may stay in place.

**Furrows.** Cingulum delineated by processes and by cingular horns.

**Size.** Intermediate.

**Stratigraphic occurrence.** Early Eocene (Ypresian).

**Discussion.** Other genera with latiepeliform archeopyles are *Dracodinium*, *Kledodinium*, *Petalodinium* and *Piladinium*. *Dracodinium* differs in having non-tabular processes, although some may show alignment. *Kledodinium* has trabeculate processes, *Petalodinium* does not have processes, and *Piladinium* has a membranous ectophragm. Wetzelielloidean genera with similar ornamentation are *Castellodinium*, *Dolichodinium*, *Vallodinium* and *Wilsonidium*. In *Castellodinium* and *Dolichodinium*, the perioperculum is adnate anteriorly. *Vallodinium* has an equiepeliform archeopyle and *Wilsonidium* has a hyperepeliform archeopyle.

The holotype of *Stichodinium subtile* has a pericyst length and width (excluding processes) both of 94  $\mu\text{m}$  and the endocyst is 74  $\mu\text{m}$  across.

#### Included species.

*Stichodinium? lineidentatum* (Deflandre & Cookson 1955) comb. nov.

1955 *Wetzeliella lineidentata* Deflandre & Cookson: 253–254, pl. 5, fig. 5; text-figs. 17–18.

1976 *Wilsonidium lineidentata* (Deflandre & Cookson): Lentin & Williams: 139.

We include this species in *Stichodinium* questionably because the archeopyle in the holotype appears to be latiepeliform, but the cyst in the area of the archeopyle is damaged and the archeopyle dimensions may consequently be distorted.

\**Stichodinium subtile* (He Chengquan & Wang Kede 1990) comb. nov.

1990 *Wilsonidium subtile* He Chengquan & Wang Kede: 418, 424, pl. 2, fig. 3; text-fig. 2.

Genus *Talladinium* Williams et al. in

Fensome et al. 2009

Plate 4, figures 12–13

**Type.** Mao Shaozhi & Norris 1988, pl. 13, fig. 6, as *Charlesdowniea wulagenensis*.

**Diagnosis.** Wetzelielloidean cysts with a soleiform archeopyle and processes that are distally united by membranes (ectophragm).

#### Description.

**Shape.** Dorso-ventral outline of pericyst rhomboidal; horns usually developed but of limited length; right

antapical horn reduced or absent. Dorso-ventral outline of endocyst rhomboidal.

Wall structure. Periphragm thin, with penitabular or intratabular processes that form clusters; processes distally united by an ectophragm, the connections may form 'lists' or narrow strips that parallel plate boundaries; commonly, processes are absent from the margin toward the cingulum. Endophragm thin, smooth to granular.

Pericoels. Cornucavate to circumcavate.

Tabulation. Partly to completely delineated by processes and ectophragm.

Archeopyle. Soleiform. Periarcheopyle operculum attached at anterior margin; posterior margin of operculum and archeopyle with rounded corners. Endoarcheopyle operculum attached at anterior margin, of same size as perioepylum.

Furrows. Cingulum delineated by single row of processes which are distally connected by 'lists' or membranous ribbons of ectophragm that form linear complexes. Sulcus delineated by three to four process complexes.

Size. Intermediate to large.

**Stratigraphic occurrence.** Middle Eocene to Early Oligocene (Lutetian–Rupelian).

**Discussion.** *Talladinium* may be distinguished from other genera which have a soleiform archeopyle as follows: *Castelodinium* has penitabular to sutural ornamentation and processes that are not distally connected by ectophragm, *Michouxidinium* has trabecular processes, *Rhombodinium* has a pericyst that is smooth or ornamented only with features of low relief and *Wetzeliella* has processes that are distally free. *Charlesdownia* and *Piladinium* also have an ectophragm, but have equiepeliform and latiepeliform archeopyles, respectively.

The holotype of *Talladinium wulagenense* has a pericyst 90 µm long and 76 µm wide.

#### Included species.

*Talladinium? angulosum* (Châteauneuf & Gruas-Cavagnetto 1978) comb. nov., stat. nov.

1978 *Kisselevia clathrata* subsp. *angulosa* Châteauneuf & Gruas-Cavagnetto: 69–70, pl. 5, fig. 8–9.

1989 *Charlesdownia clathrata* subsp. *angulosa* (Châteauneuf & Gruas-Cavagnetto): Lentin & Vozzhennikova: 227.

We raise this taxon to specific rank, but assign it questionably to *Talladinium* because of uncertainty over archeopyle type.

*Talladinium? clathratum* (Eisenack 1938) Williams et al. in Fensome et al. 2009

We agree with Williams et al. in Fensome et al. (2009), who assigned this species questionably to *Talladinium* because of uncertainty over archeopyle type.

*Talladinium fusiforme* (Mao Shaozhi & Norris 1988) comb. nov.

1988 *Kisselevia fusiformis* Mao Shaozhi & Norris: 49–50, pl. 13, figs. 2–4.

1993 *Charlesdownia fusiformis* (Mao Shaozhi & Norris): Lentin & Williams: 94.

*Talladinium? marginatum* (Andreeva-Grigorovich & Savitskaya 1993) comb. nov.

1993 *Charlesdownia marginata* Andreeva-Grigorovich & Savitskaya: 43–44, pl. 2, figs. 1–3.

We assign this species questionably to *Talladinium* because of uncertainty over archeopyle type.

\**Talladinium wulagenense* (Mao Shaozhi & Norris 1988) Williams et al. in Fensome et al. 2009

Genus *Vallodinium* gen. nov.

Plate 1, figures 18–19; Plate 2, figures 1–6

**Type.** Jan du Chêne & Adediran 1985, p. 9, figs. 1–2, as *Wilsonidium nigeriaense*.

**Etymology.** From the Latin noun *vallum*, meaning rampart, palisade, in reference to the pericystal ornament.

**Diagnosis.** Wetzelielloidean cysts with an equiepeliform archeopyle, pericyst ornament that is conspicuously sutural to penitabular and processes that are distally united by trabeculae or by ectophragm.

#### Description.

Shape. Dorso-ventral outline of pericyst rhomboidal, with well-developed horns; right antapical horn often reduced but may be same length as left antapical horn. Dorso-ventral outline of endocyst rhomboidal to pentagonal.

Wall structure. Periphragm thin, ornamented with sutural to penitabular processes that are distally united by trabeculae and membranous ectophragm. Endophragm thin, smooth to scabrate.

Pericoels. Cornucavate to narrowly circumcavate.

Tabulation. Precisely delineated by sutural or penitabular processes; few if any intratabular processes.

Archeopyle. Equiepeliform. Periarcheopyle with detached operculum. Endoarcheopyle usually same size or slightly smaller than periarcheopyle.

Furrows. Cingulum delineated by single row of penitabular processes. Sulcus outlined by penitabular or

sutural processes; posterior sulcal plate clearly delineated.

Size. Intermediate to large.

**Stratigraphic occurrence.** Early Eocene (Ypresian).

**Discussion.** Other genera with an equiepeliform archeopyle are *Apectodinium*, *Axiodinium*, *Charlesdowniea*, *Epelidinium* and *Sophismatia*. *Apectodinium* and *Axiodinium* have processes that are distally free, *Charlesdowniea* has an ectophragm, *Epelidinium* has a pericyst that is smooth or ornamented only with features of low relief and *Sophismatia* has trabeculate processes. *Castellodinium*, *Dolichodinium*, *Stichodinium* and *Wilsonidium* also have conspicuously penitabular to pandasutural ornamentation; however, they differ in archeopyle type. *Castellodinium* has a soleiform archeopyle, *Dolichodinium* has a hypersoleiform archeopyle, *Stichodinium* has a latiepeliform archeopyle and *Wilsonidium* has a hyperepeliform archeopyle.

The holotype of *Vallo-dinium nigeriaense* has the following dimensions: pericyst length 110  $\mu\text{m}$ , pericyst width 104  $\mu\text{m}$  and endocyst dimensions 70 by 72  $\mu\text{m}$ . The holotype of *Vallo-dinium echinosuturatum* has a pericyst 149  $\mu\text{m}$  long and 143  $\mu\text{m}$  wide and an endocyst 99  $\mu\text{m}$  long and 91  $\mu\text{m}$  wide.

**Included species.**

*Vallo-dinium?* *echinosuturatum* (Wilson 1967) comb. nov. (Plate 2, figures 5–6)

1967 *Wetzeliiella echinosuturata* Wilson: 477, 479, figs. 3, 22–25.

1976 *Wilsonidium echinosuturatum* (Wilson): Lentin & Williams: 139.

This species is questionably included in *Vallo-dinium* because of the uncertainty over archeopyle type. According to Wilson (1967, p. 479), the ‘Archeopyle when formed is rectangular and replaces [the] 2a plate’. In the accompanying illustrations (Wilson 1967, figs. 22–25), the archeopyle cannot be discerned. Wilson (1988, fig. 6, no. 6) illustrated a specimen that appears to have a hyperepeliform archeopyle. The line drawing of this species in Wilson (1967, fig. 3b) shows that it has a distinctly epeliform archeopyle. In some specimens, such as those illustrated in Wilson (1988, pl. 25, figs. 3a–b and pl. 26, fig. 1c), the operculum appears to be in place. Thus, the true nature of the archeopyle is uncertain.

\**Vallo-dinium nigeriaense* (Jan du Chêne & Adediran 1985) comb. nov.

1985 *Wilsonidium nigeriaense* Jan du Chêne & Adediran: 31, 33, pl. 7, figs. 1–6; pl. 8, figs. 1–6; pl. 9, figs. 1–5.

*Vallo-dinium stellatum* (Damassa 1979) comb. nov.

(Plate 2, figures 1–2)

1979 *Kisselevia stellata* Damassa: 834, 837, pl. 7, figs. 1–3.

1989 *Charlesdowniea stellata* (Damassa): Lentin & Vozzhennikova: 227.

The specimen of *Vallo-dinium stellatum* illustrated in Damassa (1979, pl. 7, figs. 4–7) has a latiepeliform archeopyle. Therefore, it is assigned to *Kledodinium* as *Kledodinium filiosum*.

Genus *Wetzeliiella* Eisenack 1938 emend.

Williams et al. in Fensome et al. 2009

Plate 4, figures 2–9; Plate 5, figures 5–7

**Type.** Eisenack 1938, fig. 4, as *Wetzeliiella articulata*.

**Diagnosis.** Wetzeliielloidean cysts with a soleiform archeopyle and processes that are distally free and non-tabulate in distribution or not clearly reflecting tabulation.

**Description.**

**Shape.** Dorso-ventral outline of pericyst rhomboidal to pentagonal, usually with well-developed horns; right antapical horn varies from vestigial to approximately the same length as the left antapical horn. Dorso-ventral outline of endocyst round to ovoidal.

**Wall structure.** Periphragm usually up to 2  $\mu\text{m}$  thick, with primarily non-tabular, distally free processes. Process tips bifid to aculeate. Some processes show alignment. Endophragm 1–2  $\mu\text{m}$  thick, smooth to granular.

**Pericoels.** Usually cornucavate but may be circumcavate.

**Tabulation.** Generally not apparent, except for the archeopyle margin.

**Archeopyle.** Soleiform. Periarcheopyle with operculum attached at anterior margin; posterior margin of operculum with rounded corners. Endoarcheopyle with operculum attached at anterior margin, of same size as perio-perculum.

**Furrows.** Usually bear processes but not clearly delineated.

Size. Intermediate to large.

**Stratigraphic occurrence.** Late Paleocene to early Late Oligocene if based on published records, but based on our observations, the range is Middle Eocene to Early Oligocene (Rupelian).

**Discussion.** The four other genera with a soleiform 2a archeopyle are *Castellodinium*, *Michoux-dinium*, *Rhombodinium* and *Talladinium*. *Castellodinium* has sutural to penitabular processes, *Michoux-dinium* has trabeculate processes, *Talladinium* has a membranous ectophragm and *Rhombodinium* has a pericyst that is smooth or ornamented with features of low relief. Other genera with distally free processes but a different

archeopyle type are *Apectodinium*, *Axioidinium*, *Dracodinium* and *Stenodinium*. *Apectodinium* and *Axioidinium* have an equiepeliform archeopyle, *Dracodinium* has a latiepeliform archeopyle and *Stenodinium* has a hyper-epeliform archeopyle.

Eisenack (1954) reported the range of pericyst length in *Wetzelia articulata* was from 114 to 196  $\mu\text{m}$ ; the larger end of this range would make Eisenack's specimens among the largest known wetze-lielloids. Eisenack noted that the holotype of *Wetzelia articulata* is 167  $\mu\text{m}$  long. The holotype of *Wetzelia gochtii* has a pericyst length of 113  $\mu\text{m}$ , a pericyst width of 108  $\mu\text{m}$ , an endocyst length of 97  $\mu\text{m}$  and an endocyst width of 93  $\mu\text{m}$ . The holotype of *Wetzelia hampdenensis* has a pericyst length of 132  $\mu\text{m}$ , a pericyst width of 118  $\mu\text{m}$  and an endocyst 83 by 88  $\mu\text{m}$ .

#### Included species.

\**Wetzelia articulata* O. Wetzel in Eisenack 1938 emend. Williams et al. in Fensome et al. 2009 (Plate 4, figures 6–8)

*Wetzelia articulata* subsp. *articulata* (autonym)

*Wetzelia articulata?* subsp. *scabrata* (Shaw Chenglong 1999) stat. nov.

1999 *Wetzelia articulata* var. *scabrata* Shaw Chenlong: 45, figs. 49–57.

We retain this taxon questionably in *Wetzelia articulata* because in the diagnosis Shaw Chenglong (1999, p. 45) stated, 'operculum sometimes attached along anterior margin, generally free...'. However, the archeopyle in one specimen (Shaw Chenglong 1999, figs. 52–54) appears to be equiepeliform. We raise the taxon from variety status to subspecies status.

*Wetzelia articulata?* subsp. *taiwaniana* (Shaw Chenglong 1999) stat. nov.

1999 *Wetzelia articulata* var. *taiwaniana* Shaw Chenlong: 42, 44–45, figs. 37–48.

We retain this taxon questionably in *Wetzelia articulata* because in the diagnosis, Shaw Chenglong (1999, p. 45) stated, 'operculum sometimes attached along anterior margin, generally free...'. However, the archeopyle in the holotype (Shaw Chenglong 1999, figs. 37–39) appears to be latiepeliform. We raise the taxon from variety status to subspecies status.

*Wetzelia? astroides* Islam 1983b

We retain this species questionably in *Wetzelia* because of uncertainty over archeopyle type.

*Wetzelia caviarticulata* Fensome et al. 2009

*Wetzelia? crassa* Mao Shaozhi & Norris 1988

We retain this species questionably in *Wetzelia* because of uncertainty over archeopyle type.

*Wetzelia distalis* He Chengquan 1991

*Wetzelia elongata* He Chengquan 1991

*Wetzelia? flexibilis* Yu Jingxian 1989

We retain this species questionably in *Wetzelia* because of uncertainty over archeopyle type.

*Wetzelia gochtii* Costa & Downie 1976 (Plate 4, figure 2; Plate 5, figures 5–7)

*Wetzelia? hampdenensis* Wilson 1967 (Plate 4, figures 3–4)

We retain this species questionably in *Wetzelia* because of uncertainty over archeopyle type.

*Wetzelia ovalis* Eisenack 1954

subsp. *ovalis* (autonym)

subsp. *rotundata* Andreeva-Grigorovich & Savitskaya 1993

*Wetzelia? robusta* Yu Jingxian 1989

We retain this species questionably in *Wetzelia* because of uncertainty over archeopyle type.

*Wetzelia simplex* (Bujak 1979) Lentin & Vozzhennikova 1989

*Wetzelia? spinulosa* Wilson 1988

We retain this species questionably in *Wetzelia* because of the uncertainty over the archeopyle type. Wilson (1988, p. 33) stated that sometimes the operculum remained attached. In the accompanying illustrations of the holotype (Wilson 1988, pl. 25, figs. 3–4), the shape of the archeopyle appears to be soleiform but the periarcheopyle appears to extend anteriorly into the apical pericoel, which would indicate that the species has a hyperepeliform archeopyle.

*Wetzelia symmetrica* Weiler 1956

*Wetzelia symmetrica* subsp. *incisa* Gerlach 1961

*Wetzelia symmetrica?* subsp. *scabrata* (Shaw Chenglong 1999) stat. nov.

1999 *Wetzelia symmetrica* var. *scabrata* Shaw Chenlong: 42, figs. 31–36.

We retain this taxon questionably in *Wetzelia symmetrica* because, in the diagnosis, Shaw Chenglong (1999, p. 42) stated, 'operculum sometimes attached along anterior margin, generally free...'. However, the archeopyle in the holotype (Shaw Chenglong 1999, figs. 31–33) appears to be latiepeliform. We raise the taxon from variety status to subspecies status.

*Wetzelia symmetrica* subsp. *symmetrica* (autonym)

*Wetzeliella symmetrica?* subsp. *taiwaniana* (Shaw Chenglong 1999) stat. nov.

1999 *Wetzeliella symmetrica* var. *taiwaniana* Shaw Chenlong: 41–42, figs. 22–30.

We retain this taxon questionably in *Wetzeliella symmetrica* because, in the diagnosis, Shaw Chenglong (1999, p. 42) stated: ‘operculum sometimes attached along anterior margin, generally free. . .’. However, the holotype (Shaw Chenglong 1999, figs. 22–24) is too badly damaged to determine the true nature of the archeopyle. We raise the taxon from variety status to subspecies status.

*Wetzeliella? tianshanensis* He Chengquan 1991

We retain this species questionably in *Wetzeliella* because of uncertainty over archeopyle type.

*Wetzeliella xinjiangensis* He Chengquan 1991

Genus *Wilsonidium* Lentin & Williams 1976  
emend. nov.

Plate 2, figures 18–20, Plate 3, figure 1

**Type.** Wilson 1967, fig. 4–6, as *Wetzeliella tabulata*.

**Emended diagnosis.** Wetzelielloidean cysts with hyperepeliform archeopyle and pericyst ornamentation that is conspicuously sutural to penitabular.

#### Description.

Shape. Dorso-ventral outline of pericyst rhomboidal to pentagonal, with well-developed horns. Right antapical horn prominent but never as long as the left antapical horn. Dorso-ventral outline of pericyst subcircular to rhomboidal.

Wall structure. Periphragm up to about 2 µm thick, ornamented with features of low relief or short processes that may be distally free or united. Endophragm thin, smooth to scabrate.

Pericoels. Circumcavate, but the endocyst and pericyst may occasionally come into contact.

