

**Dinoflagellate Taxonomy and Biostratigraphy
of the Mid- to Late Eocene and Early Oligocene
of New Zealand**

by

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Abstract

This document presents results from a study of the Mid- to Late Eocene and earliest Oligocene marine palynomorphs from on-shore and near-shore New Zealand. Eighty samples of appropriate age from across mainland New Zealand were examined for fossil dinoflagellates. Acritarchs encountered in the study are described, also, and the phenetic taxonomy of the Acritarcha provides an interesting contrast to the present 'mixed' state of dinoflagellate taxonomy: phylogenetic above the genus rank, and arguably below it, but predominantly phenetic at the genus rank.

Extensive single mount collections were harvested from a number of samples which were found to be especially rich, well preserved, or which contained new taxa. The outcome has included descriptions of 25 new species, in addition to two (*Corrudinium regulare* and *Corrudinium otagoense*) published in an earlier paper (Clowes & Wilson 2006), namely:

<i>Achilleodinium echinatum</i>	<i>Graptodinium inconditum</i>	<i>Phthanoperidinium dentatum</i>
<i>Achilleodinium improcerum</i>	<i>Graptodinium reticulatum</i>	<i>Phthanoperidinium granulatum</i>
? <i>Areoligera hampdenensis</i>	<i>Nummus inornatus</i>	<i>Phthanoperidinium spumosum</i>
<i>Batiacasphaera perforata</i>	<i>Operculodinium crouchii</i>	<i>Phthanoperidinium tenuimurum</i>
<i>Chlamydothorea neopilata</i>	<i>Operculodinium schioleri</i>	<i>Pyxidinopsis mundus</i>
<i>Chlamydothorea pilata</i>	<i>Operculodinium pulcher</i>	<i>Pyxidinopsis teuriensis</i>
<i>Corrudinium bujakii</i>	<i>Operculodinium vulgare</i>	<i>Samlandia tenuis</i>
<i>Deflandrea totara</i>	<i>Phthanoperidinium aculeatum</i>	
<i>Disphaerogena morgansii</i>	<i>Phthanoperidinium australe</i>	

Although there remain some difficulties where the adopted suprageneric phylogeny meets the traditionally phenetic generic constructs, adopting an explicitly phylogenetic approach to dinoflagellate taxonomy was found to be a fruitful approach. Investigation into some of the new taxa described herein was first prompted by geographic or temporal occurrence criteria which hinted that relationships might be other than those immediately suggested by gross morphology. Only upon closer inspection were subtler morphological distinctions noticed.

To adopt a wholly phylogenetic approach almost certainly requires the abandonment of taxa, particularly genera, which are uniquely defined by mutually exclusive morphological criteria. Other clues to phylogeny, such as stratigraphic and regional occurrence data, may also have to be recognised. Notwithstanding, all taxa described herein are, in fact, defined by means of conventional morphological distinctions. This study does not take the bold step to suggest a new taxon based wholly on geographical and temporal criteria. Doing so, however, is clearly a rational extension to the ideas presented herein, and is thought worthy of further investigation.

A subordinate goal of this study was to further refine the younger part of Wilson's dinoflagellate biozonation for New Zealand (Wilson 1984d, 1987, 1988; Morgans et al. 2004), to:

- improve resolution, if possible;
- clarify an ambiguous boundary remaining in the literature, between the *Wetzeliella hampdenensis* and *Wilsonidium tabulatum* zones;
- incorporate more common taxa, which are not restricted to particular ecological settings.

This has been progressed by a number of measures, including adopting a consistent approach to defining zone boundaries; replacement of the *Wilsonidium echinosuturatum* and *Wilsonidium lineidentatum* Zones with three new zones, *Deflandrea convexa* (early Porangan – late Porangan), *Graptodinium inconditum* (late Porangan – early Bortonian), and *Impagidinium elegans* (early Bortonian – late Bortonian); and the establishment of an additional new zone, the *Stoveracysta kakanuiensis* Zone, straddling the Eocene-Oligocene boundary.

Since phylogenetic concepts played no role in formulating the classification [of Sarjeant & Downie 1966, 1974], one should be cautious in criticizing its authors for seeming to suggest relationships at suprageneric levels when that was not intended. However, one can also question whether, under such circumstances, a detailed family-like classification of “non-families” is any more useful than an alphabetical listing or some other systematic but frankly arbitrary ordering.

— Evitt 1985, p. 278

This contribution is dedicated to the founder and uncontested doyen of fossil dinoflagellate studies in New Zealand,
Dr. Graeme J. Wilson
of GNS Science (formerly the New Zealand Geological Survey)
until his retirement at the end of 2007.

A wonderful mentor, field-trip companion, and kind friend.

Thanks Graeme!

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Introduction

Objectives

This document presents results from a study of the Mid- to Late Eocene and earliest Oligocene acritarchs and dinoflagellates from on-shore and near-shore New Zealand. The focus is primarily taxonomic, but effort is also made to characterise and compare whole assemblages, with emphasis upon refining the biozonation scheme for the interval.

Some specific objectives of the present study are:

1. First and foremost, this study aims to evaluate the effectiveness of having adopted an explicitly phylogenetic approach to dinoflagellate taxonomy.

The background, motivation, and evaluation of this approach are explored further in the section entitled *Taxonomic Approach*.

2. The approach was trialled by applying it to “genuine” (i.e., not a contrived experiment) taxonomic research, which was expected to further elucidate the taxonomy of the middle Eocene to early Oligocene dinoflagellate cyst biota of New Zealand. This is the second objective.

The resulting systematic descriptions, including 25 new taxa, are documented in the systematic section.

3. A third goal is to further refine the younger part of Wilson’s (1984d¹, 1987, 1988; Morgans et al. 2004) dinoflagellate biozonation for New Zealand, to:

- improve resolution, if possible;
- clarify an ambiguous boundary occurring between the *Wetzeliella hampdenensis* and *Wilsonidium tabulatum* zones (Morgans et al. 2004, p. 149);
- incorporate more common taxa, which are not restricted to particular ecological settings.

This goal has been progressed (I would not claim to have written the final word on any part of the zonation) by replacing the *Wilsonidium echinosuturatum* and *Wilsonidium lineidentatum* Zones with three new zones and the establishment of a new zone straddling the Eocene-Oligocene boundary, as discussed in the *Biostratigraphy* section.

Previous Work

Previous accounts of Paleogene dinoflagellate cysts from mainland and near-shore New Zealand include Deflandre 1933, Couper 1960, Wilson 1967c, 1968, 1977, 1978, 1982a, 1982b and 1982c, Clowes & Morgans 1984, Wilson 1985, Clowes 1985, Wilson 1988, Beggs et al. 1992, Strong et al. 1995, Wilson & McMillan 1996, Edbrooke et al. 1998, Crouch 2001, Willumsen 2003, Morgans et al. 2004, Willumsen 2004, Hollis et al. 2005 and Clowes & Wilson 2006. The majority of the publications describe material from localities in eastern New Zealand ranging from Hawkes Bay to Otago, although Beggs et al. 1992 deals exclusively with material from petroleum exploration wells in the offshore Taranaki Basin west of North Island.

Of the several papers dealing with detailed taxonomy, the two most significant contributions are Wilson 1967c and Wilson 1988 which together include full systematic descriptions and stratigraphic ranges for over 35 dinoflagellate species. These form the basis of the current New Zealand-wide dinoflagellate zonation for the Paleocene and Eocene, part of which is also used in Australia (Wilson 1984d, 1985, 1987, Partridge & Dettmann 2003, Morgans et al. 2004). Recent refinements to parts of the scheme have resulted from the doctoral research studies of Crouch (2001) and Willumsen (2003).

However, the Late Eocene and Early Oligocene dinoflagellate cyst fossils of New Zealand have been relatively little documented compared to older sections. The earliest publication is Deflandre 1933, in which a siliceous dinoflagellate, *Lithoperidinium* (now *Peridinites*) *oamaruense*, is described from an Oamaru diatomite, and then there is a hiatus until a small string of publications by Wilson (1982a, 1982b, 1982c, 1985, Beggs et al. 1992, Wilson & McMillan 1996) and the present writer (Clowes & Morgans 1984, Clowes 1985, Clowes & Wilson 2006).

¹ References are cited without commas separating the authors’ names and dates of publication. Where a researcher is referred to in person, any supporting references are listed in parentheses, generally without repeating the author’s name.

Materials and Methods

Sample Preparation and Housing

The fossil locality numbers, denoted by “f” and recorded in the New Zealand Fossil Record File, refer to the NZMS 260 Topographical Map Series.

Standard preparation techniques – comprising hydrofluoric acid digestion, heavy liquid flotation (SG = 2.0), and oxidation in Schulze’s reagent – were used throughout. The practice of oxidation is now thought to selectively remove certain cysts, and is used with more caution than in the past. Most (all but eight) of the samples used in this study, however, were prepared long ago: many as early as the 1970s, and are likely to have been treated to approximately 15 minutes or more of oxidation. Moreover, it remains true, even today, that oxidation is a simple, practical technique which yields good results.

Strew slides are identified by a laboratory preparation number prefixed by the letter ‘L.’ Single grain mounts were prepared, wherever possible, to obtain clean, oriented specimens for photography. These were hand-picked from glycerine jelly with a mounted needle and are identified by a serial number prefixed by the letters ‘SM.’

L and SM numbers refer to the corresponding catalogues maintained by GNS Science, Lower Hutt, New Zealand. All rock samples, palynological residues and prepared slides will be deposited in the collections of GNS Science.

Stratigraphic Treatment

In the pioneer days of New Zealand geology, Thomson formulated a system of local stages for the New Zealand marine sequence (Thomson 1916). The philosophy represented by this paper is at once the greatest single advance and the greatest impediment to further progress in New Zealand biostratigraphy today. The scheme allows for the convenient pigeon-holing of New Zealand sediments into an overall succession, with a resolution at least equal to that of the international standard. However, the wholesale continued use of Thomson’s stages could lead us into a parochial science, born and bred in isolation.

Globally, biostratigraphic data are increasingly reported in international units – stages anchored to GSSPs or magnetostratigraphic chrons – and this trend appears to be gaining some acceptance locally as well. Cooper 2004 represents a major milestone in our coming of age. Following this major undertaking, it is now possible to correlate almost any local stratigraphic datum with the international chronology (Table 1). Thus, a major objective of this study has been to relate the New Zealand stage material to more regional data.

However, to me, there seems little point in simply substituting one set of problematic units for another – worse, indeed, because at least the New Zealand stages are relatively well-agreed by practising geologists and defined by the paleontology of relatively few organisms (most New Zealand Cenozoic stages are essentially foraminiferal zones) whereas definitions for many international stages are still being agreed.

The samples used in the present study are all dated independently of the study itself, generally by means of foraminifera (or interpolation from other samples which are dated by foraminifera), although palynological results are also important (e.g. in the Puketeraki section).

Although the distinction rarely surfaces in the text, the underlying data for this study consistently distinguishes between “sections” (a delimited sequence of sediments at a particular locality) and “collections” (a sampling made from a particular section, made on a given day or

Ma	NZ Stage	Intl Stage	Chron
33		Rupelian	C13n
34			C13r
35	Runangan (Ar)	Priabonian	C15r
36	Kaiatan (Ak)		C16n
37			C17n
38			
39		Bartonian	C18n
40	Bortonian (Ab)		C18r
41			
42			C19r
43			C20n
44	Porangan (Dp)	Lutetian	C20r
45			
46			
47	Heretaungan (Dh)		C21n
48			C21r

Table 1: Approximate correlations between New Zealand and international stages; after Cooper 2004.

a few successive days). It is assumed that the sequence of samples from a single collection is precisely known. But, because different collections may be made years apart, and even the most reliable of landmarks can change over time, it is not assumed that the exact ordering of samples combined from different collections can be exactly known. Thus, for example, when a composite section was assembled for the main species range chart given in Appendix 2, only a single collection from each section was utilised, so as to avoid the uncertain ordering of samples from overlapping collections.

Range Charts

The stratigraphic ranges of various taxa are presented (Appendix 2) as a series of range charts. Individual charts are presented for a handful of genera, for which the member species are sufficiently numerous, common, and distinctive to make it worthwhile to do so. These are referenced from the appropriate systematic sections.

Additionally, a composite range chart is provided for all taxa which have been found to be stratigraphically useful in the studied interval. The column for this chart was assembled from various sections by hand. Samples were selected so as to avoid uncertain correlations. As noted above, only a single collection (generally the most extensive) from each section was utilised, so as to avoid the uncertain ordering of samples collected on different occasions.

In all cases, the charts were prepared programmatically from raw occurrence records, ignoring identifications marked as uncertain. Rows in the charts, corresponding to individual samples, were omitted if they contained neither a FAD nor a LAD for any taxon included in the chart.

Descriptive Terminology and Notation

General

Descriptive terminology generally follows Evitt et al. 1977, Stover & Evitt 1978, Evitt 1985, and Fensome et al. 1993b, extended by a small number of additions proposed by subsequent authors. A schematic diagram, illustrating the most fundamental features of dinoflagellate morphology is reproduced in Text-Fig. 1, and many of the important individual terms employed here are defined in the glossary.

This contribution adopts the recommendation of Norris (1978a) to omit the unnecessary para- prefix from terms such as paraplate, parasuture, and so on.

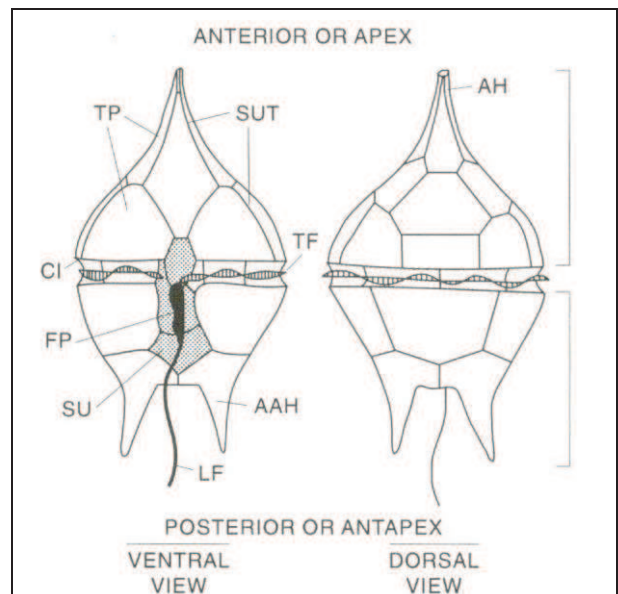
It adopts the most popular of the tabulation notation systems, based on Kofoid's original, because it is a strictly descriptive notation system. Although there are others, such as the Evitt-Taylor and Edwards systems, and no doubt each has some advantages (e.g. see Fensome et al. 1996), they share a common failing in attempting to codify presumed plate homologies within the notation itself. While there may yet come a day when these homologies are so well-understood that they acquire near-factual status, for the present they remain interpretive, and interpretation has no place in a descriptive notation.

Archeopyle Morphology

Detailed archeopyle morphology is nowadays considered less important than it once was ("highly overrated" in the words of Evitt 1985, p. 280). Nevertheless, it still has its place and many genera in widespread use today are distinguished by archeopyle characteristics and little else (e.g. *Cerebrocysta* and *Pyxidinopsis*). Indeed, the rather fragile distinction between the subfamilies Deflandreioideae and Palaeoperidinioideae is entirely based upon archeopyle characteristics (Fensome et al. 1993b, p. 129, text-fig. 133) with the genus *Phthanoperidinium* uncomfortably straddling both.

Two particular points are noted here:

1. An archeopyle metric widely employed in the description of peridiniaceans is the transverse archeopyle index (width of the widest part of the archeopyle divided by the total width of the cyst at the same "latitude"). Lentin & Williams 1976 (p. 22) also defines a "transverse archeopyle ratio" (not to be confused with the unqualified term, *archeopyle ratio*, e.g. as defined in Evitt 1985, p. 133) but Lentin & Williams's ratio is



Text-Fig. 1: Schematic diagram, illustrating the most fundamental features of dinoflagellate morphology. AH = apical horn; AAH = antapical horn; TP = plates; SUT = sutures; CI = cingulum; TF = transverse flagellum (not fossilised); FP = flagellar pore; SU = sulcus (shaded area); LF = longitudinal flagellum (not fossilised). The upper or portion of the cysts, anterior to the cingulum, is known as the episome, and the posterior portion as the hyposome. [After Fensome et al. 1996]

algebraically equivalent to the index $[1/R = (1/l) - 1]$ and so it adds no new information. Specifically, it should not be used (e.g. as in Lentin & Williams 1976, table 7) to provide a second dimension on a scatter plot. It is here proposed that use of the transverse archeopyle ratio metric be discontinued altogether.

All of the numeric archeopyle metrics presented herein are transverse archeopyle indices.

2. Here, and in a previous study (Clowes & Wilson 2006), certain species attributed to *Pyxidinospis* and *Corrudinium* were observed to possess a distinctive plate 3" which is very narrow at the top, lending a roughly triangular appearance to the archeopyle. The term "subtriangular" is applied to this morphology, and "pentagonal" to the usual, *Gonyaulax*-style of precingular archeopyle, in which the top margin is broader and typically angled where the suture between plates 2' and 3' connects.

Density of Ornament

A common characteristic of several different kinds of surface ornament – whether a reticulum, or rugulum, or whatever – is the density of the ornamental features. Typically in the literature, ornament is described using absolute measurements. However, ornamental features often scale in proportion to the overall cyst diameter. Recognising this, an approach experimentally used in this study is to count the number of ornamental "units" across the visible diameter of the cyst.

The approximate measure is obtained simply by counting across a number of radii and averaging the counts for \pm round forms; across the cingulum for peridinioids. I'll revisit the wording of this section to address any ambiguity.

It might be expected that this number becomes difficult to ascertain as one approaches the ambitus, or limb, of the cyst, where the surface retreats until it becomes perpendicular to the observer. In practise, however, an approximate measure is easy to obtain, quicker than absolute measurement, and automatically compensates for differences between small and large individuals. It has been found to have considerable merit.

A Note on Illustrations and Descriptions

A principle adopted in the preparation of this document is that illustrations without accompanying descriptions are completely useless, and descriptions without accompanying illustration are not greatly better. Accordingly, descriptions have been provided for many taxa, even if they be well-described already, and supposedly well-understood. Any taxonomist who has tried to assemble a dataset for cladistic analysis – even for such a well-known taxon as *Deflandrea*, for example – is well-aware that observations for corresponding characters of most species are difficult to locate in the literature. Comparable descriptions of even a few taxa are difficult to come by, and broad datasets, including many taxa, rare indeed.

As a consequence of the second part of the proposition, almost all of the taxa identified during the study have been illustrated by at least one specimen, the result being something in the order of 90 plates. The intention is that all of my identifications can be readily verified by the reader, who may then make an informed decision whether or not to include the occurrences reported here into their own synonymies. Merely listing a taxon name as "present" does not afford such confidence.

In respect of the photographs themselves, digital images were cropped and sometimes rotated, using Adobe Photoshop. However, no images have been enhanced by any means – including brightness, contrast or sharpness manipulation – nor has any debris close to the imaged specimens been masked. I have attempted to produce published images as close as possible to the first-hand experience of seeing the specimens down a microscope.

Many of the dinoflagellate descriptions provided below are computer generated. This is an approach to taxonomic description which is becoming increasingly popular. Observations are collected in some kind of database – perhaps something as simple as a spreadsheet – and computer generate the description text, or at least a draft of it, from there. Some of the practical advantages of this technique are that it ensures consistency of the format and coverage of features, and, because the author is typically compiling descriptions from raw data in a database anyway, reduces the likelihood of copying errors.

A similar approach was attempted here, with the dinoflagellate descriptions only. Results were mixed.

I took some pains to generate text in an acceptable final form. Once computer-generated text (of any kind) has been hand-edited, it can no longer be recreated if a new observation requires a change to be made to the base data, unless one also reapplies the manual changes. This requires keeping a record of all such manual changes which, for a large database, is a considerable overhead., which does not require subsequent hand-editing. In practice, however, I found that fully computer-generated descriptions were often inferior to those that were "hand written" and some manual editing was necessary in many cases. Notwithstanding these few shortcomings, the computer generated descriptions provided a useful place to start, and, I believe, saved a great deal of time.

Rather than a series of observations ("character states") being attached to fixed set of morphological features ("characters"; think of columns in a spreadsheet), the characters themselves are also defined in a table, together with various annotations describing their relationship to one another. This nuance permitted new characters to be defined, or existing characters to be modified, without any requirement to change the programme which generates the descriptions, and was found to be very effective.

Exactly the same table of characters and character states was also used to generate the keys described below. This approach ensured consistency between the descriptions and the keys, and, assuming the keys are able to resolve of all taxa, further ensured that the descriptions are truly diagnostic – at least within the context of taxa defined in the tables. Certain character states are flagged as unsuitable for use in the keys. Typically, exact plate counts, especially of minor series such as the sulcal plates, are not useful in keys, either because they are variable between individuals which we would otherwise recognise as belonging to the same species, or because they are too difficult to observe in all but the most perfect specimens. The keys are discussed further, below.

Identification Keys

Identification keys are common in modern floras, yet, despite an early outing in the influential Evitt 1985, and some notable exceptions such as Jan du Chêne et al. 1986a, for some reason the technique does not seem to have become widespread practice in palynological studies. Some limited use of keys for selected genera and higher taxa has been introduced in the present endeavour. Some, typically those for supra-generic taxa have been assembled by hand; others are computer-generated from the table of morphological features (“characters”) and observations (“character states”) for each species.

A key comprises a number of questions, or decision points (“is the operculum free or attached?”) known as nodes, from which arise one or more branches, depending upon the answer. Near the beginning of a typical key, most branches will lead to further questions. Later, though, the branches will lead to answers from which no further branches arise (“leaves”). Ideally, most of these will provide resolved identifications.

At the first node in a key, and at each subsequent node, are assembled one or more taxa, each taxon having one or more characteristics and its associated character state. An artificially simplified set for a key to subspecies of *Hystrichosphaeridium tubiferum* might look something like this:

Taxon	Character	Character State
<i>H. tubiferum</i> subsp. <i>brevispinum</i>	archeopyle type	apical
	operculum attachment	free
	length of processes	less than diameter of body
<i>H. tubiferum</i> subsp. <i>tubiferum</i>	archeopyle type	apical
	operculum attachment	free
	length of processes	more than diameter of body

In the special case where there is only a single species present, then we have arrived at a leaf and the only task required is to write down the “answer.”

In the case of non-leaf nodes, however, we have a more complex task. The first decision is which character is best to distinguish between the taxa. One approach would be to calculate the outcomes of using each character in turn, potentially carrying this calculation forward through many nodes, and choose the best approach in retrospect. Where there is only a small number of taxa and characters, it might even be possible make an exhaustive calculation of every possible key. Many chess- and other game-playing programmes use some variation of this technique.

The computer programme employed here, though, takes a different approach. Instead of calculating many outcomes, and retrospectively choosing the best character, a heuristic is used to try to *predict* the best character to use. This approach may occasionally produce suboptimal results, but it is no less “accurate” in the sense that it doesn’t make actual errors, and keys are able to be constructed much more quickly. The entire systematics section of this thesis, together with all keys, descriptions, references, range charts, text-figures and plates, is generated in three or four minutes on a regular desktop PC.

The best character to use at a given node is chosen by scoring all characters using a handful of criteria, as follows:

- The choice of a specific character divides the taxa into one or more groups, depending upon the states each has for that character. Dichotomous keys require that the taxa at each node are always divided into two groups (i.e., that the node has two outgoing branches); polytomous keys (as these are) do not have that restriction. One outcome which is useless, however, is where a character produces only a single group; i.e., it cannot differentiate between any of the taxa. Such characters are assigned a high (effectively infinite) negative “score”.
- In both dichotomous and polytomous keys, it is considered best for the groups to be of approximately equal size. This criterion promotes shorter keys. The programme handles this criterion by calculating the difference between the sizes of the smallest and largest group, multiplying by a weighting factor, and setting the resulting number as a negative score against the character being assessed.
- The overall number of groups is also multiplied by a weighting factor, and set as a negative score against the character being assessed. This criterion favours characters which divide the taxa into fewer groups:

ideally two (producing a dichotomous node) but the weighting is not overwhelming. Nodes with three or four outgoing branches are common in the following keys.

- Finally, the number of “unknown” character states is multiplied by a high weighting factor, and set as a negative score against the character being assessed, so as to favour characters for which the data are complete, at the expense of characters which are poorly understood. (Characters which are ambiguous, difficult to determine, or problematic in some other way, are simply not made available to the key generating programme in the first place.)

Having evaluated each character against all criteria, the one with the best score is chosen for use at the current node, and taxa are divided into groups depending on their states for the chosen character. In cases where the state is variable (“the operculum is free or attached”), both character states are evaluated. Thus it is possible for a single taxon to pass down two (or more) branches from a node and so appear at more than one leaf in a key. Then, taking each group in turn, the programme invokes itself (an operation known as “recursion”) to consider the subset of taxa, characters, and character states for that group. The idea of recursion can seem astonishing to non-programmers, but in fact it is standard practice in cases where a large data set is to be broken into subsets, and each subset treated the same way in turn.

The programme terminates successfully when a leaf is reached. Here, it simply prints out the name of the remaining taxon and “returns” without invoking itself further.

However, there is also an “unsuccessful” termination, which arises when there is more than one taxon left, but no character can be found to differentiate between them. This situation arises when there is insufficient morphological data available to differentiate between genuinely different forms, and also in the case of true synonyms. The programme explicitly checks for this possibility and simply treats it as a special kind of leaf. It prints out a list of the undifferentiated taxa, and returns. Some of these cases have been picked up in earlier drafts of this document, and additional characters defined so as to permit full resolution.

In practice, the keys so produced were found to be of highly variable quality, and the majority are omitted in the following text. Only a few have been retained where they seem to make a useful contribution to the discussion. In other cases, minor problems have been overlooked or corrected by hand, this being a primarily taxonomic study rather than a computer science project. Before persisting any further with this initiative, I believe it would be necessary to improve the computer programme considerably, so as to better accommodate multiple character states, and to support both phylogenetic and phenetic keys.

Taxonomic Approach

Scope

Although fossil palynomorphs are taxonomically diverse, in practice, individual taxonomists do tend to specialise. In New Zealand, at least, the tradition has been for our researchers to specialise in either terrestrial pollen and spores, or marine acritarchs, dinoflagellates and various “algae”.

A variety of palynomorphs has been encountered during this study. I have not attempted to report them all. Only dinoflagellates, acritarchs, and a handful of PterospERMATALES have been studied.

Introduction and Motivating Philosophy

Sir Earnest Rutherford, who was born in Nelson, near what is now Brightwater, before travelling to Manchester and discovering the atomic nucleus², once famously proclaimed that “All science is either physics or stamp-collecting” (e.g. Gallagher & Appenzeller 1999). While strongly disagreeing with this assessment, it is nevertheless true that, without some unifying theory behind it – evolution, obviously – a catalogue of dinoflagellate taxa is, indeed, little more than a stamp album. Describing and illustrating taxa has its uses, certainly, but alone it is only part of the story. It is phylogeny that breathes meaning into the names, and makes the pictures tell a story. In my first period of working with dinoflagellates, some twenty or more years ago, I was unsettled by the lack of it (the words “gonyaulaccean lineage” on p. 29 of Clowes 1985 were a poor attempt to fill a perceived vacuum) and in the present study, I was determined to try out the new developments which have been made since then.

The science of biological taxonomy has undergone a revolution during the past 50 or so years, initiated at least in part by ideas published by Hennig in 1950 and 1966, and the last of the dust has yet to settle, even now. Some cherished morphological constructs have been eroded as the cladistic movement has gained traction and brought the phylogenetic world-view into collision with established form-taxonomy.

The debate has been robust, intemperate at times, and the cladists have – easily, in my view – won the high ground from a purely theoretical standpoint. There have even been proposals to eventually replace the Linnaean nomenclatural system currently in use (see, for example, Brochu & Sumrall 2001 and references therein). But, although few have been brave enough to challenge the logic of adopting a phylogenetically-based taxonomy on theoretical grounds, some grass-roots dinoflagellate (and other) paleontologists have simply refused to acknowledge that anything is fundamentally different; they have continued organising their material exactly as they have always done or, arguably worse, have adopted phylogenetic frameworks merely as an alternative to alphabetical or some other arbitrary order.

One referee of a recent paper of mine asked, rhetorically, whether it would ever be possible to truly know the phylogenetic relationships between our taxa. Insofar as fossils are our objects of study, it can be said that morphology is the only objective evidence we have available, but this argument is a more than a little disingenuous: We can certainly deduce phylogeny in some cases, perhaps many. One of the earliest attempts along these lines was that of Eaton (1971), who examined some sequences of *Areosphaeridium* and close allies. Eaton’s sequences have been dismissed as “not phyletic” by some subsequent authors (e.g. Damassa et al. 1994, p. 4-5), because the break-up of the genus *Areosphaeridium* by Stover & Williams 1995, dispersed several of the species across two or three genera which are purported to belong to different families. It will later be contended herein that the analysis of Stover & Williams 1995 is fundamentally flawed, and that many of the species are not greatly different. Eaton’s lineages may yet prove to be phyletic, after all. However, whether they are or are not, in this particular case, is beside the point: As long ago as 1971 – more than thirty years ago – Eaton was able to propose a plausible evolutionary succession of fossil dinoflagellate cyst taxa. It is surely not beyond our means to effect similar work today.

Some other well-known papers which make the attempt to deduce the phylogeny of various dinoflagellate cysts are Davey 1969c (*Amphorosphaeridium* and *Cordosphaeridium*), Bujak 1976 (*Areosphaeridium* and close allies), Bujak 1979 (*Rhombodinium* and *Gochtodinium*), Costa & Downie 1979a (Wetzeliellaceae), and Dörhöfer & Davies 1980 (Rhaetogonyaulacineae). However correct or otherwise the proposed lineages are eventually determined to be, these examples should be inspirational. They prove that we *can* deduce phylogeny, with sufficient application. We certainly can do much better than we have done to date.

There are very pragmatic reasons to eschew a single-mindedly morphological taxonomy of dinoflagellates too. A key failing of any form-taxonomy to the working stratigrapher is that form-taxa have no *general* stratigraphic value: ranges can be discontinuous or of a length which defies credibility. Any stratigraphic relationship between form-taxa is coincidental. Consider the following real-world situation: A form-taxonomic group – say the dinoflagellate genus *Pyxidinospis* – contains species ranging geographically from the North Atlantic to New

² “Geiger recalled that, early in 1911, ‘one day Rutherford, obviously in the best of spirits, came into my room and told me that he now knew what the atom looked like and how to explain the large deflections of alpha particles’” (Weinberg 1993, p. 127).

Zealand, and temporally from Late Jurassic to Quaternary. The taxon thus defined has very little to offer the practising paleontologist. Identifying a specimen as belonging to this genus leaves the researcher none the wiser. (Of course there are some dinoflagellate genera which are genuinely, and perhaps unavoidably, like this, though *Pyxidinosopsis* isn't one of them – refer to the Systematic section.)

It is obvious (or, at any rate, it will be adopted as such in the following text) that the phylogenetic approach has the greater interpretative and predictive value. As noted in Grimaldi & Engel 2005, p. 15: "Besides identifying lineages of organisms, [a phylogeny] can record the success and demise of those lineages, and perhaps even provide explanations for these outcomes. Phylogenies also allow the interpretation of evolutionary patterns. Another salient scientific advantage to understanding phylogeny, though, is that it allows predictions. Armed with knowledge about the closest relatives, accurate predictions can be made about any species, and so phylogenies explain very well. There are many ways to classify organisms – things good to eat, bad to eat, things that sting – but a phylogenetic classification, one that reflects and summarises phylogeny, is the most useful and a goal of modern systematists."

While far from blind to the *practical* difficulties and shortcomings of the phylogenetic scheme followed herein (Fensome et al. 1993b), it seems to me to offer the greatest hope for the future. Developing a better form-taxonomic framework, perhaps something analogous to Potonié's *turma* concept (Traverse 1988) used for pollen, might yield better short-term results, but to me it seems backward-looking and carries the additional risk that it may simply detract from the collective effort even further. Working with the phylogenetic philosophy and evaluating its contribution to (or detracting from) the study is the key element of this research project.

Suprageneric Classification

Over the past few decades, a number of authors have attempted to synthesise suprageneric classification schemes for all or part of the Dinoflagellata. A handful of examples, by no means comprehensive, are Eisenack 1961, Sarjeant & Downie 1966, Norris 1978a, b, Bujak & Davies 1983, Taylor 1987d, 1990. Some of these schemes were early attempts at a phylogenetic approach; others phenetic (i.e., presenting a form taxonomy). Some considered only fossil cysts, or considered modern and fossil dinoflagellates separately; others attempted to unify fossil and modern classifications.

By far the most comprehensive attempt to date is Fensome et al. 1993b. (A number of the authors of earlier attempts, mentioned above, are bundled up in the "et al.") This landmark work provides a suprageneric classification for both modern and fossil dinoflagellates which is explicitly phylogenetic.

In this work, the Dinoflagellata is divided into two subdivisions (subphyla) and three classes, primarily on characteristics of the nucleus (obviously a neontological feature). Lower taxa – comprising five subclasses, fourteen orders, ten suborders and fifty six families – are recognised on the basis of tabulation patterns, which can, at least in principle, be recognised in both fossil and modern material. Below the level of family, a broader variety of features is employed. This is the part of the scheme which is least systematised, and, one gets the impression, most likely to be modified in the future for that reason.

The phylogenetic philosophy underpinning the entire Fensome et al. work is made explicit as early as the third paragraph of the abstract, which is worth quoting in its entirety:

The classification, and the phylogenetic hypothesis that derives from it, supports the following premises: 1) that below the rank of class, amphiesmal structure, especially tabulation, is the most valuable and meaningful criterion in classifying dinoflagellates; 2) that the use of cell or cyst habit (i.e. general shape or morphology) in classifying dinoflagellates should be restricted in its use primarily to subfamily and, less commonly, higher rank; 3) that, although incomplete and despite the sporadic evidence of Paleozoic dinoflagellates, the fossil record supports a major adaptive radiation of dinoflagellates during later Triassic and earlier Jurassic times; 4) that the majority of living thecate dinoflagellate[s] can be interpreted as having either a peridinialean or gonyaulaclean tabulation, and that these tabulations, and hence the orders Gonyaulacales and Peridiniales, have been separate since at least the Early Jurassic.

A corollary to their premise is that ornamental features, *per se*, have less significance than plate topologies. This is an observation which deserves explicit recognition: It is quite evident that gross ornamental morphologies, such as spinose processes or whatever, recur again and again in taxa which are as distantly related as peridiniaceans and gonyaulacaceans. These kinds of features, while useful species-level distinctions, offer little insight at higher taxonomic levels. Indeed, it seems likely that ecological considerations exert as much control over the development of these features as do genomics.

It is with these concepts firmly in mind that the present study was undertaken.

Dual Nomenclature

It is quite contrary to the spirit of a phylogenetic classification to retain a dual nomenclature for motile and cyst forms of the same taxon. However, two major methodological difficulties stand in the way of a unified approach at present:

1. Although Fensome et al. 1993b does much to reconcile the higher taxa, there is still no usable correspondence between thecal and cyst taxonomies at the generic level.
2. In most cases the association of cysts, particularly of older fossil cysts, with motile forms is not convincingly established. It is this uncertainty which, for example, led Matsuoka et al. (1997) to recommend the retention of '*Hystrichosphaeridium*' *centrocarpum* and similar forms within the cyst genus *Operculodinium*, rather than in the thecal genus *Protoceratium*.

Consequently (and with some misgivings) I have followed the standard practice of using exclusively cyst taxa at the generic and species rank.

Splitting, Lumping, and the Use of Subspecies

Authorities differ in their interpretations of taxonomic boundaries, and no doubt always will. Those favouring fine division are colloquially known as splitters; the opposite extreme as lumpers. This contribution adopts the philosophy set out below.

Morphological breaks, or discontinuities, between taxa are sampling artefacts. If every organism that ever lived could be called to heel, it would be possible to assemble an insensible gradation from elephants to pond-scum. In the more prosaic phrasing of Brochu & Sumrall (2001, p. 754), "An evolutionary group exists because of common ancestry. The only natural boundaries for these groups are [splitting of lineages] and extinction." Richard Dawkins (2004) hammers home a final nail with a sledgehammer: "[W]e have a continuous historical lineage in evolution. At the borderline between any fossil species and its immediate predecessor, there must be some individuals about whom it is absurd to argue, since the *reductio* of such an argument must be that parents of one species gave birth to a child of the other. It is even more absurd ... [in the case of higher taxa]. These are evolutionary regions into which our zoological naming conventions were never designed to go" (p. 69).

A widespread though erroneous impression of the punctuated equilibrium hypothesis (Eldredge & Gould 1972) is that it conceives of evolution as proceeding in a series of quantum jumps, or saltations. In fact, punctuated equilibrium isn't, and never was, a theory of saltations. For authenticity, this is perhaps best explained by one of its original authors: "Our theory entails *no new or violent mechanism*, but only represents the *proper scaling of ordinary events* into the vastness of geological time. An isolated population may take a thousand years to speciate, and its transformation would therefore appear glacially slow if measured by the irrelevant scale of our personal lives. But a thousand years, appropriately recorded in geological time, is only an unresolvable moment, usually preserved on a single bedding plane, in the lifetime of species that often live for several million years in stasis" (Gould 1992; italics added).

Punctuated equilibrium is not relevant to the present study – it is concerned with the allopatric speciation of sexually reproducing metazoans (Eldredge & Gould 1972, p. 94) – but, even if it were, it would not represent a contradiction to the view presented in the preceding paragraphs. Notwithstanding one or two real saltations, if there are such things, as paleontologists we all believe in evolution, and we are all aware of transitional forms between neatly circumscribed taxa. Thus, whether they arise slowly or quickly, punctuated by stasis or not, divisions between taxa – morphospecies – are gradational and arbitrary. Published fossil taxa are simply convenient, though somewhat random, "signposts" scattered over a phylogenetic tree. The presence or otherwise of *known* intermediates has no phylogenetic meaning. Specifically, it is irrational to combine – to lump – taxa simply because intermediates are observed, rather than lying undiscovered in some rock we have yet to examine. In this respect I am an unapologetic splitter and quite reconciled to living with the imprecision inherent in gradational boundaries between taxa.

It is a commonly held view that taxa should be distinguished – split – where they have stratigraphic value; left combined otherwise. But this idea is equally absurd since we cannot know, *a priori*, which taxa will have future stratigraphic value, and which will not. Where consistent morphological differences exist, they should be recognised, and that's all there is to it. The reverse argument does have some merit, though. Different taxa, whose occurrences are widely separated in time or space, should not be lumped, in my opinion, even if morphologically very similar.

If we accept that species will be recognised, even where they may intergrade with one another, then the manner in which we employ subspecies suggests itself for review. Given that we are dealing with fossils, we are deprived of the semi-objective (at best) fertility and genome criteria available to neontologists. We must recognise that our decision is almost entirely arbitrary: practical usability alone can be our guide.

In the past, implementation of the subspecies construct has been quite inconsistent, with some authorities making extensive use of the concept and others ignoring it. Where it has been used, there may be some implied phylogenetic relationship, generally absent from our present use of higher order taxa. Developments of the past few years, however, have seen an increasing phylogenetic philosophy brought to bear above the genus level. Although that work is still far from complete, the new front line in our battle to understand these organisms more fully, lies at the level of genera and species. We must pick apart the old catch-all genera which have been used as dumping places for species with superficial resemblance, but no seriously implied kinship, and assemble a new taxonomy of genera reflecting true (or, at least, hypothesised) phylogenetic relationships. In that endeavour, subspecies are something of a distraction. Their time may yet come, but for the moment I have chosen to ignore the construct.

Nor have I yielded to the temptation to assign difficult forms to “complexes” or superspecies. Some specimens exhibit morphologies which are intermediate – sometimes in different and conflicting degrees for different characteristics – between neatly circumscribed taxa. They are difficult to identify, and that is just a fact of life. The taxonomist still has to stand up and commit to a view: otherwise his discipline becomes, indeed, “just stamp-collecting.”

Presentation of Findings

The findings of the study are presented as follows:

- A brief review – essentially annotated references to the available literature – of the localities and geology of the sections from which the samples were drawn is provided next. The localities occur across the country, including both North and South Islands; both west and east coasts.

A list of the 80 or so individual samples examined in this study is provided in Appendix 1.

- Next, the Systematics section describes almost all of the acritarch and dinoflagellate taxa encountered in the study, including a small number which could not be identified to even generic level. Only the poorest and most ambiguous material is omitted from the Systematics section entirely.

An extensive collection of more than 1000 individually mounted specimens was harvested from a number of samples which were found to be especially rich, well preserved, or which contained new taxa.

Where sufficient material, of sufficient quality, was found, new taxa have been described. If the material was too sparse, or poor, to be reliable, informal tags are provided. (As the writer encountered new forms during the study, informal tags were applied consecutively. Subsequent identification or description, however, means they are no longer so.) The outcome has included descriptions of 25 new taxa, including two (*Corrudinium regulare* and *Corrudinium otagoense*) published in an earlier paper (Clowes & Wilson 2006).

It is recognised that description in a limited-run thesis does not constitute effective publication in the sense of the International Code of Botanical Nomenclature (Article 29). However, it is intended to publish the present text with minimal modification as soon as practical, so the usual trappings of formal publication (specifying holotypes, repository, etc.) have been provided in preference to using manuscript names.

All taxa are described by means of morphological distinctions. As further elaborated in the Conclusion section, this study does not take the bold step to suggest a new taxon based wholly on geographical and temporal criteria. Doing so, however, is clearly a rational extension to the present ideas, and such an approach is advocated as worthy of further investigation.

- A Biostratigraphy section discusses the dinoflagellate biozonation for New Zealand, as it is presently known, and presents a number of proposals to refine the scheme, including:
 - a. redefining zone boundaries using the lower boundary only, so as to eliminate the possibility for gaps or overlaps to arise;
 - b. replacing the *Wilsonidium echinosuturatum* and *Wilsonidium lineidentatum* Zones with three new zones;
 - c. replacing the *Wilsonidium tabulatum* Zone with an approximate equivalent defined by the more commonly found *Rhombodinium glabrum*; and
 - d. defining a new zone marked by the FAD of *Stoveracysta kakanuiensis* at or very close to the Eocene-Oligocene boundary.
- Finally, a concluding section revisits the principal taxonomic theme of the study, and summarises the major findings.

Appendices and plates complete the document.

Study Areas

A map locating the broad study areas described below, is provided in Text-Fig. 2.

Waikato

Basement in the region is provided by the massive, largely undifferentiated graywackes of the Torlesse Supergroup. Graywackes of the Manaia Hill Group, ranging in age up to late Jurassic, crop out east of the Waipa Fault. Over this, a transgressional sequence, the Te Kuiti Group, comprises basal coal measures overlain by marine sediments, deposited as the early Cenozoic shoreline moved south and westward.

The economically significant Waikato Coal Measures are of Arnold age; further south, the coals are Landon: possibly as young as Duntroonian at Tongariro National Park (Suggate et al. 1978, p. 449). The oldest marine beds are Whaingaroan.

Old Mountain Road

The Old Mountain Road site (Text-Fig. 3) is located at grid reference S14/937707, below a prominent bluff, 60 m south west of the summit of Old Mountain Road, situated approximately half way between Hamilton and Raglan, Waikato, North Island, New Zealand.

Hawkes Bay

Rocks of the Hawkes Bay area comprise predominantly marine sediments ranging from about mid-Cretaceous to Quaternary in an almost complete sequence.

General accounts of the geology of the area include Kingma 1971.

Pre-Cretaceous greywacke basement is overlain throughout the region by sediments laid down in a shallow synclinal setting. Material was apparently derived from the east and southeast during the Cretaceous, and afterwards from the west. The rate of deposition was slow prior to the Miocene; sediments are generally thin, fine grained, and conformable throughout the Eocene and early Oligocene.

Akitio River

The Akitio River flows through the east coast ranges of north Wairarapa, New Zealand. The general geology of the Akitio area is described in Neef 1992. The locality for the sample analysed in the present study is shown in Text-Fig. 4.

Te Uri Stream

Te Uri Stream is located on the southern flank of the Whangai Range in southern Hawkes Bay, North Island, New Zealand.

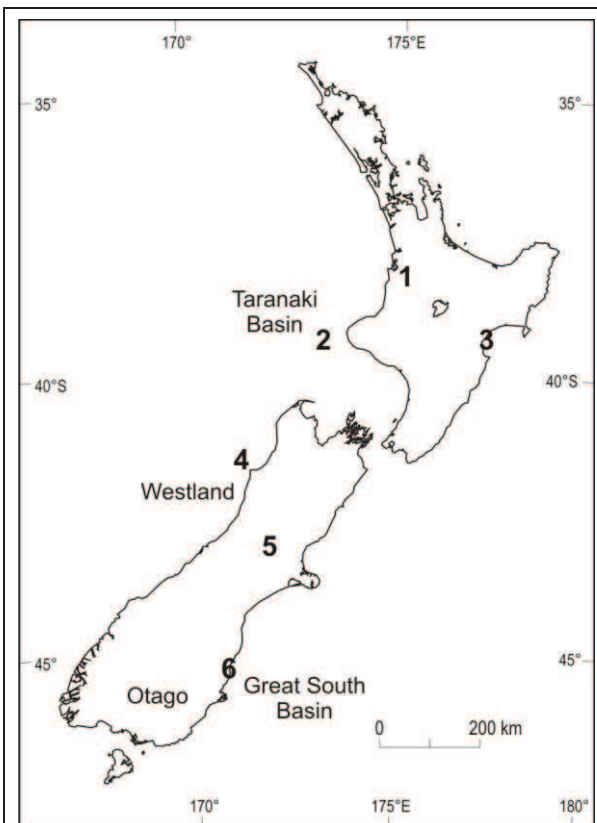
The type Porangan material analysed in this study was collected from between grid reference U24/031959 and U24/032959 (Text-Fig. 5). It is the original stratotype for the entire Dannevirke Series, although exposures are often poor and stage boundaries seldom available for close study.

Waipawa Section

Waipawa township is located on State Highway 2, north of Waipukurau, North Island, New Zealand.

The area was mapped by Kingma 1971. The section itself is a standard for the Dannevirke Series, supplementing the incomplete type section at Te Uri Stream (Hornibrook & Harrington 1957, Wilson 1988). Columns and a taxon range chart for Waipawa Section are provided in Wilson 1988.

The section has been extensively studied for foraminifera (Hornibrook & Harrington 1957; Hornibrook 1971; Jenkins 1971), calcareous nannofossils (Edwards 1971), and palynomorphs. Couper 1960 describes some terrestrial palynomorph taxa from the section but, of marine taxa, he records only the presence of unspecified



Text-Fig. 2: Map of New Zealand locating the broad study areas discussed herein:

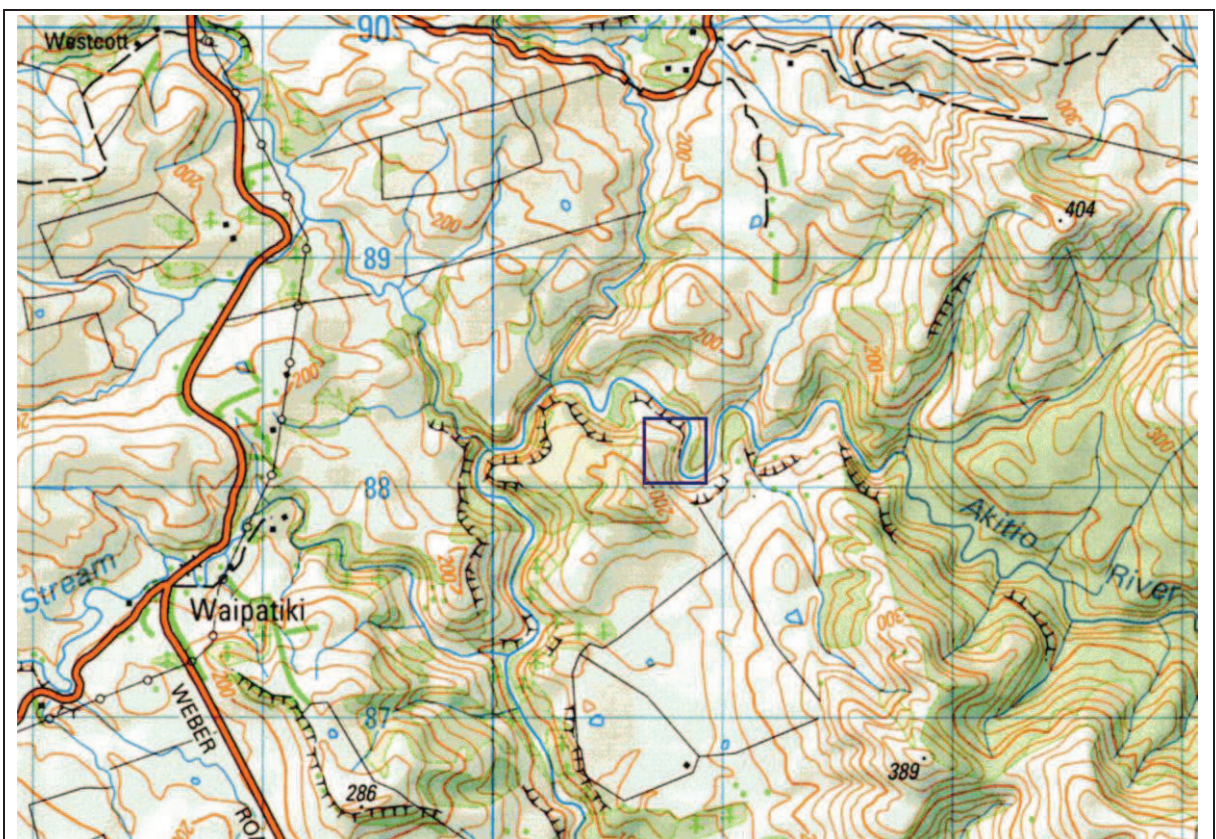
(1) Waikato, (2) Taranaki Basin, (3) Hawkes Bay, (4) Cape Foulwind, (5) Central Canterbury, (6) Oamaru-Dunedin area, including Kakanui River mouth, Hampden Beach, Puketeraki, and Abbotsford.

microplankton. The earliest dinoflagellate taxonomy from the section is Wilson 1967c and the definitive account is provided by Wilson 1988.

The locality for the sample analysed in the present study is shown in Text-Fig. 6.



Text-Fig. 3: Location map for the Old Mountain Road sample.



Text-Fig. 4: Location map for the Akitio River sample.



Text-Fig. 5: Location map for the Te Uri Stream samples.



Text-Fig. 6: Location map for the Waipawa Section sample.

Westland

Upper Cretaceous coals are overlain, after a (probably region-wide) break, by Cenozoic sediments laid down in a transgression which lasted through to the Oligocene, when limestone (e.g., the Cobden Limestone) was

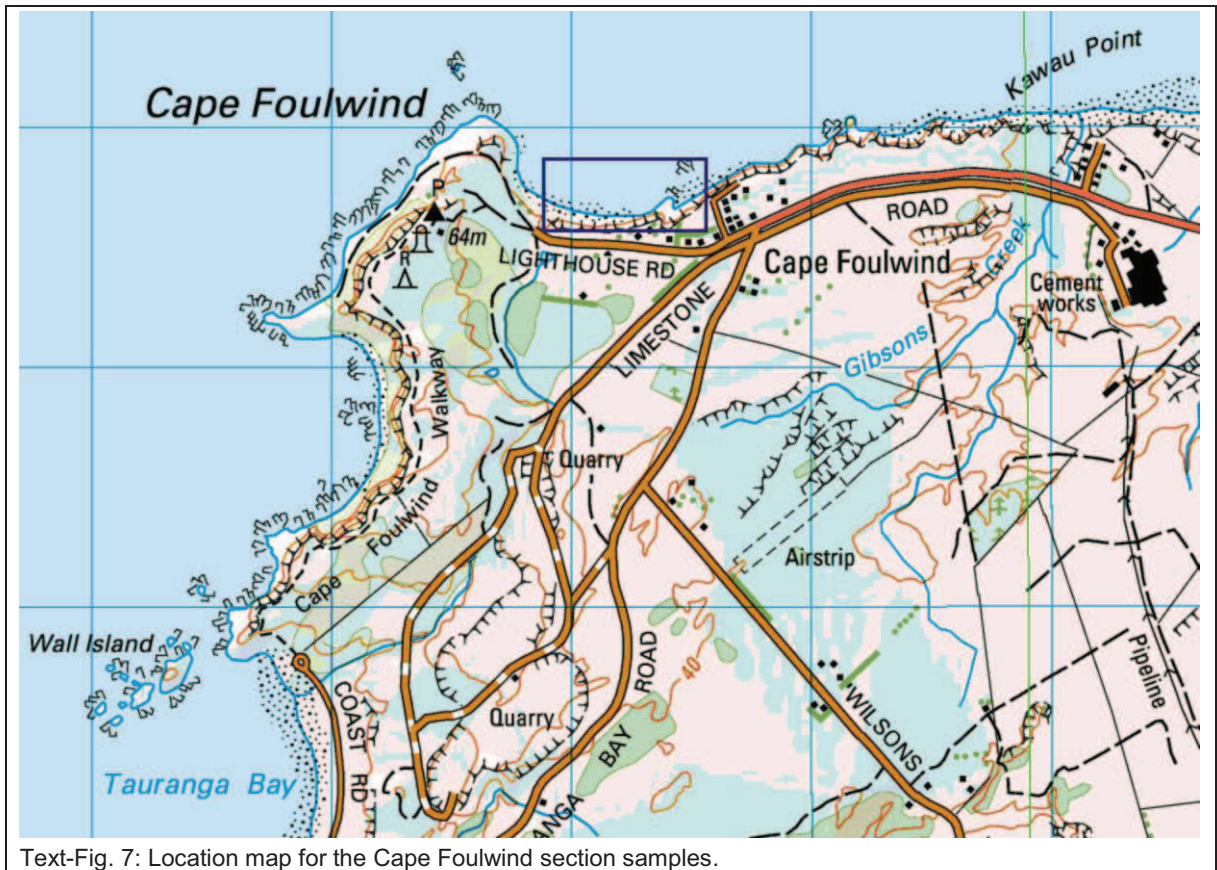
deposited in most areas, followed by a regressional sequence (e.g., the Miocene to Pliocene Blue Bottom Formation).

The transgressional sequence commences with coals, which generally young to the north (Suggate 1950, Couper 1960, p. 13-14), and include the economically significant Brunner Coal Measures, overlain by marine sediments ranging in age from ?Teurian upwards. The earliest marine sediments are Bortonian in the Greymouth Coalfield, Kaiatan in the Buller Coalfield. The Kaiata Siltstone may be wholly Kaiatan.

Cape Foulwind Section

Cape Foulwind forms a prominent headland on the west coast of the South Island, New Zealand (Text-Fig. 2). The section crops out along the base of the sea cliffs extending south from the headland, roughly between grid references K29/829386 and K29/834388 (Text-Fig. 7).

The sea cliffs along the west and north coasts of Cape Foulwind provide key reference sections through the Runangan and Lower Whaingaroan Stages.



Text-Fig. 7: Location map for the Cape Foulwind section samples.

Nine Mile Bluff

Nine Mile Bluff, where marine sandstones of probable Kaiatan age overlie brown coal, is located north of Point Elizabeth and the Grey River mouth, on the Westland coast (Text-Fig. 8).

Canterbury

Principal accounts of the general geology of the area include Gair 1959, Wilson 1956, and Wilson 1963.

Base comprises indurated Triassic or Jurassic rocks of the Torlesse Supergroup, overlain by late Cretaceous and early Cenozoic basal coals and marine sediments laid down as the shoreline migrated generally west and south. Transgression reached a maximum in the Oligocene, followed by regression associated with uplift of the alpine range.

Upper Eyre River

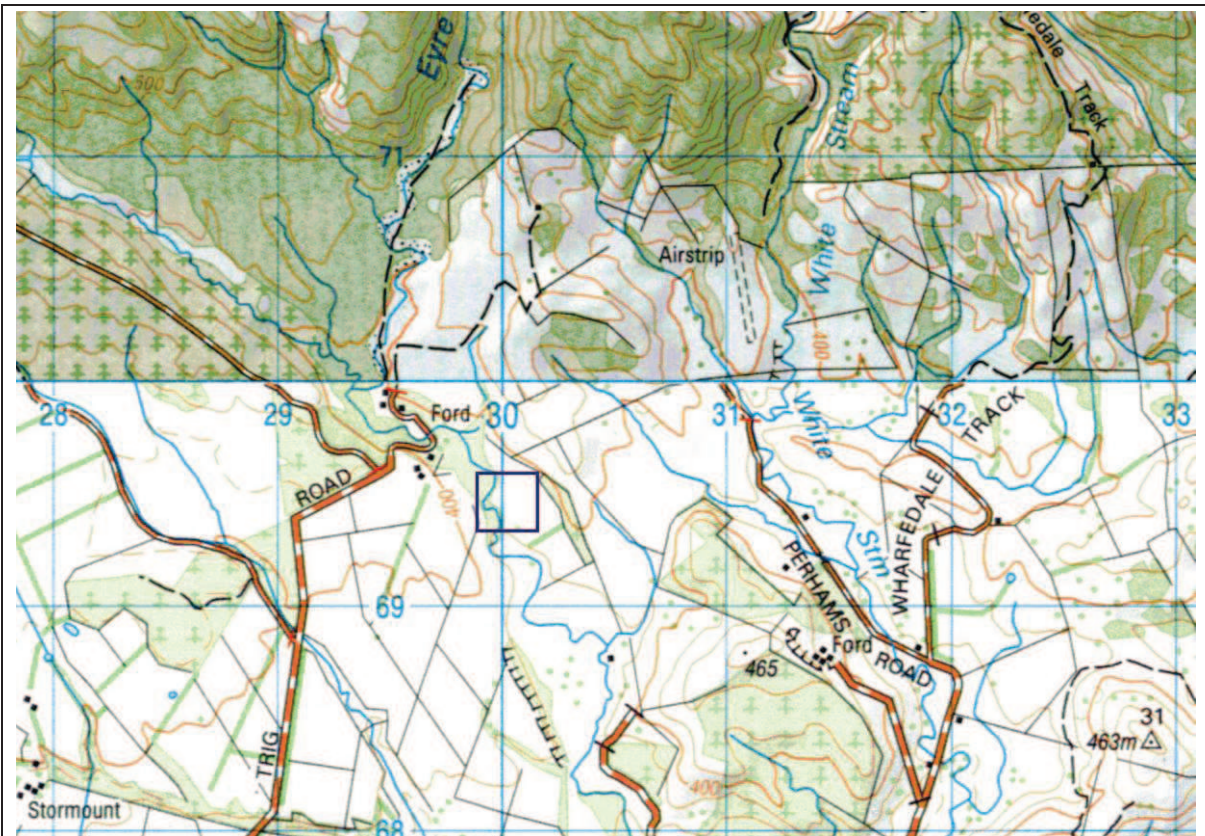
The headwaters of the Eyre River lie in the Puketeraki Ranges, north of the Waimakariri River and to the west of Oxford, central Canterbury, South Island, New Zealand (Text-Fig. 9).

The geology of the area is mapped by Gregg 1964 and further described in MacPherson 1947, McLennan 1981, and Wilson 1982c.

Dinoflagellate assemblages from two samples recovered from the area, at grid reference L34/294700, are described in Wilson 1982c.



Text-Fig. 8: Location map for the Nine Mile Bluff section samples.



Text-Fig. 9: Location map for the Upper Eyre River samples.

Oamaru-Dunedin

The Great South Basin and the on-shore correlative sediments of coastal Otago range from Late Cretaceous to mid-Miocene.

General accounts of the geology of the Oamaru area include Park 1918, Gage 1957, and Mutch 1963. A detailed allostratigraphic analysis is provided by McMillan & Wilson 1997.

Basement in northern Otago comprises a ?Cretaceous peneplain, principally of schist, which became inundated from the north, beginning in the latest Cretaceous, allowing the accumulation of marginal coals and fully marine sediments. Sedimentation appears to have ceased for a time early in the Eocene, and been reversed by erosion in places (Gage 1957, p. 16) before recommencing. Intermittent basaltic intrusion marked the late Eocene-early Oligocene interval, followed by slowing sedimentation through to the middle or late Oligocene, when sediment accumulation increased again.

Burnside Marl Pit

The Burnside Marl Pit (or Burnside Quarry) is located to the west of central Dunedin, South Island, New Zealand (Text-Fig. 10).

The section is described in Benson 1968.

A column and description of the sequence exposed in the Pit are provided in Wilson & McMillan 1996 (p. 4-5, figs. 8-11).

Descriptions of foraminifera (p. 5, 133) and dinoflagellate (p. 5, 128-132) assemblages for this section are provided in Wilson & McMillan 1996.



Text-Fig. 10: Location map for the M26 core (west) and Burnside Marl Pit (east).

Hampden Beach Section

Hampden Beach is located to the north of Hampden township, south of Oamaru, South Island, New Zealand (Text-Fig. 11).

The Hampden Beach area is mapped by Brown 1938 and the section has been well-known and repeatedly studied for many years, acquiring the working status of Bortonian stage lectostratotype (Cameron & Waghorn 1985, Wilson 1985, Hornibrook et al. 1989) owing to the poor exposure and fossil content of the original stratotype at Bortons, in the Waitaki River valley.

Low coastal cliffs expose an extensive section, ranging from possibly Teurian (Wilson & McMillan 1996, p. 13) to at least Bortonian. A stratigraphic column for the Hampden Section is provided by Jenkins based on unpublished work by D.A. Brown (Jenkins 1971, Column 3).

Previous paleontological studies include Finlay & Marwick 1940, Jenkins 1971 and Edwards 1971. Dinoflagellates are recorded from the section in Wilson 1967c, Wilson 1977, and, more expansively, in Wilson 1985 and Wilson & McMillan 1996.



Text-Fig. 11: Location map for Kakanui River mouth (north) and Hampden Beach section (south).

Jacksons Paddock

Jacksons Paddock is located near Cormacks, to the west of Oamaru, north Otago, South Island, New Zealand (Text-Fig. 12).

Relevant stratigraphic details for the Waiareka Volcanic Formation are provided by Gage (1957).

"*Lithoperidinium oamaruense*" of Deflandre (1933) is from a sample from Cormacks Top, near the Jacksons Paddock locality and probably from the same stratigraphic horizon. Organic-walled dinoflagellates from sample S136/f914, recovered from immediately below 'basalt' 20 m below diatomite in an exposure at Jacksons Paddock, is dated as Lower Runangan (Upper Eocene) on foraminifera and nannoplankton (Wilson 1982b).

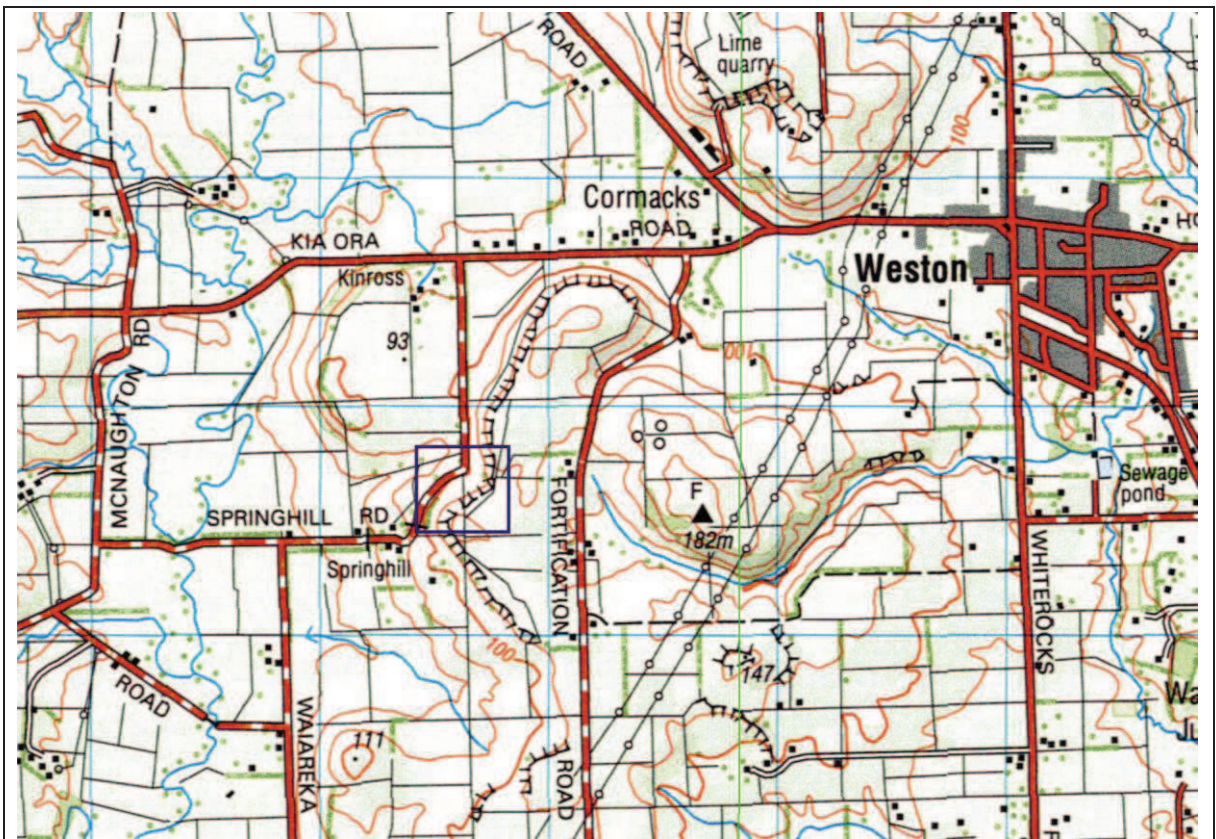
Kakanui River

The Kakanui River section is well-exposed for ~300 metres along the south bank of Kakanui River, south of Oamaru, South Island, New Zealand (Text-Fig. 11), approximately 300 metres inland from a sand bar across the river mouth, grid reference J42/446558.

The section includes a Runangan-Whaingaroan boundary, and maybe also an Eocene-Oligocene boundary within the early Whaingaroan (Clowes & Morgans 1984). Early reports include studies of the section's macrofauna (Gage 1957) and microfauna (Jenkins 1971).

The section exposes the Totara Limestone formation, comprising Runangan aged thin-banded calcareous tuffs and marls, passing up into a Whaingaroan polyzoan limestone, overlain by the coarse grey and brown tuffs of the Deborah Volcanics (Gage 1957, column S136/1; Clowes & Morgans 1984, text-fig. 2).

Previous dinoflagellate studies are reported in Wilson 1982b, Clowes & Morgans 1984, and Clowes 1985.



Text-Fig. 12: Location map for Jackson's Paddock.



Text-Fig. 13: Location map for the Puketeraki core.

M26 Core

The M26 core, grid-reference I44/109760, was the longest of 30 cores recovered from holes drilled in the Abbotsford area (Text-Fig. 10) following the landslide of August 1979 which damaged homes and required the permanent evacuation of a small residential subdivision.

Terrestrial palynomorphs from the core are provided in preliminary (Mildenhall 1979a) and expanded reports (Mildenhall 1979b) from the time of the landslide. Foraminifera and dinoflagellate assemblages from M26 are discussed in Wilson & McMillan 1996.

Puketeraki Core

Puketeraki is located on the coast, north of Dunedin, South Island, New Zealand (Text-Fig. 13). The Puketeraki core was drilled in 1993 at grid reference I43/26550313, in the course of an investigation into landslides affecting the main trunk railway line in the area (Glassey 1994, Wilson & McMillan 1996).

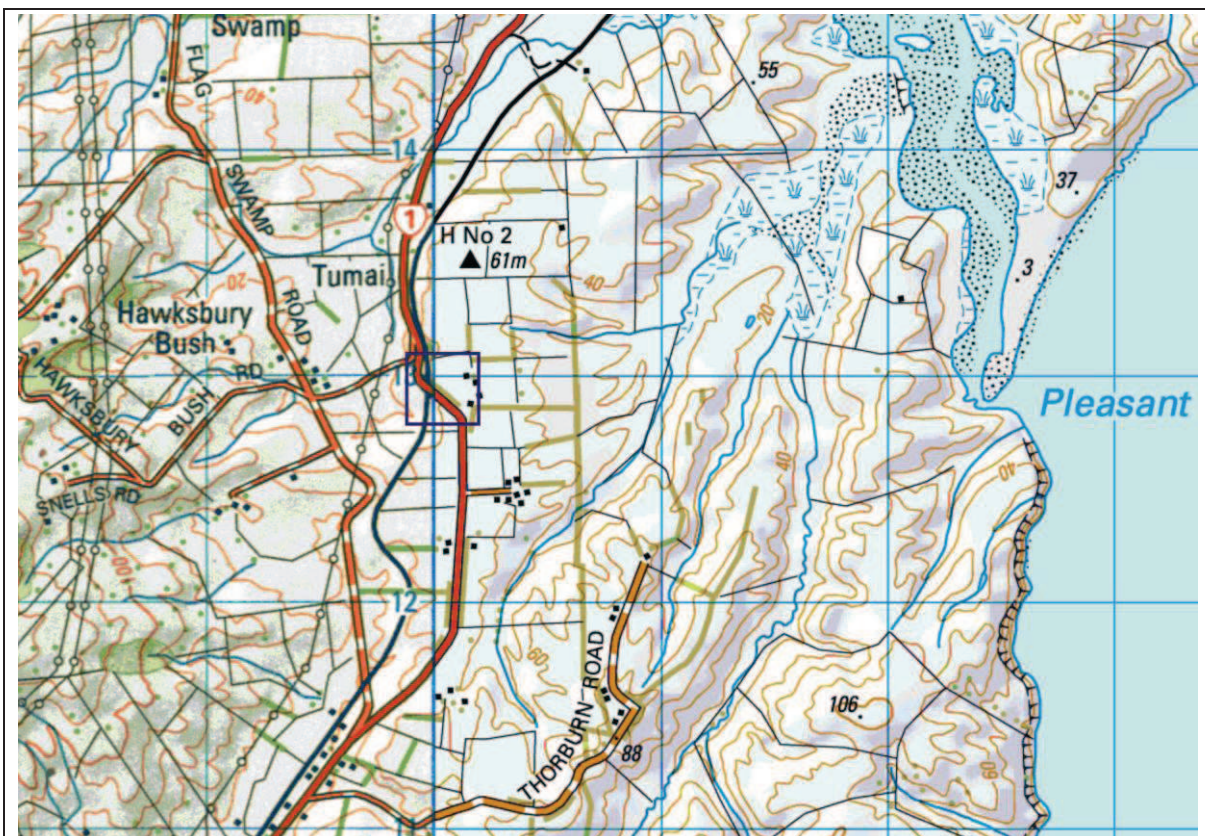
The majority of the core comprises “alternating zones of silty claystone and claystone of variable thickness” (Wilson & McMillan 1996, fig. 21) of the Burnside Formation. The lowest ~65 m. are of late Bortonian-age, separated from overlying Kaiatan sediments by a discontinuity, those in turn separated from overlying Runangan sediments by a second discontinuity. Discontinuously overlying the Burnside Formation is ?Waitakian-aged Concord Greensand and Otaian Caversham Sandstone.