Tabulation. Clearly delineated by strongly aligned rows of processes, which are usually sutural but may be penitabular.

Archeopyle. Hyperepeliform. Periarcheopyle with operculum free. Endoarcheopyle equal in width but shorter than periarcheopyle, endoperculum free.

Furrows. Cingulum delineated by a single discontinuous row of processes or low relief ornamentation.

Size. Large.

**Stratigraphic occurrence.** Eocene.

**Discussion.** *Wilsonidium* may be distinguished from other genera having hyperepeliform archeopyles as follows: *Rhadinodinium* has a pericyst that is smooth or ornamented only with features of low relief. *Sagenodinium* has trabeculate processes. *Stenodinium* has processes that are distally free. Other genera with penitabular to sutural ornamentation are *Castellodinium*, *Dolichodinium*, *Stichodinium* and *Valloodium*. *Castellodinium* has a soleiform archeopyle, *Dolichodinium* has a hypersoleiform archeopyle, *Stichodinium* has a latiepeliform archeopyle and *Valloodium* has an equiepeliform archeopyle.

The holotype of *Wilsonidium tabulatum* has a pericyst length of 149 µm, a pericyst width of 138 µm, and endocyst 83 by 85 µm. The holotype of *Wilsonidium ornatum* has a pericyst length of 156 µm, a pericyst width of 151 µm, an endocyst length of 99 µm and an endocyst width of 102 µm.

#### Included species.

*Wilsonidium conspicuum* (He Chengquan 1991) stat. nov.

1991 *Wilsonidium lineidentatum* subsp. *conspicuum* He Chengquan: 103–104, pl. 44, figs. 6–12.

*Wilsonidium ornatum* (Wilson 1967) Lentin & Williams 1976 (Plate 3, figure 1)

\**Wilsonidium tabulatum* (Wilson 1967) Lentin & Williams 1976 (Plate 2, figures 18–20)

Subfamily DEFLANDREOIDEAE Bujak & Davies 1983

Genus *Spinidinium* Cookson & Eisenack 1962

*Spinidinium rugosum* (Stanley 1965) Costa & Downie 1979

1965 *Wetzeliella rugosum* Stanley: 222–223; pl. 21, figs. 6–11.

1978 *Wetzeliella? rugosum* Stanley: Stover & Evitt: 132.

1976 *Wilsonidium? rugosum* (Stanley): Lentin & Williams: 140.

1979 *Spinidinium rugosum* (Stanley): Costa & Downie: 45.

**Discussion.** Fensome & Williams (2004) retained this species in *Wilsonidium*. However, the morphology appears to conform with *Spinidinium* rather than any wetzelielloidean genus; hence, we retain the species as *Spinidinium rugosum*.

#### 6. Stratigraphic significance

Numerous studies have acknowledged the importance of wetzelielloidean taxa in delineating ages within the late Paleocene to Oligocene (Figures 4a–b), although ranges must be treated with caution as species were commonly not constrained by the archeopyle morphology of their holotypes. In a pioneering study, Wilson

(1967) recognised the usefulness of *Wetzeliella* in refining stratigraphic control in the Paleocene–Eocene strata of New Zealand. Of the eleven species he recorded, seven were restricted to individual New Zealand regional stages and three occurred in two stages. One of the species that Wilson identified was *Wetzeliella* (now *Charlesdowniea*) *coleothrypta*. The only species that did not appear to be useful stratigraphically was *Wetzeliella articulata*.

Caro (1973) was first to propose a zonation based primarily on *Wetzeliella*. In a study of Paleocene–lower Eocene strata of the Spanish Pyrenees, Caro named five zones, which are shown in Figure 4a. According to Caro, the zones were total range zones, with the nominative species being restricted to its zone.

A comparison of the data of Wilson (1967) and Caro (1973) prompts interesting questions. Why, for example, is the total range of *Wetzeliella articulata* restricted to the earliest middle Ilerdian (a regional early Eocene stage) in Caro's scheme, whereas according to Wilson the species has no stratigraphic value? A plausible explanation, if one uses the archeopyle type for the initial separation, is that specimens identified as *Wetzeliella articulata* by many authors represent several species. Another possibility is that ranges of many species in the Northern and Southern hemispheres are different, rendering it difficult to compare zonations.

A second question is whether the specimens identified as *Wetzeliella coleothrypta* by the two authors represent the same species. The specimen illustrated in Wilson (1967, figs. 12–14) appears assignable to *Charlesdowniea columna*, whereas the specimen that Caro illustrated (1973, his pl. 5, fig. 8) agrees with our concept of *Charlesdowniea coleothrypta*. But Caro also illustrated a specimen that he assigned to *Wetzeliella clathrata* (his pl. 5, fig. 7), which appears, like Wilson's specimen, to be assignable to *Charlesdowniea columna* (now *Piladinium*).

Jan du Chêne et al. (1975) identified five dinoflagellate-cyst associations in the Thanetian–Lutetian of Haute-Savoie, France, three of which were named after wetzelielloidean species. One diagnostic wetzelielloidean dinoflagellate cyst found only in the youngest – the *Areosphaeridium diktyoplokum* association – is *Wetzeliella* (now *Rhombodinium*) *perforata*.

A comprehensive zonation based on peridinioid taxa, mainly species of *Wetzeliella*, is that of Costa & Downie (1976). These authors proposed a zonation for the Paleocene–Oligocene strata of northwestern Europe, which was applicable in southern England, Belgium, northern Germany and the Paris Basin and keyed to the nannofossil zonation. Eight of the nine zones in the scheme proposed by Costa & Downie (1976, text-fig. 5) were named for wetzelielloidean species (Figure 4a).

Châteauneuf & Gruas Cavagnetto (1978; Figure 4a) proposed a fourteenfold zonation extending from the late Thanetian to the Rupelian in the Paris Basin. All fourteen zones were named for wetzelielloidean taxa, many of which had been noted as having stratigraphically restricted ranges by Costa & Downie (1976). In their text-figure 2, Châteauneuf & Gruas Cavagnetto (1978) showed what they regarded as morphologic variations and stages of evolution in four of the taxa: we pursue this hypothesis in the next section.

Costa & Downie (1979) reiterated the value of the Wetzelielloideae (which they referred to as the Wetzeliellaceae) in biostratigraphy. In their text-fig. 3, they plotted the stratigraphic range of 42 species, which they variously assigned to the genera *Apectodinium*, *Kisselevia*, *Wetzeliella*, *Dracodinium* and *Rhombodinium*. One example is *Kisselevia* (now *Sophismatia*) *ten-uivirgula*, which extends from nannofossil zones NP 12 to NP 20. Unfortunately, Costa & Downie (1979) did not reference their data sources.

Wilson (1984) proposed a dinoflagellate-cyst zonation for the Late Jurassic to Eocene of New Zealand. One of the Paleocene and most of the Eocene zones were named after species of the Wetzelielloideae. Wilson (1988; Figure 4a) proposed a minor modification of the Early Eocene zonation, with the uppermost zone being named after the areoligeracean species *Membranophoridium perforatum*. Most of the zones named after wetzelielloidean species represent the total range of the index species. Exceptions are: the *Apectodinium homomorphum* Zone, whose top is based on the FAD (First Appearance Datum) of *Wetzeliella* cf. *hyperacantha* (Wilson 1988, named this taxon *Wetzeliella spinulosa*); the *Charlesdowniea* (as *Kisselevia*) *edwardsii* Zone, whose base is marked by the LAD (Last Appearance Datum) of *Charlesdowniea coleothrypta* and whose top is marked by the LAD of the index species; and the *Stichodinium* (as *Wilsonidium*) *lineidentatum* Zone, whose base is defined by the LAD of *Castellodinium* (as *Wilsonidium*) *echinosuturatum* and whose top is defined by the FAD of *Wetzeliella hampdenensis*.

The archeopyles in most of the wetzelielloidean species after which the zones of Wilson (1984) are named fit with our observed trends relating to changes in archeopyle type through time. One possible exception is *Wetzeliella? spinulosa*, which may have a soleiform archeopyle. Wilson (1988), when erecting the species, stated that the 'operculum [is] sometimes attached along the anterior margin, generally free'. The shape of the archeopyle cannot be determined from the illustrated specimens. But an attached operculum would be a first for an Early Eocene wetzelielloidean dinoflagellate cyst. Another exception is *Vallodinium? echinosuturatum*. In the line drawing of Wilson (1967, fig. 3b), the shape of



| Ma | EPOCH     | AGE | NP       | Caro (1973) | Costa & Downie (1976) | Châteauneuf & Gruas-Cavagnello (1978) | Wilson (1984, 1988) | Andreeva-Grigorovich (1991) |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
|----|-----------|-----|----------|-------------|-----------------------|---------------------------------------|---------------------|-----------------------------|------------|-----------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|---|---|---|---|---|
| 24 | OLIGOCENE | L   | 25       |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 25 |           |     |          |             |                       |                                       |                     |                             | Chattian   |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 26 |           | E   | Rupelian |             |                       |                                       |                     |                             |            | 24        | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 |
| 27 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 28 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 29 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 30 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 31 | EOCENE    | L   | 19       |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 32 |           |     |          |             |                       |                                       |                     |                             | Priabonian | 23        | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9  | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| 33 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 34 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 35 |           | M   | 17       |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 36 |           |     |          |             |                       |                                       |                     |                             |            | Bartonian | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3 | 2 | 1 |   |   |   |   |   |
| 37 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 38 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 39 |           | E   | 16       |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 40 |           |     |          |             |                       |                                       |                     |                             |            | Lutetian  | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2 | 1 |   |   |   |   |   |   |
| 41 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 42 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 43 |           | E   | 15       |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 44 |           |     |          |             |                       |                                       |                     |                             |            | Ypresian  | 15 | 14 | 13 | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1 |   |   |   |   |   |   |   |
| 45 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 46 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 47 | E         | 14  |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 48 |           |     |          |             |                       |                                       |                     |                             | Ypresian   | 14        | 13 | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1  |    |   |   |   |   |   |   |   |   |
| 49 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 50 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 51 | E         | 13  |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 52 |           |     |          |             |                       |                                       |                     |                             | Ypresian   | 13        | 12 | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1  |    |    |   |   |   |   |   |   |   |   |
| 53 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 54 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 55 | E         | 12  |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 56 |           |     |          |             |                       |                                       |                     |                             | Ypresian   | 12        | 11 | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1  |    |    |    |   |   |   |   |   |   |   |   |
| 57 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 58 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 59 | E         | 11  |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 60 |           |     |          |             |                       |                                       |                     |                             | Danian     | 11        | 10 | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1  |    |    |    |    |   |   |   |   |   |   |   |   |
| 61 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 62 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 63 | E         | 10  |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 64 |           |     |          |             |                       |                                       |                     |                             | Danian     | 10        | 9  | 8  | 7  | 6  | 5  | 4  | 3  | 2  | 1  |    |    |    |    |    |   |   |   |   |   |   |   |   |
| 65 |           |     |          |             |                       |                                       |                     |                             |            |           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |   |   |   |   |   |   |   |

Figure 4A. Some Paleogene zonations published from 1973 to 1991 showing use of wetzelielloidean taxa. The generic assignments are as used in the original publication. Generic abbreviations are as follows: Ap = *Apectodinium*, Ch = *Charlesdowniea*, Dr = *Dracodinium*, Ki = *Kisselevia*, Rh = *Rhombodinium*, We = *Wetzeliella*, Wi = *Wilsonidium*. The abbreviation “s.l.” means sensu lato, as used by original author. Under Costa & Downie (1976), ‘1’ denotes *Wetzeliella similis* and ‘2’ denotes *Wetzeliella varielongituda*. To determine the present generic assignment of species, please see Appendix 2.

the 2a plate is epeliform. But in several illustrations (e.g. Wilson 1967, figs. 22–25; Wilson 1988, pl. 25, fig. 3b and pl. 26, fig. 1c); the operculum seems to remain in place. Thus, *Vallocladon?* *echinosuturatum* may have an attached epeliform operculum.

Williams & Bujak (1985), in a review of dinoflagellate-cyst zonations, plotted the stratigraphic ranges of 21 wetzelielloidean species. Some of their stratigraphic information is erroneous: an example is the FAD of *Charlesdowniea* (as *Kisselevia*) *edwardsii* and *Rhadinodinium* (as *Dracodinium*) *politum* at 63.7 Ma in the

Danian. Williams & Bujak indicated the range of *Wetzeliella articulata* to be from 54.25 to 36.2 Ma, which is less than the range of 53.2 to 30.4 Ma for *Charlesdowniea* (as *Kisselevia*) *coleothrypta*. However, the sequence of the individual ranges does show a consistency that is close to the present view, with the general order of appearances of the genera being *Apectodinium*, *Wetzeliella* (if one includes species now assigned to *Axioidinium*), *Dracodinium* and *Rhombodinium*. No species of *Wilsonidium* were included in the plots of Williams & Bujak (1985).

| Ma | EPOCH       | AGE          | NP                                     | Bujak & Mudge (1994)                  | Sub Zones               | Powell (1992)              | Partridge in McGowan et al. (2000) | Andreeva-Grigorovich et al. (2011)                       | Iakovleva & Aleksandrova (2013)                |  |
|----|-------------|--------------|--|---------------------------------------|-------------------------|----------------------------|------------------------------------|--|--|--|
| 24 | OLIGOCENE   | L Chattian   | 25                                     |                                       |                         |                            |                                    |  |  |  |
| 26 |             |              | 24                                     |                                       |                         |                            |                                    |  |  |  |
| 27 |             | E Rupelian   | 23                                     |                                       |                         |                            |                                    |  |  |  |
| 28 |             |              | 22                                     |                                       |                         | <i>We. gochtii</i>         |                                    | <i>We. gochtii</i>                                       |  |  |
| 29 |             |              | 21                                     |                                       |                         |                            |                                    | <i>Ph. amoenum</i> / <i>We. symmetrica</i>               |  |  |
| 30 | EOCENE      | L Priabonian | 19                                     |                                       |                         | <i>Rh. perforatum</i>      | <i>Rh. perforatum</i>              | <i>Ch. clathrata angulosa</i> /<br><i>Rh. perforatum</i> | <i>Ch. clathrata</i><br>subsp. <i>angulosa</i> |  |
| 31 |             |              | 20                                     |                                       |                         |                            | <i>Rh. perforatum</i>              |  |  |  |
| 32 |             | M Bartonian  | 17                                     | <i>He. porosa</i> (E-7)               | E7b                     | <i>We. simplex</i>         | <i>Wi. tabulatum</i>               | <i>Rh. porosum</i>                                       |  |  |
| 33 |             |              | 16                                     |                                       | E7a                     | <i>Rh. porosum</i>         |                                    | <i>Rh. draco</i>   |  |  |
| 34 |             |              | 16                                     | <i>Di. colligerum</i> (E-6)           | E6c*                    | <i>Rh. draco</i>           | <i>We. hampdenensis</i>            | <i>We. articulata</i>                                    | <i>Ki. ornata</i>                              |  |
| 35 |             | M Lutetian   | 15                                     | <i>Cl. placacanthum</i> (abund) (E-5) | E6b                     | <i>Gl. intricata</i>       | <i>Wi. lineidentatum</i>           |  | <i>Rh. draco</i>                               |  |
| 36 |             |              |  | <i>Di. ficusoides</i> (E-4)           | E6a                     | <i>Ar. arcuatum</i>        | <i>Wi. echinosuturatum</i>         |  |  |  |
| 37 |             |              | 14                                     |                                       | E5a                     |                            |                                    |  |  |  |
| 38 |             |              | 14                                     | <i>Ea. ursulae</i> (E-3)              | E4d                     | <i>Ph. comatum</i>         |                                    |  |  |  |
| 39 |             |              | 14                                     |                                       | E4c                     |                            |                                    |  |  |  |
| 40 | E Ypresian  | 13           | <i>Ar. medusetiformis</i> (acme) (E-3) | E4b*                                  | <i>Ph. comatum</i>      |                            |                                    |  |  |  |
| 41 |             |              |  | E4a*                                  |                         |                            |                                    |  |  |  |
| 42 |             |              |  | E3d                                   |                         |                            |                                    |  |  |  |
| 43 |             | 12           |  | E3c                                   | <i>Pe. laticinctum</i>  | <i>Ch. edwardsii</i>       |                                    | <i>We. eocaenica</i> ( <i>Dr. pachydermum</i> )          |  |  |
| 44 |             | 12           |  | E3b*                                  |                         | <i>Ch. n.sp.</i>           |                                    | <i>Am. diktyoplokum</i>                                  |  |  |
| 45 |             | 12           |  | E2c                                   |                         | <i>Wi. ornatum</i>         |                                    | <i>Oc. romanum</i> /<br><i>Ch. columna</i> -group        |  |  |
| 46 |             | 12           |  | E2b*                                  | <i>Ch. coleothrypta</i> | <i>Rh. waipawaense</i>     |                                    | <i>Ch. coleothrypta</i>                                  |  |  |
| 47 | PALEOCENE   | L Thanetian  | 11                                     |                                       | E2a*                    | <i>We. spinulosa</i>       | <i>We. spinulosa</i>               | <i>Dr. varielongitudum</i>                               | <i>Dr. varielongitudum</i>                     |  |
| 48 |             |              | 10                                     | <i>Hm. tubiferum</i> (E-1)            | E1b                     | <i>We. meckelfeldensis</i> | <i>Rh. subtilis</i>                | <i>Dr. simile</i>  | <i>Dr. simile</i>                              |  |
| 49 |             | 9            | <i>Ap. augustum</i>                    | E1a                                   | <i>We. astra</i>        | <i>Ap. homomorphum</i>     | <i>Ap. homomorphum</i>             | <i>We. meckelfeldensis</i>                               | <i>Ap. hyperacanthum</i>                       |  |
| 50 |             | 9            |  |                                       | <i>Ap. augustum</i>     | <i>Ap. hyperacanthum</i>   | <i>Ap. hyperacanthum</i>           | <i>Ap. hyperacanthum</i>                                 |  |  |
| 51 | L Selandian | 8            |  |                                       |                         |                            |                                    |  |  |  |
| 52 |             |              | 7                                      |                                       |                         |                            |                                    |  |  |  |
| 53 |             | 6            |  |                                       |                         |                            |                                    |  |  |  |
| 54 |             | 5            |  |                                       |                         |                            |                                    |  |  |  |
| 55 |             | E Danian     | 4                                      |                                       |                         |                            |                                    |  |  |  |
| 56 | 3           |              |  |                                       |                         |                            |                                    |  |  |  |
| 57 | 2           |              |  |                                       |                         |                            |                                    |  |  |  |
| 58 |             |              | 1                                      |                                       |                         |                            |                                    |  |  |  |

Figure 4B. Some Paleogene zonations published from 1994 to 2013 showing use of wetzelielloidean taxa. The generic assignments are as used in the original publication. Generic abbreviations are as follows (with non-wetzelielloidean genera denoted by an asterisk): Am = *Areosphaeridium*\*, Ap = *Apectodinium*, Ar = *Areoligera*\*, Ch = *Charlesdowniea*, Cl = *Cleistosphaeridium*\*, Di = *Diphyes*\*, Dr = *Dracodinium*, Ea = *Eatonicysta*\*, En = *Enneadocysta*\*, Gl = *Glaphyrocysta*\*, He = *Heteraulacacysta*\*, Hm = *Hystriochosphaeridium*\*, Ki = *Kisselevia*, Oc = *Ochetodinium*\*, Pe = *Pentadinium*\*, Ph = *Phthanoperidinium*\*, Rh = *Rhombodinium*, We = *Wetzeliella*, Wi = *Wilsonidium*. The subzones denoted by an asterisk in the Bujak & Mudge (1994) column are based on the following wetzelielloidean species: E2a, *Dracodinium solidum*; E2b, *Dracodinium politum*; E3b, *Charlesdowniea columna*; E4a *Dracodinium pachydermum*; E4b, *Wetzeliella articulata brevicornuta*; E6c, *Rhombodinium rhomboideum*. To determine the present generic assignment of species, please see Appendix 2.