Dinoflagellate assemblages from the Puketeraki Core are reported in Wilson & McMillan 1996.

Tumai

The section exposed at the Tumai Overbridge, just south of Goodwood, South Island, New Zealand (Text-Fig. 14), “is known for its exposure of the rarely observed contacts of the Burnside Formation, Concord Greensand and Caversham Sandstone outside of the immediate Dunedin area” (Wilson & McMillan 1996, p. 16).

Foraminifera (two samples) and dinoflagellate (one sample) assemblages from Tumai are reported in Wilson & McMillan 1996, p. 16-17, 89-91).



Text-Fig. 14: Location map for the Tumai sample.

Systematics

In the subsequent systematic text, the following points apply.

The sequencing of the taxa is, first of all, determined by the suprageneric classification of Fensome et al. 1993, updated where appropriate. Genera are arranged within subfamilies, and species within genera, so as to position the most similar forms together, wherever possible. The type, if it is represented within the study material, appears first, followed by any other taxa. There is no concession to alphabetical order, and the reader is directed to Appendix 5 to locate individual taxa alphabetically.

The synonymies are not exhaustive, and are not intended to be. Various databases are available for readers wishing to locate all citations of a particular name in the literature. Necessarily, these lists are constantly growing, and any printed version is doomed to obsolescence as soon as the ink dries. There is limited value in such an activity.

Instead, the synonymies presented below include two types of entry:

1. Important orthographic or nomenclatural variations have been captured.
2. Other entries are “just” citations from the literature, but with the added distinction that each has been individually examined, to determine that the cited occurrence does indeed correspond to my own view of the taxon circumscription. Of course I could be as easily mistaken as the next person, but the reader may be assured that the presence of a citation in one of the following synonymies implies more than just the mention of a name.

For both types of entry, I have relocated the original reference in nearly all cases, and attempted to reproduce the citation exactly, including any misspellings or other typographical irregularity.

Occurrences listed in the *Distribution* section for each species may include a few from the literature; typically those also listed in the synonymy. As for the synonymy, these are not intended to be exhaustive, nor even representative of the global distribution.

Distribution lists for each taxon include only the FAD and LAD from each collection (not section) and intervening occurrences are omitted.

The lists are ordered approximately by the age/stage for the occurrence, as far as can be determined. Ages for occurrences derived from the literature are reproduced in their original terms; not converted to New Zealand ages. The sample reference column in the distribution table provides previously published references to the sample, if one exists. Note these are references to the *sample*, not necessarily to the taxon.

Group Acritarcha Evitt 1963a

1963a Acritarchs Evitt, p. 158

1963b Acritarchs Evitt, p. 300-302

1963 Acritarcha Evitt 1963; Downie et al., p. 7

Remarks: Evitt (1963a, p. 158) proposed the name acritarchs be applied to a “new informal group of microfossils of organic composition and unknown affinity”. Later (1963b, p. 300-301) he elaborated his vision of the group in two important ways, (1) noting that the group is polyphyletic, and (2) restricting his definition, morphologically, to microfossils having “a central cavity enclosed by a wall of single or multiple layers and of chiefly organic composition; symmetry, shape, structure, and ornamentation varied; central cavity closed or communicating with the exterior by varied means, for example: pores, a slitlike or irregular rupture, a circular opening (the pylome).”

The characteristic of polyphyletic and unknown affinity necessitates a wholly morphological (phenetic) form taxonomy for the group as a whole: Acritarchs are acritarchs precisely because we do not know their phylogenetic affiliations. Of course, that need not preclude us from attempting to assemble groups of species into “genera” that are at least potentially phylogenetic units, although any such approach is necessarily constrained. Thus, for example, it was perfectly reasonable for Prössl (1994) to recognise the essential similarity between *Paucilobimorpha* and *Tritonites* and to combine the species into a single form-genus. More stands to be gained from considering them together than separately.

Before the dinoflagellate affinities of many fossil cyst taxa had been convincingly demonstrated, several acritarchs and dinoflagellate cysts were collectively known as “hystrichospheres” – an informal term derived from the now disused family name, Hystrichosphaeridae O. Wetzel 1933b (p. 32). The type genus and species of Hystrichosphaeridae, *Hystrichosphaera furcata*, is nowadays considered a junior synonym of *Spiniferites ramosus* (Lentin & Williams 1973, p. 128-129), a dinoflagellate. The Hystrichosphaeridae was effectively dismantled by Evitt (1963a, b) and various members transferred to either the acritarchs or to “Peridinales” (= dinoflagellates, in the sense Evitt meant it), as appropriate. Since then, a number of taxa have continued to shuffle back and forth between the two groups, as various workers have observed, or thought they observed, characteristics diagnostic of a dinoflagellate affinity. Most often, a clearly polygonal shape to the archeopyle,

taken to indicate boundaries with surrounding plates and, by implication, the existence of the plates themselves, has been considered to be strong enough evidence of a dinoflagellate affinity, provided, of course, that size, shape, etc., are within the appropriate ranges. This is the standard of “proof” adopted herein, also. As further discussed below, the form known as *Membranilarnax* (or *Valensiella*) *clathroderma*, and usually grouped with the dinoflagellates, fails this test and is herein treated as an acritarch.

Subgroup Sphaeromorphae Downie et al. 1963

Genus *Indet 2*

Remarks: A number of unidentified sphaeromorphs have been encountered. Two of the more striking forms are grouped together below.

Indet 2 sp. 1

Pl. 1, figs. 1-3

Description: Small, thick-walled, prolate to more or less spherical cyst, with a broad pylome in the “precingular” position; evidence of thickened ridges on the wall do not appear to delineate any kind of tabulation.

Size Range: Length = 23 (29) 35 μm (2 measurements). Width = 21 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996

Indet 2 sp. 2

Pl. 1, figs. 4-6

Description: Small, thick-walled, prolate to more or less spherical cyst, with an almost circular pylome in the “precingular” position, showing evidence of splitting below the posterior margin, as if splitting along the two sutures lateral to a plate 3” analogue.

Size Range: Length = 20 μm (one measured specimen). Width = 20 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984

Remarks: A very tiny form which could, conceivably, be a fungal spore or similar.

Subgroup Uncertain

Genus *Cystidiopsis* Nagy 1965

1965 *Cystidiopsis* Nagy, p. 209

1978 *Cystidiopsis* Nagy 1965; Stover & Evitt, p. 291

1990 *Cystidiopsis* Nagy, 1965b, p. 209; Fensome et al., p. 178

Type Species: *Cystidiopsis certa* Nagy 1965, p. 209-210, pl. 5, figs. 27-30 [Mid Miocene]

Original Description: Regularly arranged cysts on the globular central body (E. Nagy, p. 209).

Remarks: This genus of small but distinctive acritarchs is seldom reported, though it is apparently cosmopolitan.

***Cystidiopsis certa* Nagy 1965**

Pl. 1, figs. 7-9

- ?1960 *Dinoflagellata* cyst; Kuprijanova, p. 78, pl. 14, fig. 1
1965 *Cystidiopsis certa* Nagy, p. 209-210, figs. 27-30, text-fig. 8
1977 *Litosphaeridium?* *mamellatum* De Coninck, p. 42, pl. 6, figs. 8-13
1990 *Cystidiopsis certa* Nagy, 1965b, p. 209-210; pl. 5, figs. 27-30; Fensome et al., p. 178
2002 *Litosphaeridium?* *mamellatum* De Coninck, 1977; De Coninck, pl. 8, figs. 21-22

Original Description: [Diagnosis] Shell 21 μ in diameter, its globular central body is 12 μ large covered with a smooth cyst of roughly 1 μ thickness. To this cyst from outside, around and in groups of three about twelf [sic] smooth-walled vesicles of 1 μ [sic] seize [sic] adhere, each of which has an approximately 8 μ long appendage ending in a point....

[Remarks] An entirely identical form was published by Kuprijanova (1960, Pollen et Spores, p. 78, Table 14, Fig. 1) from the Lower Oligocene of West-Kazakhstan.... Beside the holotype one more specimen was found so far in the sample from 755 to 757 m. depth of the [Zengövárkony] bore-hole No. 59 at Hidas [Mecsek Mountains, southern Hungary]. Both samples are of maritime origin... (Nagy 1965, p. 209-210).

Size Range: Length including any processes = 20 (31) 42 μ m (5 measurements). Width including any processes = 25 μ m (one measured specimen).

Distribution: Rare. To date, recorded in New Zealand from the Bortonian only.

Age/Stage	Location	Sample	Sample Reference
Miocene-middle Miocene	Zengövárkony bore-hole No. 59, Hidas, Mecsek Mountains, southern Hungary		Nagy 1965
early Oligocene	west Kazakhstan		Kuprijanova 1960
late Eocene-early Oligocene	Grimmeringen section, eastern Belgium	+0.9 m.	De Coninck 2002
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Eocene	Woensdrecht borehole, southern Netherlands	329-392m	De Coninck 1977

Remarks: The holotype is from 30.9 to 34.0 m. in Zengövárkony borehole No. 59 and is stated to be Middle Miocene. The paper does not specifically state the age of another specimen occurring in the 755 to 757 m. interval, other than noting (p. 199) that the entirety of the core is Miocene. The examples encountered in this study, however, are late Middle Eocene (Bortonian).

De Coninck 1977 (re)described this form as *?Litosphaeridium mamellatum* noting that "about 13" of the inflated, ribbed processes "seem to communicate with the interior of the central body" and have a small opening at the distal extremity.

New Zealand specimens seem identical to the type material.

?*Cystidiopsis* sp. 1

Pl. 1, figs. 10-12

- 1988 *Hystrichosphaeridium* cf. *H. astartes* Sannemann 1955; Wrenn & Hart, p. 354, fig. 24, 4-5

Description: Small cysts constructed as a collection of 25 or so, straight to gently convex-sided, cones joined at their wide ends to form a polyhedral vesicle.

Size Range: Length including any processes = 30 μ m (one measured specimen). Width including any processes = 28 (29) 30 μ m (2 measurements).

Distribution: Rare. Apparently confined to the Bortonian in New Zealand.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
late early Eocene	northern Seymour Island, West Antarctica	8462	Wrenn & Hart 1988

Comparison: This form differs from *Cystidiopsis certis* in possessing processes which are more acutely conical than the lower, more rounded processes of *C. certis*.

Genus *Nummus* Morgan 1975

1975 *Nummus* Morgan, p. 163

1978 *Nummus* Morgan 1975; Stover & Evitt, p. 295

1989 *Nummus* Morgan, 1975, p. 163; Lentin & Williams, p. 258

1990 *Nummus* Morgan, 1975, p. 163, emend. Backhouse, 1988, p. 112; Fensome et al., p. 367

Type Species: Nummus monoculatus Morgan 1975, p. 163, pl. 3, figs. 1a-d, 4a-c [Aptian]

Original Description: Lenticular fossil is single-walled, with a slight thickening around the margin in dorsal-ventral view. A subcircular to rounded angular pylome is located in an "intercalary" position, and most of the "ventral" wall is lost, apparently by disintegration (Morgan 1975, p. 163).

Comparison: *Nummus* superficially resembles *Cyclopsiella*, but differs in being single-walled and in lacking an ambital thickening or flange. Additionally, it commonly appears to lose the majority of its ventral wall, leaving a construction reminiscent of the periphragm of *Thalassiphora*, though the significance of this characteristic is enigmatic, to say the least.

Nummus inornatus Clowes n. sp.

Pl. 2, figs. 1-6

?2004 *Cyclopsiella* sp. A; Ramirez, pl. 9, fig. 3

?2005 *Cyclopsiella* sp. 1; Schiøler, pl. 6, fig. 7

Derivation of Name: Latin, *inornatus*, unadorned or uncelebrated; with reference to the lack of distinctive surface ornament.

Holotype: Sample I43/f093, slide L16341/SM100; Burnside Formation, Puketeraki Core (Bortonian); Pl. 2, figs. 1-3

Description: Vesicle elliptical in outline. Wall apparently single layered; typically lacking from most of the central ventral surface, the rim being relatively smooth; thin (~0.5 µm or less) and hyaline; lacking any thickened ambital flange. Surface irregularly and very shallowly wrinkled, especially near the ambitus, sparsely punctate; otherwise apparently completely smooth. Pylome subapical, circular to ellipsoidal; pylome rim thickened (~1.5 to 2 µm), slightly irregular or wrinkled. No operculum has been observed.

Although the rim of the ventral "opening" exhibits occasional tears, it is generally quite smooth, suggesting that the ventral surface separates along some kind of pre-formed line of weakness rather than tearing away at random.

Size Range: Length including any processes = 80 (94) 120 µm (6 measurements). Width including any processes = 68 (87) 122 µm (5 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Rupelian-Burdigalian	Alma-1X well, Danish North Sea	LVR23764	Schiøler 2005
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f178 (L11927)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f128 (L11939)	
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New	J42/f301 (L23131)	

	Zealand		
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
middle Eocene-late Eocene	north west Venezuela	Pica-1X, 2119 ft.	Ramírez 2004

Comparison: This taxon differs from *Nummus similis* (Cookson & Eisenack 1960b) Burger 1980b, in possessing a relatively smooth rather than a granular wall, and from *Nummus monoculatus* Morgan 1975 in having a smaller pylome which is noticeably thickened around the rim and in the relatively smooth rather than a “granulo-punctate” wall.

Genus *Paucilobimorpha* De Coninck 1986b emend. Prössl 1994

- 1986b *Paucilobimorpha* De Coninck, p. 22
- 1988 *Tritonites* Marshall & Partridge, p. 244-245
- 1990 *Paucilobimorpha* De Coninck, 1986b, p. 22; Fensome et al., p. 387
- 1990 *Tritonites* Marshall and Partridge, 1988, p. 244-245; Fensome et al., p. 496-497
- 1994 *Paucilobimorpha* De Coninck 1986b emend. Prössl, p. 400

Type Species: *Paucilobimorpha triradiata* De Coninck 1986b, p. 23, pl. 11, figs. 19-20 [Eocene (Bartonian)]

Original Description: The vesicle is single-layered and consists of a few hollow lobes diverging from a common centre. Each lobe may eventually terminate distally in a few, more or less pronounced bulbous parts. The vesicle wall may be smooth or granular and/or ornamented with short spines (De Coninck 1986b, p. 22).

Remarks: Prössl 1994 emends *Paucilobimorpha* and considers *Tritonites* Marshall & Partridge 1988 to be a junior synonym.

Prössl included two Late Cretaceous forms (?*P. apiculata* and *P. extrema*, both described in Cookson & Eisenack 1962a) within *Paucilobimorpha*. They seem unusual because their age is very different from those of the Eocene species comprising the majority of the genus.

- ?*P. apiculata* appears to be a typical *Paucilobimorpha*, somewhat like *P. incurvata* with the addition of a small “apical” projection. Only a single specimen is illustrated (presumably the holotype, though neither the description nor the figure caption states this to be the case) and only the holotype is measured. It is not clear that additional specimens have ever been found. The photograph is tiny (12 mm high) and grainy; as far as can be seen, the apical projection could be the result of mechanical damage.
- *P. extrema* appears (Cookson & Eisenack 1962a, pl. 37, fig. 10) to possess an extensively folded and otherwise textured wall which is quite atypical for the genus, however, and might have been better left in *Horologinella*.

A range chart for the species of *Paucilobimorpha* encountered in this study is provided in Appendix 2, chart 6.

***Paucilobimorpha inaequalis* (Marshall & Partridge 1988) Prössl 1994**

Pl. 2, figs. 7-12, Pl. 3, figs. 1-3

- 1988 *Tritonites inaequalis* Marshall & Partridge, p. 251, fig. 11A-U
- 1990 *Tritonites inaequalis* Marshall and Partridge, 1988, p. 251, figs. 11A-U; Fensome et al., p. 497
- 1994 *Paucilobimorpha inaequalis* (Marshall & Partridge 1988) Prössl, p. 402, figs. 6a-b

Original Description: Vesicle consisting of 3 lobes; longitudinal axes of lobes generally coplanar and symmetrically arranged around common junction. Lobe tips expanded into rounded subtriangular shapes.... One triangular expansion approximately in same plane as the 3 longitudinal axes; the other 2 near 90° to this plane. Distal lobe margins flattened or, more commonly, concave. On specimens with markedly concave distal margins, lobe termini bifurcate with branches forming 2 rounded bulges. Wall usually single layered, 0.5-1 µm thick; occasionally with diaphanous inner layer 0.3 µm thick evident where detached from outer wall near lobe tips.... Wall thinning on rare specimens at tip of one lobe. Surface ornamented with granules, bacula, and spines up to 2.5 µm high, 1.5 µm in diameter, and usually more than µm apart. Spine bases usually rounded, occasionally stellate with 4-5 points; spines may be hollow. Ornament concentrated towards lobe tips (Marshall & Partridge 1988, p. 251; ellipses replace figure references in the original).

Description of Study Material: Vesicle constructed as two pairs of lobes, here referred to as apical and antapical, separated by a constricted waist; the apical pair of lobes characteristically poorly developed, in extreme cases

barely distinguishable as a pair at all; the overall outline resembling a thickly formed, inverted, letter T, with varying degrees of lateral expansion evident at the apex; approximately 20 µm high. Lobes closed and rounded distally; more or less tubular, neither attenuating nor expanding greatly; the antapical pair essentially equal in size, though rarely exactly so. The waist is typically constricted to around a third of the width of the antapical pair of lobes. Walls either single layered or comprising two indistinguishable layers, approximately 1 µm thick; hyaline; generally not folded; completely smooth over most of the surface except for sparse spines ornamenting the distal surfaces of the lobes. Spines small and conical, in the order of 0.5 µm diameter and 1 µm high; apparently solid, and hyaline like the wall itself.

Size Range: Length including any processes = 18 (26) 33 µm (10 measurements). Width including any processes = 15 (24) 27 µm (9 measurements).

Distribution: Rare. Recorded from the ?latest Porangan at Hampden Beach, and several Bortonian locations. Not recorded from the type Porangan at Te Uri Stream, which may be a little older than the Porangan at Hampden Beach.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	

Paucilobimorpha incurvata (Cookson & Eisenack 1962a) Prössl 1994

Pl. 3, figs. 4-6

1962a *Horologinella incurvata* Cookson & Eisenack, p. 272, pl. 37, fig. 5

1982b *Horologinella incurvata* Cookson & Eisenack; Wilson, p. 7, pl. 1, fig. 15

1994 *Paucilobimorpha incurvata* (Cookson & Eisenack 1962) Prössl, p. 402-403

Original Description: Shell small, without fields and apical projection approximately isodiametric with deeply concave sides, no opening observed. Wall relatively thick, surface smooth (Cookson & Eisenack 1962a, p. 272).

Description of Study Material: Vesicle comprising two pairs of lobes, essentially indistinguishable, separated by a variably constricted waist; the outline of the upper and lower surfaces generally convex, strongly concave at the sides; approximately 13 µm high. The shape in polar view (i.e., whether the solid form is dorso-ventrally flattened or essentially cylindrical) has not been determined. Lobes closed and rounded distally. Walls either single layered or comprising two indistinguishable layers, approximately 1 µm thick; hyaline; generally not folded; surface completely smooth.

A very small species: the holotype is just 16 µm high and the same broad, and the New Zealand specimens encountered in this study slightly smaller. The overall shape can vary somewhat (e.g. contrast Pl. 3, fig. 5 and Pl. 3, fig. 6).

Size Range: Length including any processes = 12 (15) 27 µm (9 measurements). Width including any processes = 13 (16) 23 µm (5 measurements).

Distribution: Rare. Cookson & Eisenack's type material is recorded as "probably lower Eocene" but in New Zealand it seems to be one of the younger species of *Paucilobimorpha*, persisting possibly as late as the Oligocene.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f064 (L09221)	Wilson 1985
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

***Paucilobimorpha panda* (Marshall & Partridge 1988) Prössl 1994**

Pl. 3, figs. 7-12

1988 *Tritonites pandus* Marshall & Partridge, p. 248-250, fig. 10A-W

1990 *Tritonites pandus* Marshall and Partridge, 1988, p. 248-251, figs. 10A-W; Fensome et al., p. 497

1994 *Paucilobimorpha panda* (Marshall & Partridge 1988) Prössl, p. 403, fig. 1

Original Description: Vesicle with 2 arcuate lobes forming a horseshoe shape. Lobes planar or more frequently distal tips of lobes twisted above and below this plane...; tips occasionally overlap.... Vesicle outline in side view (i.e., normal to plane containing the lobes) subcircular, oval, subrectangular, to slightly v-shaped..., with outer margin along which lobes connect nearly straight to concave. Lobes circular in cross-section, of fairly uniform diameter on individual specimens, tips rounded to slightly bulbous. Wall single-layered, 0.5-1.5 µm thick, thinning on most specimens at tip or on inward-facing side of one lobe, where wall is flattened..., wrinkled..., or ruptured. Surface with granules; straight to arcuate rugulae, bacula, and spines up to 2 µm high and 0.5 µm in diameter. Elements usually 1 µm apart, distributed on outward-facing surfaces of lobes and concentrated towards tips, occasionally arranged in discontinuous rows (Marshall & Partridge 1988, p. 248; ellipses replace figure references in the original).

Size Range: Length including any processes = 15 (18) 20 µm (7 measurements). Width including any processes = 17 (19) 21 µm (4 measurements).

Distribution: Infrequent. This species appears to be the earliest appearing *Paucilobimorpha*, possibly occurring as early as the Heretaungan.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan-Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f298 (L23128)	

Remarks: New Zealand forms, while falling within the range of the type material, are quite variable in overall shape (contrast, for example, Pl. 3, figs. 7-8 and Pl. 3, figs. 11-12). Further, some specimens seem completely smooth, whereas others carry small spines (e.g. Pl. 3, fig. 9).

***Paucilobimorpha spinigera* (De Coninck 1969) Prössl 1994**

Pl. 4, figs. 1-3

1969 *Diacrocanthidium spinigerum* De Coninck, p. 43-44, pl. 13, figs. 11-13

1988 *Tritonites bilobus* Marshall & Partridge, p. 247, fig. 8A-O

1990 *Tritonites bilobus* Marshall and Partridge, 1988, p. 247, figs. 8A-O; Fensome et al., p. 497

1994 *Paucilobimorpha spinigerum* (De Coninck 1969) Prössl, p. 403, fig. 2

Original Description: The organism consists of a small elongated body with inflated ends on which are a variable number of short spines (De Coninck 1969, p. 43-44).

Description of Study Material: Vesicle apparently constructed as two pairs of lobes separated by a constricted waist, as in other species of *Paucilobimorpha*, but each pair of lobes reduced to a mere swelling; approximately 25 µm high. Vesicle closed, presumed to be more or less circular in cross-section. Walls either single layered or comprising two indistinguishable layers, approximately 1 µm thick; hyaline; generally not folded; completely smooth over most of the surface except for scattered spines ornamenting the apical and antapical lobes. Spines relatively elongated, in the order of 0.5 µm diameter and up to 5 µm high; apparently solid, and hyaline like the wall itself.

Size Range: Length including any processes = 23 μm (one measured specimen). Width including any processes = 15 μm (one measured specimen).

Distribution: Very rare. Occurs low in the Bortonian (Hampden Beach) in New Zealand and at the early/middle Eocene boundary in the Gippsland Basin, according to Marshall & Partridge 1988.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	

***Paucilobimorpha spinosa* (Cookson 1965a) Prössl 1994**

Pl. 4, figs. 4-6

- 1965a *Horologinella spinosa* Cookson, p. 89, pl. 10, figs. 10-12, pl. 11, fig. 10
 1982 *Horologinella spinosa* Cookson; Cookson & Eisenack, p. 44, pl. 5, fig. 11
 1986b *P. spinosa* (Cookson 1965) De Coninck, p. 22 [invalid comb.]
 1988 *Tritonites spinosus* (Cookson) Marshall & Partridge, p. 251, 253, figs. 12A-P
 1990 *Tritonites spinosus* (Cookson, 1965, p. 89, pl. 10, figs. 10-12, pl. 11, fig. 10) Marshall and Partridge, 1988, p. 251-253; Fensome et al., p. 497
 1994 *Paucilobimorpha spinosa* (Cookson 1965) Prössl, p. 403-404, figs. 3a-b
 1995a *Paucilobimorpha spinosa* (Cookson, 1965); De Coninck, pl. 7, figs. 20-21
 1999b *Paucilobimorpha spinosa* (Cookson, 1965); De Coninck, pl. 1, fig. 13

Original Description: Cyst without fields, with deeply concave sides and straight to slightly concave ends (cf. *H. incurvata* ...). Wall c. 0.5-1 μm , thick mainly smooth, except at the distal rounded ends of the 4 arms where it is ornamented with small, solid, spine-like projections. One of the arms at the 'anterior' end is slightly longer than the other 3 and sometimes narrows slightly towards the apex. In 2 examples ... the apex of the longer arm is open, apparently as the result of a natural transverse break (Cookson 1965a, p. 89; ellipses replace figure references in the original).

Description of Study Material: Vesicle comprising two pairs of lobes, here referred to as apical and antapical, separated by a constricted waist, the outline thus resembling a thickly formed letter H laid on its side; generally concave on all sides, strongly so at the waist; approximately 25-30 μm high. The two pairs of lobes are almost, but usually not quite, coplanar, being slightly rotated with respect to one another about an imaginary polar axis. Lobes closed and rounded distally; more or less tubular, neither attenuating nor expanding greatly; very close to being equal in size, but rarely exactly so, the slightly smaller pair herein referred to (and oriented in the figures) as the apical pair. The waist is typically constricted to around a third of the width of the lobes. Walls either single layered or comprising two indistinguishable layers, approximately 1 μm thick; hyaline; generally not folded; completely smooth over most of the surface except for the characteristic sparse spines ornamenting the distal surfaces of the lobes. Spines small and conical, in the order of 0.5 μm diameter and 1 μm high; apparently solid, and hyaline like the wall itself.

Size Range: Length including any processes = 23 (28) 35 μm (17 measurements). Width including any processes = 25 (29) 33 μm (3 measurements).

Distribution: Frequent. Occurs widely, though it is never common, from the Bortonian to at least the early Whaingaroan in New Zealand.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f182 (L11931)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f171 (L11920)	
late Eocene-early Oligocene	Kallo borehole, north-western Belgium	-110 m. - slide 3	De Coninck 1999b
?Kaiatan-Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996

Age/Stage	Location	Sample	Sample Reference
Bartonian-early Rupelian	Kallo borehole, north-western Belgium	-115 m. - lame 1; -115 m. - lame 2	De Coninck 1995a
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: Marshall & Partridge 1988 (p. 251) describe the lobes of *Paucilobimorpha* (as *Tritonites*) *spinosa* as “planar” and subsequently refer to a “plane containing the lobes.” Although this is approximately the case, neither their figures (see especially their figs. 12E-G) nor the specimens observed in this study possess lobes which are *exactly* coplanar. Instead, as noted in the foregoing description, the apical and antapical (insofar as we may recognise those concepts) pairs are usually slightly rotated with respect to one another, about an imaginary polar axis. Marshall & Partridge 1988 also observed “a diaphanous inner layer 0.2 µm thick, which is only clear where detached from the outer wall near lobe tips” (p. 251, fig. 12K). Nothing similar was encountered in the present study.

De Coninck (1986b) published the combination “*P. spinosa* (Cookson 1965)” without further elaboration, thus failing to meet the requirements of Art. 33.2 for valid publication of a new combination.

***Paucilobimorpha tricornus* (Marshall & Partridge 1988) Clowes n. comb.**

Pl. 4, figs. 7-12

1985 *Incertae Sedis* sp. B in De Coninck 1976; De Coninck, p. 69, pl. 2, fig. 19 (not 18)

1988 *Tritonites tricornus* Marshall & Partridge, p. 245-247, figs. 6A-U

1990 *Tritonites tricornus* Marshall and Partridge, 1988, p. 245-247, figs. 6A-U; Fensome et al., p. 497

Original Description: Vesicle of 3 arcuate lobes extending from their common junction. Lobes radial and symmetrical about axis normal to plane in which they join. Lobes diverging from proximal junction, subparallel or convergent distally. Vesicle outline subcircular when viewed normal to axis of symmetry.... Lobes circular in cross-section, of constant diameter or tapering slightly distally, tips rounded. Wall single-layered, c. 0.5 µm thick, frequently thinning slightly towards inward-facing side of tip of one lobe...; this lobe usually slightly flattened, rarely ruptured. Surface bearing rugulae, bacula, and spines up to 2.5 µm high, 1.5 µm in diameter, and usually more than 1.5 µm apart. Projections usually solid, occasionally hollow. Spine bases usually circular, occasionally star-shaped. Ornament distributed over outward facing convex surfaces; concentrated towards tips (Marshall & Partridge 1988, p. 245).

Description of Study Material: Vesicle comprising three, approximately equal-sized and equally spaced, lobes which radiate from their common centre in a plane, then curve inwards. Sometimes this curvature is strong enough that the lobes almost touch at their tips, though generally it is less so; the approximate sphere thus formed being about 20-25 µm in diameter. Lobes closed and rounded distally; more or less tubular, neither attenuating nor expanding greatly. Walls either single layered or comprising two indistinguishable layers, approximately 1 µm thick; hyaline; generally not folded; completely smooth over most of the surface except for the characteristic sparse (Pl. 4, figs. 7-9) to fairly dense (Pl. 4, fig. 12) spines ornamenting the distal or, less frequently, more proximal surfaces of the lobes. Spines small and conical, in the order of 0.5 µm diameter and 1 µm high; apparently solid, and hyaline like the wall itself.

Size Range: Length including any processes = 18 (21) 23 µm (5 measurements). Width including any processes = 20 (22) 23 µm (4 measurements).

Distribution: Infrequent. Somewhat less common than *P. tripa* (see below) though the stratigraphic range is broadly similar in New Zealand.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f041 (L09198)	Wilson 1985
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
middle Eocene	Sands of Ledde, Mol borehole, Belgium	-319.8m - prep. 1	De Coninck 1985

Remarks: Considered to be a junior synonym of *P. tripa* by Prössl 1994 (p. 404) as it may yet prove to be; see further remarks under *P. tripa*.

***Paucilobimorpha tripa* De Coninck 1986b**

Pl. 5, figs. 1-6

- ?1982b ?*Horologinella spinosa* Cookson; Wilson, p. 7, pl. 1, fig. 14
1986b *Paucilobimorpha tripus* De Coninck, p. 23, pl. 11, fig. 25
1990 *Paucilobimorpha tripus* De Coninck, 1986b, p. 23, pl. 11, fig. 25; Fensome et al., p. 387
1994 *Paucilobimorpha tripa* De Coninck 1986; Prössl, p. 404, figs. 5a-b

Original Description: The vesicle consists of three lobes diverging from a common centre, but curving to one side as the legs of a tripus (three-legged stool) (latin: tripus -odis). The vesicle wall is single-layered and ornamented with short spines irregularly scattered all over the vesicle (De Coninck 1986b, p. 23).

Description of Study Material: Vesicle comprising three, approximately equal-sized and equally spaced, lobes which radiate from their common centre in a plane, then curve inwards, the approximate diameter of the whole being about 20-25 µm. Sometimes the curvature of the lobes is very weak (Pl. 5, figs. 1-3, Pl. 5, figs. 4-5); at other times it is much stronger (Pl. 5, fig. 6) though rarely sufficient to bring the lobe tips close to touching. Lobes closed and rounded distally; more or less tubular, neither attenuating nor expanding greatly. Walls either single layered or comprising two indistinguishable layers, approximately 1 µm thick; hyaline; generally not folded. The surface varies from almost completely smooth (Pl. 5, figs. 4-5), through somewhat granular (Pl. 5, figs. 1-3) to quite densely spinose (Pl. 5, fig. 6); the spines, when present, small and conical, in the order of 0.5 µm diameter and 1 µm high; apparently solid, and hyaline like the wall itself.

Size Range: Width = 25 µm (one measured specimen). Length including any processes = 15 (22) 31 µm (8 measurements). Width including any processes = 17 (25) 37 µm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	

Comparison: A more "gracile" version of *P. tricornus* (Marshall & Partridge), as noted in Prössl 1994 (p. 404), although the two may yet prove to be conspecific (as regarded by Prössl). For the present, however, I prefer to retain them separately because they are usually readily distinguished (although some intermediates are difficult) and their ranges, though similar, do not seem to be identical.

Genus *Fenestridium* Clowes n. gen.

Derivation of Name: Latin, *fenestra*, window; with reference to the window-like areas occurring on the outer wall of the type species.

Type Species: *Fenestridium clathrodermum* (Deflandre & Cookson 1955) Clowes n. comb.

Description: Cyst comprising two, concentric, more or less spherical bodies, connected together by numbers of membranous lamellae. Where the lamellae connect to the outer wall they divide the surface up into numerous polygonal fields within which are typically one or a small number of fenestrae.

Remarks: The genus *Membranilarnax* O. Wetzel 1933b (p. 51) has long been recognised as a problematic taxon: Stover & Evitt 1978 (p. 295) considered it to be an acritarch genus, whereas Sarjeant 1985b (p. 149, 151-152) considered it to be a skolochorate dinoflagellate cyst. In fact, however, the genus is quite likely to be polyphyletic and a more tractable approach might be to consider the various species individually. The species, '*Membranilarnax*' *clathroderma*, is almost certainly not a dinoflagellate. As noted in Clowes & Morgans 1984, p. 37, the unusual ramifying lamellae between the wall layers, apparent lack of an archeopyle (a fact also noted by Stover & Evitt 1978, p. 86), and surface pattern inconsistent with any obvious dinoflagellate tabulation, fail to provide any support for an affinity with the dinoflagellates (although one might argue that the structure of the wall layers has an approximate analogue in *Samlandia*).

It is, however, a very distinctive element of southern palynofloras around the Eocene-Oligocene boundary. The new genus, *Fenestridium*, is here proposed to accommodate this form, which bears no apparently close relationship with the type species of either *Membranilarnax* (*M. pterospermoides*, Late Cretaceous) or *Valensiella* (*V. ovulum*, Middle Jurassic).

Fenestridium clathrodermum (Deflandre & Cookson 1955) Clowes n. comb.

Pl. 5, figs. 7-12, Pl. 6, figs. 1-6

- 1955 *Membranilarnax clathroderma* Deflandre & Cookson, p. 290, pl. 7, fig. 6, text-fig. 51
1963a *Valensiella clathroderma* (Deflandre & Cookson 1955, p. 290, pl. 7, fig. 6, text-fig. 51) Eisenack, p. 101
?1974 *Membranilarnacia densa* Cookson & Eisenack, p. 71, pl. 25, fig. 19; pl. 29, fig. 19
1978 *Valensiella? clathroderma* (Deflandre & Cookson 1955) Eisenack 1963a; Stover & Evitt, p. 86
1984 '*Valensiella*' *clathroderma* (Deflandre & Cookson 1955); Clowes & Morgans, p. 37, pl. 2, figs. 19-20
?1986b *Valensiella? clathroderma* (Deflandre & Cookson 1955); De Coninck, pl. 10, figs. 26-27
2002 *Valensiella? clathroderma* Deflandre & Cookson, 1955; De Coninck, pl. 10, figs. 8-10

Original Description: Shell practically spherical with an angular outline and thin wall surrounded by a 2nd very fine membrane that is indistinctly punctate and perforated with relatively large rounded holes. External membrane attached to the shell, not by individual processes but by membranaceous lamellae, which form a kind of wide-meshed reticulate surface design wholly independent of the above-mentioned holes. External outline irregularly rounded, not exactly concentric with the shell (Deflandre & Cookson 1955, p. 290).

Description of Study Material: Cyst comprising an approximately central, more or less spherical inner body, connected to a more polygonal outer wall by numbers of membranous lamellae. Where the lamellae connect to the outer wall they divide the surface up into numerous polygonal fields within which are typically one large or several smaller fenestrae.

Size Range: Length including any processes = 45 (54) 65 μm (12 measurements). Width including any processes = 42 (49) 60 μm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f184 (L11933)	
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f169 (L11918)	
late Eocene-early Oligocene	Grimmertingen section, eastern Belgium	+2.15 m.	De Coninck 2002
Priabonian (Tongrien)	Sands of Asse, Woensdrecht borehole, southern Netherlands	263m	De Coninck 1986b
latest Bartonian-Priabonian (Tongrien)	Sands of Asse, Woensdrecht borehole, southern Netherlands	277m	De Coninck 1986b

Remarks: The fossil taxon *Membranilarnax clathroderma* was described by Deflandre & Cookson (1955, p. 290) who regarded it as a dinoflagellate cyst. Despite the apparent lack of an archeopyle or any other indications of a dinoflagellate tabulation, it has continued to be treated as a dinoflagellate cyst by most subsequent authors. For many years it has been assigned *Valensiella*. However, the non-dinoflagellate nature of '*Membranilarnax*' *clathroderma* was recognised at least 30 years ago (e.g. Stover & Evitt 1978, p. 86).

As far as can be judged from the single, somewhat poor figure of the holotype provided in Deflandre & Cookson 1955 (pl. 7, fig. 6), the New Zealand forms encountered in the present study are conspecific.

Membranilarnacia densa Cookson & Eisenack 1974 is regarded as a junior synonym in Stover & Evitt 1978 (p. 86) though I'm not convinced myself. The original illustrations of this taxon depict only mid-section foci and show no evidence of the characteristic fenestrae.

Domain Eukarya Woese et al. 1990

Kingdom Alveolata Cavalier-Smith 1991

Phylum Dinoflagellata Bütschli 1885

1831	Peridiniaea Ehrenberg, p. 32
1885	Dinoflagellata Bütschli
1914	Pyrrophyta Pascher
1981	Dinozoa Cavalier-Smith, table 10
1985	Pyrrophyta; Evitt, p. 26
1993b	Dinoflagellata (Bütschli 1885) Fensome et al., p. 39

Remarks: Dinoflagellates are protists – neither plants nor animals. The botanical code of nomenclature has been settled upon for naming dinoflagellates, more or less by historical accident. Botanists frequently refer to the phylum-level taxonomic rank as a “division”.

Key to classes (principally after Fensome et al. 1998):

1	Dinoflagellates possessing a nucleus rather than a dinokaryon	2
	Dinoflagellates possessing a dinokaryon during at least one stage of the life cycle	3
2	Class Syndiniophyceae – Dinoflagellates with motile cells (dinospores or gametes) with a dinokont arrangement of flagella, and in which the nucleus possesses histones (Fensome et al. 1998); intracellular parasites without known fossil record (Evitt 1985, p. 27).	
3	Dinokaryon present throughout life-cycle	4
	Dinokaryon present during part of life-cycle only	5
4	Class Dinophyceae – Dinoflagellates with a dinokaryon throughout their entire life-cycle (Fensome et al. 1998).	
5	Parasitic dinoflagellates with non-vacuolated cells	6
	Non-parasitic dinoflagellates with vacuolated cells	7
6	Class Blastodiniophyceae – Parasitic dinoflagellates having a dinokaryon during part of the life-cycle only. Cells are not highly vacuolated (Fensome et al. 1998).	
7	Class Noctiluophyceae – Dinoflagellates with a dinokaryon during part of the life-cycle only. The principal life-cycle stage comprises a large free-living motile cell inflated by vacuoles (Fensome et al. 1998).	

Note: The key to classes does not include the problematic class Ebriophyceae – non-photosynthetic, biflagellate, free-living organisms, variously classified as dinoflagellates, protozoans and *incertae sedis* – which lack a resistant external covering but having an internal siliceous skeleton which can fossilise. Examples are known from at least the Paleocene.

Only the class Dinophyceae is considered further herein.

Class Dinophyceae (Bütschli 1885) Pascher 1914

Dinoflagellates with a dinokaryon throughout their entire life-cycle (Fensome et al. 1998); in which one flagellum is whip-like and extends longitudinally, while the second is ribbon-like and follows a circular path in a plane about at right angles to the first (Evitt 1985, p. 26).

Key to subclasses (principally after Fensome et al. 1998):

1	Cysts tabulate	2
	Cysts non-tabulate	8
2	Plates arranged into latitudinal series	3
	Plates not arranged into latitudinal series	5
3	Plates arranged in seven or more latitudinal series	8
	Plates arranged in five to six latitudinal series	4

	Plates arranged into four or fewer latitudinal series; hyposome with sagittal suture	9
4	Subclass Peridiniphycidae – Dinophyceans with a tabulation which accords with, or derives from, a pattern in which there are five or six latitudinal plate series; sagittal suture lacking (Fensome et al. 1998); includes by far the majority of fossil dinoflagellate cysts, see below.	
5	Episome and hyposome separated by a cingulum	7
	Cingulum absent; tabulation comprising two large lateral plates plus a small apically located cluster of periflagellar platelets in a periflagellar area	6
6	Subclass Prorocentrophycidae – Dinophyceans in which the flagella are inserted apically and in which there is no cingulum or sulcus; thecal plates and a wavy flagellum, the latter being clearly homologous to the transverse flagellum of other dinoflagellates, are present (Fensome et al. 1998); no fossil record is known for this group.	
7	Numerous plates, arranged in no obvious tabulation pattern other than division into episome, cingulum and hyposome	8
	Relatively few plates; episome divisible into two latitudinal series of plates and an apical pore complex; hyposome divided into two large lateral plates by a sagittal suture	9
8	Subclass Gymnodiniphycidae – Dinophyceans in which: 1) amphiesmal vesicles are numerous and arranged nonserially or in more than six latitudinal series; or 2) the pellicle is the principal amphiesmal element; or 3) the amphiesmal structure is uncertain but does not comprise a theca divisible into six or fewer latitudinal series (Fensome et al. 1998); comprises the Gymnodiniales, Ptychodiscales, and Suessiales, all of which include fossil members though none have been encountered in the present study.	
9	Subclass Dinophysiphycidae – Dinophyceans which possess a cingulum, sulcus and sagittal suture (Fensome et al. 1998); normally exhibits moderate to strong lateral compression; comprises the Dinophysiales, which have no certain fossil record, and the Nannoceratopsiales, which are known only from the Jurassic.	

Note: The key has been constructed using only preservable characteristics, so cannot be applied to extant taxa, and without consideration of a few problematic fossil genera including *Cobricosphaeridium*, *Prolixosphaeridium*, *Suibindia* and *Xylochoarion*.

Only the subclass Peridiniphycidae includes members which are considered further herein.

Subclass Peridiniphycidae Fensome et al. 1993b

Dinophyceans with a tabulation which accords with, or derives from, a pattern in which there are five or six latitudinal plate series; sagittal suture lacking.

Key to orders (principally after Fensome et al. 1998):

1	Cells with two more or less symmetrical fundital (antapical) plates, neither being clearly dorsal to the other	2
	Cells in which one fundital (antapical) plate is clearly in a more dorsal than the other	3
2	Order Peridiniales Haeckel 1894 – Tabulation with one or both of the following arrangements: (a) the first apical plate is symmetrical, the left lateral triple junction or pair of left lateral triple junctions being essentially level with the right lateral triple junction or pair of right lateral triple junctions; (b) there are two antapical plates, placed more or less symmetrically about the midventral (middorsal) plane. (Fensome et al. 1998)	
3	Order Gonyaulacales Taylor 1980 – Tabulation with one or both of the following arrangements: (a) the first apical plate is asymmetrical, its left lateral triple junction being higher (i.e. more anterior) than the right lateral triple junction; (b) there are two to four fundital plates – always the posterior intercalary plate (1p) and first antapical plate (1'''), sometimes the posterior sulcal homologue (*ps), and possibly in rare cases also the right sulcal homologue (*rs) or subdivisions of these plates. Among the fundital plates, 1''' is almost always larger and is in a clearly more dorsal position than the other(s). (Fensome et al. 1998)	

Order Peridinales Haeckel 1894

Suborder Peridiniineae Haeckel 1894 [autonym]

Family Peridiniaceae Ehrenberg 1831

Subfamily Deflandreoideae Bujak & Davies 1983

Genus *Deflandrea* Eisenack 1938b emend. Lentin & Williams 1976

1938b *Deflandrea* Eisenack, p. 187

1966c *Deflandrea* Eisenack 1938 emend. Williams & Downie, p. 231

1974 *Deflandrea* Eisenack 1938 emend. Stover, p. 169-170

1976 *Deflandrea* Eisenack 1938 emend. Lentin & Williams, p. 35-36

1978 *Deflandrea* Eisenack 1938 emended Lentin & Williams 1976; Stover & Evitt, p. 99-101

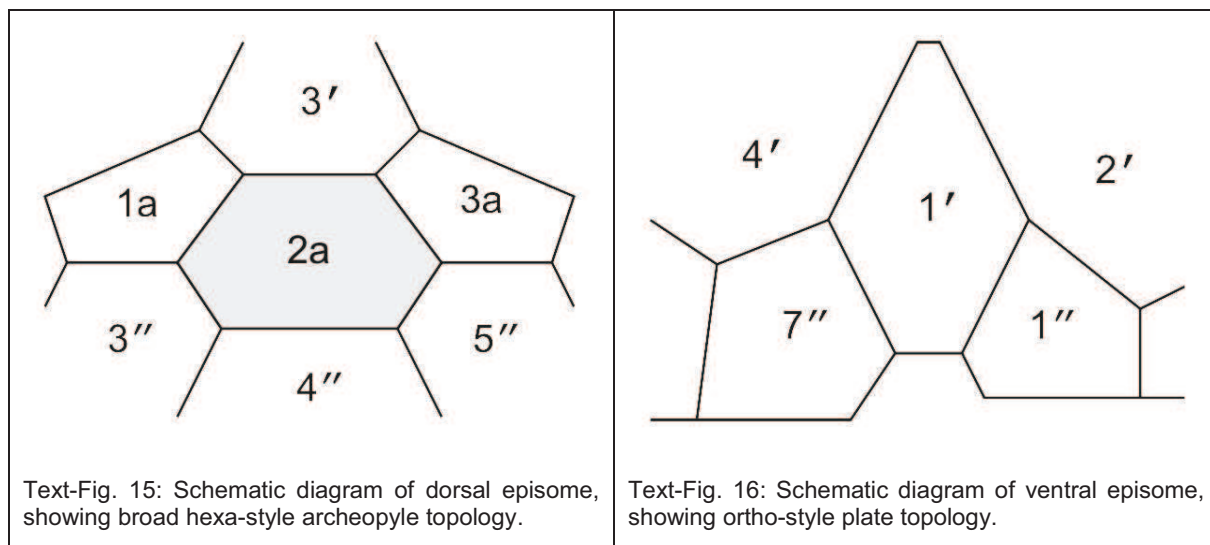
Type Species: Deflandrea phosphoritica Eisenack 1938b, p. 187, text-fig. 6 [Late Eocene-Early Oligocene]

Original Description: [Given for the type species.] *Deflandrea phosphoritica* is characterized by its rounded inner body in apical view, oval in cross section, provided with a transverse band within its flattened, characteristically three pointed outer shell (translation from Eisenack 1938, p. 187, by Stover & Evitt 1978, p. 99).

Remarks: *Deflandrea* and related genera were the subjects of a major revision by Lentin & Williams 1976 (p. 35-45) in which the diagnostic value of the archeopyle shape was explored thoroughly. In particular, the broad hexa style archeopyle (Text-Fig. 15) lends this genus a characteristically high transverse archeopyle index.

It seems to me, though, that *Deflandrea* is still in need of further work. For the present purposes, I have grouped together the species which appear similar and, indeed, to intergrade in at least some cases, such as *D. phosphoritica* and *D. heterophlycta*. I have stopped short of proposing new genera or subgenera to formalise such groupings, however. Doing so may be a very good idea, but will require a broader study than that attempted here.

The ventral episome appears to have an ortho-style configuration (Text-Fig. 16) for most *Deflandrea* species, and a more ambitious reassessment of the genus could make this feature a starting point for an emended diagnosis, as is attempted below for *Phthanoperidinium*. Although this feature is subtle and often difficult to observe, there seems no reason, in principle, to regard it as any less significant than, say, the L-type versus S-type ventral dichotomy used to classify gonyaulacaceans.



Several Australian species of *Deflandrea* which also occur in New Zealand are analysed in Stover 1974.

A range chart for species of *Deflandrea* is provided in Appendix 2, chart 3.

***Deflandrea phosphoritica* Eisenack 1938b**

Pl. 6, figs. 7-12, Pl. 7, figs. 1-9

- 1938b *Deflandrea phosphoritica* Eisenack, text-fig. 6
1953 *Deflandrea phosphoritica* Eisenack; Klumpp, p. 393, pl. 19, fig. 6
1954b *Deflandrea phosphoritica* Eisenack 1938; Eisenack, p. 52-54, pl. 9, figs. 8-12, pl. 12, figs. 8-9, text-fig. 1
1955 *Deflandrea phosphoritica* Eisenack; Deflandre & Cookson, p. 249, pl. 4, fig. 5, text-fig. 5
1960 *Deflandrea phosphoritica* Eisenack; Manum, p. 18-20, figs. 4-8, text-fig. 1
1961 *Deflandrea phosphoritica* Eisenack 1938; Gerlach, p. 150-152, pl. 25, fig. 1
1961b *Deflandrea phosphoritica* Eisenack subsp. *phosphoritica*; Cookson & Eisenack, p. 39, pl. 1, figs. 1, 4
1963 *Deflandrea phosphoritica*; Brosius, p. 36, pl. 5, fig. 1
1965a *Deflandrea phosphoritica* Eisenack; Cookson & Eisenack, p. 121, pl. 11, fig. 11
1965a *Deflandrea granulosa* Cookson & Eisenack, p. 122, pl. 11, figs. 8-9
1966 *Deflandrea phosphoritica*; Eisenack, pl. 60, figs. 3, 7-8
1966c *Deflandrea phosphoritica* subsp. *phosphoritica* Cookson & Eisenack; Williams & Downie, p. 231-232, pl. 26, figs. 3, 9
1967 *Deflandrea phosphoritica*; Agelopoulos, p. 13-14, pl. 1, figs. 1-6
1974 *Deflandrea phosphoritica* Eisenack, 1938; Stover, p. 177-178, pl. 4, figs. 3-4
1982b *Deflandrea phosphoritica* Eis.; Wilson, p. 7, pl. 4, figs. 4-5
1983 *Deflandrea phosphoritica* Eisenack, 1938; Goodman & Ford, p. 864, pl. 1, figs. 1-2
1984 *Deflandrea phosphoritica* Eisenack 1938 s. ampl.; Clowes & Morgans, p. 34, pl. 2, fig. 15
1984d *Deflandrea phosphoritica* Eisenack; Wilson, p. 114, fig. 6 (12)
1994 *Deflandrea phosphoritica*; Stover & Hardenbol, pl. 10, fig. 64
2005 *Deflandrea phosphoritica*; Schiøler, pl. 5, fig. 11

Original Description: *Deflandrea phosphoritica* is characterized by its rounded inner body in apical view, oval in cross section, provided with a transverse band within its flattened, characteristically three pointed outer shell (translation from Eisenack 1938, p. 187, by Stover & Evitt 1978, p. 99).

Description of Study Material: Pericyst fairly large, with pointed apical horn and two relatively pointed antapical horns. Periphragm thin; surface ornamented with scattered grana which may be clustered or linear. Endophragm thicker, up to 2.5 µm; smooth. Intercalary archeopyle broad, up to 45 µm; operculum free, inner and outer layers adherent. Pericingulum apparent to well-defined by parallel rows of grana and by straight to concave profile in dorso-ventral view; width ~7 µm. Sulcus prominent, broad, largely confined to hypocyst. Tabulation peridiniacean, indicated by archeopyle, cingulum, and occasionally by intratabular or penitabular clusters of grana on the pericyst; inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2''', 0-5s.

Size Range: Length = 110 (131) 175 µm (29 measurements). Width = 87 (104) 117 µm (9 measurements).

Distribution: Common.

The published stratigraphic range for *Deflandrea phosphoritica* is broad: at least early Ypresian to early Aquitanian. Previously, however, in New Zealand (pers. obs.; Graeme Wilson pers. comm.) and also in Australia (Alan Partridge pers. comm.), *Deflandrea phosphoritica* has generally been regarded as confined to the Middle Eocene (no older than Bartonian) and younger. Of course the first and last appearances of this, or any, taxon may be strongly diachronous, but in the case of *D. phosphoritica* there are also likely to be questions of taxonomic interpretation complicating the picture (see *Remarks*, below) and we must look more deeply.

For example, Crouch 2001, p. 36, records *Deflandrea phosphoritica* first appearing in her NZE1b subzone (early Waipawan/early Ypresian, C24r), further noting (p. 44) “[a]t Tawanui, *Deflandrea phosphoritica* first occurs at the P/E boundary. This is earlier than recorded from northwest Europe, where it first occurs within the lower part of calcareous nannoplankton Zone NP10 (Bujak and Brinkhuis 1998); this suggests the species may have evolved in a Southern Hemisphere region.” Whereas Crouch’s pl. 3, fig. 2 (p. 52) could conceivably be dismissed as *Deflandrea scabrata*, which is to be expected in sediments of that age, her pl. 3, fig. 1 is much harder to ignore.

The top of its range was not pin-pointed in this study, but may occur in the lowest Oligocene (lower Rupelian) in New Zealand.

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/1, 77	Gerlach 1961
early Oligocene	Samland, Germany	Ph 7	Eisenack 1954b
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f184 (L11933)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f169 (L11918)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
Runangan	North Otago, New Zealand	SM422	Wilson 1984d
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	
Runangan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f098 (L10953)	Clowes & Morgans 1984
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f262 (L13546)	
late Eocene	Wöhrden	W-622-a	Klumpp 1953
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f057 (L09214)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: Deflandrea phosphoritica is at once one of the most familiar dinoflagellate cyst species – almost every study of Eocene material reports it – and one of the most problematic. One source of confusion extends back to at least 1954 when Eisenack incorrectly nominated, as the holotype, a specimen other than that illustrated in his original 1938 publication of the name. Nomenclatural rules require that the holotype of *D. phosphoritica* is the specimen illustrated in Eisenack 1938b, text-fig. 6, and Eisenack 1954b, pl. 9, fig. 11, rather than the specimen Eisenack explicitly designated subsequently (Eisenack 1954b, pl. 9, fig. 8; refer to his figure caption on p. 91).

The distinction is important because there may be more than one species involved. It is quite clear that Eisenack favoured forms with a broad pentagonal “jodhpur” outline to the periphragm as best exemplifying this taxon (e.g. Eisenack 1954b, p. 52-54, pl. 9, fig. 8; Eisenack 1966, pl. 60, figs. 3, 7-8; also see Text-Fig. 17, herein). This particular form differs from the New Zealand pentagonal forms attributed herein to *Deflandrea phosphoritica*, in possessing a seemingly perfectly smooth periphragm and a periarcheopyle which extends upwards almost to the tip of the apical horn, but is otherwise the same.

Another source of difficulty is immediately apparent from a review of the plates. It is evident that *D. phosphoritica* intergrades with several other forms in shape and in the ornamentation of the endocyst.

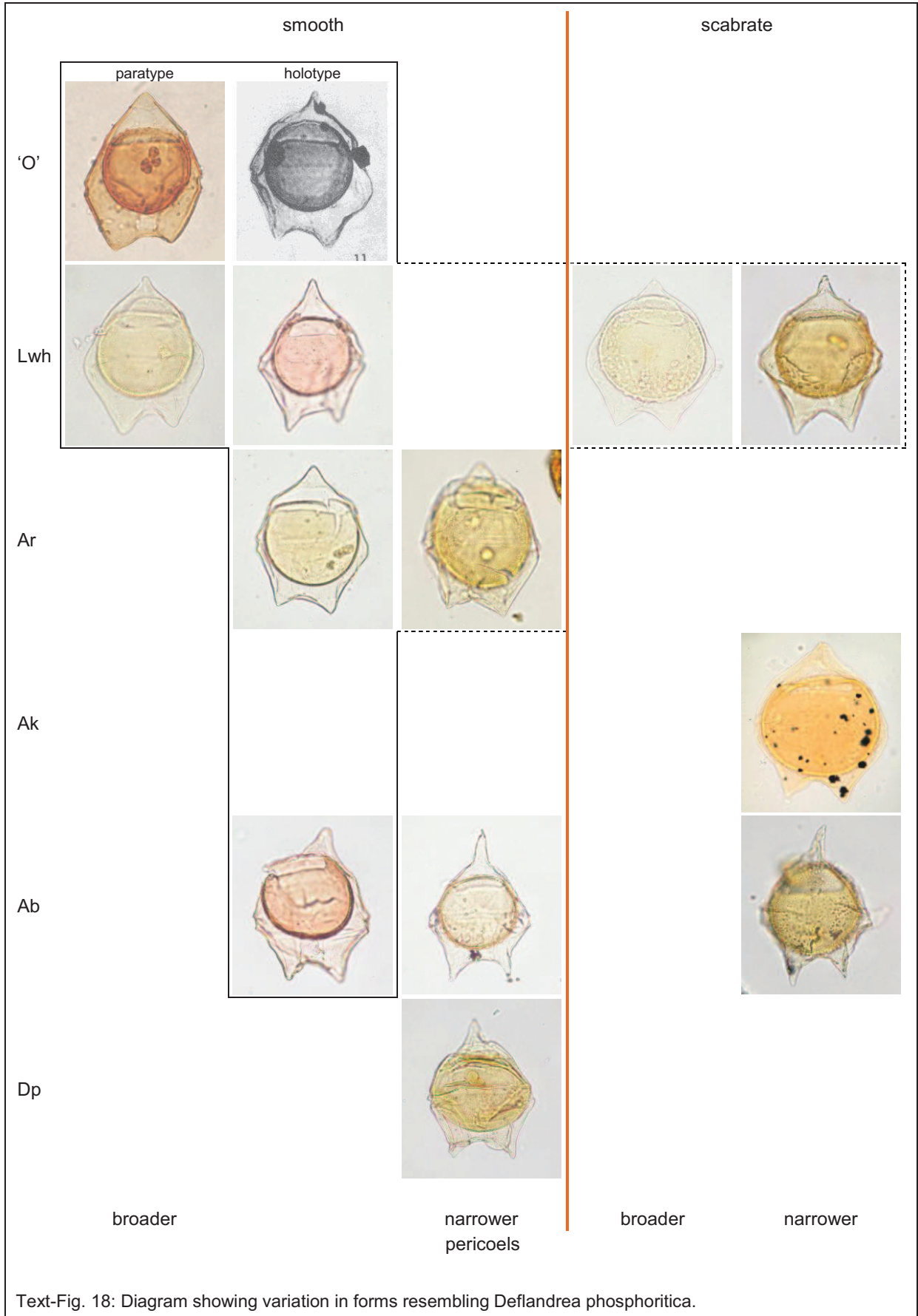
So, what is *Deflandrea phosphoritica*? And is it confined to only the uppermost Eocene and early Oligocene or does it extend into older rocks? Several dimensions of the variation discussed above are represented in Text-Fig. 18. There may be some age-significance in this variation, though it is not easy to discern any linear trends.

Deflandrea granulosa is identified as a junior synonym by Stover 1974 (p. 177). Observations made in the



Text-Fig. 17: Paratype of *Deflandrea phosphoritica*; the specimen apparently favoured by Eisenack to typify the species.

course of this study are quite consistent with this view.



Text-Fig. 18: Diagram showing variation in forms resembling *Deflandrea phosphoritica*.

Deflandrea aff. phosphoritica

Pl. 7, figs. 10-12, Pl. 8, figs. 1-6

2005 *Deflandrea heterophlycta* Deflandre & Cookson 1955; Heilmann-Clausen & Van Simaey, pl. 3, fig. 10

Description of Study Material: Cysts large, proximate, only slightly dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome and hyposome more or less equal in length. Apex more or less conical, episome more or less straight-sided; antapical horns strongly developed. Lateral pericoels strongly developed. Archeopyle intercalary, type I (2a); eurydeltaform. Surface of endophragm verrucate. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2"', 0-5s. Cingulum moderately expressed, indicated by folds in the periphragm, 10-12 µm wide; offset not readily visible on ventral surface.

Size Range: Length including any processes = 123 (134) 149 µm (6 measurements). Width including any processes = 102 (109) 117 µm (6 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Priabonian	Kysing Marl, Kysing-4 Borehole, central Danish Basin, eastern Jylland, Denmark	1928	Heilmann-Clausen & Van Simaey 2005

Remarks: A ?variety of *Deflandrea phosphoritica* having a scabrate endocyst, but retaining all other characters of the species, notably the characteristic periphragm outline and associated relative development of the pericoels (cf. *D. heterophlycta*).

Cookson & Eisenack 1965a, p. 121, comments "Specimens with the general characteristics of *D. phosphoritica*, but with tuberculate thickenings on the wall of the capsule, similar to, but less prominent than those of *D. heterophlycta*, are not uncommon in the upper beds of the Browns Creek section. Furthermore, the shape of the shell differs from that of the holotype of *D. heterophlycta* and more particularly that of additional specimens of this species recently isolated from the type locality at Castle Cove, Victoria."

The authors were clearly making a distinction between a scabrate *D. phosphoritica* and *D. heterophlycta*, most usefully on the basis of its different periphragm shape. Such a distinction is supported by observations from the present study, but, although some specimens of the "scabrate *D. phosphoritica*" differ markedly from *D. heterophlycta* in possessing a far more pronounced cingulum underlain by well-developed pericoels, it will be seen that many intermediates (e.g. Pl. 8, figs. 1-3) provide an insensible gradation from one to the other.

***Deflandrea ?heterophlycta* Deflandre & Cookson 1955**

Pl. 8, figs. 7-12, Pl. 9, figs. 1-9

?1955 *Deflandrea heterophlycta* Deflandre & Cookson, p. 249-250, pl. 5, fig. 6, text-fig. 5

1982b *Deflandrea heterophlycta* Defl. & Cooks.; Wilson, p. 7, pl. 4, fig. 11

1982b *Deflandrea heterophlycta* Defl. & Cooks.; Wilson, p. 7, pl. 2, fig. 10

1983 *Deflandrea heterophlycta* Deflandre and Cookson, 1955; Goodman & Ford, p. 864, pl. 1, fig. 3

1984 *Deflandrea phosphoritica* Eisenack 1938 s. ampl.; Clowes & Morgans, p. 34, pl. 2, fig. 16

1996 *Deflandrea cf. heterophlycta* Deflandre & Cookson; Wilson & McMillan, fig. 3 (7)

2005 *Deflandrea heterophlycta*; Schiøler, pl. 11, fig. 10

Original Description: Epitheca broadly conical with slightly convex flanks and a somewhat rounded, unthickened apex; hypotheca a little smaller than the epitheca and provided with 2 short, blunt, slightly divergent horns. Transverse girdle clear but shallow. Cyst spheroidal, ornamented with irregularly dispersed tubercles more numerous and coarser towards the poles. Cyst membrane finely punctate. Opening laterally extended situated towards the apical pole. Membrane of theca very finely and sparsely punctate (Deflandre & Cookson 1955, p. 249-250).

Description of Study Material: Cysts large, proximate, only slightly dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns. Apical horn well developed, apex more or less conical to

pointed, episome somewhat attenuated to markedly attenuated; antapical horns strongly developed, relatively pointed. Cyst wall two-layered; circumcavate, lateral pericoels developed to strongly developed; endophragm thicker than periphragm, up to 2.5 µm in thickness. Archeopyle intercalary, type I (2a); eurydeltaform; operculum free, inner and outer layers adherent. Processes lacking; surface ornament present, non-tabular, comprising scattered grana; occasionally forming lineations, especially along the margins of the cingulum. Surface of endophragm scabrate to tuberculate, often coarser below the cingulum. Tabulation weak to lacking, peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', Ops, 2''', Xs. Cingulum clearly expressed, indicated by shape of the periphragm, 8-10 µm wide. Sulcus clearly expressed, indicated by depression of the periphragm; largely confined to the hyposome.

Size Range: Length including any processes = 98 (118) 153 µm (33 measurements). Width including any processes = 82 (90) 100 µm (8 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f115 (L11051)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: Deflandre & Cookson 1955 illustrates the holotype of *Deflandrea heterophlycta* with a line drawing (text-fig. 5). The specimen appearing in the plates (pl. 5, fig. 6) is a paratype: an isolated endocyst. To the best of my knowledge, there is no published photograph of the holotype. Topotype material (Castle Cove, Victoria, Australia) subsequently illustrated by Cookson & Eisenack 1965a (pl. 12, figs. 1-4), however, appears quite similar to the line drawing of the holotype.

As noted above, Cookson & Eisenack 1965a, p. 121, distinguished between scabrate forms of *Deflandrea phosphoritica* and *D. heterophlycta*, the former having "tuberculate thickenings on the wall of the capsule, similar to, but less prominent than those of *D. heterophlycta*" and a different shape to the periphragm. As noted above, the periphragm shape is continuously variable across both smooth and scabrate/tuberculate forms. Subsequent studies suggest that the prominence of the tuberculae may be highly variable and, in fact, those of the Castle Cove (holotype and topotype) specimens appear quite extreme compared to most other published material. Specimens of *D. heterophlycta* recovered from the Gippsland Basin rarely exhibit tubercles as tall as those of the type, more typically resembling the present form (Alan Partridge pers. comm.)

The present material is considerably less tuberculate than the Castle Cove specimens, but agrees in other respects with the concept of *D. heterophlycta* as usually applied in Australasia.

Deflandrea ?heterophlycta differs from *Deflandrea scabrata* Wilson 1988 in lacking the thick (up to 6 µm), spongy endocyst.

***Deflandrea* sp. 3**

Pl. 9, figs. 10-12, Pl. 10, figs. 1-9

Description: Cysts large, proximate, only slightly dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome and hyposome more or less equal in length. Apex more or less attenuated, episome more or less straight-sided; antapical horns strongly developed and also somewhat attenuated. Lateral pericoels moderately to strongly developed. Archeopyle intercalary, type I (2a); eurydeltaform. Surface of endophragm finely to moderately scabrate. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', Ops, 2''', 0-5s. Cingulum well expressed by folds in the periphragm, ~10 µm wide; offset not readily visible on ventral surface.

Size Range: Length including any processes = 127 (127) 127 µm (3 measurements). Width including any processes = 82 (85) 88 µm (3 measurements).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Age/Stage	Location	Sample	Sample Reference
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	

Remarks: Differs from *Deflandrea phosphoritica* in its longer, more attenuated horns, especially the apical horn, and from *Deflandrea oebisfeldensis* in having a smaller antapical pericoel which is more wholly incorporated into the antapical horns.

***Deflandrea cygniformis* Pöthe de Baldis 1966**

Pl. 10, figs. 10-12, Pl. 11, figs. 1-3

1966 *Deflandrea cygniformis* Pöthe de Baldis, p. 221, pl. 2, fig. c

1975 *Deflandrea cygniformis* Pöthe de Baldis; Haskell & Wilson, pl. 1, fig. 14

cf. 1984b *Deflandrea* cf. *D. cygniformis* Pöthe de Baldis, 1966; Helenes, p. 94, 104, pl. 5, figs. 15-16

1988 *Deflandrea cygniformis* Pöthe de Baldis 1966 Wrenn & Hart, p. 350, fig. 20, 2-5, fig. 21, 1-4, fig. 42, 3-5, fig. 44, 4

?2000 *Deflandrea* cf. *D. cygniformis* Pöthe de Baldis, 1966; Levy & Harwood, p. 206, pl. 3, figs. d-e

Original Description: [Diagnosis] Theca fusiform and elongated, surface finely granulated. Epitheca three times larger than the hypotheca. Hypotheca with poorly defined antapical appendages, which terminate in an irregular edge. Cyst sub-rounded, large, occupying a little more than half of the specimen. The opening of the dorsal face is also large and ovoid. The cingulum is narrow, poorly demarcated with a smooth edge.

[Description] All specimens examined possess, in general, the same characteristics, although some variations exist with respect to the length of the epitheca with respect to the rest of the theca, but nevertheless maintaining this variation within specific characters. The theca has a pentagonal outline, is fusiform, and may exhibit either granulate or somewhat plain surface. The epitheca is much higher than the hypotheca. After separating itself from the cyst, the epitheca converges smoothly and uniformly, forming a long neck. In its lower part the epitheca is separated a little from the cyst, whereas the hypotheca is found completely separated from it. The cingulum is excavated and its border is plain or very finely granulate. The cyst is of oval form, and its larger diameter is the transverse. In all the samples observed one does not observe a good development of the antapical appendages, from which it is believed that the form in which they are found is their typical form. The antapical appendages are united, forming an irregular border (translated from Pöthe de Baldis 1966, p. 221).

Description of Study Material: Cysts large, proximate, not appreciably dorso-ventrally compressed, outline peridinioid, with one apical horn; episome much longer than hyposome. Apical horn extraordinarily developed, apex pointed, episome markedly attenuated; antapical horns weak to lacking. Lateral pericoels developed. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2''', 0-5s. Cingulum clearly expressed, indicated by shape of the periphragm. Sulcus weakly expressed to moderately expressed, indicated by folds in the periphragm.

Size Range: Length including any processes = 120 µm (one measured specimen). Width including any processes = 72 µm (one measured specimen).

Distribution: Very rarely encountered in this study. The global distribution of *D. cygniformis* includes a number of southern and, possibly, Pacific localities, and at least some correspondence with elements of the Trans-Antarctic assemblage (Appendix 3).