Michoux (1988) provided some critical stratigraphic information in his paper by showing that *Wilsonidium* (now *Castellodinium compactum*, the oldest known wetzelielloidean with a soleiform archeopyle, occurs in the Lutetian nannofossil zone NP 16.

Several papers presenting Paleogene zonations based primarily on wetzelielloidean species have been published by Russian authors. Andreeva-Grigorovich (1991) published an elevenfold zonation for the late Thanetian to early Rupelian of the former USSR, with the

index taxa including species of *Apectodinium*, *Wetzeliella*, *Kisselevia*, *Dracodinium* and *Rhombodinium* (Figure 4a). The general ordering is similar to that in Costa & Downie (1976) but with less control in the Ypresian. Andreeva et al. (2011) provided a slightly modified version of this zonation for the late Thanetian to Rupelian of the Ukraine, but retained the same 11 zones.

Powell (1992; Figure 4b) proposed a formal zonation for the Paleogene of Britain and adjacent areas that was based in large part on wetzelielloideans. Of the 27 zones,

12 were named after species of this group. Powell illustrated some of the wetzelielloidean species that he used as zonal index markers. Where it can be seen, the archeopyle type shown in these illustrations accords with our concepts. The exception, however, is *Wetzeliella articulata*, which Powell did not use as an index species. The specimen he illustrated (Powell 1992, pl. 4.6, fig. 10) has an equiepeliform archeopyle, rather than a soleiform archeopyle. Our redefining of wetzelielloidean taxa according to archeopyle type restricts some stratigraphic ranges in Powell (1992). For example, Powell gives a range for *Wetzeliella articulata* as extending from the early Ypresian into the Rupelian. Although precise ranges for our new configurations of species remain to be refined, the morphology represented by the type of *Wetzeliella articulata* does not extend below the late middle Eocene and is likely restricted to Bartonian through Rupelian strata. Other species also significantly restricted because of the new morphological understanding are *Wetzeliella* (now *Stenodinium*) *meckelfeldensis*, *Charlesdowniea coleothrypta*, *Charlesdowniea* (now *Sophismatia*) *reticulata* and probably *Wetzeliella ovalis*.

Bujak (1994, fig. 1; also Bujak & Mudge 1994, fig. 2; see Figure 4b herein) presented a dinoflagellate cyst zonation for the latest Paleocene and Eocene of the North Sea in which he erected nine zones and 23 sub-zones. The one zone named after a wetzelielloidean was the oldest, the *Apectodinium augustum* Zone. However, he named five subzones after wetzelielloideans. In the accompanying events chart, Bujak also included the LADs of *Dracodinium simile* (frequent occurrence), *Dracodinium* (now *Petalodinium*) *condylos* (consistent), *Dracodinium varielongitudum* (common), *Dracodinium* (now *Rhadinodinium*) *politum* (consistent), *Dracodinium varielongitudum* (consistent), *Dracodinium pachydermum* (now a junior taxonomic synonym of *Axiodinium eoceanicum*) (common), *Rhombodinium* (now *Petalodinium*) *rhomboideum* and *Wetzeliella ovalis*. Since Bujak (1994) did not illustrate any of the wetzelielloidean species, it is not possible to determine archeopyle types.

Williams et al. (1998), using the Paleogene time scale of Berggren et al. (1995), gave two sets of values for dinoflagellate cyst stratigraphic ranges. The first was for northwestern Europe, the second was for the Mediterranean area. These authors recorded 24 species and one subspecies of wetzelielloidean taxa from northwestern Europe, but only 7 species from the Mediterranean area. Most of the species, especially those of *Apectodinium*, appeared earlier in the Mediterranean than in northwestern Europe but this was not always the case. For example, *Rhombodinium porosum* had its Mediterranean FAD at 37.00 Ma whereas its FAD for northwestern Europe was 37.34 Ma. The exclusion of data regarding the stratigraphic range of *Wetzeliella*

*articulata* reflects that Williams et al. (1998) had reservations about its stratigraphic range.

Williams et al. (1999) also gave ages in a similar format to that of Williams et al. (1998), and with the same control. The oldest wetzelielloidean taxa were four species of *Apectodinium*, which had late Thanetian LADs that ranged from 56.42 to 55.86 Ma. The first species of *Wetzeliella*, *Wetzeliella* (now *Sophismatia*) *meckelfeldensis*, had a FAD of 53.94 Ma, marginally older than *Dracodinium waipawaense* and *Charlesdowniea reticulata*, both at 53.82 Ma. Thus within a very short interval of time the three genera, which we would now refer to as *Sophismatia*, *Petalodinium* and *Stenodinium*, had made their first appearances. This means that the equiepeliform (*Sophismatia*) was soon joined by the latiepeliform (*Petalodinium*) and hyperepeliform (*Stenodinium*) archeopyle types. The equiepeliforms had earlier been represented by *Apectodinium* only.

Determining when the soleiform archeopyle first appeared is not easy from the ranges provided by Williams et al. (1999). If *Wetzeliella? spinulosa*, described by Wilson (1988) from the Waiwapan Stage (Early Eocene) of New Zealand, does indeed have a soleiform archeopyle, then its FAD would be within the Ypresian. Otherwise, the FAD of *Rhombodinium draco* is given as 39.39 Ma, which is within the Bartonian. *Wetzeliella articulata* was given an FAD of 49.73 Ma, but this reflects the broad definition of this species as used at that time.

According to Williams et al. (1999), and probably in reality, *Dracodinium* is restricted to the Ypresian. The biggest surprise is the stratigraphic range of *Charlesdowniea*, which according to Williams et al. (1999) is 53.82 Ma (FAD of *Charlesdowniea reticulata*) to 37.34 Ma (LAD of *Charlesdowniea coleothrypta*). We suspect that the younger records are of morphologically similar forms that have soleiform archeopyles. If confirmed, such forms would now be included in *Talladinium*.

Partridge in McGowran et al. (2000; Figure 4b) compared the Paleogene dinoflagellate cyst zonation for the Gippsland Basin, southeastern Australia, with that for New Zealand as proposed by Wilson (1984, 1988) and for Antarctica as proposed by Wrenn & Hart (1988). None of the marker species for the Paleogene of Antarctica are wetzelielloideans. But the similarity between the Gippsland Basin and the New Zealand zonation is striking, especially the series of events that Partridge recognised for the Wetzelielloideae. The events, which include FADs and LADs, cover the late Paleocene to Early Oligocene and highlight the restricted stratigraphic ranges of many of the species.

Further refinements in our understanding of the stratigraphic ranges of wetzelielloidean species were

provided by Williams et al. (2004). Recognizing the variability in FADs and LADs according to paleolatitudes, or more correctly also according to control by paleoceanic currents, these authors gave values for five regions: low latitudes, northern- and southern-hemisphere middle latitudes, and northern- and southern-hemisphere high latitudes. Unfortunately, they listed only 14 wetzelielloidean taxa, including one species of *Apectodinium*, three of *Charlesdownia*, four of *Dracodinium*, three of *Rhombodinium*, two of *Wetzeliella* and one of *Wilsonidium*. The sparse data make it impossible to comment on stratigraphic changes in morphology in the wetzelielloideans.

Recent updates of the stratigraphic ranges of wetzelielloidean species are published in Powell & Brinkhuis (in Gradstein et al. 2004, fig. 20.3 and in Gradstein et al. 2012, fig. 28.9; with identical information in both publications). Gradstein et al. (2004) provided FADs and/or LADs for 18 wetzelielloidean taxa, which included two species of *Apectodinium*, three of *Charlesdownia*, five of *Dracodinium*, four (and one subspecies) of *Wetzeliella* and three of *Rhombodinium*. The data were based on northwestern European sections. With such a relatively low number of taxa, important trends are hard to delineate, but there is a definite clustering of *Dracodinium* species in the Ypresian between 53.6 and 48.7 Ma. Likewise, *Rhombodinium* is recorded from the Bartonian to Rupelian. *Charlesdownia* appears in the Ypresian but, since LADs are not given for two of the three species, the overall range of the genus cannot be determined. *Apectodinium* is restricted to the late Thanetian–Ypresian. The widest range from Ypresian to Chattian is for *Wetzeliella*. This is not surprising considering the present, in our view confused, records in the literature.

Andreeva-Grigorovich et al. (2011; Figure 4b) proposed a slightly modified version of the zonation erected by Andreeva-Grigorovich (1991). The major difference was in the designation of two non-wetzelielloidean taxa as index species.

A significant paper on the Paleogene dinoflagellate cysts of western Siberia is that of Iakovleva & Aleksandrea (2013; Figure 4b), who proposed 15 zones spanning the late Thanetian to the mid Priabonian. Thirteen of the zones are named for wetzelielloidean taxa, and show a logical sequence when the morphology of the species is considered. The oldest, as in some other wetzelielloidean-based zonations, is named after *Apectodinium hyperacanthum*. Sequentially, this is followed by *Apectodinium* (now *Axiodinium*) *augustum*, *Deflandrea oebisfeldensis*, *Wetzeliella* (now *Axiodinium*) *astra*, *Wetzeliella* (now *Stenodinium*) *meckelfeldensis*, *Dracodinium simile*, *Dracodinium varielongitudum*, *Charlesdownia coleothrypta*, *Charlesdownia* (now *Piladinium*) *columna*, *Areosphaeridium diktyoplokum*,

*Dracodinium pachydermum* (now considered a taxonomic junior synonym of *Axiodinium eocaenicum*), *Rhombodiniu draco*, *Rhombodinium porosum*, *Kisselevia ornata* and *Charlesdownia clathrata* subsp. *angulosa* (now *Talladinium angulosum*). The zonal index species reflect the stratigraphic ranges of the wetzelielloidean archeopyle types, with the oldest being the equiepeli-form and hyperepeli-form and the youngest being solei-form. For example all the index species of the uppermost four zones have soleiform archeopyles.

## 7. Phylogeny

The problem of establishing evolutionary relationships among fossil dinoflagellates was expressed, perhaps overly pessimistically, by Evitt (1981). Fensome et al. (1993; see also Medlin & Fensome 2013) nevertheless established a broad, evolutionarily based classification for dinoflagellates, including fossils, that has largely withstood the test of time. Still, trying to establish meaningful phylogenetic relationships both within the Wetzelielloideae and between the subfamily and other groups is challenging. Nevertheless, the difficulty of determining phylogenetic relationships of wetzelielloidean taxa has not deterred some from attempting to do so.

The first attempt to propose a phylogenetic tree for wetzelielloideans was that of Châteauneuf & Gruas Cavagnetto (1978, text-figure 2), who considered the root stock to be *Apectodinium*. From this root stock the authors postulated the evolution of four taxa — *Wetzeliella meckelfeldensis* subsp. *lobisca* (now *Dracodinium lobiscum*), *Dracodinium simile*, *Wetzeliella symmetrica* and *Kisselevia* (now *Sophismatia*) *tenuivirgula*. Châteauneuf & Gruas Cavagnetto's line drawings of these four taxa show equiepeli-form (*Wetzeliella meckelfeldensis* subsp. *lobisca* and *Dracodinium simile*), hyperepeli-form (*Wetzeliella symmetrica*) and latiepeli-form (*Kisselevia tenuivirgula*) archeopyles. That *Wetzeliella symmetrica* would have a hyperepeli-form archeopyle and be restricted to the late Ypresian to Bartonian does not fit with our interpretation, nor with the middle Oligocene age of the holotype of this species — an age later endorsed by Andreeva-Grigorovich (1991), who considered *Wetzeliella symmetrica* to be a marker species for the early Rupelian. Thus, the evolutionary sequence postulated by Châteauneuf & Gruas-Cavagnetto (1978) seems questionable.

Costa & Downie (1979) presented a 'morphogenetic chart' for the wetzelielloideans, in part based upon archeopyle type but also on other morphological features and stratigraphic occurrences. These authors considered *Apectodinium* to have been the ancestral taxon for the group, evolving from the deflandroid peridiniacean *Spinidinium*. Costa &

Downie based this idea on the similarity of the archeopyle and the weakly developed pericoel, features that they deemed common to both genera. However, *Spinidinium* has a hexa 2a plate whereas *Apectodinium* has a quadra 2a plate. Moreover, *Spinidinium* commonly exhibits an adnate operculum that remains posteriorly connected to the rest of the cyst, with the 2a joined along the boundary with the 4" plate. In wetzelielloideans with an attached operculum, the attachment is along the anterior margin of the 2a plate, with the 3' and 2a plates remaining connected. Also, such attachment does not occur in the earliest wetzelielloideans, but is a consistent feature in taxa occurring in younger, Bartonian-Rupelian rocks. Recognition of *Apectodinium* as the wetzelielloidean 'root stock' is understandable if based on its first appearance as early as the Selandian and on its possession of an equiepeliform archeopyle. Costa & Downie (1979) viewed *Apectodinium* as giving rise to *Wetzeliella* (now *Stenodinium*) *meckelfeldensis*, with its hyperepeliform archeopyle, and thence directly or indirectly to most other wetzelielloideans within a short interval during the early Ypresian.

Costa & Downie (1979) had major problems determining the affinities of *Wilsonidium*, which they had correctly determined had a hyperepeliform archeopyle (in our terminology). They concluded that *Wilsonidium* derived from *Alterbidinium* (as *Alterbia*) *pentaradiatum*. Similar caveats apply to this suggestion as to the *Apectodinium*-*Spinidinium* relationship discussed above — indeed *Alterbidinium* could be thought of as a spineless *Spinidinium* with the same tendency to have a posteriorly attached hexa archeopyle/operculum.

Bujak (1979) and Bujak & Davies (1983) also developed significant ideas on wetzelielloidean relationships. Bujak (1979) emphasised the continuity of the quadra archeopyle in the wetzelielloideans, concluding that it is found only in that group and is thus a diagnostic feature. However, he expressed uncertainty over the nature of the intercalary archeopyle in *Apectodinium*.

Bujak & Davies (1983) modified the phylogenetic model of Costa & Downie (1979), primarily by regarding *Alterbidinium?* *pentaradiatum* subsp. *precedum* as the root stock. These authors reasoned that the quadra 2a plate evolved because of the lateral extension of the cingulum in the wetzelielloideans. According to Bujak & Davies (1983), one offshoot from *Alterbidinium?* *pentaradiatum* subsp. *precedum* gave rise to *Wilsonidium*, which they regarded as an evolutionary dead end. Another branch led to *Apectodinium*, the root stock of all other wetzelielloideans.

Evitt (1985, p. 201) commented that 'It seems probable that the ... cingular arrangement [seen in *Proto-peridinium*] occurred throughout the *Wetzeliella*-*Apectodinium* complexes ...'. This would involve only

three cingular plates plus a transitional plate, in contrast to the peridiniacean condition with five or six cingular plates plus a transitional. Evitt gave no direct evidence for this feature and further added '... but there is little likelihood that this will be provable in very many instances.' Despite the speculative nature of Evitt's comments, they have been the basis for the widely held belief that the wetzelielloideans are closely related to modern protoperidinioids and thus, by extension, heterotrophic. In contrast, we view the wetzelielloids as not being closely related to the protoperidinioids. Scanning electron micrographs presented herein (Plate 5, figs. 4 and 11) suggest at least one and probably two breaks in the cingular plate series on the dorsal surface. Protoperidinioids have only three cingular plates (Fensome et al. 1993), with no sutures on the dorsal surface. The evidence presented here indicates that wetzelielloids have at least four, and possibly five, cingular plates plus a small transitional plate on the ventral surface. The only significant differences between wetzelielloid and deflandroid/palaeoperidinioid tabulation are the quadra versus hexa 2a plate and associated differences in adjacent plates (Figure 1). This, together with the stability and consistent symmetry of the epicystal tabulation, tentatively allies the wetzelielloids with the deflandroids and palaeoperidinioids. As the wetzelielloidean archeopyle invariably involves only the 2a plate, its affinity may lie closer to the deflandroids. But this is speculative, and the origin of the wetzelielloids among peridiniaceans remains unclear.

That wetzelielloideans are probably not related to protoperidiniaceans also accords with their usual lack of brown pigmentation of the cyst wall, the latter being a feature of protoperidiniacean cysts and suggestive of a heterotrophic habit (Mudie 1992). In extensive studies of Paleogene deep-sea material, one of us (SPD) has rarely encountered wetzelielloids in samples; the reverse would be expected if wetzelielloids were heterotrophic. This sparsity of wetzelielloideans in deeper water deposits accords with the findings of Downie et al. (1971), who recognised a *Wetzeliella* association in the London Clay of southeastern England and postulated that it denoted estuarine conditions. Thus, there seems substantive evidence that the wetzelielloids preferred shallow-water environments and hence were probably autotrophic rather than heterotrophic.

Modern ideas emphasise evolution's bush-like rather than tree-like nature, and so it follows that the wetzelielloidean fossil record represents isolated branches. In this context, it is perhaps not advisable to try to connect or place individual species on the overall bush. However, evolution did occur and morphologies did change over time in ways that we can recognise — the trick is to pick out which morphological features are telling the most meaningful evolutionary story.