Age/Stage	Location	Sample	Sample Reference
late middle Eocene-late Eocene	northern Seymour Island, West Antarctica	8455	Wrenn & Hart 1988
late middle Eocene-late Eocene	northern Seymour Island, West Antarctica	8479	Wrenn & Hart 1988
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Lutetian	Bateque Formation; Sebastian Vizcaino Basin, Baja California		Helenes 1984b
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000

Remarks: A distinctive taxon, though apparently very rare on mainland New Zealand.

Wrenn & Hart 1988 (p. 350) notes that "*D. cygniformis* is similar to *D. antarctica* and may prove to be an evolutionary offshoot of that species." To me, however, they look no more similar than any other pair of *Deflandrea* species, and less so than many.

Deflandrea sp. 4

Pl. 11, figs. 4-6

Description: Cysts large, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome slightly longer than the hyposome. Apex slightly attenuated; antapical horns well developed, rounded, sub-equal. Pericoels characterised by numerous lamellae apparently connecting the endocoel with the periphragm, imparting a reticulate pattern to the latter when viewed end-on; lateral pericoels well developed. Archeopyle intercalary, type I (2a); eurydeltaform. Surface of endophragm smooth to finely scabrate (the described specimen may be somewhat corroded). Tabulation not indicated by any surface features or by the pericoel lamellae; assumed to be peridiniacean. Cingulum moderately expressed by folds in the periphragm, ~12 µm wide; offset not readily visible on ventral surface.

Size Range: Length including any processes = 117 µm (one measured specimen). Width including any processes = 92 µm (one measured specimen).

Distribution: Extremely rare. Known from a single specimen only.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	

Remarks: The single specimen of this form is remarkable for highly unusual infilling between the endocyst and periphragm. It is unknown if it is a genuine character or a taphonomic effect.

Deflandrea antarctica Wilson 1967a

Pl. 11, figs. 7-12

- 1967a *Deflandrea antarctica* Wilson, p. 58, 60, figs. 23-24, 26-27
1975 *Deflandrea antarctica* Wilson; Haskell & Wilson, pl. 1, fig. 12
1982c *Deflandrea antarctica* Wilson; Wilson, p. 4, pl. 1, figs. 1-4
1983 *Deflandrea antarctica* Wilson, 1967; Goodman & Ford, p. 864, pl. 1, figs. 4-6
1988 *Deflandrea antarctica* Wilson 1967; Wrenn & Hart, p. 349, fig. 19, 1-4, fig. 44, 3
1989 *Deflandrea antarctica* Wilson; Wilson, pl. 1, fig. 1
2000 *Deflandrea antarctica* Wilson, 1967; Levy & Harwood, p. 204, 206, pl. 2, figs. c-e, pl. 3, figs. a-c

Original Description: Test peridinioid in shape, bi-layered, divided into epitheca and hypotheca by a slightly laevorotatory transverse girdle. Apical horn broad at base, narrow at apex which is usually capped with a small papilla; antapical horns short, approximately equal in size. Outer cyst usually covered with numerous granules forming a dotted pattern. Inner cyst fairly thick-walled, smooth, and approximately circular in outline. Archeopyle broad, intercalary, subhexagonal. Operculum free, bi-layered; inner layer smaller, denser, and of more regular shape than the membranous outer layer; the large and small layers of the operculum represent segments of the outer and inner cysts respectively.... Apparently atabulate, although granules sometimes concentrated into polygonal clusters possibly indicative of reflected tabulation (Wilson 1967a, p. 58, 60; ellipses replace figure references in the original).

Description of Study Material: Cysts large, proximate, not dorso-ventrally compressed, outline peridinioid, with one apical horn; episome longer than hyposome. Apex with nipple-like projection, episome inflated (more or less bell-shaped); antapical horns weak to lacking. Lateral pericoels weakly developed. Archeopyle intercalary, type I (2a); eurydeltaform; operculum free. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2"', 0-5s. Cingulum moderately expressed, indicated by shape of the periphragm.

Size Range: Length including any processes = 105 (115) 125 µm (4 measurements). Width including any processes = 65 µm (one measured specimen).

Distribution: The strict form of *D. antarctica* (see remarks provided under *D. aff. antarctica*, below), though widely reported from Antarctica and environs, is apparently quite rare on the New Zealand mainland.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
mid Eocene	DSDP Leg 71, Falkland Plateau, south Atlantic Ocean	512-18-3, 14-16 cm	Goodman & Ford 1983
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
late early Eocene	northern Seymour Island, West Antarctica	8465	Wrenn & Hart 1988

Age/Stage	Location	Sample	Sample Reference
late early Eocene	northern Seymour Island, West Antarctica	8506	Wrenn & Hart 1988
Mangaorapan	Oxford area, central Canterbury, New Zealand	SM1556, 1645	Wilson 1982c
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	SM3781	Wilson 1989
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4737	Wilson 1967a
Eocene	erratics, McMurdo Sound, Antarctica	MTD 1B	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000

Deflandrea aff. antarctica

Pl. 12, figs. 1-3

1967 *Deflandrea oebisfeldensis* Alberti; Cookson & Cranwell, p. 205, pl. 1, figs. 1-4

1988 *Deflandrea antarctica* Wilson, 1967; Wilson, p. 17, pl. 5, figs. 5-7

Description: Cysts large, proximate, outline peridinioid, with one apical and two antapical horns; episome much longer than hyposome. Apex more or less conical, episome more or less straight-sided; antapical horns weak to lacking. Lateral pericoels weak to lacking. Archeopyle intercalary, type I (2a); eurydeltaform. Inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2''', 0-5s. Cingulum moderately expressed, indicated by folds in the periphragm.

Description of Study Material: Cysts large, proximate, outline peridinioid, with one apical and two antapical horns; episome much longer than hyposome. Apex more or less conical, episome more or less straight-sided; antapical horns weak to lacking. Lateral pericoels weak to lacking. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2''', 0-5s. Cingulum moderately expressed, indicated by folds in the periphragm.

Size Range: Length including any processes = 123 (137) 150 µm (7 measurements). Width including any processes = 68 µm (one measured specimen).

Distribution: Common.

Age/Stage	Location	Sample	Sample Reference
late Eocene-Oligocene	Leña Dura Formation, Río Leña Dura valley, SW of Punta Arenas, Chile	JSB-56	Cookson & Cranwell 1967
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Porangan	Waipawa standard section, Hawkes Bay, New Zealand	V22/f7401 (L976)	Wilson 1988
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Waipawan	Waipawa standard section, Hawkes Bay, New Zealand	V22/f7400 (L12098)	Wilson 1988

Remarks: *Deflandrea antarctica* s.s. (erratics, Minna Bluff, Antarctica; Wilson 1967a) is characterised by an inflated, bell-shaped episome capped by a small, nipple-like horn, which is very distinctive. Later, however, Wilson (1988) illustrated a slightly different form, also under the name *D. antarctica*, which differs from the type material in possessing an essentially straight-sided, conical episome. He explained his identification of the two morphotypes by noting that “[t]he type Antarctic material possesses a more rounded epicyst with a short apical horn, although that material varies more than is indicated by the illustrated specimens (Wilson 1967a and unpublished data)” (Wilson 1988, p. 17).

Between *Deflandrea antarctica* s.s. and *D. antarctica* sensu Wilson 1988 lies a range of forms, here recorded as *Deflandrea aff. antarctica*, in which the shape of the episome varies, apparently continuously, between the two extremes. It is difficult to assign any age significance to the difference, owing to continuing uncertainty over exact age correlation between assemblages from Antarctica (typically confused by wholesale reworking) and those from lower latitudes, including New Zealand.

Wilson 1988, p. 17, notes that *Deflandrea antarctica* – both s.s. and s.l. varieties – “is possibly conspecific with” *Deflandrea flounderensis* Stover 1974. However, he did not formally propose synonymy.

As further noted by Wilson (1988, p. 17), “*Deflandrea medcalfii* Stover is similar in many respects but differs in having a longer and narrower apical horn, a smooth and thinner endophragm, and by having distinctly separated, longer, antapical horns.”

***Deflandrea convexa* Wilson 1988**

Pl. 12, figs. 4-12

1988 *Deflandrea convexa* Wilson, p. 17, pl. 6, figs. 3-5

Original Description: Pericyst intermediate to large, ovoidal, elliptical to almost circular in dorso-ventral view with a subrounded apex and broadly convex antapical margin lacking horns. Surface finely reticulate, 1-1.5 µm thick. Paracingulum may be defined by lineation of reticulum; on other specimens it is not seen. Parasulcus defined by narrow smooth area on ventral surface of some specimens. Endocyst circular, smooth, slightly thicker walled than pericyst (2-3 µm). Narrow pericoels (length up to 12 µm) are developed only at the apex and antapex. Intercalary archeopyle broad (width 37-42 µm), hexagonal; operculum free and comprises two adherent pieces from periphragm and endophragm (Wilson 1988, p. 17).

Description of Study Material: Cysts of intermediate size, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical horn; episome longer than hyposome. Apex rounded to subconical, episome more or less straight-sided; antapical horns weak to lacking. Lateral pericoels absent. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation not indicated by surface features; assumed to be peridiniacean. Generally not indicated.

Size Range: Length including any processes = 66 (91) 105 µm (15 measurements). Width including any processes = 61 (80) 98 µm (11 measurements).

Distribution: Infrequent. Generally infrequent, but one notable sample (L23126, U24/f418) is dominated by the species.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	

Remarks: The strict form is relatively old – Porangan to perhaps earliest Bortonian – but there is also a younger form higher in the Bortonian (Pl. 12, figs. 10-12) which looks very similar but may differ systematically in possessing a hypopericoel which extends up and laterally as far as the cingulum.

***Deflandrea ?leptodermata* Cookson & Eisenack 1965a**

Pl. 13, figs. 1-3

?1965a *Deflandrea leptodermata* Cookson & Eisenack, p. 121-122, pl. 11, figs. 6-7

1974 *Deflandrea leptodermata* Cookson & Eisenack, 1965; Stover, p. 177, pl. 5, figs. 1a, 1b

1984 *Deflandrea* aff. '*leptodermata*' sensu Stover 1974; Clowes & Morgans, p. 34, pl. 2, fig. 14

2005 *Deflandrea leptodermata*; Schiøler, pl. 15, fig. 11-12

Original Description: Shell untabulated, longer than broad with strongly convex sides, a short blunt apical horn and two short, broad, slightly pointed antapical horns. Girdle usually not indicated. Wall of shell thin, distinctly granular. Capsule large, circular in outline, almost filling the shell, wall very thin and densely granular. Archeopyle usually indistinctly outlined, broader than long, possibly 6-sided. In the specimen shown in Pl. 11, fig. 7 [the single paratype, like the holotype, apparently badly corroded] the basal suture of the archeopyle is evident as a fine line crossing the upper part of the shell at a right angle (Cookson & Eisenack 1965a, p. 121-122).

Description of Study Material: Cysts large, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome longer than hyposome. Apex rounded to subconical, episome more or less straight-sided; antapical horns developed. Lateral pericoels weakly developed. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation not indicated by surface features; assumed to be peridiniacean. Cingulum weakly expressed, indicated by shape of the periphragm.

Size Range: Length including any processes = 97 (115) 138 µm (6 measurements). Width including any processes = 98 (100) 101 µm (2 measurements).

Distribution: Occurs infrequently in the present study material. The type material from the Browns Creek Clays, southwest Victoria, Australia, is recorded as "Upper Eocene" Cookson & Eisenack 1965a) but this date is not well-constrained.

Age/Stage	Location	Sample	Sample Reference
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f259 (L13545)	
Runangan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f098 (L10953)	Clowes & Morgans 1984
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: As noted in Clowes & Morgans 1984, p. 34, the forms attributed to *D. leptodermata* by Stover 1974, p. 177, pl. 5, figs. 1a-b, possess a very broad archeopyle, "a feature which is not apparent from the holotype illustration" of Cookson & Eisenack 1965a (pl. 11, fig. 6). It is assumed that Stover may have been able to determine the archeopyle width from his re-examination of the type material, but some uncertainty surely remains.

***Deflandrea micropoda* Cookson & Eisenack 1974**

Pl. 13, figs. 4-6

1974 *Deflandrea micropoda* Cookson & Eisenack, p. 49, pl. 27, fig. 11

?1975 *Deflandrea cornumammillata* Jan du Chêne & Chateaufeuf, p. 31-32, 34, pl. 2, figs. 1-13

Original Description: Overall shape is oval, with an apex shaped in the form of a slight arch and a straight-edged antapex, with two nearly equal, widely separated and very short antapical horns, no indication of a girdle or a longitudinal furrow. Periphragm is smooth and transparent with thin walls. The endophragm has a somewhat elliptical outline, is also smooth but has thick walls, crossing the archeopyle in its centre in the epitract, in the hypotract a narrow zone is left free at the antapex.

Archeopyle in the periphragm close under the apex, wide hexagonally rounded. Cap still in situ (Cookson & Eisenack 1974, p. 49).

Description of Study Material: Cysts of intermediate size, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns, characterised by small, nipple-like thickenings of the periphragm at the tips; episome and hyposome more or less equal in length. Apex rounded to subconical, episome more or less straight-sided; antapical horns weak to lacking. Lateral pericoels developed below the cingular region. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation not indicated by surface features; assumed to be peridiniacean. Cingulum weakly indicated.

Size Range: Length including any processes = 100 µm (one measured specimen). Width including any processes = 80 µm (one measured specimen).

Distribution: Very rare. Only one specimen found in the present study.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: Considered to be a junior synonym of *Deflandrea leptodermata* by Stover & Evitt 1978 (p.101), and there appears some substance to this view. Other than papillae terminating the antapical horns there seems little to distinguish them; the one specimen found in the present study may very well be an outlier of *D. leptodermata*.

***Deflandrea* sp. 1**

Pl. 13, figs. 7-9

Description: Cysts of intermediate size, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two weakly developed antapical horns; episome and hyposome more or less equal in length. Apex rounded to subconical, episome more or less straight-sided; antapical horns small and bluntly rounded. Lateral pericoels developed below the cingular region. Archeopyle intercalary, type I (2a); eurydeltaform. Tabulation not indicated by surface features; assumed to be peridiniacean. Cingulum very weakly indicated.

Distribution: Extremely rare. Only one encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f106 (L11042)	

Remarks: This form, which is known from a single specimen, is nevertheless highly distinctive, and included in the hope that further specimens may be encountered.

***Deflandrea totara* Clowes n. sp.**

Pl. 13, figs. 10-12, Pl. 14, figs. 1-3

1984 *Deflandrea* sp. 2; Clowes & Morgans, p. 37, pl. 2, figs. 17-18

Derivation of Name: Named after the type formation: the Totara Limestone.

Holotype: Sample J42/f096, slide L10951/SM091; Totara Limestone, Kakanui River (early Whaingaroan); Pl. 13, figs. 10-11

Description: Cysts large, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome longer than hyposome. Apex more or less conical, episome more or less straight-sided; antapical horns developed. Lateral pericoels weak to lacking. Archeopyle intercalary, type I (2a); eurydeltaform; ratio (AR) about 0.5; operculum free. Tabulation not indicated by surface features; assumed to be peridiniacean. Cingulum clearly expressed, indicated by folds in the periphragm. Sulcus weakly expressed to moderately expressed, indicated by folds in the periphragm.

Size Range: Length including any processes = 112 (124) 135 μ m (9 measurements). Width including any processes = 92 (96) 98 μ m (5 measurements).

Distribution: Common. Apparently of limited stratigraphic occurrence, nevertheless, it is often occurs commonly where it occurs at all.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f064 (L09221)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985

Comparison: *Deflandrea totara* most closely resembles *D. leptodermata*, but differs in possessing a narrower archeopyle, a higher, more conical apical horn, and a periphragm which is more closely appressed to the endocyst laterally. It is readily distinguished from *D. phosphoritica* and similar forms with well-developed well-developed pericoels below the cingulum, because it typically possesses almost none, and from *D. antarctica* in its shorter, less inflated apical horn.

***Deflandrea* sp. 2**

Pl. 14, figs. 4-6

Description: Cysts large, proximate, somewhat dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome and hyposome or more or less equal length. Apex quite pointed and more or less conical, episome more or less straight-sided; antapical horns also quite pointed, developed unequally. Lateral pericoels developed below the cingular region. Archeopyle intercalary, type I (2a); eurydeltaform; ratio (AR) about 0.5; operculum free. Tabulation not indicated by surface features; assumed to be peridiniacean. Cingulum moderately well expressed, indicated by folds in the periphragm. Sulcus weakly expressed to moderately expressed, indicated by folds in the periphragm.

Distribution: Very rare; only a single specimen recorded in the present study.

Age/Stage	Location	Sample	Sample Reference
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	

Genus *Alterbidinium* Lentin & Williams 1985 emend. Khowaja-Ateequzzaman et al. 1991

- 1967 *Albertia* Vozzhennikova, p. 150-151
1976 *Alterbia* Lentin & Williams, p. 47-48
1978 *Alterbia* Lentin & Williams 1976; Stover & Evitt, p. 92-93
1985 *Alterbidinium* Lentin & Williams, p. 14
1991 *Alterbidinium* Lentin & Williams 1985 emend. Khowaja-Ateequzzaman et al., p. 38

Type Species: Alterbidinium recticorne (Vozzhennikova 1967, p. 151-152, pl. 77, figs. 1-4; pl. 78, figs. 1-3; pl. 79, figs. 1-2) Harker & Sarjeant 1990, p. 104 [Cretaceous (Turonian)]

Original Description: Theca pentagonal, rhomboid, subdivided into almost equal parts [presumably by the cingulum]. Epithea bell-shaped, triangular with a small apical horn. Hypotheca with one or two unequal antapical horns. Transverse furrow equatorial, annulate; longitudinal furrow situated on hypotheca and extends to the antapex. Internal body has the same outline of that of the theca. Pylome triangular with rounded or truncated angles, thus appearing somewhat trapeziform (translated from Vozzhennikova 1967, p. 150-151, by Lees 1971, reproduced in Stover & Evitt 1978, p. 92).

Remarks: *Alterbidinium* (as *Alterbia*) and related genera were the subjects of a major revision by Lentin & Williams 1976 (p. 47-50) in which the diagnostic value of the archeopyle shape was explored. Note, however, that the transverse archeopyle ratio value given for *Alterbia* in text-fig. 5A is incorrect [R is given as 0.92; it should be 0.86] and in tables 6 & 7 the transverse archeopyle index and ratio values are mutually inconsistent [if I is 0.33, then R must be 0.49, not 0.57, whereas if R is 0.57, then I must be 0.36, not 0.33].

Stover & Evitt 1978, p. 93, notes that *Alterbidinium* differs from *Senegalinium* in having an epipericoel which is in communication with the exterior through the archeopyle, and in having a reduced or absent right antapical horn instead of two nearly equally developed antapical horns. However, Goodman & Ford 1983 reports populations of *Alterbidinium distinctum* (as *Alterbia distincta*) from the upper Eocene of the Falklands Plateau (DSDP Hole 511) which display archeopyles where communication between the epipericoel and the exterior is variable. Goodman & Ford go on to suggest that "archeopyle morphology should possibly be treated as an intergeneric variable rather than a generic character for these taxa" (p. 864). Although this cautious statement stops short of proposing any synonymy, it definitely amounts to a warning shot across the bows. (Note also that Herngreen 1975, p. 60-61, considers *Senegalinium* to be a junior synonym of *Deflandrea*.)

Eucladinium is also similar to *Alterbidinium* in having a reduced right antapical horn, but is mainly epicavate rather than circumcavate (Stover & Evitt 1978, p. 93).

Alterbidinium cf. acutulum (Wilson 1967b) Lentin & Williams 1985

Pl. 14, figs. 10-12

Original Description: Test narrow, bi-layered, comprising smooth outer cyst tapering at poles, and small inner cyst. Apical horn long ($l = 22-32 \mu$), bluntly terminated. Right antapical horn long ($l = 14-36 \mu$), pointed. Left antapical horn absent, but position represented by minor angularity in margin of outer cyst. Archeopyle long, narrow, intercalary, situated on dorsal epithea; operculum hinged to shell by posterior margin. Spiral transverse girdle represented by a folding of outer cyst (Wilson 1967b, p. 225-226).

Size Range: Length including any processes = 57 (64) 70 μ m (2 measurements). Width including any processes = 45 (48) 51 μ m (2 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	

Remarks: A few specimens resembling *A. acutulum*, at least superficially, were encountered in the present study. However, the identification seems unlikely: if they really are *A. acutulum*, then they would extend the known stratigraphic range of that species from the Late Cretaceous to the Eocene.

Genus *Cerodinium* Vozzhennikova 1963 emend. Lentin & Williams 1987

- 1963 *Cerodinium* Vozzhennikova, p. 181
1963 *Ceratiopsis* Vozzhennikova, p. 181
1980b *Ceratiopsis* Vozzhennikova, 1967 [sic] emend. Bujak et al., p. 27
1987 *Cerodinium* Vozzhennikova 1963 emend. Lentin & Williams, p. 114
1988 *Ceratiopsis* Vozzhennikova, 1963 emend. Bujak et al., 1980c; Wilson, p. 15

Type Species: Cerodinium sibiricum Vozzhennikova 1963, p. 181, text-figs. 9-10 [Paleocene-Eocene]

Original Description: Cells spherical or lenticular, with one apical and two widely spaced antapical horns. Girdle annular; longitudinal furrow present on hypovalve. Width of furrow varies. Membrane thin, delicate, smooth hyaline. Internal body occupies the whole cell cavity, which is darker than the membrane (translation from Vozzhennikova 1963, p. 181, by Lentin & Williams 1976, p.154).

Remarks: *Cerodinium* is treated as a junior synonym of *Deflandrea* by, for example, Lentin & Williams 1976 (p.154) which notes similarities between the type species, *C. sibiricum* and *Deflandrea oebisfeldensis*. This treatment was followed for some years, for example by Stover & Evitt 1978 (p. 99) and Lindgren 1984 (p. 153).

A subsequent analysis by Lentin & Williams (1977b, p. 20) reinstated *Ceratiopsis* and transferred the former *Cerodinium* species, *C. sibiricum* and *C. balticum*, into that genus.

Lindgren (1984, p. 153-154) reverted to the earlier approach, regarding both *Cerodinium* and *Ceratiopsis* as junior synonyms of *Deflandrea*, and further pointing out that *Ceratiopsis* Vozzhennikova 1963 is a junior homonym of *Ceratiopsis* De Wildeman 1896, a fungus.

In 1987, however, Lentin & Williams (p. 114) again resurrected the *Cerodinium/Ceratiopsis* concept, this time using *Cerodinium* as the name-bearer and, generally, the genus has remained in use since.

Lentin & Williams 1987, p. 113, notes that: "*Ceratiopsis* and *Cerodinium* were considered to be congeneric by Lentin and Williams (1976) who gave priority to the name *Ceratiopsis*." In fact, the analyses of *Ceratiopsis* and *Cerodinium* provided in Lentin & Williams 1976, on pages 153 and 154 respectively, do not reference one another at all, and both genera, as noted above, are considered to be junior synonyms of *Deflandrea*. It seems likely that this was a simple reference error, and that the authors mistakenly referenced Lentin & Williams 1976 when they meant Lentin & Williams 1977b, in which *Cerodinium* and *Ceratiopsis* are indeed interpreted as synonyms of one another, but distinct from *Deflandrea* (p. 22).

The convoluted nomenclatural history notwithstanding, the status of this genus remains unconvincing. Lentin & Williams 1987, p. 114, concludes that *Cerodinium* differs from *Deflandrea* in possessing an isodeltaform rather than a latideltaform [= eurydeltaform] archeopyle. In preparing a dataset from which to build a key for *Deflandrea* species, however, archeopyle ratios for numerous similar taxa were compared and, at ~0.85, that of *Cerodinium dartmoorium* hardly stands out as remarkable.

***Cerodinium medcalfii* (Stover 1974) Lentin & Williams 1987**

Pl. 15, figs. 1-6

- 1974 *Deflandrea medcalfii* Stover, p. 175-176, pl. 3, figs. 3a-c, text-fig. 3G, 6C
1976 *Deflandrea dartmooria* subsp. *medcalfii* (Stover 1974, p. 175-176, pl. 3, figs. 3a-c; text-figs. 3G, 6C) Lentin & Williams, p. 39
1985 *Ceratiopsis medcalfii* (Stover 1974, p. 175-176, pl. 3, figs. 3a-c; text-figs. 3G, 6C) Heilmann-Clausen, p. 19
1987 *Cerodinium medcalfii* (Stover 1974, p. 175-176, pl. 3, figs. 3a-c; text-figs. 3G, 6C) Lentin & Williams, p. 114
1988 *Deflandrea medcalfii* Stover, 1974; Wilson, p. 18, pl. 7, figs. 1-3

Original Description: Cysts are tricornate with an elongate, tapered apical horn and prominent antapical horns of about equal size and with narrowly rounded or pointed tips. Antapical horns separated by a broad medial concavity.

Lateral margins of periphragm are gently convex anterior to the cingulum, and straight to slightly concave posterior to the cingulum. Periphragm less than 1 μ thick and clear except for areas with small coni. The species has a typical peridinioid tabulation of 4', 3a?, 7", 5", 2''' with the size, shape, and position of the plates represented by the conate areas. Cingulum defined by transverse parallel ridges about 1 μ high, 5-7 μ apart, and fringed with coni, denticles, or spinules. On some specimens the cingulum is subdivided by longitudinal ridges

and its floor is smooth or bears scattered con. Sulcal margins generally indefinite, and on most specimens, a hook-shaped scar occurs in the sulcus near its junction with the cingulum and generally a little right of centre.

Endoblast is comparatively large, broadly elliptical to ovoid in dorso-ventral view, generally wider than long although on some specimens the reverse is true, and located about centrally with respect to the periphragm. Endoblast configuration approximates that of the periblast laterally but deviates apically and antapically. Endophragm is smooth and ca 0.5µ thick.

Archeopyle intercalary, large, irregularly hexagonal in outline, and with a narrower apical than antapical margin. Opening in endophragm corresponds with that in the periphragm. Operculum free.

Length of periphragm is 106-140µ, width of periphragm is 68-75µ and the specimens have a length:width ratio between 1:0.53 and 1:0.73 (mean 1:0.64). Length of endophragm is 53-70µ, width 58-76µ. Apical horn is 22-34µ long; antapical horns 20-36µ long. Measurements based on 12 complete specimens (Stover 1974, p. 175).

Description of Study Material: Cysts large, proximate, not dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome longer than hyposome. Apical horn well developed, apex pointed, episome markedly attenuated; antapical horns strongly and approximately equally developed, relatively pointed. Cyst wall two-layered; bicavate, lateral pericoels absent; thin (< 1 µm) in thickness. Archeopyle intercalary, type I (2a); isodeltaform, large; operculum free. Surface ornament present, non-tabular, comprising con; sometimes forming incomplete, apparently sutural, lineations. Tabulation peridiniacean, inferred formula: 4', 3a, 7", Xc, 5"', 0ps, 2''', 0-5s. Cingulum clearly expressed, surface ornament and folds in the periphragm, 7-8 µm wide; offset only slightly.

Size Range: Length including any processes = 125 (136) 155 µm (7 measurements). Width including any processes = 72 (80) 87 µm (3 measurements).

Distribution: Frequent. The younger occurrences reported here represent a significant extension to the previously reported range of the species (Stover 1974, Wilson 1988).

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Waipawan	Waipawa standard section, Hawkes Bay, New Zealand	V22/f8978	Wilson 1988
Teurian	Waipawa standard section, Hawkes Bay, New Zealand	V22/f8692	Wilson 1988

Remarks: *Cerodinium medcalfii* appears to differ from *C. dartmoorium* principally in possessing a tabulation less well-delineated by linear sutural features.

Genus *Isabelidinium* Lentin & Williams 1977a

1976 *Isabelia* Lentin & Williams, p. 56

1977a *Isabelidinium* Lentin & Williams, p. 167

1978 *Isabelidinium* Lentin & Williams 1977a; Stover & Evitt, p. 108-109

Type Species: *Isabelidinium korojonense* (Cookson & Eisenack 1958, p. 27-28, pl. 4, figs. 10-11) Lentin & Williams 1977a, p. 167 [Cretaceous (Campanian-Maastrichtian)]

Original Description: Pericyst: Ambitus commonly pentagonal, elongated in an anteroposterior direction, rarely rhomboidal or rectangular. Apex prolonged into a broad short apical horn which may merge imperceptibly into the epipericyst, or be developed into shoulders. Antapex produced into two symmetrically located short antapical horns, usually of unequal length. The left antapical horn is always the longer, the right is reduced or vestigial. The apical and two antapical horns sometimes reduced. There is usually a slight to prominent equatorial bulge in ambital view. Compression dorso-ventral.

Endocyst: Ambitus ovoidal with longest axis equatorially aligned to circular, to elongate ovoidal. May be equatorially in contact with endocyst. Pericoels: When endocyst and pericyst are appressed in precingular, cingular and postcingular regions, they are separated apically and antapically by a large apical and a large antapical pericoel, respectively. Alternatively the apical and antapical pericoels may be united by an ambital pericoel. Compression dorso-ventral, may be negligible.

Periphragm: Usually of constant thickness. Surface laevigate, scabrate, granulate or verrucate. Ornamentation nontabular. Endophragm: Surface laevigate to scabrate to granulate. Pericyst: Paratabulation indeterminate other than in the vicinity of the periarcheopyle. Pericingulum: Almost always absent or rudimentary and never complete, occasionally visible on the ambitus as an indentation. Perisulcus: Not observed. Endocyst: Paratabulation unknown.

Periarcheopyle: Omegaform intercalary resulting from the partial detachment of the second anterior intercalary paraplate, 2a, with perioperculum usually remaining along parasuture H4. Transverse periarcheopyle index is 0.33-0.55. Transverse archeopyle ratio is 0.50-1.25. Endoarcheopyle: Where observable appears to result from the loss of the second anterior intercalary paraplate (2a), or all three anterior intercalaries.

Archeopyle Formula: I/I (2a/2a) or I/3I (2a/1-3a) (Lentin & Williams 1976, p. 56, 57).

Remarks: *Isabelidinium* is a substitute for the original name applied to this genus, *Isabelia* Lentin & Williams 1976, which is a junior homonym of the orchid genus *Isabelia* Barbosa-Rodrigues 1877.

A number of older New Zealand species (or species occurring in New Zealand) previously assigned to this genus have been moved to other genera (e.g. *I. haumuriense* to *Satyrodinium*; *I. druggii/seelandicum* to *Manumiella*). The genus as currently defined dates back to at least the Paleocene: Wilson 1988 records *I. bakeri* and a new species, *I. cingulatum*, from the Teurian at Waipawa.

As far as I am aware, however, the following record is the youngest occurrence yet reported from New Zealand.

Isabelidinium cf. bakeri (Deflandre & Cookson 1955) Lentin & Williams 1977a

Pl. 15, figs. 7-9

Original Description: [Description of *I. bakeri*] Cell generally but not always encysted. Theca widely fusiform, somewhat obliquely truncated posteriorly; transverse girdle faint, neither hollowed nor shallow, sometimes quite indistinct, dividing the theca into 2 unequal parts. Longitudinal furrow not observed. Epithea larger than the hypotheca, widely conical or bell-shaped, surmounted by a short, more or less bluntly pointed, slightly thickened prominence. Hypotheca like a frustum of a cone, sometimes with 2 very short unequal horns and occasionally a 3rd submedian conical expansion, sometimes with the lower angles simple or 1 of the 2 rounded. In lateral view ... the encysted cells have an asymmetrical outline with, at the level of the cyst, 1 face plane and the other convex. This convexity does not seem to exist in the rare non-encysted examples that have been examined. The cyst also causes a slight frontal enlargement.

The cysts is ellipsoidal, more or less regular when viewed from the front, more asymmetrical in lateral view. The encysted cells have a rather regular polygonal aperture on the convex side of the epithea (Deflandre & Cookson 1955, p. 251; ellipses replace figure references in the original).

Size Range: Length including any processes = 165 µm (one measured specimen). Width including any processes = 96 µm (one measured specimen).

Distribution: Extremely rare. Known from a single specimen.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f063 (L09220)	Wilson 1985

Remarks: The present form closely resembles *I. bakeri* though, if it were truly conspecific, would represent a considerable extension to the stratigraphic range. It seems more probable that the specimen is reworked.

Genus ***Planoperidinium*** De Coninck 1986b

1986b *Planoperidinium* De Coninck, p. 18

Type Species: *Planoperidinium gracile* De Coninck 1986b, p. 18, pl. 6, fig. 44, pl. 8, figs. 1-10 [Oligocene (Rupelian)]

Original Description: Small, dorsoventrally flattened pericyst with peridinioid ambitus. Pericyst and endocyst separate from each other in the antapical horns and often in the apical horn as well unless it is very poorly developed. Between horns and cingulum peri and endocyst generally not separate; in some specimens however a narrow separation is visible. Cingulum mainly marked at the lateral margin. Sulcus generally invisible or slightly marked. The archeopyle is intercalary and relatively wide. No ornamentation of the periphragm, hence no tabulation indicated (De Coninck 1986b, p. 18).

Planoperidinium ?gracile De Coninck 1986b

Pl. 15, figs. 10-12, Pl. 16, figs. 1-3

?1986b *Planoperidinium gracile* De Coninck, p. 18, pl. 6, fig. 44; pl. 8, figs. 1-10

Original Description: The pericyst is dorsoventrally flattened. Its ambitus is peridinioid. The epicyst is generally a little longer than the hypocyst and has a more or less triangular outline. The apical horn is poorly developed and rounded. The cingular margins are marked on the ambitus by short protrusions between which the cingulum is represented by a shallow depression. Generally the cingulum and sulcus are invisible on the dorsal and ventral surfaces of the pericyst. The hypocyst is trapezium-shaped with two protruding antapical horns with a pointed, often flexuous tip. One of the antapical horns is a little longer than the other. Between the antapical horns the pericyst is concave. The surface of the pericyst is unornamented. The endocyst is generally appressed against the pericyst except in each of the antapical horns where the separation is clearly indicated. In the poorly developed apical horn, the separation of endo- and pericyst is not always marked. The archeopyle, generally not developed, is intercalary and relatively large (De Coninck 1986b, p. 18).

Description of Study Material: Cysts of intermediate size, proximate, dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome slightly longer than hyposome. Apical horn moderately well-developed; antapical horns strongly developed, acuminate. Cyst wall two-layered; cornucavate. Archeopyle intercalary, type I (2a); large. Surface ornament lacking. Indicated by folds in the periphragm.

Size Range: Length including any processes = 78 (82) 87 μm (2 measurements). Width including any processes = 57 (63) 67 μm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	

Remarks: The general outline and “over-size” archeopyle recall *Lentinia*. According to De Coninck (1986b, p. 18) *Planoperidinium* differs from *Lentinia* “by its extreme dorso-ventral flattened body” and, more obviously, by the “absence of any ornamentation and tabulation of the pericyst.”

?*Planoperidinium* sp. 2

Pl. 16, figs. 4-9

Description: Cysts of intermediate size, proximate, dorso-ventrally compressed, outline peridinioid, with one apical and two antapical horns; episome slightly longer than hyposome. Apical horn moderately well-developed; antapical horns strongly developed, acuminate. Cyst wall two-layered; cornucavate. Archeopyle intercalary, type I (2a); large. Surface ornament lacking. Cingulum indicated by folds in the periphragm.