Building on the work of Evitt (1985), Fensome et al. (1993) concluded that for dinoflagellates as a whole (and especially for fossil forms), changing tabulation was the feature that revealed the most meaningful evolutionary story. Features such as surface ornamentation, horn and process morphology and cavation had their place in defining taxa at lower ranks, but for determining taxa at higher rank and understanding evolutionary trends, tabulation was key.

In the peridiniaceans, the stability of the tabulation makes recognition of evolutionary trends difficult. But if we can relate even subtle changes in, say, archeopyle shape, that reflect changes in tabulation, we may be able to develop a workable model. Our focus on archeopyle types in the wetzelielloideans gives us a window into changes in the tabulation of this subfamily. In contrast, variations in horn length and periplasm ornamentation probably reflect environmental controls rather than broader phylogenetic patterns, as has been suggested for other groups of dinoflagellate cysts (e.g. Monteil 1991). By utilising changing archeopyle form, we can discern the broader evolutionary story.

As *Apectodinium*, the earliest known wetzelielloidean, has an equiepiliform archeopyle type, it seems logical to propose that this type reflects the ‘root stock’ of the subfamily, developing in the Selandian (Figure 5). Accepting this, the other archeopyle types evolved very rapidly, since taxa with hyperepiliform, latiepiliform and hypersoleiliform types are known from the Ypresian, when ‘experimentation’ in the group was obviously rife. Such experimentation followed by stabilisation has occurred in archeopyle development in other peridiniaceans; an example can be found among fossil deflandroids and palaeoperidinioids (taken collectively), which show a variety of combinations of archeopyle types in the Middle to Late Cretaceous (for example, *Chichaouadinium* and *Luxadinium*); in contrast most Cenozoic members of these two subfamilies have a simple one-plate anterior intercalary archeopyle.

The latiepiliform archeopyle, which characterises *Dracodinium*, like the hyperepiliform type, is stratigraphically restricted to the Ypresian and Lutetian. Forms with the soleiliform archeopyle appear in the late Lutetian. Hyperepiliform types do not fit into the evolutionary pattern if Wilson (1967) is right in considering *Wilsonidium tabulatum* to be late Eocene. C. Clowes (pers. comm., 2014) considers this species to be no younger than middle Bartonian, which – although still later than expected – would not be so anomalous. Latiepiliform types seem not to have survived into the Middle Eocene, though hypersoleiliforms did, and perhaps gave rise to the earliest soleiliform types in the Lutetian (see Michoux 1988). However, taxa with this archeopyle type are rare until the Bartonian, when

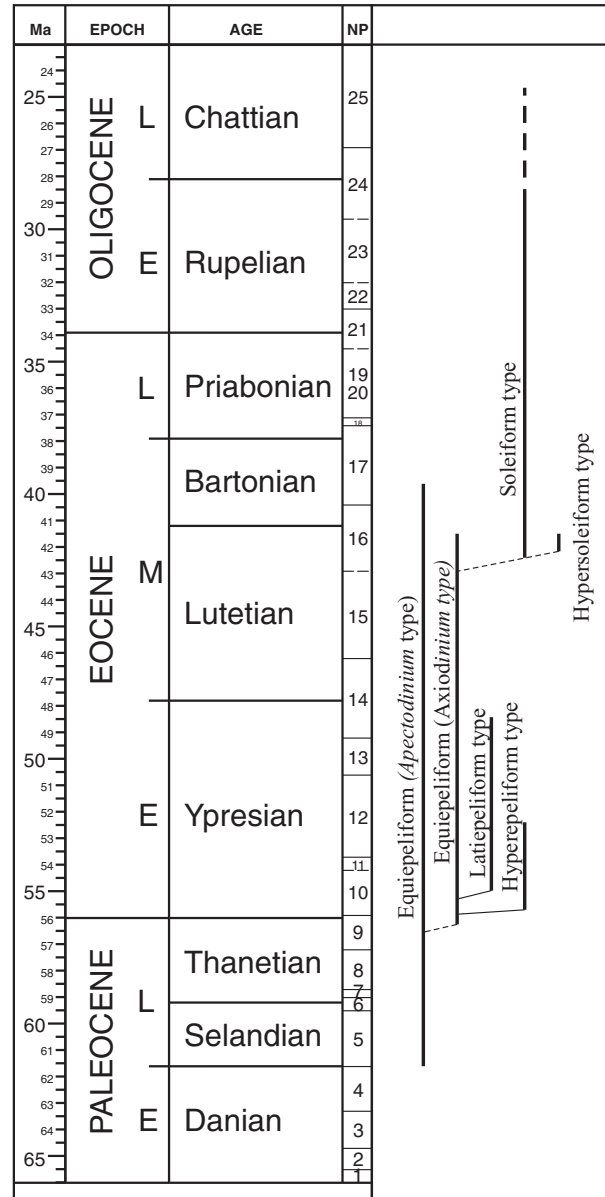


Figure 5. Postulated stratigraphic ranges of the wetzelielloidean archeopyle types defined in this paper.

they come to dominate wetzelielloidean assemblages. At the same time, there is a rapid decline in those taxa with equiepiliform archeopyles, which disappear in the Bartonian. Thus, by the Priabonian and Rupelian, taxa with soleiliform archeopyles don't simply dominate assemblages – they are the only wetzelielloideans present. There is much uncertainty over the occurrence of wetzelielloideans in the Chattian but, if present, we would expect them to have soleiliform archeopyles.

Why the hypersoleiliform and soleiliform archeopyle types have opercula that remain attached anteriorly is a mystery. In peridiniaceans, this anterior attachment

is found only in the wetzelielloideans, so perhaps it has some relationship to the distinctive quadra tabulation. Why the soleiform archeopyle type became dominant is also puzzling; perhaps it somehow offered better protection before and during the initial stages of encystment. Another mystery is the identity of the non-wetzelielloidean group that the subfamily evolved from. They are so similar to other fossil peridiniaceans, yet so distinctive in the morphology of their 2a plate, that at present, any ideas would be pure speculation.

Archeopyle type shows a significant relationship to apical horn length. As would be expected, the hyperepeliform and hypersoleiform archeopyles occur only in taxa with long apical horns, whereas in forms with the latiepeliform archeopyle, the apical horn is reduced. In equiepeliform and soleiform types, the apical horns can vary from short to long. The lengths of other horns vary considerably in all five archeopyle types, suggesting that, as observed in the *Phoberocysta-Muderongia* group (Monteil 1991), general horn length may be related to environmental parameters. Also, as shown by Iakovleva & Heilmann-Clausen (2007), the left antapical horn can be reduced, with the right antapical horn being the longer. Their observations highlight some of the drawbacks in using relative horn length for generic and specific separation.

Pericyst-endocyst relationships also tend to change with time, with circumcavation largely disappearing in the Bartonian–Priabonian. Endophragm thickness decreased, so that Bartonian–Rupelian taxa almost invariably have a thin endophragm.

## 8. Conclusions

The peridiniacean subfamily Wetzelielloideae shows considerable morphological variability, particularly in horn development and ornamentation. The impressive array of wetzelielloidean forms has tended to deflect attention from the more phylogenetically important but less striking morphology of the archeopyle, and this has led to problems with the taxonomy and consequent biostratigraphic utility of the group. Following Fensome et al. (1993), we believe that the overriding criterion for generic assignment must be tabulation. Within the wetzelielloidean complex, the general tabulation is strikingly consistent, a tendency for tabulation stability echoed among fossil peridiniaceans as a whole but in contrast to modern peridiniaceans (and fossil and modern protoperidiniaceans).

Members of the Wetzelielloideae are unique in possessing a second intercalary (2a) plate that is four-sided (quadra), in contrast to the six- (or, rarely, five-) sided 2a plate of other fossil peridiniaceans. Unlike many peridiniaceans, only the 2a plate in the wetzelielloideans is involved in archeopyle formation. However, this plate shows variation in shape and relative dimensions in the peri- and endoarcheopyle, either of which may have a detached or an attached operculum. We have used these variations in the archeopyle as the primary morphological features in defining or redefining genera in the Wetzelielloideae, leading us to a proposed new classification (Figure 3). Based on this concept, we suggest possible relationships of wetzelielloidean genera in the form of a cladogram (Figure 6).

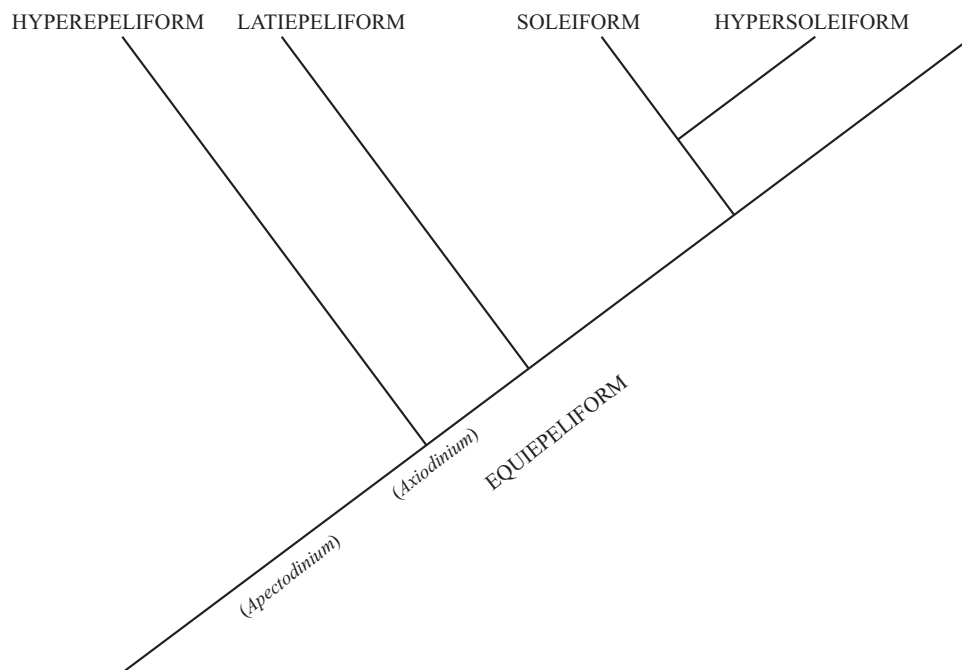


Figure 6. Cladogram depicting possible relationships of the five wetzelielloidean archeopyle types.

We recognise six genera with an equiepiliform archeopyle, five with a soleiform archeopyle, four with a hyperepiliform archeopyle, five with a latiepiliform archeopyle and one with a hypersoleiform archeopyle. As our understanding of the wetzelielloideans increases, more new genera may fill the morphological gaps that currently exist.

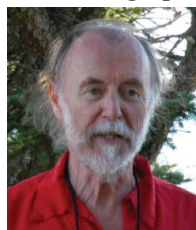
We have used ornamentation type and distribution as secondary features for differentiation at the generic level. Our proposed scheme with regard to ornamentation in part reflects prior definitions of existing genera. *Wetzeliella* is characterised by processes that are distally free, whereas *Rhombodinium* has ornamentation of low relief and *Charlesdowniea* has an ectophragm. Forms like *Wilsonidium* but with a soleiform archeopyle are included in the new genus *Castellodinium*. When such variations in ornamentation are related to archeopyle type, and the genera redefined accordingly, it provides a more realistic view of the evolution of the group emerges and, hence, more meaningful and useful stratigraphic ranges.

Our proposed classification is, in itself, an evolution of previous ideas. Without the pioneering studies of Costa & Downie (1976, 1979), Bujak (1979) and Michoux (1988), we would have struggled to make sense of the wetzelielloideans. We still have much to learn, but we believe that application of the ideas expressed herein will point the way forward. We have told the 'hole' story as we presently understand it. Let us hope that we can build on this story and thereby provide greater insight into the stratigraphic and palaeoenvironmental utilisation of the wetzelielloideans in the Paleogene.

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### Author biographies



GRAHAM WILLIAMS's main field of interest is Mesozoic-Cenozoic palynostratigraphy of offshore eastern Canada, including arctic areas. His interest in dinoflagellates 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 Bedford Institute of Oceanography in Nova Scotia, where he has the good fortune to work with some outstanding colleagues.



In a previous existence, SARAH PIERCE Damassa was a Palaeogene dinoflagellate specialist, having studied with Bill Evitt, Al Loeblich and Helen Loeblich. She then worked as a consulting palynologist for around fifteen years. A career change then led her to Lexington, Massachusetts, where she has taught Environmental Earth Science to ninth-grade students for twenty years. She has also coached the school's National Ocean Science Bowl team for the last twelve years. Thanks to her co-authors, she has managed to retain a tenuous toehold in the world of fossil dinoflagellates, and has thoroughly enjoyed working with them on the *Wetzeliella* paper.



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



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**Appendix 1. Assignment of species in Fensome & Williams (2004) compared to assignment in the present paper. \* = type.**

| Fensome & Williams (2004)  | This paper          |
|----------------------------|---------------------|
| <b><i>Apectodinium</i></b> |                     |
| <i>augustum</i>            | <i>Axiodinium</i>   |
| <i>capitulatum</i>         | <i>Apectodinium</i> |
| <i>cornufruticosum</i>     | <i>Apectodinium</i> |
| <i>geometricum</i>         | <i>Apectodinium</i> |
| * <i>homomorphum</i>       | <i>Apectodinium</i> |
| <i>hyperacanthum</i>       | <i>Apectodinium</i> |
| <i>longispinosum</i>       | <i>Apectodinium</i> |
| <i>paniculatum</i>         | <i>Apectodinium</i> |
| <i>paradoxum</i>           | <i>Apectodinium</i> |

(continued)

| Fensome & Williams (2004)   | This paper                       |
|-----------------------------|----------------------------------|
| <i>parvum</i>               | <i>Apectodinium</i>              |
| <i>quinguelatum</i>         | <i>Apectodinium</i>              |
| <i>raritubiformium</i>      | <i>Apectodinium</i>              |
| <i>summissum</i>            | <i>Apectodinium</i>              |
| <i>williereae?</i>          | <i>Apectodinium?</i>             |
| <b><i>Charlesdownia</i></b> |                                  |
| <i>aculeata</i>             | <i>Michouxdinium</i>             |
| <i>clathrata</i>            | <i>Talladinium?</i>              |
| subsp. <i>angulosa</i>      | <i>Talladinium? angulosum</i>    |
| subsp. <i>clathrata</i>     | (now redundant)                  |
| * <i>coleothrypta</i>       | <i>Charlesdownia</i>             |
| subsp. <i>coleothrypta</i>  | (now redundant)                  |
| subsp. <i>rotundata</i>     | <i>Charlesdownia? rotundata</i>  |
| <i>columnna</i>             | <i>Piladinium</i>                |
| <i>crassiramosa</i>         | <i>Sophismatia</i>               |
| <i>edwardsii</i>            | <i>Piladinium</i>                |
| <i>fasciata</i>             | <i>Charlesdownia?</i>            |
| <i>fusiformis</i>           | <i>Talladinium</i>               |
| <i>limitata</i>             | <i>Michouxdinium</i>             |
| <i>marginata</i>            | <i>Talladinium?</i>              |
| <i>pengchiahsuensis</i>     | <i>Charlesdownia?</i>            |
| <i>proserpina</i>           | <i>Michouxdinium</i>             |
| <i>reticulata</i>           | <i>Sophismatia</i>               |
| <i>rhomboidalis</i>         | <i>Michouxdinium?</i>            |
| <i>stellata</i>             | <i>Valloadinium</i>              |
| <i>taiwaniana</i>           | <i>Charlesdownia?</i>            |
| <i>tenuivirgula</i>         | <i>Sophismatia</i>               |
| subsp. <i>conopia</i>       | <i>Sophismatia conopia</i>       |
| subsp. <i>exouros</i>       | <i>Sophismatia? exouros</i>      |
| subsp. <i>tenuivirgula</i>  | (now redundant)                  |
| <i>variabilis</i>           | <i>Michouxdinium</i>             |
| <i>wulagenensis</i>         | <i>Talladinium</i>               |
| <b><i>Dracodinium</i></b>   |                                  |
| <i>condylos?</i>            | <i>Petalodinium</i>              |
| <i>granulatum</i>           | <i>Epelidinium?</i>              |
| <i>laszczynskii</i>         | <i>Petalodinium</i>              |
| <i>politum</i>              | <i>Rhadinodinium</i>             |
| subsp. <i>politum</i>       | (now redundant)                  |
| subsp. <i>spinula</i>       | <i>Petalodinium spinula</i>      |
| <i>rhomboideum</i>          | <i>Petalodinium</i>              |
| subsp. <i>ovale</i>         | <i>Petalodinium rhomboideum?</i> |
|                             | subsp. <i>ovale</i>              |
| subsp. <i>rhomboideum</i>   | <i>Petalodinium rhomboideum</i>  |
|                             | subsp. <i>rhomboideum</i>        |
| <i>simile</i>               | <i>Dracodinium</i>               |
| * <i>solidum</i>            | <i>Dracodinium</i>               |
| <i>variabile</i>            | <i>Rhombodinium</i>              |
| <i>varielongitudum</i>      | <i>Dracodinium</i>               |
| <i>waipawaense</i>          | <i>Petalodinium</i>              |
| <b><i>Kisselevia</i></b>    |                                  |
| <i>insolens?</i>            | <i>Sophismatia?</i>              |
| <i>major</i>                | <i>Rhombodinium?</i>             |
|                             | <i>vozzhennikovae</i>            |
| * <i>ornata</i>             | <i>Rhombodinium</i>              |