Size Range: Length including any processes = 72 (74) 75 μm (2 measurements). Width including any processes = 50 (52) 55 μm (2 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	

Remarks: A few specimens, though apparently of *Planoperidinium*, differ from *Planoperidinium gracile* in lacking the characteristically delicate, very attenuated antapical horns.

Genus *Spinidinium* Cookson & Eisenack 1962b

1962b *Spinidinium* Cookson & Eisenack, p. 489

1978 *Spinidinium* Cookson & Eisenack 1962b emended Lentin & Williams 1976; Stover & Evitt, p. 124-125

Type Species: *Spinidinium styloniferum* Cookson & Eisenack 1962b, p. 489, pl. 1, figs. 1-5 [Cretaceous (Aptian-Albian)]

Original Description: Shell longer than broad, concavo-convex, with straight or slightly convex slanting sides. Epithea horned, hypotheca with a small projection on one side. Girdle equatorial, circular; longitudinal furrow more or less well developed. Wall of shell two-layered, the outer layer which is covered with small spines forming the apical horn and antapical projection. A pylome may develop on the dorsal surface of the epithea (Cookson & Eisenack 1962, p. 489).

Remarks: The ventral plate topology of the type species, *Spinidinium styloniferum*, appears to exhibit the same ortho-style arrangement as *Deflandrea* (Cookson & Eisenack 1962b, pl. 1, fig. 4; Morgan 1975, pl. 2, fig. 1b). This topology is herein taken to be a diagnostic character for the genus as a whole.

Spinidinium has historically been distinguished from broadly similar forms, such as *Phthanoperidinium*, by various features of its intratabular ornament. As noted elsewhere, these sorts of ornamental distinctions have little

phylogenetic meaning, and more profound distinctions should be sought at the generic and higher taxonomic ranks. It is more significant that *Spinidinium* has an attenuated to standard hexa-style plate 2a in the sense of Lentin & Williams 1976 (text-fig. 4). In particular, that of the genoholotype is very narrow (Cookson & Eisenack 1962b, pl. 1, fig. 2; Morgan 1975, pl. 2, fig. 1d), which distinguishes *Spinidinium* from *Gippslandia*, *Lentinia*, *Phthanoperidinium*, *Vozzhennikovia*, etc.

Spinidinium differs from *Vozzhennikovia* in possessing a deltaform archeopyle, as opposed a thetaform or even slightly omegaform archeopyle in *V. apertura*. *Spinidinium* further differs from *Vozzhennikovia* in possessing a tabulation which is a known, as a consequence of having the ornamentation arranged in penitabular rows or intratabular clusters, or both, rather than being nontabular.

It differs from *Gingiodinium* in having a type I rather than a type 3I archeopyle (Stover & Evitt 1978, p. 124).

***Spinidinium cf. styloniferum* Cookson & Eisenack 1962b**

Pl. 16, figs. 10-12

1962b *Spinidinium styloniferum* Cookson & Eisenack, p. 489, pl. 1, figs. 1-5

Description of Study Material: Cysts small to intermediate, proximate, not dorso-ventrally compressed, more or less spherical to prolate, with one apical and one or two unequal antapical horns; episome and hyposome more or less equal in length. Apical horn well developed, apex rounded; antapical horns weakly developed, relatively pointed. Cyst wall two-layered; cornucavate. Archeopyle intercalary, type I (2a); ?stenodeltaform; operculum attached. Processes lacking; surface ornament present, intratabular, comprising coni; about 1-2 µm high. Crests sutural, low (less than about 1 µm), margins of crests smooth. Tabulation clearly expressed, peridiniacean, 3a, 7", 5", ?ps, 2""; ventral organisation probably ortho-style. Cingulum clearly expressed, indicated by sutural septa; offset only slightly. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 30 (43) 56 µm (2 measurements). Width including any processes = 47 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: One or two specimens have been encountered which superficially resemble *Spinidinium styloniferum*. This identification is unlikely, however, because the true *S. styloniferum* has not previously been reported from the Eocene.

***Spinidinium colemanii* Wrenn & Hart 1988**

Pl. 17, figs. 1-9

1988 *Spinidinium colemanii* Wrenn & Hart, p. 366-367, fig. 36, 1-2; fig. 39, 2

2000 *Spinidinium colemanii* Wrenn & Hart, 1988; Levy & Harwood, p. 208, 210, pl. 9, fig. a

Original Description: Shape: Cornucavate, subpentagonal to subelliptical dinocysts bearing one hundred or more penitabular spines. The paracingulum separates the epicyst from the hypocyst; the former is usually two to three times the length of the hypocyst. The paracingular area may bulge laterally, giving the dinocyst a subpentagonal shape.

Phragma: Both the endophragm and the periphragm are smooth. The wall layers are appressed except in the basal regions of the horns. The periphragm gives rise to capitate spines, whereas the endophragm lacks projections. The short apical horn is capped by two or more capitate spines. The right antapical horn is rarely evident, whereas the left horn is a long, spike-shaped projection bearing one or more accessory spines.

Paratabulation: A paratabulation of x', 3a, 7", xc, 5", ?2"" is delineated by penitabular capitate spines. The distribution and number of paraplates is obscured by the abundance of the closely spaced spines and by the presence of accessory rows of spines. The paracingulum and the parasulcus are not divided by rows of spines.

Paracingulum: Low folds capped with short capitate spines delimit the shallow excavation of the paracingulum. Paraplate divisions within the paracingulum were not observed.

Parasulcus: A broad, bare area bordered by rows of spines indicates the location of the parasulcus. Spines are usually absent within the parasulcal area, although isolated spines occur on some specimens.

Archeopyle: The archeopyle is formed by the partial detachment of the 2a paraplate, and occasionally by the partial detachment of the 4" paraplate. The operculum is adnate along the H4 parasuture. A row of penitabular capitate spines occurs on each side of all archeopyle parasutures, except the H4 parasuture. The rows of spines along the H2-H3 and the H5-H6 parasutures of the 2a intercalary paraplate continue below the base of that paraplate and along the margins of the 4" paraplate to the anterior margin of the paracingulum (Wrenn & Hart 1988, p. 366-367).

Size Range: Length including any processes = 47 (54) 60 µm (2 measurements). Width including any processes = 37 (40) 42 µm (2 measurements).

Distribution: Very rare. Just two specimens resembling *Spinidinium colemanii* (one rather dubiously) were encountered in the type Porangan material from Te Uri Stream.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Eocene	erratics, McMurdo Sound, Antarctica	MB 181(2)	Levy & Harwood 2000
late early Paleocene	northern Seymour Island, West Antarctica	8496	Wrenn & Hart 1988

Remarks: This species differs from *Spinidinium essoii* and *S. macmurdoense* in its far coarser ornamentation and, rather more variably, a more prominent antapical horn.

***Spinidinium essoii* Cookson & Eisenack 1967a**

Pl. 17, figs. 10-11

1967a *Spinidinium essoii* Cookson & Eisenack, p. 135, pl. 19, figs. 1-8

2000 *Spinidinium essoii* Cookson & Eisenack, 1967; Levy & Harwood, p. 210, pl. 9, fig. b

Original Description: Shell small, somewhat flattened and oval in outline, with straight to convex sides, a relatively broad, circular, equatorial girdle with high ledges bearing short thin spines, a short blunt apical horn and a single sharply-pointed horn on the left-hand side of the antapex. Both surfaces of the shell are partially tabulated, the areas being delimited by short spines. On the ventral surface of the epitheca a small, roughly rectangular area outlined by small dot-like thickenings is usually clearly evident, and a wide furrow-like region, delimited by small spines, is typically present in the hypotheca. An intercalary, trapezoidal archeopyle is developed on the dorsal surface of the epitheca.

In one specimen ... a relatively thin-walled cyst-like body, circular in outline, occupies approximately three-quarters of the cavity of the shell [this is either a different taxon or else an accidental superposition of some other palynomorph; it is difficult to determine from the published image – CC].

The wall of the shell, which is rather sparsely ornamented with pointed or knobbed spines, appears to consist of two closely opposed layers which separate from one another only at or near the bases of the horns, the position of the diaphragm varying in individual specimens. The apical horn tends to be straight-sided and its apex incurved; the antapical horn, which tapers to a sharp point, bears a few downwardly directed spines (Cookson & Eisenack 1967a, p. 135).

Size Range: Length including any processes = 35 (45) 55 µm (3 measurements). Width including any processes = 30 (36) 42 µm (3 measurements).

Distribution: Rare. Very seldom encountered in the present study, but known from older New Zealand sediments (Erica Crouch pers. comm.)

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Eocene	erratics, McMurdo Sound, Antarctica	MB 181(2)	Levy & Harwood 2000

***Spinidinium macmurdoense* (Wilson 1967a) Lentin & Williams 1976**

Pl. 17, fig. 12, Pl. 18, figs. 1-3

1967a *Deflandrea macmurdoensis* Wilson, p. 60-62, figs. 2a, 11-16, 22

1975 *Deflandrea macmurdoensis* Wilson; Haskell & Wilson, pl. 1, fig. 13

- 1976 *Spinidinium macmurdoense* (Wilson 1967a, p. 60-62, figs. 11-16, 22; text-fig. 2a) Lentin & Williams, p. 64
- 1988 *Deflandrea macmurdoense* (Wilson 1967) Lentin and Williams 1976 Wrenn & Hart, p. 369, fig. 36, 6; fig. 44, 1
- 1989 *Spinidinium macmurdoense* (Wilson) Lentin & Williams; Wilson, pl. 1, fig. 9
- 2000 *Spinidinium macmurdoense* (Wilson 1967) Lentin & Williams, 1976; Levy & Harwood, p. 210, pl. 9, figs. c-d

Original Description: Test bi-layered, dorso-ventrally flattened, angular, bilaterally asymmetric. Outer cyst divided into fields by small spines ($l = 5-9 \mu$); smooth hyaline inner cyst closely follows outline of outer cyst. Horns formed by polar extensions of outer cyst; apical horn relatively long ($l = 14-20\mu$) narrow, blunt-ended and bordered by very small spines; right antapical horn pointed ($l = 13-17 \mu$) and usually bordered with small spines; left antapical horn either non-existent or very small. Prominent slightly laevo-rotatory transverse girdle delimited by a double row of spines or sometimes, on dorsal surface, by a spiny ridge. Archeopyle intercalary, hoof-shaped or subhexagonal, located on dorsal epitheca; operculum always fixed to shell by its posterior margin; remainder of archeopyle perimeter bordered by a double row of spines, one on operculum, the other on outer cyst, with line of rupture between the two rows.... Tabulation uncertain, but that of dorsal epitheca apparently consistent with *Gonyaulax*... (Wilson 1967a, p. 60, 62; ellipses replace figure references in the original).

Size Range: Length including any processes = 55 μ m (one measured specimen). Width including any processes = 46 μ m (one measured specimen).

Distribution: Extremely rare in the present study; only a single specimen was recovered from Hampden Beach.

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	SM3792	Wilson 1989
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4729	Wilson 1967a
Eocene	erratics, McMurdo Sound, Antarctica	MTD 153(1)	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000
late early Paleocene	northern Seymour Island, West Antarctica	8457	Wrenn & Hart 1988

Genus *Vozzhennikovia* Lentin & Williams 1976

- 1976 *Vozzhennikovia* Lentin & Williams, p. 65-66
- 1978 *Vozzhennikovia* Lentin & Williams 1976; Stover & Evitt, p. 129-130

Type Species: *Vozzhennikovia apertura* (Wilson 1967a, p. 64-65, figs. 3-5, 8) Lentin & Williams 1976, p. 65 [Paleocene-Oligocene]

Original Description: Pericyst: Ambitus rounded to ovoidal. Apex occasionally rounded, more frequently produced into a short apical horn which distally may be acuminate, oblate or invaginated. Antapex rounded or commonly with one eccentrically located left antapical horn. Rarely there are two symmetrically located antapical horns which are unequal in length, the right antapical horn being reduced or vestigial. Epipericyst and hypopericyst of more or less equal size or epipericyst somewhat larger. Ambital outline widest in pericingular region. Compression dorso-ventral, moderate to extreme.

Endocyst: Ambitus rounded to ovoidal, almost always appressed against pericyst apart from in the vicinity of the horns. Usually difficult to delineate, Compression dorso-ventral, often extreme. Pericoels: A small apical pericoel in the vicinity of the apical horn. If an antapical horn is present there may be a small antapical pericoel. Periphragm: Epipericyst and hypopericyst ornamented with nontabular echinae or processes rarely exceeding 10 μ in length. The processes may be distally acuminate, oblate or invaginated. Processes often oriented in pericingular or perisulcal regions only.

Endophragm: Laevigate. Usually thin and difficult to delineate. Pericyst: Paratabulation never discernible other than in the vicinity of the periarcheopyle. Pericingulum: Generally present and indented. Planar or slightly helicoidal. Anterior and posterior parasutures delineated by a continuous or discontinuous row of echinae or processes. Area of pericingulum within parasutures is devoid of a surface ornamentation. Perisulcus: Commonly delineated by absence of ornamentation. Indented. Extending onto epipericyst but considerably longer and wider on the hypopericyst reaching almost to the antapex. Endocyst: Paratabulation not observed.

Standard hexa or broad hexa intercalary [archeopyle] resulting from the partial or complete detachment of the anterior intercalary paraplate 2a. The operculum may be free or remain attached along parasuture H4. Since the endophragm and periphragm are appressed in the vicinity of the archeopyle, there is no separation of the endoperculum and perioperculum so that effectively there is one archeopyle and one operculum. Transverse archeopyle index is 0.33-0.50. Transverse archeopyle ratio is 0.50-1.0.

Archeopyle Formula: I (Lentin & Williams 1976, p.65-66).

Remarks: *Vozzhennikovia* differs from *Spinidinium* in possessing a broader, thetaform or slightly omegaform archeopyle, whereas that of *Spinidinium* is narrow and deltaform (q.v.), and also in generally lacking evidence of plate boundaries. The latter characteristic, while presenting methodological difficulties, of course, is not considered to have any phylogenetic significance per se. Ornament which fails to delineate the plate boundaries is still "just another kind" of ornament.

Vozzhennikovia differs from *Dioxya* in having two wall layers rather than an autophragm only, and in the shape of the antapex which clearly indicates two plates, although only one horn may be developed, rather than the single antapical projection of *Dioxya* which is less typical of peridiniaceans. Additionally, most *Dioxya* species appear confined to the Cretaceous, whereas most southern (Gondwana) species of *Vozzhennikovia* appear to be Eocene or younger. The Paleocene species, *Vozzhennikovia spinulosa* Wilson 1984c is somewhat atypical in this regard, although in all other respects its generic placement appears sound.

Vozzhennikovia apertura (Wilson 1967a) Lentin & Williams 1976

Pl. 18, figs. 4-12

- 1967a *Spinidinium aperturum* Wilson, p. 64-65, figs. 3-5, 8
1975 *Spinidinium aperturum* Wilson; Haskell & Wilson, pl. 1, fig. 6
1976 *Vozzhennikovia apertura* (Wilson 1967a, p. 64-65, figs. 3-5, 8) Lentin & Williams, p. 65
1982c *Vozzhennikovia* cf. *apertura* (Wilson); Wilson, p. 4, pl. 2, fig. 16
1983 *Vozzhennikovia apertura* (Wilson, 1967) Lentin and Williams, 1976; Goodman & Ford, p. 864-865, pl. 4, figs. 1-6
1988 *Vozzhennikovia apertura* (Wilson 1967) Lentin and Williams 1976; Wrenn & Hart, p. 371-372, fig. 37, 6-9, fig. 43, 3-4
1989 *Vozzhennikovia apertura* (Wilson) Lentin & Williams; Wilson, pl. 1, fig. 5
2000 *Vozzhennikovia apertura* (Wilson, 1967) Lentin & Williams, 1976; Levy & Harwood, p. 210, pl. 11, figs. h-j

Original Description: Test broadly rounded to sub-angular, differentiated into two closely joined layers forming inner and outer cysts. Surface of outer cyst thickly covered with pointed or flat-tipped spines, evenly distributed over the dorsal and ventral surfaces except on transverse girdle and longitudinal furrow. Transverse girdle wide, deeply grooved, either non- spiral or very slightly laevo-rotatory, delimited by two parallel rows of closely spaced spines. Longitudinal furrow a very prominent deep groove devoid of spines. Apical horn relatively long ($l = 8-10 \mu$) rectangular and usually terminated by either one or two small spines; right antapical horn short ($l = 2-3 \mu$) pointed; left antapical horn absent but position defined by slight angularity in shell outline. Archeopyle very prominent, intercalary, hexagonal. located on dorsal epitheca. Operculum free, distinctive, often occurs totally separated from parent shell.... Atabulate (Wilson 1967a, p. 64-65).

Description of Study Material: Cysts small, proximate, somewhat dorso-ventrally compressed, with one apical horn; episome usually slightly longer than the generally rounded hyposome. Apical horn well developed, apex bluntly terminated; antapical horns small and weakly developed to completely lacking. Cyst wall two-layered; cornucavate. Archeopyle intercalary, type I (2a); eurythetaform to slightly euryomegaform; operculum free to attached, inner and outer layers adherent. Processes lacking; surface ornament comprising small non-tabular granules to short spines. Tabulation not expressed. Cingulum lacking to weakly expressed by surface ornament and folds in the periphragm. Sulcus generally moderately clear, expressed by an absence of surface ornament; more or less vertical; largely confined to the hyposome; lacking any clear indications of subdivision.

Size Range: Length including any processes = 33 (38) 45 μ m (9 measurements). Width including any processes = 31 (33) 35 μ m (3 measurements).

Distribution: Occurs infrequently in a handful of samples, although in one only (I43/f092, L16340) specimens are common.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
late early Eocene	northern Seymour Island, West Antarctica	8463	Wrenn & Hart 1988
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	SM3786	Wilson 1989
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4729	Wilson 1967a
Eocene	erratics, McMurdo Sound, Antarctica	MB 109(1)	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 1B	Levy & Harwood 2000

Remarks: The older forms included here, from the lower part of Hampden Beach (J42/f301, L23131; Porangan to ?Bortonian) have distinctly longer spines than the younger forms (and the Antarctic type material) and may represent a distinct species.

Vozzhennikovia rotunda is treated as a synonym of *Vozzhennikovia apertura* in Wrenn & Hart 1988 (p. 371-372) on account of the existence of intermediates and the authors' observation that the two species are "end members of a morphologic continuum." As noted elsewhere herein, the existence of intermediates, per se, does not imply synonymy.

Subfamily Palaeoperidinioideae (Vozzhennikova 1961) Bujak & Davies 1983

Genus *Phthanoperidinium* Drugg & Loeblich Jr. 1967 emend. Clowes

- 1967 *Phthanoperidinium* Drugg & Loeblich Jr., p. 182
1978 *Phthanoperidinium* Drugg & Loeblich 1967; Stover & Evitt, p. 118-119
?1980 *Vectidinium* Liengjarern et al., p. 490
1981 *Phthanoperidinium* Drugg & Loeblich 1967 emend. Edwards & Bebout, p. 36, 38
1982 *Phthanoperidinium* Drugg et Loeblich 1967 emend. Islam, p. 306
2004 *Phthanoperidinium* Drugg & Loeblich Jr., 1967, p. 182; Fensome & Williams, p. 524-526

Type Species: *Phthanoperidinium amoenum* Drugg & Loeblich Jr. 1967, p. 182, pl. 1, figs. 1-5; text-fig. 1a-e [Oligocene]

Original Description: Proximate fossil cysts, more or less ovoidal in shape, with short apical projection. Tabulation 4', 3a, 7", 5"', 2'''. Additional furrow platelets may be present. The archeopyle is formed by the removal of intercalary plate 2a. Sutures delimited by low ridges, crests, or lines of spines (Drugg & Loeblich 1967, p. 182).

Emended Description: Small to medium sized peridinioid cysts; apical horn typically present though small, antapical horns either very much reduced or absent; cyst walls two-layered but with the layers closely appressed everywhere (acavate), except sometimes at horn bases (cornucavate); typically exhibiting a clear tabulation, formula 4', 3a, 7", X-6c, 5"', 0p, 2''', X-4s; dorsal epicyst topology broad hexa-style; ventral epicyst topology ortho-style; archeopyle primarily type I (2a) but sometimes involving additional plates 1a-3a and 3"-5", operculum or opercular pieces variably free or attached.

Remarks: The genus *Phthanoperidinium* was established by Drugg & Loeblich Jr. 1967 (p. 182) to accommodate proximate peridinioid fossil cysts with a "more definite" tabulation, formula 4', 3a, 7", 5"', 2''', and a single 2a intercalary archeopyle. The authors described but did not draw particular attention to the broad six-sided (hexa-style) archeopyle. Drugg & Loeblich Jr. 1967, text-figure 1, depicts five cingular plates, although these are not enumerated in the text, and it is assumed that there are in fact six in the series (e.g. as noted by Stover & Evitt 1978, p. 118) but that plate 1c is not clearly differentiated from the sulcus (contrast Drugg & Loeblich Jr. 1967, pl. 1, fig. 5, with Evitt 1985, fig. 5.2A). It is clear there is no posterior intercalary plate; references to this plate in some older descriptions of *Phthanoperidinium* species are assumed to be misinterpretations.

The archeopyle is a broad hexa-style (Text-Fig. 15).

Goodman & Ford 1983 draws attention to the importance of ventral epicyst plate topology in any analysis of *Phthanoperidinium*. Plate 1' of the type species, *Phthanoperidinium amoenum*, is clearly five-sided and in contact with plates 4', 2', 7", 1", and the anterior sulcal: a configuration known as the ortho-style (Text-Fig. 16). To my knowledge, however, this seminal suggestion has not previously been pursued with any enthusiasm, possibly because the diagnostic features are sometimes difficult to observe, even in specimens which can be studied at first hand, and all the more difficult when only published illustrations are available. Ignoring the practical difficulties, however, there is no reason to suppose there is any difference – in principle – between this distinction and other much better recognised distinctions, such as that between the L-type and S-type gonyaulacaceans.

Some species currently assigned to *Phthanoperidinium* are apparently ortho-style, some are not, and others are unknown. (Perhaps some are variable, but I am unaware of it. If that were found to be the case, the present emendation would be invalidated.) Observing that both ortho- and non-ortho types included within the genus, and believing the distinction to be important, has prompted this reappraisal of the genus.

In overall appearance, the genera most closely resembling *Phthanoperidinium* are *Ginginodinium*, *Lentinia*, *Luxadinium*, and *Vectidinium* among the Palaeoperidinioideae, and *Gippslandia*, *Spinidinium*, and *Vozzhennikovia* among the Deflandreioideae.

- ***Ginginodinium*:** Stover & Evitt 1978 (p. 118) notes that *Phthanoperidinium* differs from *Ginginodinium* in having a Type I rather than the Type 3I archeopyle of *Ginginodinium*, and in either lacking antapical horns or having a single, medial, antapical projection rather than two, more or less equally developed, antapical horns as in *Ginginodinium*. Subsequent studies have shown that most species of *Phthanoperidinium* are

somewhat variable in respects of both plate involvement in the archeopyle, and in antapical horn formation, very much weakening the utility of these characteristics as differentiators. However, the fact remains that the type species of *Ginginodinium* is quite dissimilar in overall appearance, and is very much older than the core group of “good” *Phthanoperidinium* species which appear tightly knit in both morphology and in their Paleocene to mid-Oligocene stratigraphic ranges.

- **Lentinia:** The alignment of granules on the ventral epicyst of the genoholotype of *Lentinia* (Bujak 1980, pl. 18, fig. 9) strongly supports an ortho-style interpretation (Bujak 1980, text-fig. 18A, C). However, *Lentinia* differs from *Phthanoperidinium* in possessing two well and approximately equally developed antapical horns, and an unusually large archeopyle.
- **Luxadinium:** *Luxadinium* is variously described as cavate (Brideaux & McIntyre 1975, p. 36), bicavate, circumcavate, or “possibly cornucavate” (Stover & Evitt 1978). Only the last condition is comparable with *Phthanoperidinium*, but this does appear to be the case for the holotype of the type species of *Luxadinium*, *L. primulum*. But, although there may be some mechanistic difficulty formulating a clear morphological distinction between these two genera, the wide separation in time between *Luxadinium primulum* (mid Albian) and *Phthanoperidinium*, as defined herein, militates against any proposal for synonymy.
- **Vectidinium:** *Vectidinium* was considered a junior synonym of *Phthanoperidinium* by Islam (1982), having reviewed the type material of the type and only species, *Vectidinium stoveri*. Although Lentin & Williams 1985 (p. 364) and subsequent editions of the Catalogue, including the most recent (Fensome & Williams 2004), retain *Vectidinium*, Islam’s view is provisionally accepted here. Islam did not, however, re-describe the species in any detail, so no further comment is made.

The Deflandreioideae differ from *Phthanoperidinium* at the subfamilial level in possessing archeopyles which involve the intercalary plates only (Fensome et al. 1993b, p. 129). However, as noted above and in many previous works, this is often true for *Phthanoperidinium* and it is true for some other Palaeoperidinioideae genera also.

- **Gippslandia:** *Gippslandia* shares the broad, hexa-style archeopyle of *Phthanoperidinium* (and is in several respects reminiscent of *Lentinia*, also). The topology of the ventral epicyst is neither discussed nor clearly shown by any of the illustrations in the type species description (Stover 1974) and is not mentioned in the original generic diagnosis (Stover & Williams 1987). Topotype material generously provided to the writer by Alan Partridge, although less than fully conclusive, includes several specimens with an alignment of granules that is entirely consistent with the ortho-style (Text-Fig. 19). Remaining distinctions between *Gippslandia* and *Phthanoperidinium* are that precingular plates are never involved in the archeopyle formation of *Gippslandia*, and the ornament type: sutural or penitabular in the case of *Phthanoperidinium* and intratabular in the case of *Gippslandia*. It is quite evident, however, that similar ornament types recur again and again in genera which are as distantly related as peridiniaceans and gonyaulacaceans; these kinds of features, while useful species-level distinctions, offer little insight at higher taxonomic levels.
- **Spinidinium:** Historically, *Phthanoperidinium* has been distinguished from *Spinidinium* by its possession of sutural features of various sorts, rather than intratabular ornament only. As noted above, these sorts of ornamental distinctions clearly have little phylogenetic meaning, so more profound distinctions are desirable at generic and higher taxonomic ranks. I consider it far more significant that *Phthanoperidinium* possesses a standard to broad hexa-style plate 2a, whereas *Spinidinium* has an attenuated to standard hexa-style plate 2a in the sense of Lentin & Williams 1976 (text-fig. 4). That of the genoholotype of *Spinidinium* is very narrow (Cookson & Eisenack 1962b, pl. 1, fig. 2; Morgan 1975, pl. 2, fig. 1d). The ventral plate topology of *S. styloniferum* appears to exhibit the same ortho-style arrangement as *Phthanoperidinium* (Cookson & Eisenack 1962b, pl. 1, fig. 4; Morgan 1975, pl. 2, fig. 1b).
- **Vozzhennikovia:** *Vozzhennikovia* differs from all of the above in possessing non-tabular ornament and, in consequence, having a tabulation which is unknown apart from the archeopyle, which is clearly intercalary. However, as noted above, this is a methodological problem with no intrinsic phylogenetic significance at generic and higher taxonomic rank.



Text-Fig. 19: Topotype of *Gippslandia extensa* showing ventral surface of episome. The alignment of spines seems to indicate an ortho-style tabulation.

A range chart for species of *Phthanoperidinium* is provided in Appendix 2, chart 7.

Key to selected species: The following key distinguishes most of the forms found in the present study; it is not intended to comprehensively address the entire genus.

0.	Surface ornament of very low relief (less than ~1 µm)	1.
	Surface ornament slightly elevated (2-3 µm)	2.
	Surface ornament of relatively high relief (a significant fraction of the cyst diameter)	3.
1.	Sutural ridges present	1.1.
	Sutural plus penitabular ridges present	1.2.
	Surface ornament is non-tabular	1.3.
1.1.	Intratabular areas smooth, or varying from shagreenate to vermiculate	1.1.1.
	Intratabular areas distinctly scabrate	1.1.2.
1.1.1.	<i>Phthanoperidinium amoenum</i>	
1.1.2.	<i>Phthanoperidinium granulatum</i>	
1.2.	<i>Phthanoperidinium geminatum</i>	
1.3.	<i>Phthanoperidinium spumosum</i>	
2.	Surface ornament comprising low crests	2.1.
	Surface ornament comprising squat, non-tabular (or intratabular) echinae	2.2.
	Surface ornament comprising sutural or penitabular papillae	2.3.
2.1.	Antapical horns absent or weak	2.1.1.
	A single antapical horn developed	2.1.2.
2.1.1.	<i>Phthanoperidinium ?crenulatum</i>	
2.1.2.	<i>Phthanoperidinium eocenicum</i>	
2.2.	<i>Phthanoperidinium dentatum</i>	
2.3.	<i>Phthanoperidinium echinatum</i>	
3.	Spines very thin and delicate	3.1.
	Spines slender and sinuous	3.2.
	Spines robust and dagger-like	3.3.
3.1.	<i>Phthanoperidinium tenuimurum</i>	
3.2.	<i>Phthanoperidinium tritonium</i>	
3.3.	<i>Phthanoperidinium aculeatum</i>	

Phthanoperidinium ?crenulatum (De Coninck 1975) Lentin & Williams 1977b emend. Heilmann-Clausen 1985

Pl. 19, figs. 1-6

1975 *Peridinium crenulatum* De Coninck, p. 96, pl. 17, figs. 5-7, 12-15

1977b *Phthanoperidinium crenulatum* (De Coninck, 1969, p. 96, pl. 17, figs. 5-7, 12-15) Lentin & Williams, p. 131

1995a *Phthanoperidinium crenulatum* (De Coninck, 1969); De Coninck, pl. 7, figs. 3-5

Original Description: The outline of the body is roundly pentagonal. The archeopyle is intercalary. Serrated ridges (Latin: *crenulatus*) show the tabulation. I could see 7 precingular plates and 5 postcingular plates. The girdle is relatively large and helicoidal; The distance between the extremities is roughly equivalent to its width. The longitudinal furrow is larger than the girdle. There is a short horn on the apex on which the serrated ridges rise up. At the antapex the ridges become higher and suggest two weakly developed antapical horns (De Coninck 1975, p. 96).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, prolate to peridinioid, usually with one apical horn; episome usually somewhat longer than hyposome. Apical horn variably developed up to about 5µm; antapical horns weak to lacking. Cyst wall two-layered; acavate. Archeopyle intercalary, type I (2a). Processes lacking; surface ornament present, sutural, comprising crests; slightly elevated. Crests sutural, 2-3 µm, margins of crests granulate. Inferred formula: 4', 3a, 7", 6c, 5"', ?ps, 2''', X-5s; ventral organisation probably ortho-style. Cingulum clearly expressed, indicated by sutural septa; offset only slightly. Sulcus moderately expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 58 μm (one measured specimen). Width excluding any processes = 47 μm (one measured specimen). Length including any processes = 45 (53) 61 μm (9 measurements). Width including any processes = 37 (45) 53 μm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Lutetian	Mol borehole, Belgium	309.8m	De Coninck 1995a

***Phthanoperidinium dentatum* Clowes & Wilson n. sp.**

Pl. 19, figs. 7-12, Pl. 20, figs. 1-3

1982b *Phthanoperidinium cf. resistente* (Morgenroth); Wilson, p. 7, pl. 1, figs. 4-6

1985 *Spinidinium* sp.; Wilson, p. 99, pl. 1, figs. 9-10

Derivation of Name: Latin, *dentatus*, toothed; with reference to the tooth-like processes.

Holotype: Sample J42/f8690, slide L06958/SM0382; Hampden Formation, Hampden Beach Section (Bortonian); Pl. 19, figs. 7-12

Description: Cyst small, ellipsoidal, bilayered, with both layers closely appressed. A short relatively broad tooth-like apical horn is present (length $\sim 4 \mu\text{m}$) and a short narrow left antapical horn is sometimes present in the middle part of the antapical margin; the right antapical horn is not developed. Tabulation defined by parasutural rows of short solid tooth-like processes (length $\sim 2 \mu\text{m}$), often joined proximally by low solid septa. Tabulation pattern peridiniacean: 4', 3a, 7'', Xc, 5''', 2''''', Xs. Isolated intratabular processes may be present in the central part of some plates; otherwise surface smooth. Archeopyle fairly prominent, intercalary type I; operculum generally free or may be partly attached. Cingulum relatively broad ($\sim 5 \mu\text{m}$) and not generally segmented. Sulcus expressed as narrow midventral depression on the hypocyst; not usually differentiated into plates.

Size Range: Length including any processes = 40 (42) 43 μm (2 measurements). Width including any processes = 34 (37) 40 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f8690 (L06958)	Wilson 1982b
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	

Comparison: *Phthanoperidinium dentatum* is distinguished from other species mainly by its robust, tooth-like sutural processes. The spines of *P. ?crenulatum* occupy the same position on the cyst, but are far smaller; those of *P. echinatum* and *P. geminatum* are penitabular rather than sutural.

Remarks: At its type locality, the Hampden Beach section, *Phthanoperidinium dentatum* is associated with abundant *Wetzeliella hampdenensis*, a typical mid Bortonian species. (Also see Wilson 1985.)

***Phthanoperidinium echinatum* Eaton 1976**

Pl. 20, figs. 4-12

1976 *Phthanoperidinium echinatum* Eaton, p. 298-299, pl. 17, figs. 8-9, 12; text-fig. 23B

1980 *?Phthanoperidinium pseudoechinatum* Bujak, p. 75-76, pl. 19, fig. 20, text-fig. 20c

1982 *Phthanoperidinium echinatum* Eaton 1976; Islam, p. 309, 311, pl. 1, fig. 1

1995a *Phthanoperidinium echinatum* Eaton, 1976; De Coninck, pl. 7, fig. 6

2000 *Phthanoperidinium echinatum* Eaton 1976; Levy & Harwood, p. 208, pl. 8, figs. g-l

Original Description: Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries accentuated by a distinctive ornament concentrated at the plate margins, consisting of short hair-like projections [up to 3 μm long], each with a bulbous spherical distal termination. Cingular zone clearly defined and slightly helicoid. Reflected tabulation 4', 3a, 7'', 5''', 2'''''; archeopyle intercalary, formed by displacement of plate 2a (Eaton 1976, p. 298).

Description of Study Material: Medium sized, proximate cysts, prolate, usually with an apical horn, cingulum equatorial, most plates defined by coarsening of the surface ornament towards the sutures, immediately adjacent to which short capitate spines may be developed. An apical horn up to approximately 5 µm long, and quite acute, may be developed; antapical horns lacking. Archeopyle intercalary; operculum free (not recognised). Cyst walls are not distinguishable into layers; assumed to comprise two layers closely appressed; thin (~1 µm). Ornament comprising small granules which are relatively small and sparse in the centres of the plates, coarsening and more frequent towards plate margins; the surface essentially smooth between granules. Immediately adjacent to the sutures, the ornament becomes roughly organised into a penitabular row where short (up to ~2-3 µm) capitate spines are variably developed. The spines are typically straight or gently arcuate, unbranched, capitate, apparently solid and non-fibrous, more or less homogenous across the entire surface although it is possible those in the gonal areas may be somewhat larger. They delineate all plate series though the tabulation is not easily determined. The cingulum is about 6 µm wide, laevorotatory, offset at the sulcus by approximately one width. The sulcus is variably delineated by alignment of relatively coarse ornamentation, having indications of division into plates.