(continued)

| Fensome & Williams (2004)           | This paper   | Fensome & Williams (2004)   | This paper   |
|-------------------------------------|--|-----------------------------|--|
| <b>Rhombodinium</b>                 |  | <i>degenerata</i>           | <i>Axiodinium</i>  |
| <i>cerciatum</i>                    | <i>Rhombodinium</i>                                      | <i>distalis</i>             | <i>Wetziella</i>   |
| <i>denticulatum</i>                 | <i>Rhombodinium</i>                                      | <i>elongata</i>             | <i>Wetziella</i>   |
| * <i>draco</i>                      | <i>Rhombodinium</i>                                      | <i>eocaenica</i>            | <i>Dracodinium</i>                                       |
| subsp. <i>draco</i>                 | <i>Rhombodinium draco</i> subsp.<br><i>draco</i>         | <i>flexibilis</i>           | <i>Wetziella?</i>  |
| subsp. <i>quadratum</i>             | <i>Rhombodinium draco</i> subsp.<br><i>quadratum</i>     | <i>forniculis</i>           | <i>Rhombodinium?</i>                                     |
| <i>elegans</i>                      | <i>Rhombodinium</i>                                      | <i>gochtii</i>              | <i>Wetziella</i>   |
| <i>elongatum</i>                    | <i>Rhombodinium</i>                                      | <i>hampdenensis</i>         | <i>Wetziella?</i>  |
| subsp. <i>elongatum</i>             | <i>Rhombodinium elongatum</i><br>subsp. <i>elongatum</i> | <i>irtyschensis</i>         | <i>Rhombodinium</i>                                      |
| subsp. <i>spinale</i>               | <i>Rhombodinium elongatum</i><br>subsp. <i>spinale</i>   | <i>lobisca</i>              | <i>Dracodinium</i>                                       |
| <i>freienwaldense</i>               | <i>Rhombodinium?</i>                                     | <i>lunaris</i>              | <i>Axiodinium</i>  |
| <i>glabrum?</i>                     | <i>Rhadinodinium</i>                                     | <i>meckelfeldensis</i>      | <i>Stenodinium</i>                                       |
| subsp. <i>crassithecum</i>          | <i>Petalodinium crassithecum</i>                         | <i>ovalis</i>               | <i>Wetziella</i>   |
| subsp. <i>glabrum</i>               | (now redundant)  | subsp. <i>ovalis</i>        | <i>Wetziella ovalis</i> subsp.<br><i>ovalis</i>          |
| <i>kunlunense</i>                   | <i>Rhombodinium?</i>                                     | subsp. <i>rotundata</i>     | <i>Wetziella ovalis</i> subsp.<br><i>rotundata</i>       |
| <i>longimanum</i>                   | <i>Rhombodinium?</i>                                     | <i>pachyderma</i>           | <i>Dracodinium</i> (as junior<br>synonym)                |
| <i>majus?</i>                       | <i>Rhombodinium?</i>                                     | <i>robosta</i>              | <i>Wetziella?</i>  |
| <i>minus</i>                        | <i>Rhombodinium?</i>                                     | <i>samlandica</i>           | <i>Dracodinium</i>                                       |
| <i>mirabile</i>                     | <i>Rhombodinium</i>                                      | <i>simplex</i>              | <i>Wetziella</i>   |
| <i>oravense</i>                     | <i>Rhombodinium?</i>                                     | <i>spinula</i>              | <i>Rhombodinium</i>                                      |
| <i>pentoganum?</i>                  | <i>Rhombodinium</i>                                      | <i>spinulosa</i>            | <i>Wetziella?</i>  |
| <i>perforatum</i>                   | <i>Rhombodinium</i>                                      | <i>symmetrica</i>           | <i>Wetziella</i>   |
| <i>porosum</i>                      | <i>Rhombodinium</i>                                      | subsp. <i>incisa</i>        | <i>Wetziella symmetrica</i><br>subsp. <i>incisa</i>      |
| <i>pustulosum</i>                   | <i>Rhombodinium?</i>                                     | var. <i>scabrata</i>        | <i>Wetziella symmetrica?</i><br>subsp. <i>scabrata</i>   |
| <i>rotundatum</i>                   | <i>Rhombodinium?</i>                                     | var. <i>taiwaniana</i>      | <i>Wetziella symmetrica?</i><br>subsp. <i>taiwaniana</i> |
| <i>rugosum</i>                      | <i>Petalodinium</i>                                      | <i>tianshanensis</i>        | <i>Wetziella?</i>  |
| <i>sinense</i>                      | <i>Rhombodinium</i>                                      | <i>triangulata</i>          | <i>Epelidinium</i>                                       |
| <i>translucidum</i>                 | <i>Epelidinium?</i>                                      | <i>uncinata</i>             | <i>Dolichodinium</i>                                     |
| <i>tuberculatum</i>                 | <i>Rhombodinium</i>                                      | <i>unicaudalis</i>          | <i>Dolichodinium?</i>                                    |
| <i>vialovii</i>                     | <i>Rhombodinium</i>                                      | <i>wetzelii</i>             | <i>Dracodinium</i>                                       |
| <i>wuqiense</i>                     | <i>Rhombodinium</i>                                      | <i>xinjiangensis</i>        | <i>Wetziella</i>   |
| <b>Wetziella</b>                    |  | <b>Wilsonidium</b>          |  |
| <i>abortiva</i>                     | <i>Axiodinium</i>  | <i>compactum</i>            | <i>Castellodinium</i>                                    |
| <i>africaensis</i>                  | <i>Apectodinium</i>                                      | <i>echinosuturatum</i>      | <i>Vallodinium?</i>                                      |
| * <i>articulata</i>                 | <i>Wetziella</i>   | <i>intermedium</i>          | <i>Castellodinium?</i>                                   |
| subsp. <i>brevicornuta</i>          | <i>Dracodinium? brevicornutum</i>                        | <i>lineidentatum</i>        | <i>Stichodinium?</i>                                     |
| subsp. <i>magnifica</i>             | <i>Dracodinium magnificum</i>                            | subsp. <i>conspicuum</i>    | <i>Wilsonidium conspicuum</i>                            |
| var. <i>scabrata</i>                | <i>Wetziella articulata?</i><br>subsp. <i>scabrata</i>   | subsp. <i>lineidentatum</i> | Now redundant  |
| var. <i>taiwaniana</i>              | <i>Wetziella articulata?</i><br>subsp. <i>taiwaniana</i> | <i>nigeriaense</i>          | <i>Vallodinium</i>                                       |
| <i>astra</i>                        | <i>Dracodinium</i>                                       | <i>ornatum</i>              | <i>Wilsonidium</i>                                       |
| <i>astroides</i>                    | <i>Wetziella?</i>  | <i>rugosum?</i>             | <i>Spinidinium</i>                                       |
| <i>crassa</i>                       | <i>Wetziella?</i>  | <i>subtile</i>              | <i>Stichodinium</i>                                      |
| <i>coronata</i> (as junior synonym) | <i>Dracodinium</i>                                       | * <i>tabulatum</i>          | <i>Wilsonidium</i>                                       |
| <i>crispa</i>                       | <i>Dracodinium</i>                                       | <i>tesselatum</i>           | <i>Axiodinium?</i>                                       |
|                                     |  | <i>tuberosuturatum</i>      | <i>Castellodinium?</i>                                   |

(continued)

**Appendix 2. Assignment of species in the present paper compared to assignment in Fensome & Williams (2004).**

\* = type.

| This paper                                | Fensome & Williams (2004)                                    |
|---|--|
| <b>Apectodinium</b>                       |  |
| <i>africaense</i>                         | <i>Wetzelia</i>  |
| <i>capitulatum</i>                        | <i>Apectodinium</i>  |
| <i>cornufruticosum</i>                    | <i>Apectodinium</i>  |
| <i>geometricum</i>                        | <i>Apectodinium</i>  |
| * <i>homomorphum</i>                      | <i>Apectodinium</i>  |
| <i>hyperacanthum</i>                      | <i>Apectodinium</i>  |
| <i>longispinosum</i>                      | <i>Apectodinium</i>  |
| <i>paniculatum</i>                        | <i>Apectodinium</i>  |
| <i>paradoxum</i>                          | <i>Apectodinium</i>  |
| <i>parvum</i>                             | <i>Apectodinium</i>  |
| <i>quinquelatum</i>                       | <i>Apectodinium</i>  |
| <i>raritubiformium</i>                    | <i>Apectodinium</i>  |
| <i>summissum</i>                          | <i>Apectodinium</i>  |
| <i>williereae?</i>                        | <i>Apectodinium?</i>   |
| <b>Axioidinium</b>                        |  |
| <i>abortivum</i>                          | <i>Wetzelia</i>  |
| <i>augustum</i>                           | <i>Apectodinium</i>  |
| <i>degeneratum</i>                        | <i>Wetzelia</i>  |
| <i>lunare</i>                             | <i>Wetzelia</i>  |
| <i>prearticulatum</i>                     | (not applicable)   |
| <i>tesselatum?</i>                        | <i>Wilsonidium</i>   |
| <b>Castellodinium</b>                     |  |
| * <i>compactum</i>                        | <i>Wilsonidium</i>   |
| <i>intermedium?</i>                       | <i>Wilsonidium</i>   |
| <i>tuberosuturatum?</i>                   | <i>Wilsonidium</i>   |
| <b>Charlesdownia</b>                      |  |
| * <i>coleothrypta</i>                     | <i>Charlesdownia</i>   |
| <i>fasciata?</i>                          | <i>Charlesdownia</i>   |
| <i>pengchiahsuensis?</i>                  | <i>Charlesdownia</i>   |
| <i>rotundata?</i>                         | <i>Charlesdownia coleothrypta</i><br>subsp. <i>rotundata</i> |
| <i>taiwaniana?</i>                        | <i>Charlesdownia</i>   |
| <b>Dolichodinium</b>                      |  |
| * <i>uncinatum</i>                        | <i>Wetzelia</i>  |
| <i>unicaudale?</i>                        | <i>Wetzelia</i>  |
| <b>Dracodinium</b>                        |  |
| <i>astra</i>                              | <i>Wetzelia</i>  |
| <i>brevicornutum?</i>                     | <i>Wetzelia articulata</i> subsp.<br><i>brevicornuta</i>     |
| <i>coronatum</i>                          | <i>Wetzelia</i> (as junior synonym)                          |
| <i>crispum</i>                            | <i>Wetzelia</i>  |
| <i>eocaenicum</i>                         | <i>Wetzelia</i>  |
| <i>lobiscum</i>                           | <i>Wetzelia</i>  |
| <i>magnificum</i>                         | <i>Wetzelia articulata</i> subsp.<br><i>magnifica</i>        |
| <i>pachydermum</i> (as junior<br>synonym) | <i>Wetzelia</i> (as junior synonym)                          |
| <i>samladicum</i>                         | <i>Wetzelia</i>  |
| <i>simile</i>                             | <i>Dracodinium</i>   |
| * <i>solidum</i>                          | <i>Dracodinium</i>   |

(continued)

| This paper                | Fensome & Williams (2004)                                   |
|---------------------------|---|
| <i>varielongitudum</i>    | <i>Dracodinium</i>  |
| <i>wetzelii</i>           | <i>Wetzelia</i>   |
| <b>Epelidinium</b>        |   |
| <i>granulatum?</i>        | <i>Dracodinium</i>  |
| * <i>pechoricum</i>       | (not applicable)  |
| <i>translucidum?</i>      | <i>Rhombodinium</i>   |
| <i>triangulatum</i>       | <i>Wetzelia</i>   |
| <b>Kledodinium</b>        |   |
| * <i>filosum</i>          | (not applicable)  |
| <b>Michouxdinium</b>      |   |
| * <i>aculeatum</i>        | <i>Charlesdownia</i>  |
| <i>limitatum</i>          | <i>Charlesdownia</i>  |
| <i>proserpina</i>         | <i>Charlesdownia</i>  |
| <i>romboidale?</i>        | <i>Charlesdownia</i>  |
| <i>variabile</i>          | <i>Charlesdownia</i>  |
| <b>Petalodinium</b>       |   |
| * <i>condylos</i>         | <i>Dracodinium?</i>   |
| <i>crassithecum</i>       | <i>Rhombodinium glabrum</i> subsp.<br><i>crassithecum</i>   |
| <i>laszczynskii</i>       | <i>Dracodinium</i>  |
| <i>rhomboideum</i>        | <i>Dracodinium</i>  |
| subsp. <i>ovale</i>       | <i>Dracodinium rhomboideum</i><br>subsp. <i>ovale</i>       |
| subsp. <i>rhomboideum</i> | <i>Dracodinium rhomboideum</i><br>subsp. <i>rhomboideum</i> |
| <i>rugosum</i>            | <i>Rhombodinium</i>   |
| <i>sheppeyense</i>        | (not applicable)  |
| <i>spinula</i>            | <i>Dracodinium politum</i> subsp.<br><i>spinula</i>         |
| <i>waipawaense</i>        | <i>Dracodinium</i>  |
| <b>Piladinium</b>         |   |
| <i>columna</i>            | <i>Charlesdownia</i>  |
| <i>edwardsii</i>          | <i>Charlesdownia</i>  |
| <b>Rhadinodinium</b>      |   |
| <i>glabrum</i>            | <i>Rhombodinium?</i>  |
| * <i>politum</i>          | <i>Dracodinium</i>  |
| <b>Rhombodinium</b>       |   |
| <i>cerciatum</i>          | <i>Rhombodinium</i>   |
| <i>denticulatum</i>       | <i>Rhombodinium</i>   |
| * <i>draco</i>            | <i>Rhombodinium</i>   |
| subsp. <i>draco</i>       | <i>Rhombodinium draco</i> subsp.<br><i>draco</i>            |
| subsp. <i>quadratum</i>   | <i>Rhombodinium draco</i> subsp.<br><i>quadratum</i>        |
| <i>elegans</i>            | <i>Rhombodinium</i>   |
| <i>elongatum</i>          | <i>Rhombodinium</i>   |
| subsp. <i>elongatum</i>   | <i>Rhombodinium elongatum</i><br>subsp. <i>elongatum</i>    |
| subsp. <i>spinale</i>     | <i>Rhombodinium elongatum</i><br>subsp. <i>spinale</i>      |
| <i>fornicale?</i>         | <i>Wetzelia</i>   |
| <i>freienwaldense?</i>    | <i>Rhombodinium</i>   |
| <i>irtyschense</i>        | <i>Wetzelia</i>   |
| <i>kunlunense?</i>        | <i>Rhombodinium</i>   |
| <i>longimanum?</i>        | <i>Rhombodinium</i>   |

(continued)

| This paper               | Fensome & Williams (2004)                                   |
|--------------------------|---|
| <i>majus?</i>            | <i>Rhombodinium?</i>  |
| <i>minus?</i>            | <i>Rhombodinium</i>   |
| <i>mirabile</i>          | <i>Rhombodinium</i>   |
| <i>oravense?</i>         | <i>Rhombodinium</i>   |
| <i>ornatum</i>           | <i>Kisselevia</i>   |
| <i>pentagonum</i>        | <i>Rhombodinium?</i>  |
| <i>perforatum</i>        | <i>Rhombodinium</i>   |
| <i>porosum</i>           | <i>Rhombodinium</i>   |
| <i>pustulosum?</i>       | <i>Rhombodinium</i>   |
| <i>rotundatum?</i>       | <i>Rhombodinium</i>   |
| <i>sinense</i>           | <i>Rhombodinium</i>   |
| <i>spinula</i>           | <i>Wetziella</i>  |
| <i>tuberculatum</i>      | <i>Rhombodinium</i>   |
| <i>variabile</i>         | <i>Dracodinium</i>  |
| <i>vialovii</i>          | <i>Rhombodinium</i>   |
| <i>vozhennikovae?</i>    | <i>Kisselevia major</i>                                     |
| <i>wuqaiense</i>         | <i>Rhombodinium</i>   |
| <b>Sagenodinium</b>      |   |
| <i>*franciscanum</i>     | (not applicable)  |
| <b>Sophismatia</b>       |   |
| <i>conopia</i>           | <i>Charlesdowniea tenuivirgula</i><br>subsp. <i>conopia</i> |
| <i>crassiramosa</i>      | <i>Charlesdowniea</i>                                       |
| <i>exouros?</i>          | <i>Charlesdowniea tenuivirgula</i><br>subsp. <i>exouros</i> |
| <i>insolens?</i>         | <i>Kisselevia?</i>  |
| <i>reticulata</i>        | <i>Charlesdowniea</i>                                       |
| <i>*tenuivirgula</i>     | <i>Charlesdowniea</i>                                       |
| <b>Spinidinium</b>       |   |
| <i>rugosum</i>           | <i>Wilsonidium?</i>   |
| <b>Stenodinium</b>       |   |
| <i>*meckelfeldense</i>   | <i>Wetziella</i>  |
| <b>Stichodinium.</b>     |   |
| <i>lineidentatum?</i>    | <i>Wilsonidium</i>  |
| <i>*subtile</i>          | <i>Wilsonidium</i>  |
| <b>Talladinium</b>       |   |
| <i>angulosum?</i>        | <i>Charlesdowniea clathrata</i><br>subsp. <i>angulosa</i>   |
| <i>clathratum?</i>       | <i>Charlesdowniea</i>                                       |
| <i>fusiforme</i>         | <i>Charlesdowniea</i>                                       |
| <i>marginatum?</i>       | <i>Charlesdowniea</i>                                       |
| <i>*wulagenense</i>      | <i>Charlesdowniea</i>                                       |
| <b>Valloodium</b>        |   |
| <i>echinosuturatum?</i>  | <i>Wilsonidium?</i>   |
| <i>*nigeriaense</i>      | <i>Wilsonidium</i>  |
| <i>stellatum</i>         | <i>Charlesdowniea</i>                                       |
| <b>Wetziella</b>         |   |
| <i>*articulata</i>       | <i>Wetziella</i>  |
| subsp. <i>scabrata</i>   | <i>Wetziella articulata</i> var. <i>scabrata</i>            |
| subsp. <i>taiwaniana</i> | <i>Wetziella articulata</i> var. <i>taiwaniana</i>          |
| <i>astroides?</i>        | <i>Wetziella</i>  |
| <i>crassa?</i>           | <i>Wetziella</i>  |
| <i>distalis</i>          | <i>Wetziella</i>  |

(continued)

| This paper                | Fensome & Williams (2004)                                    |
|---------------------------|--|
| <i>elongata</i>           | <i>Wetziella</i>   |
| <i>flexibilis?</i>        | <i>Wetziella</i>   |
| <i>gochtii</i>            | <i>Wetziella</i>   |
| <i>hampdenensis?</i>      | <i>Wetziella</i>   |
| <i>ovalis</i>             | <i>Wetziella</i>   |
| subsp. <i>ovalis</i>      | <i>Wetziella ovalis</i> subsp. <i>ovalis</i>                 |
| subsp. <i>rotundata</i>   | <i>Wetziella ovalis</i> subsp. <i>rotundata</i>              |
| <i>robosta?</i>           | <i>Wetziella</i>   |
| <i>simplex</i>            | <i>Wetziella</i>   |
| <i>spinulosa?</i>         | <i>Wetziella</i>   |
| <i>symmetrica</i>         | <i>Wetziella</i>   |
| subsp. <i>incisa</i>      | <i>Wetziella symmetrica</i> subsp. <i>incisa</i>             |
| subsp. <i>scabrata?</i>   | <i>Wetziella symmetrica</i> var. <i>scabrata</i>             |
| subsp. <i>taiwaniana?</i> | <i>Wetziella symmetrica</i> var. <i>taiwanaense</i>          |
| <i>tianshanensis?</i>     | <i>Wetziella</i>   |
| <i>xinjiangensis</i>      | <i>Wetziella</i>   |
| <b>Wilsonidium</b>        |  |
| <i>conspicuum</i>         | <i>Wilsonidium lineidentatum</i><br>subsp. <i>conspicuum</i> |
| <i>ornatum</i>            | <i>Wilsonidium</i>   |
| <i>*tabulatum</i>         | <i>Wilsonidium</i>   |

**Appendix 3. Specific epithets and their assignments herein and in Fensome & Williams (2004) (also DINO-FLAJ2 – [http://dinoflaj.smu.ca/wiki/Main\\_Page](http://dinoflaj.smu.ca/wiki/Main_Page)).**

| Epithets (as herein)   | Herein                | Fensome & Williams (2004)                                    |
|------------------------|-----------------------|--|
| <i>abortivum</i>       | <i>Axiodium</i>       | <i>Wetziella</i>   |
| <i>aculeatum</i>       | <i>Michouxdinium</i>  | <i>Charlesdowniea</i>  |
| <i>africaense</i>      | <i>Apectodinium</i>   | <i>Wetziella</i>   |
| <i>angulosum</i>       | <i>Talladinium?</i>   | <i>Charlesdowniea clathrata</i><br>subsp. <i>angulosa</i>    |
| <i>articulata</i>      | <i>Wetziella</i>      | <i>Wetziella</i>   |
| <i>astra</i>           | <i>Dracodinium</i>    | <i>Wetziella</i>   |
| <i>astroides</i>       | <i>Wetziella?</i>     | <i>Wetziella</i>   |
| <i>augustum</i>        | <i>Axiodium</i>       | <i>Apectodinium</i>  |
| <i>brevicornutum</i>   | <i>Dracodinium?</i>   | <i>Wetziella articulata</i> subsp. <i>brevicornuta</i>       |
| <i>capitulatum</i>     | <i>Apectodinium</i>   | <i>Apectodinium</i>  |
| <i>cerciatum</i>       | <i>Rhombodinium</i>   | <i>Rhombodinium</i>  |
| <i>clathratum</i>      | <i>Talladinium?</i>   | <i>Charlesdowniea</i>  |
| <i>coleothrypta</i>    | <i>Charlesdowniea</i> | <i>Charlesdowniea</i>  |
| <i>columna</i>         | <i>Piladinium</i>     | <i>Charlesdowniea</i>  |
| <i>compactum</i>       | <i>Castellodinium</i> | <i>Wilsonidium</i>   |
| <i>condylos</i>        | <i>Petalodinium</i>   | <i>Dracodinium?</i>  |
| <i>conopia</i>         | <i>Sophismatia</i>    | <i>Charlesdowniea tenuivirgula</i><br>subsp. <i>conopia</i>  |
| <i>conspicuum</i>      | <i>Wilsonidium</i>    | <i>Wilsonidium lineidentatum</i><br>subsp. <i>conspicuum</i> |
| <i>cornufruticosum</i> | <i>Apectodinium</i>   | <i>Apectodinium</i>  |
| <i>coronatum</i>       | <i>Dracodinium</i>    |  |

(continued)

| Epithets (as herein)   | Herein                                 | Fensome & Williams (2004)                               | Epithets (as herein)    | Herein                  | Fensome & Williams (2004)                                 |
|------------------------|--|---|-------------------------|-------------------------|---|
|                        |  | <i>Wetzelia</i> (as junior synonym)                     | <i>paradoxum</i>        | <i>Apectodinium</i>     | <i>Apectodinium</i>                                       |
| <i>crassa</i>          | <i>Wetzelia</i> ?                      | <i>Wetzelia</i>   | <i>parvum</i>           | <i>Apectodinium</i>     | <i>Apectodinium</i>                                       |
| <i>crassiramosa</i>    | <i>Sophismatia</i>                     | <i>Charlesdownia</i>                                    | <i>pechoricum</i>       | <i>Epelidinium</i>      | (not applicable)  |
| <i>crassithecum</i>    | <i>Petalodinium</i>                    | <i>Rhombodinium glabrum</i> subsp. <i>crassithecum</i>  | <i>pengchiahsuensis</i> | <i>Charlesdownia</i> ?  | <i>Charlesdownia</i>                                      |
| <i>crispum</i>         | <i>Dracodinium</i>                     | <i>Wetzelia</i>   | <i>pentagonum</i>       | <i>Rhombodinium</i>     | <i>Rhombodinium</i> ?                                     |
| <i>degeneratum</i>     | <i>Axioidinium</i>                     | <i>Wetzelia</i>   | <i>perforatum</i>       | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>denticulatum</i>    | <i>Rhombodinium</i>                    | <i>Rhombodinium</i>                                     | <i>politum</i>          | <i>Rhadinodinium</i>    | <i>Dracodinium</i>  |
| <i>distalis</i>        | <i>Wetzelia</i>                        | <i>Wetzelia</i>   | <i>porosum</i>          | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>draco</i>           | <i>Rhombidinium</i>                    | <i>Rhombodinium</i>                                     | <i>prearticulatum</i>   | <i>Axioidinium</i>      | (not applicable)  |
| <i>echinosuturatum</i> | <i>Vallodinium</i> ?                   | <i>Wilsonidium</i>                                      | <i>proserpina</i>       | <i>Michouxdinium</i>    | <i>Charlesdownia</i>                                      |
| <i>edwardsii</i>       | <i>Piladinium</i>                      | <i>Charlesdownia</i>                                    | <i>pustulosum</i>       | <i>Rhombodinium</i> ?   | <i>Rhombodinium</i>                                       |
| <i>elegans</i>         | <i>Rhombidinium</i>                    | <i>Rhombodinium</i>                                     | <i>quinquelatum</i>     | <i>Apectodinium</i>     | <i>Apectodinium</i>                                       |
| <i>elongata</i>        | <i>Wetzelia</i>                        | <i>Wetzelia</i>   | <i>raritybiformium</i>  | <i>Apectodinium</i>     | <i>Apectodinium</i>                                       |
| <i>elongatum</i>       | <i>Rhombodinium</i>                    | <i>Rhombodinium</i>                                     | <i>reticulata</i>       | <i>Sophismatia</i>      | <i>Charlesdownia</i>                                      |
| <i>eocaenicum</i>      | <i>Dracodinium</i>                     | <i>Wetzelia</i>   | <i>rhomboidale</i>      | <i>Michouxdinium</i> ?  | <i>Charlesdownia</i>                                      |
| <i>exouros</i>         | <i>Sophismatia</i> ?                   | <i>Charlesdownia tenuivirgula</i> subsp. <i>exouros</i> | <i>rhomboideum</i>      | <i>Petalodinium</i>     | <i>Dracodinium</i>  |
| <i>fasciata</i>        | <i>Charlesdownia</i> ?                 | <i>Charlesdownia</i>                                    | <i>robosta</i>          | <i>Wetzelia</i> ?       | <i>Wetzelia</i>   |
| <i>filosum</i>         | <i>Kledodinium</i>                     | (not applicable)  | <i>rotundata</i>        | <i>Charlesdownia</i> ?  | <i>Charlesdownia coleothrypta</i> subsp. <i>rotundata</i> |
| <i>flexibilis</i>      | <i>Wetzelia</i> ?                      | <i>Wetzelia</i>   | <i>rotundatum</i>       | <i>Rhombodinium</i> ?   | <i>Rhombodinium</i>                                       |
| <i>fornicale</i>       | <i>Rhombodinium</i> ?                  | <i>Wetzelia</i>   | <i>rugosum</i>          | <i>Petalodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>franciscanum</i>    | <i>Sagenodinium</i>                    | (not applicable)  | <i>rugosum</i>          | <i>Spinidinium</i>      | <i>Wilsonidium</i> ?                                      |
| <i>freienwaldense</i>  | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i>                                     | <i>samlandicum</i>      | <i>Dracodinium</i>      | <i>Wetzelia</i>   |
| <i>fusiforme</i>       | <i>Talladinium</i>                     | <i>Charlesdownia</i>                                    | <i>sheppeyense</i>      | <i>Petalodinium</i>     | (not applicable)  |
| <i>geometricum</i>     | <i>Apectodinium</i>                    | <i>Apectodinium</i>                                     | <i>simile</i>           | <i>Dracodinium</i>      | <i>Dracodinium</i>  |
| <i>glabrum</i>         | <i>Rhadinodinium</i>                   | <i>Rhombodinium</i> ?                                   | <i>simplex</i>          | <i>Wetzelia</i>         | <i>Wetzelia</i>   |
| <i>gochtii</i>         | <i>Wetzelia</i>                        | <i>Wetzelia</i>   | <i>sinense</i>          | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>granulatum</i>      | <i>Epelidinium</i> ?                   | <i>Dracodinium</i>                                      | <i>solidum</i>          | <i>Dracodinium</i>      | <i>Dracodinium</i>  |
| <i>hampdenensis</i>    | <i>Wetzelia</i> ?                      | <i>Wetzelia</i>   | <i>spinulosa</i>        | <i>Wetzelia</i> ?       | <i>Wetzelia</i>   |
| <i>homomorphum</i>     | <i>Apectodinium</i>                    | <i>Apectodinium</i>                                     | <i>spinula</i>          | <i>Petalodinium</i>     | <i>Dracodinium politum</i> subsp. <i>spinula</i>          |
| <i>hyperacanthum</i>   | <i>Apectodinium</i>                    | <i>Apectodinium</i>                                     | <i>spinula</i>          | <i>Rhombodinium</i>     | <i>Wetzelia</i>   |
| <i>insolens</i>        | <i>Sophismatia</i> ?                   | <i>Kisselevia</i> ?                                     | <i>stellatum</i>        | <i>Vallodinium</i>      | <i>Charlesdownia</i>                                      |
| <i>intermedium</i>     | <i>Castellodinium</i> ?                | <i>Wilsonidium</i>                                      | <i>statile</i>          | <i>Stichodinium</i>     | <i>Wilsonidium</i>  |
| <i>irtyschense</i>     | <i>Rhombodinium</i>                    | <i>Wetzelia</i>   | <i>summissum</i>        | <i>Apectodinium</i>     | <i>Apectodinium</i>                                       |
| <i>kunlunense</i>      | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i>                                     | <i>symmetrica</i>       | <i>Wetzelia</i>         | <i>Wetzelia</i>   |
| <i>laszczynskii</i>    | <i>Petalodinium</i>                    | <i>Dracodinium</i>                                      | <i>tabulatum</i>        | <i>Wilsonidium</i>      | <i>Wilsonidium</i>  |
| <i>limitatum</i>       | <i>Michouxdinium</i>                   | <i>Charlesdownia</i>                                    | <i>taiwaniana</i>       | <i>Charlesdownia</i> ?  | <i>Charlesdownia</i>                                      |
| <i>lineidentatum</i>   | <i>Stichodinium</i> ?                  | <i>Wilsonidium</i>                                      | <i>tenuivirgula</i>     | <i>Sophismatia</i>      | <i>Charlesdownia</i>                                      |
| <i>lobiscum</i>        | <i>Dracodinium</i>                     | <i>Wetzelia</i>   | <i>tesselatum</i>       | <i>Axioidinium</i> ?    | <i>Wilsonidium</i>  |
| <i>longimanum</i>      | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i>                                     | <i>tianshanensis</i>    | <i>Wetzelia</i> ?       | <i>Wetzelia</i>   |
| <i>longispinosum</i>   | <i>Apectodinium</i>                    | <i>Apectodinium</i>                                     | <i>translucidum</i>     | <i>Epelidinium</i> ?    | <i>Rhombodinium</i>                                       |
| <i>lunare</i>          | <i>Axioidinium</i>                     | <i>Wetzelia</i>   | <i>triangulatum</i>     | <i>Epelidinium</i>      | <i>Wetzelia</i>   |
| <i>magnificum</i>      | <i>Dracodinium</i>                     | <i>Wetzelia articulata</i> subsp. <i>magnifica</i>      | <i>tuberculatum</i>     | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>majus</i>           | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i> ?                                   | <i>tuberosuturatum</i>  | <i>Castellodinium</i> ? | <i>Wilsonidium</i>  |
| <i>marginatum</i>      | <i>Talladinium</i> ?                   | <i>Charlesdownia</i>                                    | <i>uncinata</i>         | <i>Dolichodinium</i>    | <i>Wetzelia</i>   |
| <i>meckelfeldense</i>  | <i>Stenodinium</i>                     | <i>Wetzelia</i>   | <i>unicaudale</i>       | <i>Dolichodinium</i> ?  | <i>Wetzelia</i>   |
| <i>minus</i>           | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i>                                     | <i>variabile</i>        | <i>Rhombodinium</i>     | <i>Dracodinium</i>  |
| <i>mirabile</i>        | <i>Rhombodinium</i>                    | <i>Rhombodinium</i>                                     | <i>variabile</i>        | <i>Michouxdinium</i>    | <i>Charlesdownia</i>                                      |
| <i>nigeriaense</i>     | <i>Vallodinium</i>                     | <i>Wilsonidium</i>                                      | <i>varielongitudum</i>  | <i>Dracodinium</i>      | <i>Dracodinium</i>  |
| <i>oravense</i>        | <i>Rhombodinium</i> ?                  | <i>Rhombodinium</i>                                     | <i>vialovii</i>         | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
| <i>ornatum</i>         | <i>Rhombodinium</i>                    | <i>Kisselevia</i>                                       | <i>vozhennikovae</i>    | <i>Rhombodinium</i> ?   | <i>Kisselevia major</i>                                   |
| <i>ornatum</i>         | <i>Wilsonidium</i>                     | <i>Wilsonidium</i>                                      | <i>waipawaense</i>      | <i>Petalodinium</i>     | <i>Dracodinium</i>  |
| <i>ovalis</i>          | <i>Wetzelia</i>                        | <i>Wetzelia</i>   | <i>wetzelii</i>         | <i>Dracodinium</i>      | <i>Wetzelia</i>   |
| <i>pachydermum</i>     | <i>Dracodinium</i> (as junior synonym) | <i>Wetzelia</i> (as junior synonym)                     | <i>williereae</i>       | <i>Apectodinium</i> ?   | <i>Apectodinium</i> ?                                     |
| <i>paniculatum</i>     | <i>Apectodinium</i>                    | <i>Apectodinium</i>                                     | <i>wuqiense</i>         | <i>Rhombodinium</i>     | <i>Rhombodinium</i>                                       |
|                        |  |   | <i>wulagenense</i>      | <i>Talladinium</i>      | <i>Charlesdownia</i>                                      |
|                        |  |   | <i>xinjiangensis</i>    | <i>Wetzelia</i>         | <i>Wetzelia</i>   |

(continued)