Size Range: Length excluding any processes = 50 µm (one measured specimen). Width excluding any processes = 40 µm (one measured specimen). Length including any processes = 42 (52) 65 µm (10 measurements). Width including any processes = 35 (39) 45 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
late Eocene	Middle Barton Beds, Barton, Hampshire, southern England	V59898	Bujak 1980
Bartonian	Kallo borehole, Belgium	135.5m	De Coninck 1995a
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
middle Eocene	Middle Bagshot Beds, Shapley Heath, southern England	C1752(2)	Islam 1982
Eocene	erratics, McMurdo Sound, Antarctica	MB 181(2)	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000

Comparison: *Phthanoperidinium echinatum* differs from *P. aculeatum* and *P. tritonium* in having considerably shorter processes (< 4 µm long), which are typically minutely capitate rather than attenuated, and which are arranged in two rows, one each side of but very close to the plate sutures, rather than in single file atop sutural crests.

Remarks: This species has been regarded as a junior synonym of *P. stockmansii* by De Coninck (1977, p. 40), "probably" by Edwards & Bebout 1981 (p. 34), and by implication in Islam 1982 (p. 315; although Islam mistakenly considered *P. echinatum* to be the senior name). Unfortunately, the scant morphological details and tiny, coarse-grained photographs of *P. stockmansii* provided by the original description do not permit a confident determination. Pending a modern redescription of the type material, I have opted to refer the present material to Eaton's more expansively described taxon.

Phthanoperidinium pseudoechinatum is regarded as a junior synonym, as first proposed by Islam (1982, p. 309, 311), because the only difference in the original descriptions is the number of plates involved in archeopyle formation which is now believed to be a variable, possibly ecologically variable, character.

***Phthanoperidinium eocenicum* (Cookson & Eisenack 1965a) Lentin & Williams 1973**

Pl. 21, figs. 1-6

1965a *Peridinium eocenicum* Cookson & Eisenack, p. 119-120, pl. 11, figs. 1-5

1973 *Phthanoperidinium eocenicum* (Cookson and Eisenack, 1965a, p. 119-120, pl. 11, figs. 1-5) Lentin & Williams, p. 113

1982b *Phthanoperidinium eocenicum* (Cookson & Eisenack); Wilson, p. 8, pl. 3, fig. 9

Original Description: Shell small, oval, tabulated and divided almost equally by a relatively broad, helicoid girdle. Both epitheca and hypotheca with a small, solid horn. Wall of shell finely granular with or without small dot-like thickenings of variable size on the surface of the plates.... The borders of the girdle and the thin transparent ledges of the plates are lightly granular and their edges dotted with evenly spaced granules and small tubercles, or sparsely denticulate. Tabulation is of the *Peridinium* type, 4' ?, 3a, 7'', 5''', 1p, 2'''''. Plate 1' is kite-like in shape, the two upper sides of the 'rhomb' being shorter than the two lower. Plate 1'''' is very narrow. Intercalary strips are sometimes evident. The archeopyle is relatively large, hexagonal, and intercalary (Cookson & Eisenack 1965a, p. 119; ellipses replace figure references in the original).

Description of Study Material: Cysts small, proximate, not dorso-ventrally compressed, prolate, with one apical and one antapical horn; episome and hyposome more or less equal in length. Apical horn moderately well-developed, apex pointed; antapical horns single antapical horn developed, relatively pointed. Cyst wall two-

layered; acavate. Archeopyle intercalary, type I (2a). Processes lacking; sutural, comprising crests; 2-3 µm high. Margins of crests granulate. Tabulation weakly expressed, apparently peridiniacean, inferred formula: 4', 3a, 7", 6c, 5"', ?ps, 2''', X-5s. Cingulum weakly expressed, indicated by sutural septa. Sulcus weakly expressed, indicated by sutural septa; lacking any clear indications of subdivision.

Size Range: Length including any processes = 42 (48) 64 µm (17 measurements). Width including any processes = 35 (41) 45 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan-Runangan	Jacksons Paddock, Oamaru-Dunedin, New Zealand	J41/f8914 (L04979)	Wilson 1982b
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: Lentin & Williams (1973, p.113) moved *Peridinium eocenicum* to *Phthanoperidinium* provisionally, as *Phthanoperidinium ?eocenicum*, without any comment as to why they regarded the assignment as provisional. The question mark over the assignment persists to this day in some publications (e.g. Fensome & Williams 2004, p. 525) although, again, without any explicit rationale as far as I am aware. The ventral episome plate topology is clearly ortho-style (Cookson & Eisenack 1965a, pl. 11, fig. 1) and in almost all other respects the species appears to be a "good" *Phthanoperidinium*. The majority of authors who have discussed *Phthanoperidinium* in some detail, including Edwards & Bebout 1981, and Islam 1982, appear to have dismissed the only apparent anomaly – the mention of plate 1p in the original description – as an error, and accepted *eocenicum* as a legitimate member of the genus. The interpretation followed here is that the "very narrow" plate 1" of the original description is, in fact, a sulcal plate, and plate "1p" is 1'''.

Stover & Evitt (1978, p.119) considered *Phthanoperidinium stockmansii* and *P. ?resistente* to be possible junior synonyms of *P. eocenicum*. However, insofar as *P. echinatum* can be taken as a proxy for *P. stockmansii*, the two taxa are easily distinguished by the penitabular versus tabular arrangement of the ornament. Moreover, *P. ?resistente* is "very small": 33-42 µm long, 25-31 µm broad, horns 3-4 µm (Morgenroth 1966a, p. 5), whereas *P. eocenicum*, by contrast, is significantly larger: 48-62 µm long, 33-48 µm broad (Cookson & Eisenack 1965a, p. 120), and also differs in possessing noticeably finer-grained sculpturing. The New Zealand material does not particularly support the contention that *P. ?resistente* and *P. eocenicum* are synonyms; Edwards & Bebout (1981, table 1) thought it "unlikely" also.

New Zealand specimens which appear identical to the Australian type material for this species.

***Phthanoperidinium geminatum* Bujak 1980**

Pl. 21, figs. 7-12

1980 *Phthanoperidinium geminatum* Bujak, p. 72, 74, pl. 19, figs. 8-12; text-figs. 20D, 22A

2004 *Phthanoperidinium geminatum*; Eldrett et al., p. 111-112, pl. III, fig. 2

2005 *Phthanoperidinium geminatum*; Schiøler, pl. 13, fig. 9

Original Description: Pericyst ovoidal with one small apical horn and one or two unequal antapical horns, the right always being strongly reduced. An endocyst is rarely visible. The periphragm is chagrinately granulate with parasutural rows of granules, short spines, or low crests. These delimit a paratabulation of 4', 3a, 7", xc, 5"', 2'''. Simulate rows or zones of similar ornament are always present and lie 1 µm to 3 µm inside the parasutures, except for those bordering the paracingulum on the precingular and postcingular paraplates. These typically merge with the cingular parasutures. An archeopyle is formed by the loss of paraplate 2a (Bujak 1980, p. 74).

Description of Study Material: Cysts small to intermediate, proximate, not dorso-ventrally compressed, prolate, with one apical and one or two unequal antapical horns; episome and hyposome more or less equal in length. Apical horn well developed; antapical horns unequal, the right strongly reduced or absent. Cyst wall two-layered; acavate; relatively robust, about 2 µm in thickness. Archeopyle intercalary, type I (2a); operculum free. Processes lacking; sutural plus penitabular, comprising crests; very low (about 1 µm or lower). Inferred formula: 4', 3a, 7", Xc, 5"', 2'''.

Size Range: Width excluding any processes = 35 (39) 43 µm (3 measurements). Length including any processes = 42 (48) 60 µm (14 measurements). Width including any processes = 32 (40) 50 µm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

?*Phthanoperidinium ?granulatum* Clowes & Wilson n. sp.

Pl. 22, figs. 1-6

Derivation of Name: Latin, *granulatus*, granulated; with reference to the granulate surface.

Holotype: Sample I43/f108, slide L16358/SM4832; Burnside Formation, Tumai (Runangan); Pl. 22, figs. 1-6

Description: Cyst small, proximate, ellipsoidal, two layered, with both layers closely appressed. A short fairly broad apical horn (length ~5 µm) with a blunt tip is usually present but the antapex is usually rounded without a horn. Tabulation defined by rows of low narrow smooth parasutural septa which are more prominent along the cingular borders. Tabulation pattern peridiniacean: 4', 3a, 7'', Xc, 5''', 2''', Xs. Surface of cyst covered with small low rounded granules. Archeopyle fairly prominent, intercalary type I; operculum generally free or may be partly attached. Cingulum relatively broad (~5 µm) and not generally segmented. Sulcus expressed as narrow mid-ventral depression on the hypocyst; not usually differentiated into plates.

Size Range: Width excluding any processes = 43 (45) 48 µm (3 measurements). Length including any processes = 46 (53) 61 µm (4 measurements). Width including any processes = 35 (44) 50 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Runangan	Tumai, Oamaru-Dunedin, New Zealand	I43/f108 (L16358)	Wilson & McMillan 1996

Comparison: *Phthanoperidinium granulatum* is characterised by its granulate surface and smooth low sutural septa, in which respect it is broadly similar to the type species, *Phthanoperidinium amoenum*. However, it differs from *Phthanoperidinium amoenum* in having a generally more rounded shape, more prominent intratabular granules, and less clearly diamond shaped plate 1'. (Indeed, there must remain some doubt about the generic assignment of this species on this account.)

***Phthanoperidinium ?resistente* (Morgenroth 1966a) Eisenack & Kjellström 1972**

Pl. 22, figs. 7-9

1966a *Peridinium resistente* Morgenroth, p. 5, pl. 2, figs. 1-2

1972 *Phthanoperidinium resistente* (Morgenroth, 1966a, p. 5, pl. 2, figs. 1-2) Eisenack & Kjellström, p. 911

Original Description: [Diagnosis] A very small species of the genus *Peridinium* Ehrenberg with the following tabulation scheme: ?4', ?3a, 7'', 5'', 2'''. Stair-like pointed antapical horn. Two tiny antapical horns. Transverse furrow defined. Longitudinal furrow clear.

[Description] The small, pear-shaped theca consists of plates with a smooth surface, only occasionally can light granulation be detected. Granulation is greater on the plate sutures. Epitheca and hypotheca are similar sizes. The epitheca tapers off in a stair-like, pointed apical horn. The 3-4 µ wide, shallow cingulum runs in a counter clockwise spiral direction. Both ends are offset from each other by approximately 1 furrow width. The wide longitudinal furrow runs from the first apical plate to the antapex. Two tiny conical antapical horns protrude from both antapical plates, only one of which is indicated. The pylome is formed from the separation of plate 2a.

[Remarks] *Peridinium resistente* n. sp. is distinguished from other well-known fossil forms by its habitus, above all however by its small dimensions [~40 µm long] (Morgenroth 1966a, p. 5).

Description of Study Material: Cysts small, proximate, not dorso-ventrally compressed, prolate. Antapical horns 2 tiny horns developed. Cyst wall two-layered; acavate. Archeopyle intercalary, type I (2a); operculum free. Surface ornament lacking to present, sutural, comprising granules; very low (about 1 µm or lower). Inferred formula: 4', 3a, 7'', 6c, 5''', ?ps, 2''', X-5s. Cingulum clearly expressed.

Size Range: Length including any processes = 43 (46) 48 µm (2 measurements). Width including any processes = 35 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: Morgenroth 1966a, p. 5, comments that the species is "very small". The dimensions given for the type material – 33-42 µm long, 25-31µm broad, horns 3-4 µm – are somewhat smaller than is usual of *Phthanoperidinium* species, though not extremely so. Usefully, however, it is significantly smaller than *P. eocenicum* (48-62 µm long, 33-48 µm broad; Cookson & Eisenack 1965a, p. 120), which it otherwise

resembles somewhat. The sutural ornament of *P. resistente* appears more coarsely granular than that of *P. eocenicum*.

The present forms are intermediate between the two in size, but more coarsely ornamented than those herein attributed to *P. eocenicum*, and are assigned to *P. resistente* provisionally.

***Phthanoperidinium spumosum* Clowes n. sp.**

Pl. 22, figs. 10-12, Pl. 23, figs. 1-3

Derivation of Name: Latin, *spumosus*, foaming or frothy; with reference to the surface texture.

Holotype: Sample I43/f093, slide L16341/SM078; Burnside Formation, Puketeraki Core (Bortonian); Pl. 22, figs. 10-12, Pl. 23, figs. 1-3

Description: Medium sized, proximate cysts, prolate, lacking horns, cingulum equatorial, most plates defined by alignment of the sculptural features above the sutures. Archeopyle intercalary; operculum attached. Sculpturing of the surface layer permits differentiation of the cyst walls into two layers when viewed in cross-section; the layers approximately equal in thickness; combined thickness ~3 µm. Ornament comprising a reticulum in which the lacunae are small (~0.5 up to, exceptionally, ~3 µm) and circular. Alignments or coarsening of the reticulum at the sutures delineates most plate series though the tabulation is not easily determined. The cingulum is about 7 µm wide. The sulcus is poorly delineated and does not exhibit division into plates.

Size Range: Length = 45 µm (one measured specimen). Width = 37 µm (one measured specimen).

Distribution: Rare, and restricted to only a few samples of Bortonian age, perhaps suggesting a narrow stratigraphic range.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: The rounded lacunae of the reticulum are quite distinctive and serve to distinguish *P. spumosum* from all other *Phthanoperidinium* known at this time.

***Phthanoperidinium aculeatum* Clowes n. sp.**

Pl. 23, figs. 4-9

?1972 *Phthanoperidinium* sp.; Benedek, p. 20, pl. 4, fig. 9

Derivation of Name: Latin, *aculeatus*, prickly, stinging; with reference to the formidable-looking spinose ornament.

Holotype: Sample I43/f093, slide L16341/SM082A; Burnside Formation, Puketeraki Core (Bortonian); Pl. 23, figs. 4-9.

Description: Cysts of intermediate size, proximochorate, prolate, with one apical horn; episome somewhat shorter than hyposome. Apical horn variably developed up to about 5µm; antapical horns weak to lacking. Cyst wall two-layered; acavate; relatively robust, about 2 µm in thickness. Archeopyle intercalary, type I (2a). Sutural, comprising spines. Nature of spines robust and dagger-like, length of spines generally less than about 12-13 µm. Inferred formula: 4', 3a, 7", 6c, 5"', ?ps, 2''', X-5s. Cingulum clearly expressed, indicated by surface ornament, about 4 µm wide; offset strongly, by about 1 width. Sulcus clearly expressed, indicated by surface ornament; more or less vertical; showing indications of subdivision into individual plates.

Size Range: Length excluding any processes = 47 (48) 50 µm (2 measurements). Width excluding any processes = 32 (35) 38 µm (2 measurements). Length including any processes = 52 (61) 70 µm (2 measurements). Width including any processes = 42 (50) 58 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: *Phthanoperidinium aculeatum* is readily distinguished by the other spinose forms discussed here, *P. comatum*, *tritonium*, and *tenuimurum*, by the more robust spines.

Phthanoperidinium tenuimurum Clowes n. sp.

Pl. 23, figs. 10-12

Derivation of Name: Latin, *tenuis*, thin, slender, slight; plus *murus*, a wall; with reference to the very thin cyst walls.

Holotype: Sample S14/f8599, slide L10662/SM014; Waikato Coal Measures, Old Mountain Road (Runangan-early Whaingaroan); Pl. 23, figs. 10-12

Description: Prolate cysts with slightly acute apex and antapex, antapical hemisphere much smaller than apical, round in cross section; cingulum represented by distinct folds and lacks significant laevorotatory offset; homogeneous, short, solid, non-fibrous, unbranched spines, 5-10 μm , with simple, acute tips mostly (?always) arise, often in groups of two or three, from sutural crests of varying but consistently low height. Cyst walls two-layered, but the different layers are not clearly discernible, being thin (combined thickness < ~0.5 μm) and very closely appressed. Archeopyle intercalary; with flat bottom edge, sides and top rounded; sometimes extending into splits between apical plates. Operculum free. A small (~1.5-7.5 μm) and sometimes indistinct apical horn is continuous with a crest which runs up the side of the sulcus and carries a cluster of four or five spines. Surface finely scabrate. Tabulation is apparent from the sutural crests, cingular folds and archeopyle; cingulum ~1.5-5 μm wide; the sulcus is indistinct. The precingular series is low to much lower than the 2a intercalary plate. The pattern is peridiniacean, presumed formula 4', 3a, 7'', Xc, 5''', 2''''', Xs.

Size Range: Length excluding any processes = 43 (53) 60 μm (16 measurements). Width excluding any processes = 40 (45) 53 μm (17 measurements). Length including any processes = 51 (61) 78 μm (16 measurements). Width including any processes = 48 (57) 73 μm (17 measurements).

Distribution: Although found in only two samples during the present study, the species is quite common in the type sample.

Age/Stage	Location	Sample	Sample Reference
Runangan-early Whaingaroan	Old Mountain Road, Waikato, New Zealand	S14/f8599 (L10662)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Comparison: Distinguished by the other spinose forms discussed here, *P. aculeatum*, *comatum* and *tritonium*, by the very thin walls and delicate spines.

Phthanoperidinium tritonium Eaton 1976

Pl. 24, figs. 1-3

1976 *Phthanoperidinium tritonium* Eaton, p. 299-300, pl. 17, figs. 2-3, 6-7, text-fig. 23c, 24

1980 '*Phthanoperidinium tritonium*' Eaton; Bujak, pl. 5, figs. 7-8

1980 *Phthanoperidinium comatum* (Morgenroth, 1966b) Eisenack and Kjellström, 1971; Bujak, p. 72

Original Description: Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries marked by thin smooth sutural crests of variable height, bearing erect or curved solid spines which may be distally simple or bifurcate. Cingular zone clearly defined and distinctly helicoid. Reflected tabulation 4', 3a, 7'', 5''', 2'''''; archeopyle intercalary, formed by displacement of plate 2a (Eaton 1976, p. 299).

Description of Study Material: Cysts small to intermediate, proximochorate, not dorso-ventrally compressed, prolate, with one apical horn; episome usually somewhat longer than hyposome. Apical horn moderately well-developed, apex bluntly terminated; antapical horns lacking to weakly developed. Cyst wall two-layered; acavate; relatively robust, about 2 μm in thickness. Archeopyle intercalary, type I (2a); operculum free to attached. Surface ornament present, intratabular, comprising granules; very low (about 1 μm or lower); minute. Crests sutural, low (less than about 1 μm), margins of crests spinose; nature of spines slender, sinuous, length of spines generally less than about 12-13 μm . Tabulation weakly expressed, apparently peridiniacean, inferred formula: 4', 3a, 7'', 6c, 5''', ?ps, 2''''', X-5s; ventral organisation probably ortho-style. Cingulum clearly expressed, indicated by surface ornament. Sulcus weakly expressed to moderately expressed, indicated by surface ornament; more or less vertical.

Size Range: Length excluding any processes = 38 (43) 45 μm (5 measurements). Width excluding any processes = 35 (36) 37 μm (5 measurements). Length including any processes = 35 (50) 70 μm (44 measurements). Width including any processes = 40 (47) 55 μm (7 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: *Phthanoperidinium tritonium* differs from *P. comatum* principally, and perhaps only, in possessing shorter spines: typically about 10 and up to 13 μm in the case of *P. tritonium* and generally in the range 14-22 μm in the case of *P. comatum* (Eaton 1976, p. 300). Bujak (1980, p. 72) considered the two species conspecific because he observed the presence of intermediate forms which "possess spines whose lengths overlap that of both species" in his Barton Bed material. However, I am far more persuaded by the argument that a complete fossil record would undoubtedly exhibit an insensible intergradation between all dinoflagellate taxa (and, indeed, all taxa). The fact that some of these intermediates have been found, whereas others have not, is a sampling artefact having neither phylogenetic nor stratigraphic significance.

The spines of *P. multispinum* arise from penitabular rather than sutural crests (Bujak 1980, text-fig. 20F) and are noticeably shorter, reaching a maximum of 4-6 μm in *P. multispinum* (Bujak 1980, p. 74) but typically ranging up to around 10 μm in the case of *P. tritonium*.

Phthanoperidinium polytrix (Benedek 1972) is possibly conspecific with *P. tritonium*, in which case it would be the senior synonym. Benedek's description is brief and inconclusive, and the original illustrations (pl. 6, figs. 1a-b) small and grainy. The holotype is reillustrated in Benedek & Sarjeant 1981 (figs. 2-4, 2-6 and 6), however, which reveals the presence of low penitabular ridges not found in *P. tritonium*.

Another similar species is *P. coreoides*. The best available image of the *P. coreoides* holotype (Benedek & Sarjeant 1981, fig. 3, numbers 2 and 4) depicts a cyst which has quite well-expressed tabulation and no discernable cavation. The line drawing in the same publication (fig. 5) shows a complete (fully expressed) tabulation, even showing 1a, 3a, 1c, and 7c, which I can't see in my specimens. Neither the line drawing nor the description hints at any cavation, whereas a small apical pericoel is easily in my material (Pl. 24, fig. 1).

Eaton (1976) does not provide measurements for the thickness of the cyst wall though his illustrations (especially pl. 7, figs. 3, the holotype, and 7) give the appearance of a thin-walled cyst, though not as thin as *P. tenuimurum*. The form described above as *P. aculeatum* differs in possessing a more robust cyst wall.

Remarks: New Zealand forms appear indistinguishable from Eaton's type material, although bifid spine tips have not been observed.

Eaton 1976, p. 299-300, notes that archeopyle formation may sometimes involve incorporation, or partial incorporation, of plates 1a, 3a, and 4", which is consistent with many subsequent observations (e.g. Edwards & Bebout 1981). This behaviour has not been observed in any of the New Zealand material, however, which exhibits type I (2a) archeopyle formation only.

***Phthanoperidinium australe* Clowes n. sp.**

Pl. 24, figs. 4-12

- ?1975 *Palaeoperidinium* sp.; Haskell & Wilson, pl. 2, fig. 8
?1982a *Phthanoperidinium* cf. *eocenicum* (Cookson & Eisenack); Wilson, pl. 1, fig. 10
1989 *Phthanoperidinium* sp. 1; Wilson, pl. 1, figs. 7-8

Derivation of Name: Latin, *australis*, southern; with reference to the species' (presently known) distribution.

Holotype: Sample I43/f090, slide L16338/SM002; Burnside Formation, Puketeraki Core (Bortonian); Pl. 24, figs. 7-12

Description: Cysts small, proximate, not dorso-ventrally compressed, prolate, with one apical horn; episome and hyposome more or less equal in length. Apical horn lacking to poorly developed, apex bluntly terminated; antapical horns weak to lacking. Cyst wall two-layered; acavate; relatively robust. Archeopyle intercalary, type I (2a); operculum attached. Surface ornament present, sutural, comprising low septa; very low (about 1 μm or lower). Margins of crests smooth. Tabulation clearly expressed, peridiniacean, inferred formula: 4', 3a, 7", 6c, 5"', ?ps, 2''', X-5s; ventral organisation probably ortho-style. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa; more or less vertical.

Size Range: Length including any processes = 38 (45) 52 μm (9 measurements). Width including any processes = 33 (34) 35 μm (3 measurements).

Distribution:

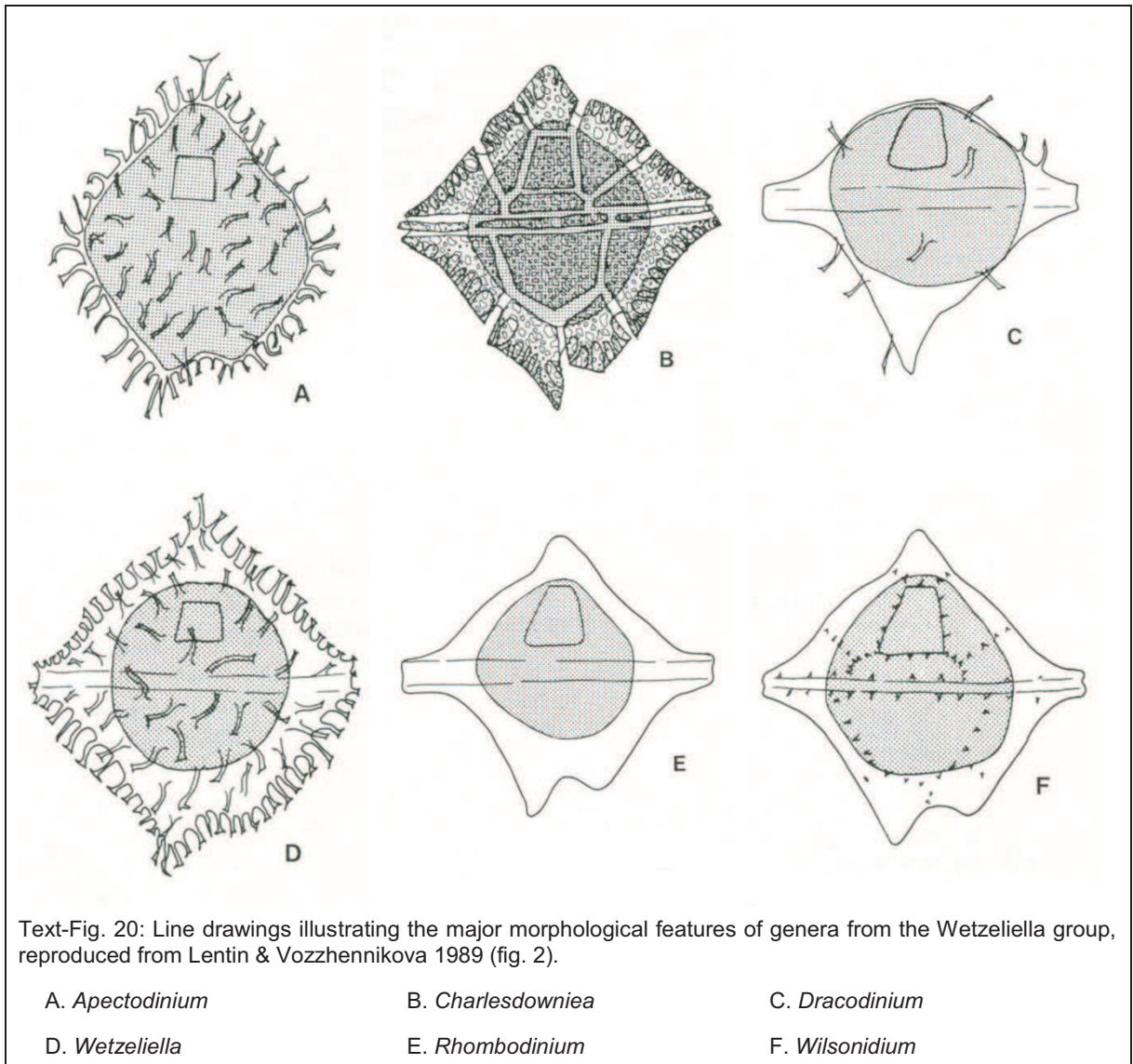
Age/Stage	Location	Sample	Sample Reference
late Eocene-early Oligocene	Chalky Island, Fiordland, New Zealand		Wilson 1982a
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	SM3796	Wilson 1989

Comparison: *P. australe* is broadly similar to *P. distinctum* but differs in possessing less prominent sutures.

Consideration of the status of other species, previously or currently placed in *Phthanoperidinium*, is given in Appendix 4.

Subfamily Wetzelielloideae (Vozzhennikova 1961) Bujak & Davies 1983

A series of line drawings illustrating the major morphological differences between several *Wetzeliella* group genera is provided in Lentin & Vozzhennikova 1989 (fig. 2; reproduced here as Text-Fig. 20).



Genus *Wetzeliella* Eisenack 1938b emend. Lentin & Williams 1976

1938b *Wetzeliella* Eisenack, p. 187

1976 *Wetzeliella* Eisenack, 1938b emend. Lentin & Williams, p. 129-133

1978 *Wetzeliella* Eisenack 1938 emended Lentin & Williams 1976; Stover & Evitt, p. 130-131

1979a *Wetzeliella* Eisenack, 1938b emend. Lentin & Williams, 1975; Costa & Downie, p. 40

Type Species: Wetzeliella articulata Eisenack 1938b, p. 187; text-fig. 4 [Late Eocene-Early Oligocene]

Original Description: [Given for the type species.] Shell more or less flattened, rhomboidal to pentagonal or also more or less oval, usually with apical horn, lateral horns on both sides and two antapical horns, all of which can be strongly reduced, without tabulation, almost always ornamented with bristles or spines. Transverse and longitudinal furrows, respectively, not determinable as flagellar groove (the former perhaps indicated sometimes). Ellipsoidal capsule present interiorly (translated from Eisenack 1954b, p. 54, by Stover & Evitt 1978, p. 130).

Remarks: Eisenack did not provide a separate generic description in his original publication of the genus (Eisenack 1938b).

Wetzeliella hampdenensis Wilson 1967c

Pl. 25, figs. 1-3

1967c *Wetzeliella (Wetzeliella) hampdenensis* Wilson, p. 480-481, figs. 17, 19

1982b *Wetzeliella hampdenensis* Wilson; Wilson, p. 7, pl. 1, figs. 12-13

1984d *Wetzeliella hampdenensis* Wilson; Wilson, p. 114, fig. 6 (10)

1985 *Wetzeliella hampdenensis* Wilson 1967; Wilson, p. 100, pl. 1, fig. 1

Original Description: Periphragm outline pentagonal, asymmetric. Horns comparatively short apart from right antapical horn which is longer and more pointed than the others. Side horns broad, short, and blunt. Left antapical horn always present, substantially shorter than right antapical horn. Periphragm bordered by short, broad, sharply tapered aculeate processes (process length 3-9 μ , bases 3-7 μ , aculei length 2-5 μ , number of aculei 3-6). The smallest processes occur on the horn margins. Processes of periphragm tapered (bases 2-7 μ), aculeate, up to 16 μ in length, and arranged in simulate complexes. Capsule sub-rhomboidal to sub-pentagonal; pericoel usually fairly well developed. Archeopyle trapezium-shaped. Tabulation apparently similar to *Wetzeliella (W.) articulata* (Wilson 1967c, p. 480-481; ellipses replace figure references in the original).

Size Range: Length including any processes = 97 (119) 140 μ m (4 measurements). Width including any processes = 102 μ m (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Hampden, Otago, New Zealand	S146/f690	Wilson 1967c, 1984d

Remarks: Considered a junior synonym of *Wetzeliella articulata* Eisenack 1938b by Costa & Downie 1979a, p. 40. However, the 1981 and subsequent editions of the Lentin & Williams catalogue (Lentin & Williams 1981, et seq., Fensome & Williams 2004) retained *Wetzeliella hampdenensis*, and the taxon remains in current use, at least in New Zealand (e.g. Wilson 1984d, 1985).

Wetzeliella hampdenensis is an index fossil for the mid Bortonian.

Genus *Charlesdowniea* Lentin & Vozzhennikova 1989

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

2004 *Charlesdowniea* Lentin and Vozzhennikova, 1989, p. 225, 227; Fensome & Williams, p. 117-119

Type Species: Charlesdowniea coleothrypta (Williams & Downie 1966b, p. 185-186, pl. 18, figs. 8-9; text-fig. 47) Lentin & Vozzhennikova 1989, p. 225 [Early Eocene]

Original Description: Dorso-ventrally compressed peridinioid cysts with one apical, two lateral and two antapical horns, the right of which may be reduced; circumcavate to cornucavate; endocyst broadly elliptical to round in outline; ectophragm incomplete, present over some or all intratabular areas and consistently absent over

pandasutural areas. Endophragm smooth or lightly ornamented with features of low relief; periphragm ornamented with smooth tubular or solid processes arranged in intratabular clusters; processes may be reduced or absent on the mid-dorsal and/or mid-ventral surfaces. Pandasutural areas smooth to faintly ornamented. Ectophragm smooth, perforate, faintly ornamented or consisting of an open reticulum of trabeculae. Paratabulation indicated on the periphragm by intratabular processes and pandasutural zones without processes and by the shape of the ectophragm pieces whose outline tends to approximate the shape of the underlying paraplate; peridiniacean, formula 4', 3a, 7", Xc or 5c, 5"', 2"', 0s or 2-4s. Archeopyle Type I/I (quadra 2a only), operculum free or attached. Paracingulum indicated by the location of the lateral horns and/or transverse alignment of processes on the dorsal and ventral surfaces, and/or fine rectilinear intratabular groups of processes. Parasulcus not indicated or indicated by a shallow depression which may or may not have intratabular clusters of processes (Lentin & Vozzhennikova 1989, p. 225-227).

Remarks: *Charlesdowniea* differs from *Kisselovia* in possessing processes and an ectophragm.

***Charlesdowniea coleothrypta* (Williams & Downie 1966b) Lentin & Vozzhennikova 1989**

Pl. 25, figs. 4-6

- 1966b *Wetzeliella coleothrypta* Williams & Downie, p. 185-186, pl. 18, fig. 8, text-fig. 47
- 1967c *Wetzeliella (Wetzeliella) coleothrypta* Williams & Downie; Wilson, p. 476, figs. 12-14
- 1976 *Kisselevia coleothrypta* (Williams & Downie 1966b, p. 185-186, pl. 18, figs. 8-9; text-fig. 47) Lentin & Williams, p. 136
- 1984d *Kisselovia coleothrypta* (Williams & Downie) Lentin & Williams; Wilson, p. 114, fig. 6 (2)
- 1989 *Charlesdowniea coleothrypta* (Williams & Downie 1966b, p. 185-186, pl. 18, figs. 8-9; text-fig. 47) Lentin & Vozzhennikova, p. 225

Original Description: Thin walled periphragm characteristic pentagonal outline with each angle produced into horns, one apical, two lateral and two antapical; left antapical horn generally reduced. Pericoel totally enclosing endophragm. Processes arising from periphragm, hollow, connecting with pericoel. Distally processes of individual simulate complex united by finely perforate membrane assuming outline of underlying plate and extending over that plate as a replica of it. Processes commonly absent from pre- and postcingular plates on side lying nearest to cingulum. Reflected tabulation of 4', 3a, 7", 5c, 5"', 2" [sic], 3-4s (Williams & Downie 1966b, p. 185).

Size Range: Length including any processes = 105 µm (one measured specimen). Width including any processes = 97 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Heretaungan	Abbotsford Mudstone, Dunedin, New Zealand	S164/f533	Wilson 1967c
Heretaungan	Otago, New Zealand	SM1002	Wilson 1984d
Heretaungan	Waipawa	N141/f994	Wilson 1967c
Mangaorapan	Waipawa	N141/f993	Wilson 1967c

***Genus Dracodinium* Gocht 1955 emend. Bujak et al. 1980**

- 1955 *Dracodinium* Gocht, p. 87
- 1979a *Dracodinium* Gocht, 1955; Costa & Downie, p. 43
- 1980b *Dracodinium* Gocht, 1955, emend. Bujak et al., p. 28

Type Species: *Dracodinium solidum* Gocht 1955, p. 88; text-figs. 3a-b, 4a-c, 5a-c [Eocene-Oligocene]

Original Description: Roughly kite-shaped dinoflagellates with well developed lateral horns and partially reduced antapical horns. Apex ± rounded, occasionally slightly pointed (as distinct from *Wetzeliella*); only in exceptional cases is there any indication of a small apical cusp. The theca is untabulated and often has bristles; furrows are absent. Inside there is always a circular to ± elliptical capsule (translation from Gocht 1955, p. 87).