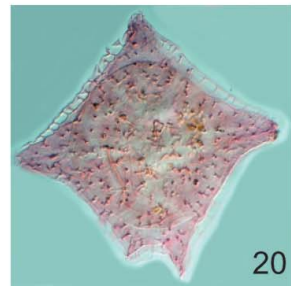
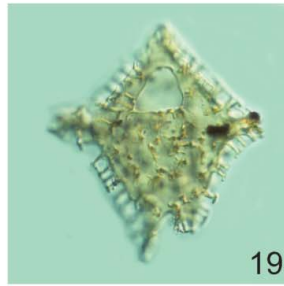
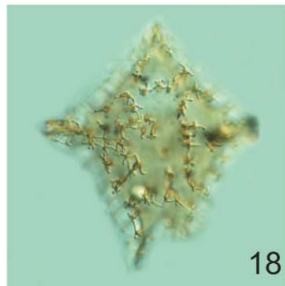
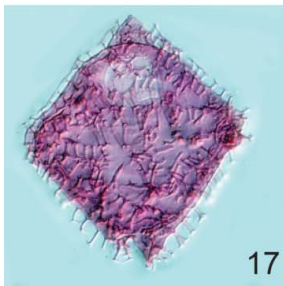
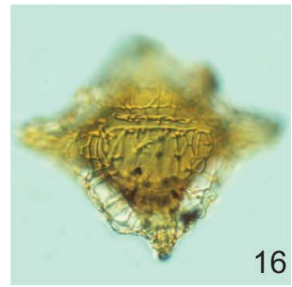
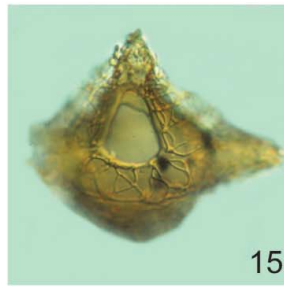
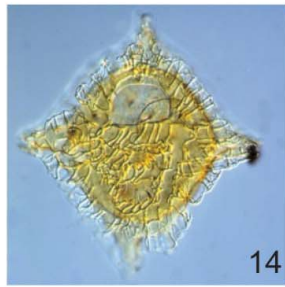
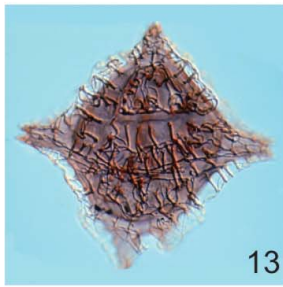
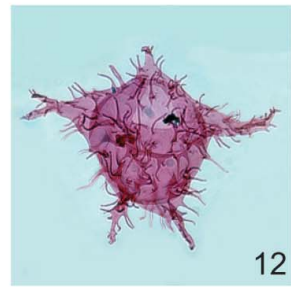
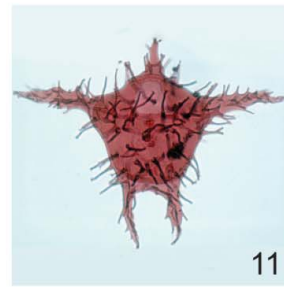
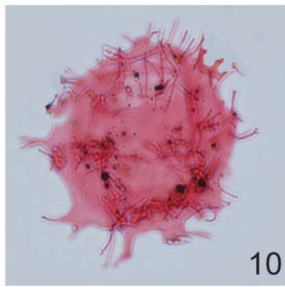
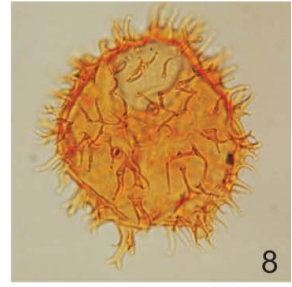
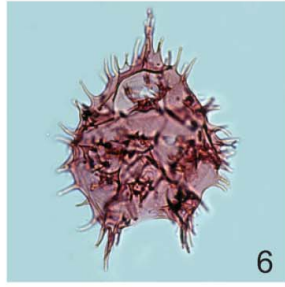
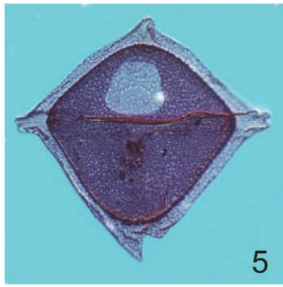
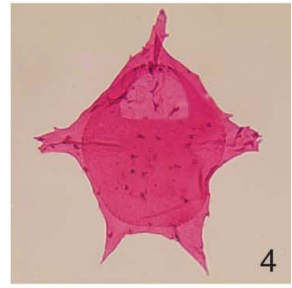
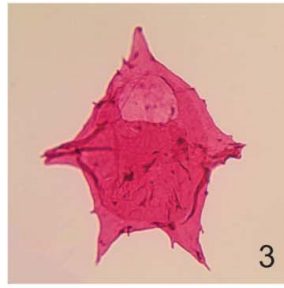
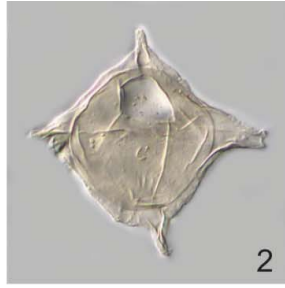
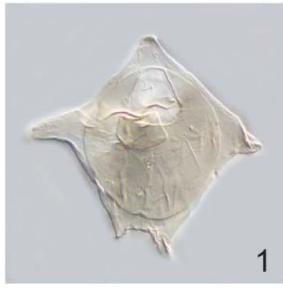
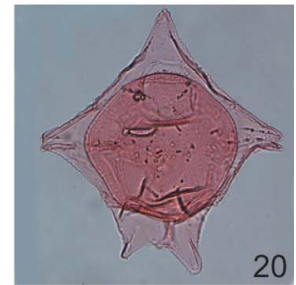
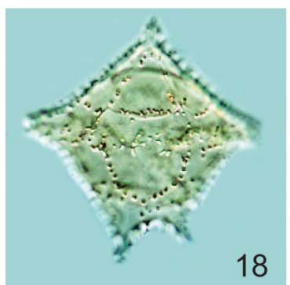
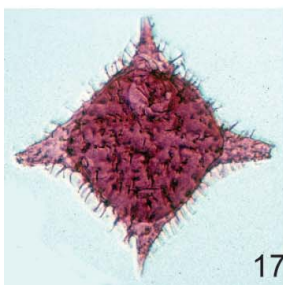
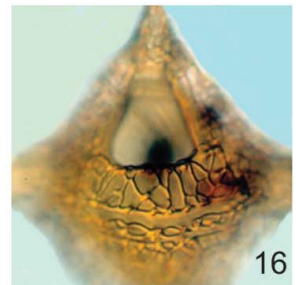
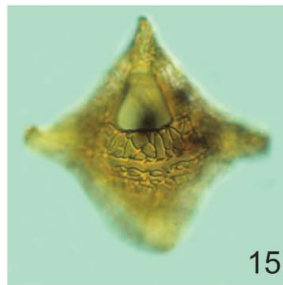
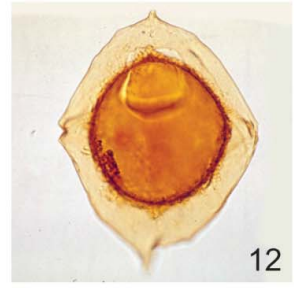
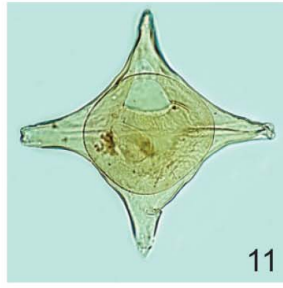
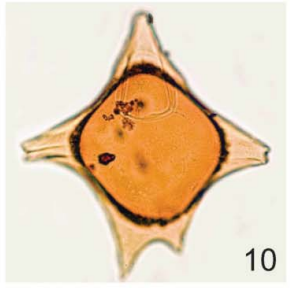
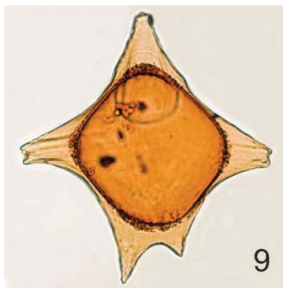
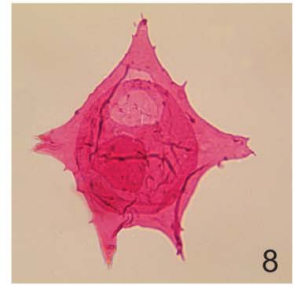
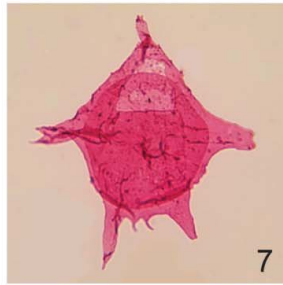
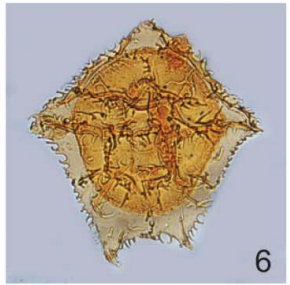
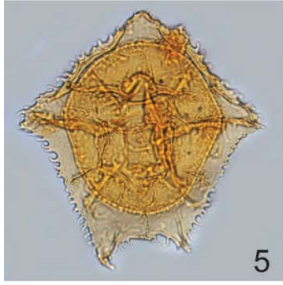
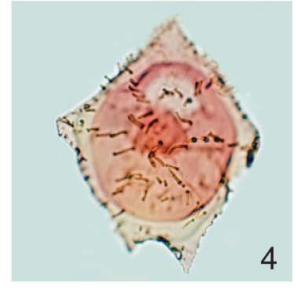
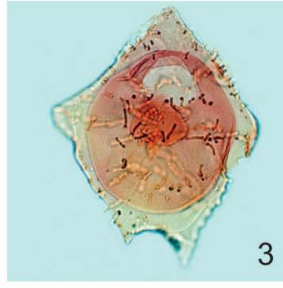
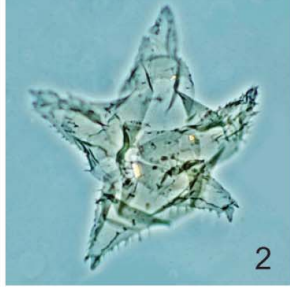
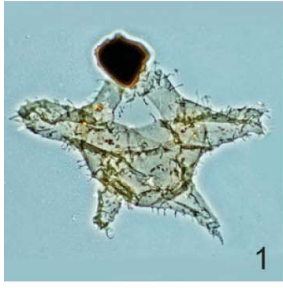


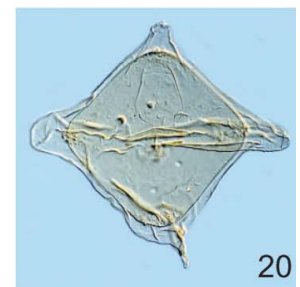
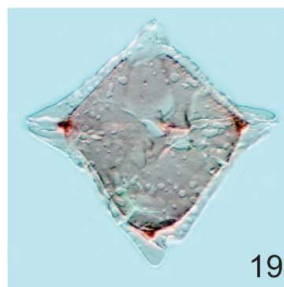
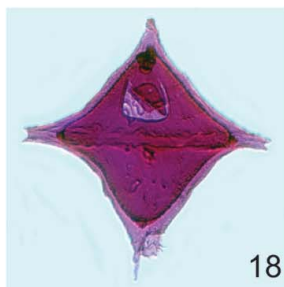
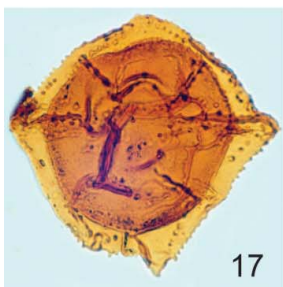
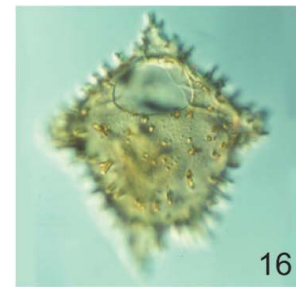
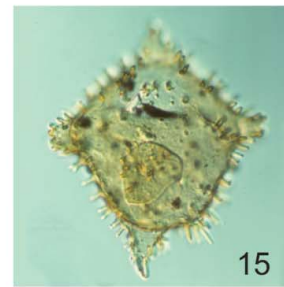
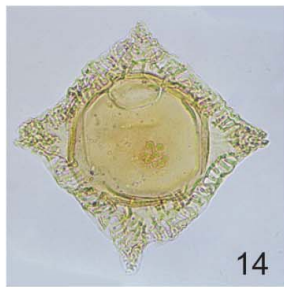
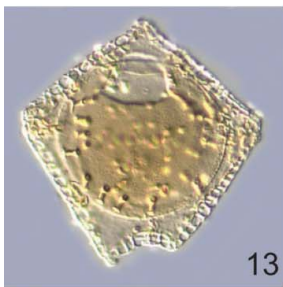
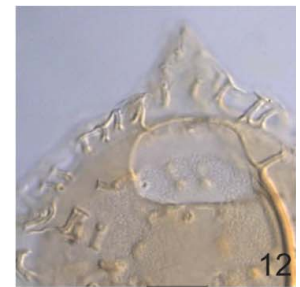
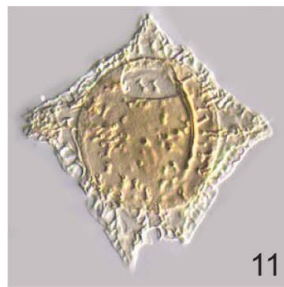
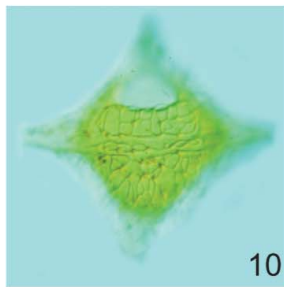
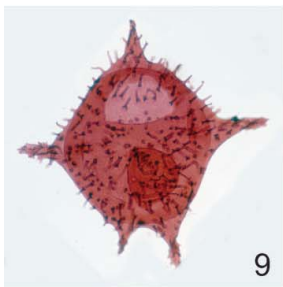
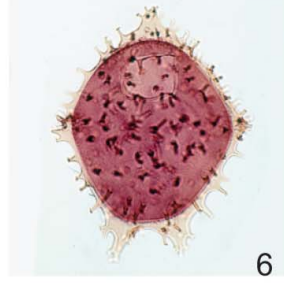
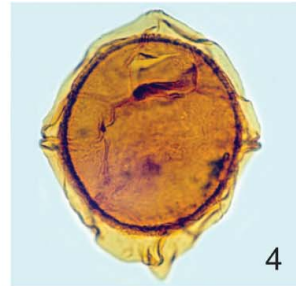
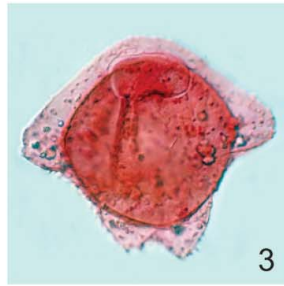
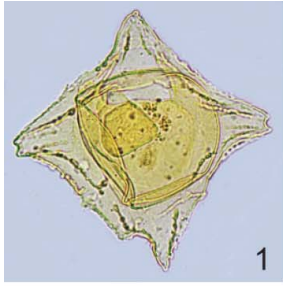
Plate 1. Note that in this plate and those following, the designation 'sp.' does not indicate that we recognise a specific informal taxon but that we can assign the specimen illustrated only to generic rank. Thus, the labelling of multiple specimens within a genus as 'sp.' implies neither that they are conspecific nor that they are separate forms. For a discussion of measurements, see General remarks in the Systematic palaeontology section. We provide measurements in the plate captions where these are known.

1. *Epelidinium? translucidum*. Holotype, ventral view of dorsal surface showing equiepeliform archeopyle. Pericyst length 126  $\mu\text{m}$ , pericyst width 135  $\mu\text{m}$ . Early Eocene, France. Photograph by Daniel Michoux.
2. *Epelidinium? translucidum*. Ventral view of dorsal surface showing equiepeliform archeopyle. Early Eocene, France. Photograph by Daniel Michoux.
3. *Epelidinium* sp. Probable ventral view of dorsal surface showing equiepeliform archeopyle. Ypresian, Taglu Formation in the eastern part of the Mackenzie Delta. Photograph provided by Graham Dolby.
4. *Epelidinium* sp. Probable ventral view of dorsal surface showing equiepeliform archeopyle. Ypresian, Taglu Formation in the eastern part of the Mackenzie Delta. Photograph provided by Graham Dolby.
5. *Epelidinium?* sp. Dorsal view of dorsal surface showing equiepeliform archeopyle. Deep Sea Drilling Project (DSDP) Leg 95, Site 612, core 18x, 0–50 cm; Late Eocene (nannoplankton zones NP 19–20). Although the archeopyle looks epeliform, its shape is more typical of a soleiform type; so the operculum may have become secondarily torn off anteriorly. In general morphology, the cyst is closely similar to *Rhombodinium porosum*. Photograph by Sarah Damassa.
6. *Apectodinium longispinosum*. Holotype, dorsal view of dorsal surface; equiepeliform archeopyle. Pericyst length 121  $\mu\text{m}$ , width 83  $\mu\text{m}$ . Paleocene or early Eocene, New Zealand. Photograph by Graham Wilson.
7. *Apectodinium quinquelatum*. Ventral view of dorsal surface showing equiepeliform archeopyle. From an unspecified North Sea well, presumably of late Paleocene to early Eocene age. Photograph by Dan Beju.
8. *Apectodinium homomorphum*. Dorsal view of ventral surface showing equiepeliform archeopyle. Early Eocene, from the cuttings sample at 2249–2259 m in Snorri J-90 well, Labrador Shelf. Photograph by Graham Williams.
9. *Apectodinium homomorphum*. Dorsal view of dorsal surface showing equiepeliform archeopyle. Early Eocene; from the cuttings sample at 2249–2259 m in Snorri J-90 well, Labrador Shelf. Photograph by Graham Williams.
10. *Axiodinium* sp. Dorsal surface showing equiepeliform archeopyle. Early Ypresian (early Eocene) of the Paris Basin, France. Photograph by Alina Iakovleva.
11. *Axiodinium augustum*. Dorsal view of dorsal surface showing equiepeliform archeopyle; the endocyst is clearly visible in the antapical region. Latest Paleocene, North Sea. Photograph by Rex Harland.
12. *Axiodinium augustum*. Ventral view of dorsal surface showing equiepeliform archeopyle. The endocyst is clearly visible in the antapical region; a similar morphology is seen in the holotype (Harland 1979, pl. 2, fig. 13). Halten well, North Sea. Photograph by Dan Beju.
13. *Sophismatia crassiramosa*. Dorsal view of dorsal surface showing equiepeliform archeopyle, operculum in place. Early Eocene, southern England. Photograph by Graham Williams.
14. *Sophismatia tenuivirgula*. Dorsal view of dorsal specimen showing equiepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
15. *Sophismatia* sp. Anterior dorsal surface showing equiepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
16. *Sophismatia crassiramosa?*. Dorsal surface. Note the large dorsal cingular plate. Early to Middle Eocene, California. Photograph by Sarah Damassa.
17. *Charlesdowniea coleothrypta*. Ventral view of dorsal surface showing equiepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
18. *Vallodinium* sp. Dorsal view of ventral surface. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
19. *Vallodinium* sp. Dorsal view of dorsal surface, showing equiepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
20. *Charlesdowniea coleothrypta*. Ventral view of ventral surface showing the 1' plate. Provenance lost. Photograph by Lew Stover.



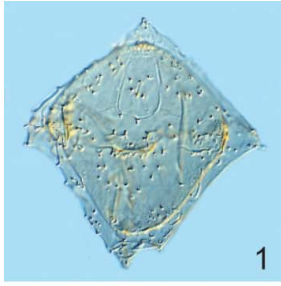
## Plate 2.

1. *Vallodinium stellatum*. Ventral view of dorsal surface showing equiepeliform archeopyle. Late Paleocene, from Alo-1 well, southern Nigeria (Antolinez-Delgado & Oboh-Ikuenobe 2007). Photograph by Hernan Antolinez-Delgado.
2. *Vallodinium stellatum*. Holotype, dorsal view of dorsal surface showing equiepeliform archeopyle. Late Paleocene, from Alo-1 well, southern Nigeria (Antolinez-Delgado & Oboh-Ikuenobe 2007). Photograph by Hernan Antolinez-Delgado.
3. *Vallodinium* sp. Ventral view of dorsal surface showing equiepeliform archeopyle. Eocene (Ypresian–Lutetian), Baldwin County, Alabama. Photograph by Sarah Damassa.
4. *Vallodinium* sp. Ventral view of ventral surface showing spinules aligned along parasutures. Eocene (Ypresian–Lutetian), Baldwin County, Alabama. Photograph by Sarah Damassa.
5. *Vallodinium?* *echinosuturatum*. Holotype; dorsal view of ventral surface. Pericyst length 149  $\mu\text{m}$ , pericyst width 143  $\mu\text{m}$ , endocyst length 99  $\mu\text{m}$ , endocyst width 91  $\mu\text{m}$ . Middle Eocene, New Zealand. Photograph by Graeme Wilson.
6. *Vallodinium?* *echinosuturatum*. Holotype; dorsal view of optical section. Pericyst length 149  $\mu\text{m}$ , pericyst width 143  $\mu\text{m}$ , endocyst length 99  $\mu\text{m}$ , endocyst width 91  $\mu\text{m}$ . Middle Eocene, New Zealand. Photograph by Graeme Wilson.
7. *Rhadinodinium* sp. Dorsal view of dorsal surface showing hyperepeliform archeopyle. Ypresian, Taglu Formation in the eastern part of the Mackenzie Delta. Photograph by Graham Dolby.
8. *Rhadinodinium* sp. Probable dorsal view of dorsal surface showing hyperepeliform archeopyle. Ypresian, Taglu Formation in the eastern part of the Mackenzie Delta. Photograph by Graham Dolby.
9. *Rhadinodinium* sp. Dorsal view of dorsal surface showing hyperepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
10. *Rhadinodinium* sp. Dorsal view of ventral surface showing hyperepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
11. *Rhadinodinium* sp. Dorsal view of dorsal surface showing hyperepeliform archeopyle. This specimen was illustrated by Nøhr-Hansen (2003, pl. 6, figs. 7–9 as *Rhombodinium* sp. 1. It is from the Early Eocene in Qulleq-1 well, offshore West Greenland. Photograph by Henrik Nøhr-Hansen.
12. *Rhadinodinium* sp. Dorsal view of dorsal surface showing hyperepeliform archeopyle. This specimen would previously have been included in *Rhombodinium rhomboideum* but the periarcheopyle extends into the apical pericoel. Provenance lost. Photograph by Lew Stover.
13. *Stenodinium meckelfeldense*. Ventral view of dorsal surface showing hyperepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
14. *Stenodinium meckelfeldense*. Ventral view of ventral surface showing hyperepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
15. *Sagenodinium franciscanum*. View of dorsal surface showing hyperepeliform archeopyle. This specimen has processes and trabeculae identical to those of *Sophismatia crassitabulata*, but the archeopyle is hyperepeliform. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
16. *Sagenodinium franciscanum*. Same specimen as Plate 2, figure 15, close-up of hyperepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
17. Genus and species undescribed, with a hyperepeliform archeopyle and processes connected by a membranous ectophragm. Provenance lost. Photograph by Graham Williams.
18. *Wilsonidium tabulatum*. Dorsal view of dorsal surface showing hyperepeliform archeopyle. Eocene, Maryland. Photograph by Graham Williams.
19. *Wilsonidium tabulatum*. Holotype, ventral view of ventral surface showing hyperepeliform archeopyle. Pericyst length 149  $\mu\text{m}$ , pericyst width 138  $\mu\text{m}$ , endocyst 83 by 85  $\mu\text{m}$ . Late Eocene?, New Zealand. Photograph by Graeme Wilson.
20. *Wilsonidium tabulatum*. Holotype, ventral view of dorsal surface, hyperepeliform archeopyle. Pericyst length 149  $\mu\text{m}$ , pericyst width 138  $\mu\text{m}$ , endocyst 83 by 85  $\mu\text{m}$ . Late Eocene?, New Zealand. Photograph by Graeme Wilson.

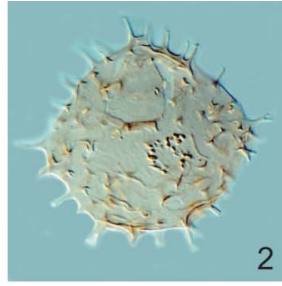


## Plate 3.

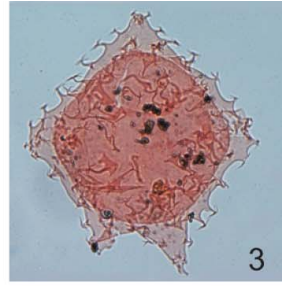
1. *Wilsonidium ornatum*. Ventral view of dorsal surface showing hyperepeliform archeopyle. Early Eocene, New Zealand. Photograph by Joe Prebble.
2. *Petalodinium* sp. Ventral view of dorsal surface showing hyperepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
3. *Petalodinium condylos*. Ventral view of dorsal surface showing latiepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
4. *Petalodinium* sp. Ventral view of dorsal surface showing latiepeliform archeopyle. Early Eocene; from Cormorant N-83 well, Grand Banks of Newfoundland. Photograph by Graham Williams.
5. *Petalodinium waipawaense*. Holotype, dorsal view of dorsal surface showing latiepeliform archeopyle. Pericyst length 102  $\mu\text{m}$ , width 118  $\mu\text{m}$ , endocyst length 69  $\mu\text{m}$ , endocyst width 69  $\mu\text{m}$ . Early Eocene, New Zealand. Photograph by Joe Prebble.
6. *Dracodinium simile*. Dorsal view of dorsal surface showing latiepeliform archeopyle. Provenance lost. Photograph by Graham Williams.
7. *Dracodinium eocaenicum*. Ventral view of dorsal surface showing latiepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
8. *Dracodinium samlandicum*. Dorsal view of dorsal surface showing latiepeliform archeopyle. Provenance lost. Photograph by Lew Stover.
9. *Dracodinium samlandicum*. Ventral view of dorsal surface showing latiepeliform archeopyle. Provenance lost. Photograph by Graham Williams.
10. *Kledodinium filosum*. Dorsal view of dorsal surface showing latiepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
11. *Piladinium columna*. Holotype, dorsal view of dorsal surface showing latiepeliform archeopyle. Pericyst length 121  $\mu\text{m}$ , pericyst width 124  $\mu\text{m}$ . Early Eocene, France. Photograph by Daniel Michoux.
12. *Piladinium columna*. Holotype, dorsal view of dorsal surface, close-up showing latiepeliform archeopyle. Pericyst length 121  $\mu\text{m}$ , pericyst width 124  $\mu\text{m}$ . Early Eocene, France. Photograph by Daniel Michoux.
13. *Piladinium columna*. Dorsal view of dorsal surface showing latiepeliform archeopyle. Early Eocene, France. Photograph by Daniel Michoux.
14. *Piladinium edwardsii*. Dorsal view of dorsal surface showing latiepeliform archeopyle. Early Eocene, New Zealand. Photograph by Joe Prebble.
15. *Stichodinium* sp. Dorsal view of ventral surface. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
16. *Stichodinium* sp. Dorsal view of dorsal surface showing latiepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979, text-fig. 1). Photograph by Sarah Damassa.
17. *Stichodinium* sp. Ventral view of ventral surface showing latiepeliform archeopyle. Provenance lost. Photograph by Graham Williams.
18. *Rhombodinium draco*. Dorsal view of dorsal surface showing soleiform archeopyle. Provenance lost. Photographer uncertain.
19. *Rhombodinium porosum*. Holotype; dorsal view of ventral surface showing soleiform archeopyle. Middle Eocene, southern England. Photograph by Jonathan Bujak.
20. *Rhombodinium? longimanum*. Ventral view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.



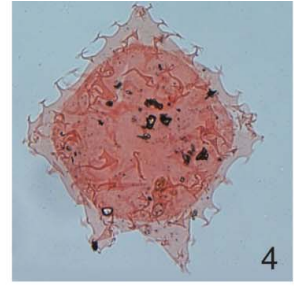
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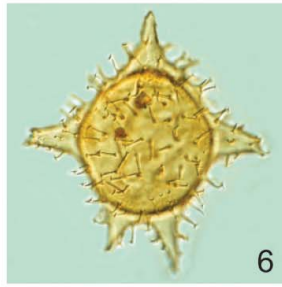
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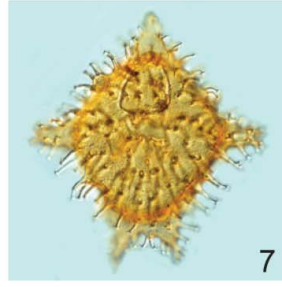
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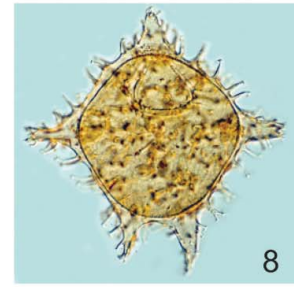
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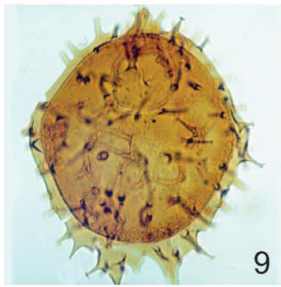
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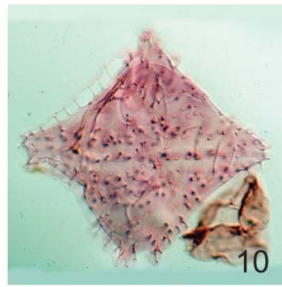
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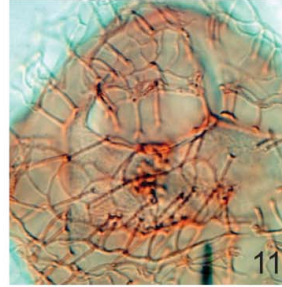
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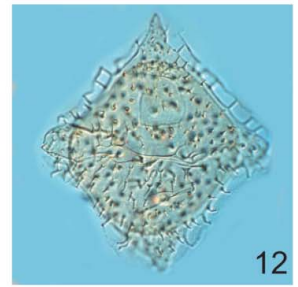
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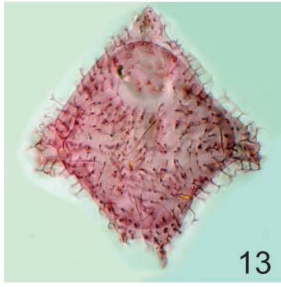
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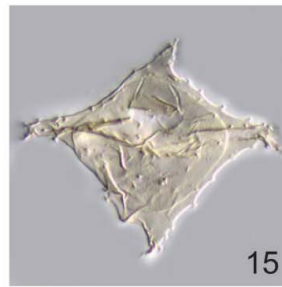
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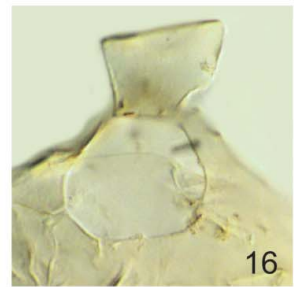
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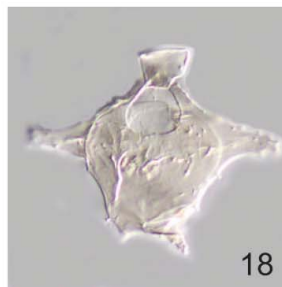
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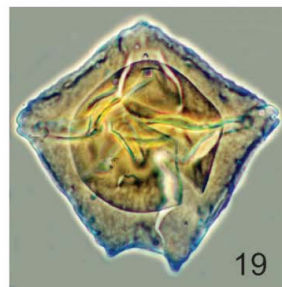
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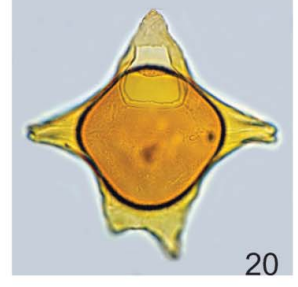
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## Plate 4.

1. *Rhombodinium spinula*. Dorsal view of ventral surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
2. *Wetzeliiella gochtii*. Dorsal view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
3. *Wetzeliiella? hampdenensis*. Holotype; ventral view, higher focus of dorsal surface showing soleiform archeopyle. Pericyst length 132  $\mu\text{m}$ , pericyst width 118  $\mu\text{m}$ , endocyst 83 by 88  $\mu\text{m}$ . Middle Eocene, New Zealand. Photograph by Joe Prebble.
4. *Wetzeliiella? hampdenensis*. Holotype, Ventral view, lower focus of dorsal surface, soleiform archeopyle. Pericyst length 132  $\mu\text{m}$ , pericyst width 118  $\mu\text{m}$ , endocyst 83 by 88  $\mu\text{m}$ . Middle Eocene, New Zealand. Photograph by Joe Prebble.
5. *Wetzeliiella caviarticulatum*. Dorsal? view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Graham Williams.
6. *Wetzeliiella articulata*. Ventral view of ventral surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
7. *Wetzeliiella articulata*. Dorsal view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
8. *Wetzeliiella articulata*. Ventral view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
9. *Wetzeliiella* sp. Dorsal view of dorsal surface showing soleiform archeopyle. Middle Eocene, Elf Hermine E-94, Grand Banks of Newfoundland. Photograph by Graham Williams.
10. *Michouxdinium variabile*. Dorsal view of ventral surface showing soleiform archeopyle. Late Eocene, Little Stave Creek, Alabama. Provenance lost. Photograph by Lew Stover.
11. *Michouxdinium* sp. Dorsal view of dorsal surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
12. *Talladinium* sp. Ventral view of ventral surface showing soleiform archeopyle. Provenance lost. Photograph by Lew Stover.
13. *Talladinium* sp. Ventral view of dorsal surface showing soleiform archeopyle. Late Eocene, Little Stave Creek, Alabama. Provenance lost. Photograph by Lew Stover.
14. *Castellodinium* sp. Dorsal view of dorsal surface showing soleiform archeopyle. Early to middle Eocene cuttings sample Onondaga E-84 well, Scotian Margin, offshore eastern Canada. Photograph by Rob Fensome.
15. *Dolichodinium uncinatum*. Ventral view of dorsal surface showing hypersoleiform archeopyle. Early Eocene, France. Photograph by Daniel Michoux.
16. *Dolichodinium uncinatum*. Ventral view of dorsal surface, close-up of archeopyle and showing the operculum folded back but still attached along its anterior margin, hypersoleiform archeopyle. Early Eocene, France. Photograph by Daniel Michoux.
17. *Dolichodinium* sp. Ventral view of ventral surface showing hypersoleiform archeopyle. Eocene, offshore Florida.
18. *Dolichodinium uncinatum*. Ventral view of dorsal surface, same specimen as figure 16 and showing the operculum folded back but still attached along its anterior margin, hypersoleiform archeopyle. Early Eocene, France. Photograph by Daniel Michoux.
19. *Dolichodinium* sp. Ventral view of dorsal surface showing hypersoleiform archeopyle. Eocene, offshore Florida. Photograph by Graham Williams.
20. *Dolichodinium?* sp. Ventral view of dorsal surface, the archeopyle outline duplicates that of the hypersoleiform archeopyle, but the operculum has been removed, probably reflecting damage. Because of the uncertainty over the nature of the archeopyle, we questionably assign this specimen to *Dolichodinium*. Provenance lost. Photograph by Lew Stover.



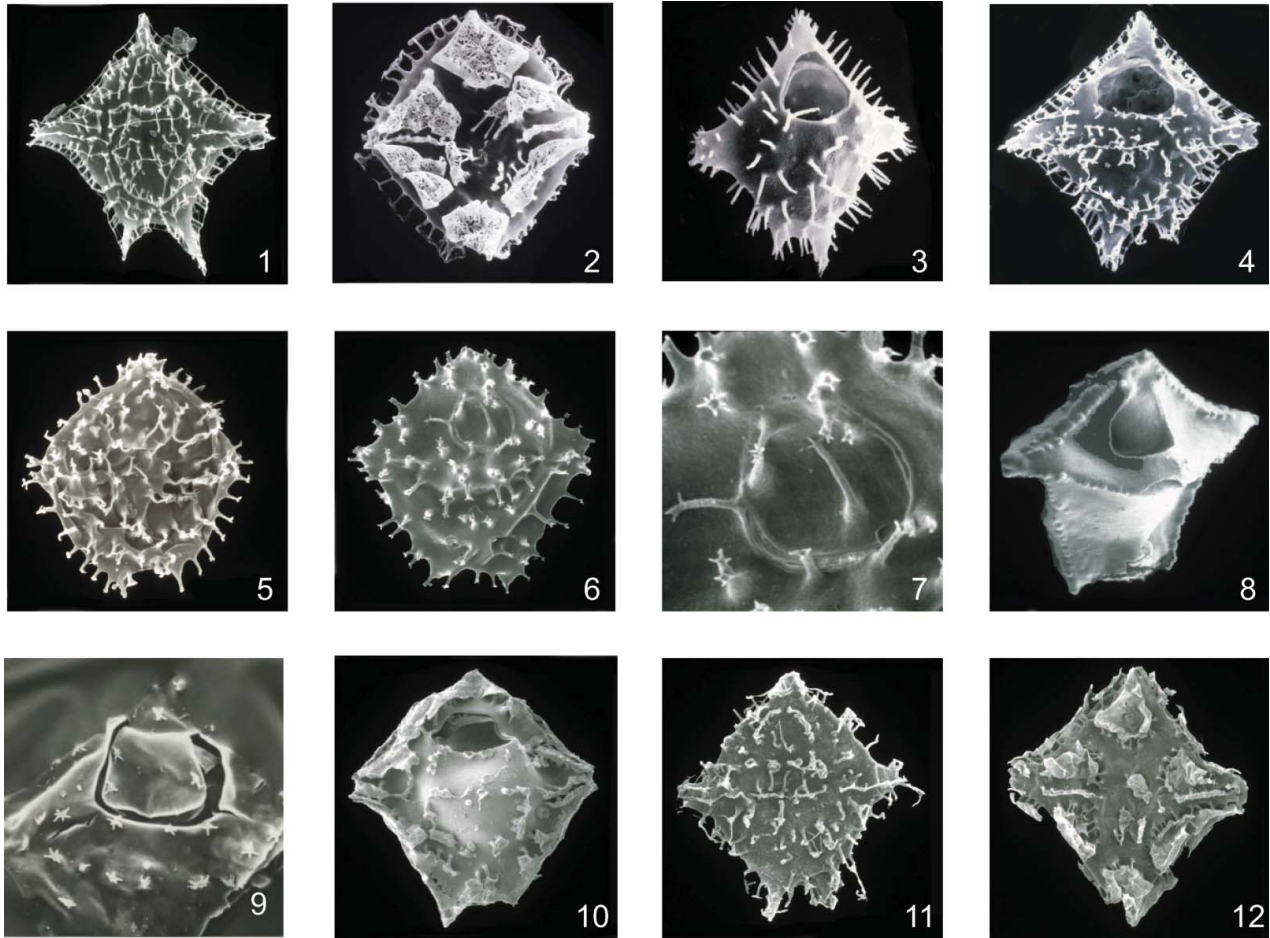


Plate 5. Scanning electron microscope images in this plate are from the collection of one of the authors (GLW) and were taken either at Pan-American Petroleum, Tulsa, or at the Geological Survey of Canada (Atlantic). Unfortunately, provenance information is now lost, but most are from the Paleogene strata of offshore eastern Canada.

1. *Sophismatia tenuivirgula*. Dorsal surface. The right antapical horn is longer than the left antapical horn in this specimen.
2. *Charlesdowniea coleothrypta*. Ventral surface.
3. *Stenodinium* sp. Dorsal surface showing hyperepeliform archeopyle.
4. *Stichodinium* sp. Dorsal surface showing latiepeliform archeopyle. Eocene; from the Franciscan Complex of the Coastal Belt, west of Willits, Mendocino County, California (Damassa 1979).
5. *Wetzeliella gochtii*. Ventral surface.
6. *Wetzeliella gochtii*. Dorsal surface.
7. *Wetzeliella gochtii*. Dorsal surface, enlargement of figure 6 showing close-up of soleiform archeopyle.
8. *Castellodinium* sp. Dorsal surface showing soleiform archeopyle. Notice cingular plate demarcation.
9. *Dolchidinium uncinatum*. Dorsal surface showing hypersoleiform archeopyle; cingulum delineated by single row of processes. Early Eocene, France (Michoux 1988).
10. *Stichodinium* sp. Dorsal surface showing latiepeliform archeopyle; cingulum delineated by single row of processes.
11. *Axiodinium* sp. Dorsal surface showing equiepeliform archeopyle but operculum still in place. There appear to be three dorsal cingular plates delineated by the process rows.
12. This is probably a specimen of *Charlesdowniea coleothrypta*. Ventral surface, archeopyle unknown. There are two distinct ventral cingular plates.