Remarks: Considered to be a junior synonym of *Wetzeliella* by Lentin & Williams 1976 and by Stover & Evitt 1978, but the genus differs in its rounded apex and has generally been found useful to retain (e.g. Costa & Downie 1979, p.36, Bujak et al. 1980b, p.28, and Lentin & Williams 1989, p.121).

As noted in Bujak et al. 1980b, p. 28, *Dracodinium* differs from *Rhombodinium* in possessing a roughly subtriangular rather than a rhomboidal pericyst, an oval rather than subrhomboidal endocyst, and an operculum which is free rather than remaining attached anteriorly, along side Q1. The last distinction is considered unreliable, however — see *Rhombodinium*.

Dracodinium granulatum (Wilson 1967c) Lentin & Williams

Pl. 25, figs. 7-9

1967c *Wetzeliella (Rhombodinium) glabra* var. *granulata* Wilson, p. 493, figs. 29-30

1973 *Rhombodinium glabrum* subsp. *granulatum* (Wilson 1967c, p. 493, figs. 29-30) Lentin & Williams, p. 120

1981 *Dracodinium granulatum* (Wilson 1967c, p. 493, figs. 29-30) Lentin & Williams, p. 92

Original Description: A variety of *W. (Rh.) glabra* with a coarsely granular periphragm. Granules sometimes aligned in rows indicating possible tabulation (Wilson 1967c, p. 493).

Size Range: Length including any processes = 87 (98) 108 µm (2 measurements). Width including any processes = 95 (98) 100 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Raki Siltstone, Rakis Table, Oamaru, New Zealand	S136/f841	Wilson 1967c
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Genus *Rhombodinium* Gocht 1955 emend. Bujak, 1979

1955 *Rhombodinium* Gocht, p. 85

1961 *Wetzeliella (Rhombodinium)* Gocht 1955; Alberti, p. 9

1967 *Rhombodinium* Gocht, 1955; Vozzhennikova, p. 167-168

1967c *Wetzeliella (Rhombodinium)* Gocht 1955; Wilson, p. 492

1975 *Wetzeliella (Rhombodinium)* Gocht, 1955, p. 85; Harker & Sarjeant, p. 225

1976 *Rhombodinium* Gocht, 1955; Lentin & Williams, p. 126-128

1977b *Rhombodinium* Gocht, 1955, p. 85; Lentin & Williams, p. 139-140

1978 *Rhombodinium* Gocht 1955; Stover & Evitt, p. 120-121

1979 *Rhombodinium* Gocht, 1955, emend. Bujak, p. 313-314

1979a *Rhombodinium* Gocht, 1955; Costa & Downie, p. 44

1989 *Rhombodinium* Gocht, 1955 emend. Bujak, 1979; Head & Norris, p. 532

1989 *Rhombodinium* Gocht 1955; non emend. Bujak 1979; Lentin & Vozzhennikova, p. 218-219

1989 *Rhombodinium* Gocht, 1955, p. 85; emend. Bujak, 1979, p. 313-314; Lentin & Williams, p. 317-318

2004 *Rhombodinium* Gocht, 1955, p. 85; Fensome & Williams, p. 571-574

Type Species: *Rhombodinium draco* Gocht 1955, p. 86, text-figs. 1a-c [Mid Oligocene]

Original Description: Dinoflagellates with an approximately rhomboidal, kite-shaped, or quadrate outline, well-developed apical and lateral horns, and mostly reduced antapical horns. Shell untabulated, smooth, not ornamented with setae or spines (difference from *Wetzeliella*), without clearly recognizable transverse or longitudinal furrow. Shell always contains an inner capsule (translated from Gocht 1955, p. 85, by Stover & Evitt 1978, p. 120).

Remarks: According to Bujak et al. 1980b, p. 28, *Rhombodinium* differs from *Dracodinium* in possessing a rhomboidal rather than a roughly subtriangular pericyst, a subrhomboidal rather than oval endocyst, and (following Bujak 1979, p. 313) an operculum which remains attached anteriorly, along side Q1, rather than becoming detached. Lentin & Vozzhennikova (1989, p. 218), however, rejected Bujak's (1979) emendation, citing a personal communication from Gocht noting that the endoperculum is free in the genoholotype. Nor do the specimens of *R. glabrum* encountered in the present study support the notion that the operculum of *Rhombodinium* remains attached along edge Q1 (see Pl. 25, figs. 10-12) or, indeed, at all (see Pl. 26, figs. 1-2).

Rhombodinium differs from *Wetziella* in having ornament of lower relief: a distinction of dubious merit at the generic level. Transitional forms are known (as lamented by several of the authors who have treated *Rhombodinium* as a subgenus of *Wetziella*).

It differs from *Wilsonidium* in lacking sutural features.

Rhombodinium glabrum (Cookson 1956) Vozzhennikova 1967

Pl. 25, figs. 10-12, Pl. 26, figs. 1-3

- 1956 *Wetziella glabra* Cookson, p. 186-187, pl. 2, figs. 1-5
 ?1961 *Wetziella (Rhombodinium) rhomboidea* Alberti, p. 10, pl. 1, figs. 1-5, pl. 12, fig. 9
 1965 *Wetziella glabra* Cookson; Williams, p. 109, fig. 3
 ?1966a *Wetziella (Rhombodinium) glabra* Cookson 1956; Morgenroth, p. 11-12, pl. 1, figs. 11-12
 1966b *Wetziella glabra* Cookson; Williams & Downie, p. 197, pl. 20, figs. 9-10
 1967 *Rhombodinium glabra* (Cookson, 1956) Vozzhennikova, p. 169
 1967c *Wetziella (Rhombodinium) glabra* Cookson; Wilson, p. 492, figs. 31-32
 1976 *Rhombodinium glabrum* (Cookson, 1956, p. 186, pl. 2, fig. 1-5) Vozzhennikova, 1967, p. 169; Lentin & Williams, p. 128
 1979a *Wilsonidium glabrum* (Cookson) Costa & Downie, p. 45
 1982b *Rhombodinium glabrum* Cookson; Wilson, p. 7, pl. 2, figs. 8-9
 1984d *Rhombodinium glabrum*; Wilson, p. 114
 ?1986b *Rhombodinium rhomboideum* (Alberti 1961); De Coninck, pl. 9, figs. 2-3, 7-8
 1989 "*Rhombodinium*" *glabrum* (Cookson, 1956) Vozzhennikova, 1967; Head & Norris, p. 532

Original Description: Cell encysted, flattened, quadrangular in outline with an entire margin, divided equally by a transverse girdle into a triangular epitheca with a short, bluntly pointed apical horn and a hypotheca with 2 short, unequal horns. The girdle is most clearly evident in the position of the lateral horns. The cell membrane is finely granular and usually completely smooth; in the holotype a few minute teeth-like outgrowths are present in the region of the horns, particularly the apical horn.

The cyst, which is separated from the cell membrane by a wide space, is ellipsoidal and flattened, and has a moderately thick, roughened wall with a granular sculpture.... An approximately quadrangular opening has been present in all specimens, and the detached "lid" can sometimes be seen lying in the cell cavity (Cookson 1956, p. 186).

Size Range: Length including any processes = 100 (120) 181 µm (19 measurements). Width including any processes = 108 (135) 160 µm (8 measurements).

Distribution: Frequent. This form is the only truly "common" *Wetziella*-group taxon found in this study.

Age/Stage	Location	Sample	Sample Reference
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
latest Bartonian-Priabonian (Tongrien)	Sands of Asse, Woensdrecht borehole, southern Netherlands	-263 to -277 m.	De Coninck 1986b
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The forms described above, and in previous New Zealand publications such as Wilson 1967c, as a group, have slightly less strongly-developed lateral horns than the Australian type material, but appear otherwise identical. Regarded as a questionable generic assignment by Head & Norris, who note that the "species was not discussed by Bujak (1979) in his emendation of *Rhombodinium*, but clearly it possesses a free, detached operculum (Cookson, 1956), which excludes it from *Rhombodinium* as emended by Bujak, and for which reason we have retained it only tentatively in this genus" (Head & Norris 1989, p. 532).

It is not completely clear (to me) that *Dracodinium* (formerly *Rhombodinium*) *rhomboideum* (Alberti 1961) differs meaningfully from this species.

Genus *Wilsonidium* Lentin & Williams 1976

- 1976 *Wilsonidium* Lentin & Williams, p. 138-139
1978 *Wilsonidium* Lentin & Williams 1976; Stover & Evitt, p. 132-133
1979a *Wilsonidium* Lentin & Williams 1975; Costa & Downie, p. 45

Type Species: Wilsonidium tabulatum (Wilson 1967c, p. 473-474, figs. 2a-b, 4-7, 10-11) Lentin & Williams 1976, p. 138, 140 [Late Eocene]

Original Description: Pericyst: Ambitus rhomboidal to pentagonal (peridinioid). Apex rounded or more commonly prolonged into an apical horn. Two equal precingular horns usually present, occasionally reduced or absent. Antapex prolonged into one eccentrically located antapical horn, the left, or two unequal symmetrically located antapical horns, the left always being the longer, the right being reduced or vestigial. From the position of the pericingular horns, the epipericyst and hypopericyst may be equal in size, or unequal, in which case the hypopericyst is always the larger. Compression dorso-ventral, usually extreme.

Endocyst: Ambitus circular to ovoidal to ellipsoidal. Rarely may be completely appressed to the pericyst when it has the same shape. Generally only partially in contact with the pericyst and then in the interhorn areas. Compression dorso-ventral. Pericoels: When the endocyst and pericyst are in contact in the interhorn areas, there result an apical, two circular and one or two antapical pericoels. Alternatively the pericoels may be united when the endocyst and pericyst are separated by a single ambital pericoel.

Periphragm: Thin (usually less than 2μ) and of a constant thickness. Surface ornamented with parasutural granules, septa and/or processes. Intratabular ornamentation reduced or absent. Endophragm: $<1\mu$ to several microns thick. Surface laevigate to granulate. Pericyst: The parasutures delineate a typical peridinioid paratabulation of 4', 3a, 7", 5"', 2'''' plus sulcals. In the apical series, paraplate 1' is pentagonal, 2', 3' and 4' are considerably smaller. The 1a and 3a paraplates appear to be pentagonal and extend closer to the pericingulum than the quadra 2a. Of the precingulars 1" and 7" are rhomboidal with their longest axis parallel to the pericingulum, 2" and 6" are elongate narrow, 3" and 5" are four-sided, and 4" is six-sided with its longest axis parallel to the pericingulum. The width of the 4" is greater than that of 2a. The postcingular paraplates consist of 1''' and 5''' which are four-sided and of more or less equal size, 2''' and 4''' which are likewise four-sided and of equal size, and the distinctive pentagonal 3'''. The two large antapicals are located primarily on the dorsal surface and are more or less equal in size. Pericingulum: Produced into two pericingular horns. Delineated by parasutural ornamentation, or apparently penetabular ornamentation as linear features. Commonly indented as can be seen at the distal extremity of the pericingular horns. Slightly helicoidal. Perisulcus: Clearly delineated. Large on both epipericyst and hypopericyst. Widening posteriorly and extending onto the antapical horns. The largest paraplate is the posterior sulcal. Flagellar pore imprints occasionally visible. Endocyst: Paratabulation indeterminate other than in the vicinity of the endoarchoepyle.

Periarchoepyle Quadra intercalary resulting from the partial or complete detachment of the second anterior intercalary paraplate 2a. Perioperculum free or remaining attached along the anterior parasuture. Endoarchoepyle: Quadra intercalary resulting from the loss of the second anterior intercalary paraplate 2a. Operculum usually free. May be of greater width than the periarchoepyle (Lentin & Williams 1976, p. 138-139).

Remarks: *Wilsonidium* differs from *Rhombodinium* in possessing parasutural ornament. It differs from *Wetzeliella* in having sutural ornament and "generally reduced intratabular ornamentation" (Lentin & Williams 1976, p. 139).

Wilsonidium tabulatum (Wilson 1967c) Lentin & Williams 1976

- 1967c *Wetzeliella* (*Wetzeliella*) *tabulata* Wilson, p. 473-474, figs. 4-7, 10-11, text-fig. 2a-b
1976 *Wilsonidium tabulatum* (Wilson 1967c, p. 473-474, figs. 2a-b, 4-7, 10-11) Lentin & Williams, p. 138-140
1982b *Wilsonidium tabulatum* (Wilson); Wilson, p. 7, pl. 2, figs. 12-13
1984d *Wilsonidium tabulatum* (Wilson) Lentin & Williams; Wilson, p. 114, fig. 6 (11)

Original Description: Periphragm outline pentagonal, bilaterally asymmetric, with well developed horns at each angle. Apical, lateral and right antapical horns all approximately equal in size; left antapical horn always shorter although still prominent. Polar horns tapered, pointed; lateral horns have a well defined notch at their extremities denoting the position of a transverse girdle. Periphragm divided into clearly defined fields by rows of slender non-tapering solid spines ($l = 2-8\mu$) which are occasionally united at their bases by a low ridge. Tabulation typical of genus.... Margin between horns concave, usually irregularly spinose, occasionally smooth. Capsule outline varies from circular to sub-angular. Archoepyle corresponds to 2a plate, shape square to rectangular; operculum often located within capsule. Transverse girdle clearly defined by double row of spines, slightly laevorotatory (Wilson 1967c, p. 473; ellipses replace figure references in the original).

Size Range: Length including any processes = 125 µm (one measured specimen).

Distribution: Rare. Only a single, poor, specimen was encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Raki Siltstone, Rakis Table, Oamaru, Otago, New Zealand	J41/f8841	Wilson 1967c
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

***Wilsonidium echinosuturatum* (Wilson 1967c) Lentin & Williams 1976**

- 1967c *Wetzeliella (Wetzeliella) echinosuturata* Wilson, p. 477-479, figs. 22-25, text-fig. 3a-b
- 1976 *Wilsonidium echinosuturatum* (Wilson 1967c, p. 477-479, figs. 3, 22-25) Lentin & Williams, p. 139
- 1984d *Wilsonidium echinosuturatum* (Wilson) Lentin & Williams; Wilson, p. 114, fig. 6 (6)
- ?1985 ?*Wilsonidium echinosuturatum* (Wilson 1967); De Coninck, p. 69, pl. 3, figs. 8-12

Original Description: Periphragm surface punctate, outline pentagonal; sides more or less straight, rarely concave. Margin adorned with prominent capitate or oblate processes (*l* = 3-10 µ). Right antapical horn invariably longer than left, although there is usually only a small difference, Ornament on periphragm comprised of very prominent ridges crested by oblate or capitate processes (*l* up to 16 µ). The ridges correspond to sutures and define a clear peridinioid tabulation.... Pericoel large. Capsule finely granular, usually more or less circular, occasionally sub-rhomboidal. Archeopyle when formed is rectangular and replaces 2a plate (Wilson 1967c, p. 477, 479; ellipses replace figure references in the original).

Distribution: Rare. Only a single, poor, specimen was encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Porangan	Waipawa, Hawkes Bay, New Zealand	N141/f1401	Wilson 1967c
middle Eocene	Sands of Ledé, Mol borehole, Belgium	-323.9m - prep. 5	De Coninck 1985

***Wilsonidium cf. echinosuturatum* (Wilson 1967c) Lentin & Williams 1976**

Pl. 26, figs. 4-6

- 1975 *Wetzeliella (Wetzeliella) echinosuturata* Wilson; Haskell & Wilson, pl. 1, fig. 2

Description of Study Material: Cysts of intermediate size, proximochorate, dorso-ventrally compressed, wetzelielloid, with one apical, two lateral, and one or two unequal antapical horns; episome and hyposome more or less equal in length. Apical horn moderately well-developed, apex more or less conical, episome more or less straight-sided; antapical horns well developed, relatively pointed. Cyst wall two-layered; circumcavate, lateral pericoels strongly developed. Archeopyle intercalary, type I (2a); quadra-style. Processes lacking; surface ornament present, non-tabular, comprising sparse granules. Crests sutural, margins of crests granulate. Tabulation clearly expressed, peridiniacean, inferred formula: 4', 3a, 7", Xc, 5", 0ps, 2"', 0s. Cingulum moderately expressed, indicated by shape of the periphragm; offset only slightly.

Size Range: Length including any processes = 94 (94) 95 µm (2 measurements). Width including any processes = 92 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985

Remarks: This taxon is very similar to *Wilsonidium echinosuturatum*, but differs in having more rounded/subdued margins to the sutural crests.

***Wilsonidium lineidentatum* (Deflandre & Cookson 1955) Lentin & Williams 1976**

Pl. 26, figs. 7-9

- 1955 *Wetzeliella lineidentata* Deflandre & Cookson, p. 253-254, pl. 5, fig. 5, text-fig. 17-18

1976 *Wilsonidium lineidentatum* (Deflandre & Cookson 1955, p. 253-254, pl. 5, fig. 5; text-figs. 17-18) Lentin & Williams, p. 139

1984d *Wilsonidium lineidentatum* (Deflandre & Cookson) Lentin & Williams; Wilson, p. 114, fig. 6 (3)

Original Description: Cell encysted, compressed, nearly quadrangular with a toothed margin. Epitheca imperfectly preserved, probably triangular, opening apparently quadrangular; hypotheca with 2 short unequal horns. Membranes of cyst thick, roughened. Cell membrane with lines of numerous short, blunt teeth, in surface view relatively widely spaced both equatorially and so as to delimit roughly polygonal areas analogous to the plates characterizing the Peridinales (Cookson & Deflandre 1955, p. 253).

Size Range: Length including any processes = 135 µm (one measured specimen). Width including any processes = 95 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	North Otago, New Zealand	L9203/1	Wilson 1984d
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985

Remarks: Cookson 1956 (p. 186) indicates that this species was described a year earlier than is commonly supposed, in Deflandre & Cookson 1954.

Family Protoperidiniaceae Bujak & Davies 1983

Subfamily Protoperidinioideae Bujak & Davies 1983 [autonym]

Genus *Lejeunecysta* Artzner & Dörhöfer 1978

1961 *Lejeunia* Gerlach, p. 169

1972 *Lejeunia* Gerlach, 1961 emend. Kjellström, p. 467

1976 *Lejeunia* Gerlach, 1961, emend. Kjellström, 1972, emend. Lentin & Williams, p. 68-71

1978 *Lejeunecysta* Artzner & Dörhöfer, p. 1381

1978 *Lejeunia* Gerlach 1961 emended Lentin & Williams 1976; Stover & Evitt, p. 111-112

Type Species: *Lejeunecysta hyalina* (Gerlach 1961, p. 169-171, pl. 26, figs. 10-11) Artzner & Dörhöfer 1978, p. 1381 [Late Oligocene]

Original Description: Theca bilaterally symmetrical-pentagonal, with apical horn and two antapical horns; without tabulation. Course of transverse furrow spiral, longitudinal furrow suggested (translated from Gerlach 1961, p. 169, by Stover & Evitt 1978, p. 111).

Remarks: Gerlach's (1961) original name for this genus is a junior homonym of *Lejeunia* (later spelled *Lejeunea*) Libert 1820, a leafy liverwort (Hepaticae).

Lejeunecysta differs from *Phelodinium* in having an autophragm and convex rather than straight or slightly concave sides. In addition, the horns on most species of *Phelodinium* are considerably longer than those on *Lejeunecysta* (Stover & Evitt 1978, p. 112).

Stover & Evitt (1978, p. 112) further note that *Lejeunecysta* differs from *Morkallacysta* in having less well-developed apical and antapical horns. This doesn't seem a lot to go on; were it not for the uncertainty remaining about the exact form of the archeopyle in *Morkallacysta*, this distinction would probably not be worth maintaining. In view of this uncertainty, the assignment of additional species to the formerly monotypic *Morkallacysta* is unfortunate.

Lejeunecysta ?fallax (Morgenroth 1966b) Artzner & Dörhöfer 1978

Pl. 26, figs. 10-12

1966b *Lejeunia fallax* Morgenroth, p. 2-3, pl. 1, figs. 6-7

1978 *Lejeunecysta fallax* (Morgenroth 1966b, p. 2-3, pl. 1, figs. 6-7) Artzner & Dörhöfer, p. 1381

Original Description: [No translation available] [Diagnosis] Eine Art der Gattung *Lejeunia* mit glatter derber Membran. Anstelle einer Gürtelfurche ist nur ein ?zirkulär verlaufender Grat vorhanden.

[Description] Die im Vergleich zu anderen Arten der Gattung kräftige Kapselmembran ist glatt. Streifungen sind nicht vorhanden. Die kegelförmige Epithek gipfelt in ein deutlich zugespitztes Apikalhorn. Eine Gürtelfurche ist nicht vorhanden. An ihrer Stelle befindet sich ein einfacher scharfer Grat, der ±zirkulär verläuft. Ventral ist er durch eine angedeutete Längsfurche unterbrochen. Die hypothek zipfelt in 2 ungefähr gleich lange Antapikalhörner aus (Morgenroth 1966b, p. 3).

Description of Study Material: Cysts of intermediate size, proximate, dorso-ventrally compressed, pentagonal, with one apical and two antapical horns; episome and hyposome more or less equal in length. Apex pointed, episome more or less straight-sided; antapical horns 2 small, unequal horns developed, relatively pointed. Cyst wall single-layered. Archeopyle intercalary. Processes lacking; surface ornament present, non-tabular, comprising irregular, loose reticulum. Cingulum clearly expressed, indicated by folds in the autophragm; offset only slightly.

Size Range: Length including any processes = 72 µm (one measured specimen). Width including any processes = 69 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	

Order Gonyaulacales Taylor 1980

Peridiniophycideans with a tabulation which accords with, or clearly derives from, a pattern in which one or both of the following arrangements occur:

- the first apical plate is asymmetrical, its left lateral triple junction being higher (i.e. more anterior) than the right lateral triple junction;
- there are two to four fundital plates – always the posterior intercalary plate and first antapical plate (or their homologues), sometimes the posterior sulcal plate, and possibly in rare cases also the right sulcal plate or subdivisions of these plates.

Among the fundital plates, 1^{'''} is almost always larger and is in a clearly more dorsal position than the other(s).

Key to suborders (principally after Fensome et al. 1998):

1	Five or more climactal plates; three or more fundital plates	2
	Generally four or more climactal plates; two fundital plates; partiform hyposome	3
	Quinqueform hyposome	4
	Sexiform hyposome	5
2	Suborder Rhaetogonyaulacineae Norris 1978a – Gonyaulacaleans in which there are at least three fundital plates, of which the dorsal-most does not contact the distal-most postcingular plate. There are more than five climactal plates. Secondary plate overgrowth may occur on all plate margins except those adjacent to the cingulum.	
3	Subclass Cladopyxiineae Fensome et al. 1993b – Gonyaulacaleans in which the tabulation is partiform: that is, it accords with, or is derived from, a pattern in which the first antapical homologue (*1 ^{'''}) contacts the distal-most postcingular plate (*6 ^{'''}) and in which the posterior sulcal homologue (*ps) is within the sulcus and extends further to the anterior than the posterior intercalary homologue (*1p), thus contacting the first postcingular homologue (*1 ^{'''}).	
4	Goniodomineae Fensome et al. 1993b – Gonyaulacaleans with a tabulation which accords with, or derives from, a pattern in which there are two or three fundital plates – always the posterior intercalary homologue (*1p) and the first antapical homologue (*1 ^{'''}), and sometimes also the posterior sulcal homologue (*ps). The first antapical homologue (*1 ^{'''}) is the dorsal-most of the fundital plates, is five-sided (quinqueform) and does not contact the distal-most postcingular plate(s) – i.e. the sixth postcingular homologue (*6 ^{'''}) – and, when it is outside the sulcus, the right sulcal homologue (*rs). There are typically five or fewer climactal plates. Secondary plate overgrowth occurs only at overlapping plate margins.	
5	Lateral horn developed	6
	No lateral horn	7
6	Ceratiineae Fensome et al. 1993b – Gonyaulacaleans having at least three horns, of which one or two are formed by contributions from postcingular plates, and in which the first antapical plate (1 ^{'''}) contacts six or seven adjacent plates, including the distal-most postcingular plate.	

- 7 Gonyaulacineae Taylor 1980 [autonym] – Gonyaulacaleans in which the hyposomal tabulation is sexiform, i.e. in which the first antapical homologue (*1^{'''}) contacts the sixth postcingular homologue (*6^{'''}) and in which the posterior intercalary homologue (*1p) extends further to the anterior than the posterior sulcal homologue (*ps). Distinctive postcingular horns are absent.

Suborder Gonyaulacineae Taylor 1980 [autonym]

Gonyaulacaleans in which the hyposomal tabulation is sexiform, i.e. in which the first antapical plate contacts the sixth postcingular plate and in which the posterior intercalary plate extends further to the anterior than the posterior sulcal plate. Distinctive postcingular horns are absent.

Family Gonyaulacaceae Lindemann 1928

Gonyaulacineans in which the sulcus is more or less midventral and may be straight, oblique from upper right to lower left, or sigmoidal. The antapical outline is more or less symmetrical and strong dorsoventral compression is lacking. There are six precingular plates.

Subfamily Gonyaulacoideae Lindemann 1928 [autonym]

Genus *Spiniferites* Mantell 1850 emend. Sarjeant 1970

- 1850 *Spiniferites* Mantell, p. 191
1866 *Gonyaulax* Diesing, p. 305, 382
1953 *Hystrichokibotium* Klumpp, p. 387
1966 *Spiniferites* Mantell, 1850, p. 191; Loeblich Jr. & Loeblich III, p. 56-57
1970 *Spiniferites* Mantell, 1850, emend. Sarjeant, p. 75
1978 *Spiniferites* Mantell 1850 emended Sarjeant 1970; Stover & Evitt, p. 189-191

Type Species: Spiniferites ramosus (Ehrenberg 1838, pl. 1, figs. 1-2, 5) Mantell 1854, p. 239 [Late Cretaceous]

Original Description: Subspiral shells with spiny processes in the shape given as characteristic for the family, but without the threefold metamerism of the body and without a closed aliform lamella, an outer shell membrane, or an outer network (translated from O. Wetzel 1933b, p. 33, description for *Hystrichosphaera*, by Stover & Evitt 1978, 189).

Remarks: Loeblich Jr. & Loeblich III 1966 (p. 56-57) appears to be the earliest publication to legally designate *Spiniferites ramosus* as the type species of *Spiniferites*.

Fensome et al. 1993b, p. 93, considers *Spiniferites* to be the possible senior synonym to *Gonyaulax*.

The genus *Hystrichosphaera* is usually treated as a junior synonym of *Spiniferites*, at least since the mid-1960s (e.g. Sarjeant 1964a, p. 174; 1970, p. 74) although, to the best of my knowledge, the type species, *H. furcata*, has never been formally transferred into *Spiniferites*. According to Fensome & Williams 2004, p. 619, the combination "*Spiniferites furcatus*" made in Lentin & Williams 1973 (p. 128) is not validly published, because the combination was not intended by Lentin & Williams, who, following Davey & Williams 1966a, p. 29-33, considered *Hystrichosphaera furcata* to be a junior synonym of *Spiniferites ramosus*.

However, Ehrenberg's (1938) illustrations of the two forms which comprise the type species for *Hystrichosphaera* and *Spiniferites*, *Xanthidium furcatum* and *Xanthidium ramosum* respectively, look quite different to my eye: I don't think it is sufficient to simply pronounce the two synonymous because intermediates exist (Lejeune-Carpentier 1937) or because Ehrenberg's types of *Xanthidium furcatum* cannot be relocated, as advocated by Davey & Williams (1966a, p. 32).

It seems to me that a better solution, since Ehrenberg's type material for *Xanthidium furcatum* cannot be relocated, is simply to confine use of the *furcatum* epithet to the (lost) type material. By this means, the name *Hystrichosphaera*, while remaining validly published, also disappears from active use, other species of the genus already having been allocated elsewhere (e.g., see Lentin & Williams 1973, p. 126-131).

Some authors (e.g. Davey & Williams 1966a, Sarjeant 1970) have described *Spiniferites* as having processes which are sometimes (or "rarely" in Stover & Evitt 1978, p. 190) hollow and open distally. Hollow processes have not been observed in the present study material, however, and only forms with solid process are assigned to *Spiniferites* herein.

Achomosphaera is considered a junior synonym of *Spiniferites* in Duxbury 1983 (p. 54-55) but herein I follow Lentin & Williams 1989 (p. 3) and many subsequent authors who have retained *Achomosphaera*.

Hafniasphaera has also been considered a junior synonym of *Spiniferites* (Stover & Williams 1987, p. 117) but herein I follow Edwards 1996 (p. 989) and subsequent authors who have preferred to retain *Hafniasphaera*.

Spiniferites ramosus (Ehrenberg 1838) Mantell 1854

Pl. 27, figs. 1-6

- 1838 *Xanthidium?* *ramosum* Ehrenberg, pl. 1, fig. 15 [not 1, 2 and 5]
 1854 *Spiniferites ramosus* (Ehrenberg 1838, pl. 1, figs. 1-2, 5) Mantell, p. 239
 1937b *Hystrichosphaera ramosa* (Ehrenberg 1838, pl. 1, figs. 1-2, 5) Deflandre, p. 64
 1961 *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel 1933; Gerlach, p. 175-176, pl. 27, fig. 3

Original Description: [No textual description provided.]

Size Range: Length excluding any processes = 36 (52) 62 µm (4 measurements). Width excluding any processes = 37 (46) 57 µm (4 measurements). Length including any processes = 55 (78) 105 µm (18 measurements). Width including any processes = 56 (80) 97 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/30	Gerlach 1961
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan 1996
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f169 (L11918)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f259 (L13545)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f262 (L13546)	
?Kaiatan-Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	

Remarks: Most commentators have unwittingly perpetuated the erroneous citation from Davey & Williams 1966a, p. 33, which lists *Xanthidium ramosum* as appearing in figures 1, 2 and 5 of plate 1 from Ehrenberg 1838. In fact, it appears in fig. 15 only.

Spiniferites furcatus (as *Xanthidium furcatum*) also appears in Ehrenberg's plate 1 (figs. 12 and 14). As noted above, the illustrations of the two taxa are noticeably different, and the reasons usually cited to support synonymy (the existence of intermediates and loss of the type material for *Spiniferites furcatus*) do not convince me. If the two are indeed synonyms, however, no particular priority attaches to the earlier-appearing name in the publication: both names have the same publication date (implied, e.g. by Recommendation 30A.1, Voss et al. 1983, p. 30).

There appears to be an earlier mention, also, in *Mittheilungen aus den Verhandlungen der Gesellschaft naturforschender Freunde zu Berlin, Viertes Quartal 1836*, published in 1837 according to the cover page, in which *Xanthidium furcatum*, *X. ramosum* (p. 47), *Peridinium pyrophorum* and *P. delitiense* (p. 48) are all

mentioned. The phrase “sie läßt sich mit dem Namen *X. ramosum* bezeichnen” (p. 47) may be significant (bezeichnen means “to define” or “designate”).

Spiniferites gracilis (Davey & Williams 1966a) n. stat.

Pl. 27, figs. 7-9

- 1966a *Hystrichosphaera ramosa* var. *gracilis* Davey & Williams, p. 34-35, pl. 1, fig. 5; pl. 5, fig. 6
 1973 *Spiniferites ramosus* var. *gracilis* (Davey & Williams 1966a, p. 34-35, pl. 1, fig. 5; pl. 5, fig. 6) Corradini, p. 165
 1973 *Spiniferites ramosus* ssp. *gracilis* (Davey & Williams 1966a, p. 34-35, pl. 1, fig. 5; pl. 5, fig. 6) Lentin & Williams, p. 130

Original Description: A variety of *H. ramosa* (Ehrenberg) with smooth, thin-walled central body bearing gonial and sutural processes. Processes solid or hollow and relatively long and slender. Crests proximal and extending along all processes often as far as the trifurcation. Gonial processes mainly trifurcate, sutural processes bifurcate, all but smallest terminating with a small trifurcation (Davey & Williams 1966a, p. 34).

Size Range: Length excluding any processes = 25 (28) 32 µm (2 measurements). Width excluding any processes = 24 (26) 28 µm (2 measurements). Length including any processes = 45 (61) 72 µm (12 measurements). Width including any processes = 43 (54) 60 µm (4 measurements).

Distribution: Common, over a lengthy stratigraphic range.

Age/Stage	Location	Sample	Sample Reference
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan 1996
?Kaiatan-Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: As noted in the introduction, the subspecies concept has not been found to be useful in this study. In a biological sense, the distinction between species and subspecies (reproductive isolation) has dubious applicability to asexual organisms, or to any fossils, and *S. gracilis* is no more or less similar to *S. ramosus* than some other full species.

Spiniferites aff. mirabilis (Rossignol 1964) Sarjeant 1970

Pl. 27, figs. 10-12

- 1964 *Hystrichosphaera mirabilis* Rossignol, p. 86-87, pl. 2, figs. 1-3; pl. 3, figs. 4-5
 1970 *Spiniferites mirabilis* (Rossignol 1964, p. 86-87, pl. 2, figs. 1-3; pl. 3, figs. 4-5) Sarjeant, p. 76

Original Description: Large ovoid *Hystrichosphaera* with scarcely visible tabulation. Trifurcated processes at the junctions of three plates and bifurcated intercalary processes along the sutures, each branch finely bifurcated. At the antapical pole the processes of the antapical plate are embedded in a large common sheet until bi- or trifurcation occurs; the combined appearance is that of a fan (Rossignol 1964, p. 87).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type). Surface ornament lacking. Processes gonial + intergonial; non-fibrous, solid; proximally connected by sutural septa proximally, trifurcate distally; the antapical process broadly expanded, with several distal trifurcating points. Tabulation clearly expressed, gonyaulacacean, inferred formula: 3 to 4', 0a, 5-6", 6c, 5-6"', 1ps, 1"', Xs; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 46 µm (one measured specimen). Width excluding any processes = 44 µm (one measured specimen). Length including any processes = 91 µm (one measured specimen). Width including any processes = 79 µm (one measured specimen).

Distribution: Rare. The published range for *Spiniferites mirabilis*, s.s., is at least Aquitanian to Recent. If the present taxon were recognised as indeed belonging to *Spiniferites mirabilis*, it might represent a significant backward extension of this range.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

Remarks: The New Zealand forms seem to be somewhat less densely ornamented than the type material, and the sutural septa are poorly developed (recalling *Achomosphaera* as much as *Spiniferites*) but is otherwise very similar.

Genus *Achomosphaera* Evitt 1963a

1963a *Achomosphaera* Evitt, p. 163

1978 *Achomosphaera* Evitt 1963; Stover & Evitt, p. 138-139

Type Species: *Achomosphaera ramulifera* (Deflandre 1937b, p. 74, pl. 14, figs. 5-6, pl. 17, fig. 10) Evitt 1963, p. 163 [Late Cretaceous]

Original Description: Test consists of a spherical to ellipsoidal central body with precingular archeopyle and furcate, spinelike processes like those on *Hystrichosphaera* in both structure and distribution, but without sutural ridges or septa connecting their bases as in that genus. Tips of processes not interconnected. Wall two-layered; layers typically in close contact between bases of processes (Evitt 1963, p. 163).

Remarks: *Achomosphaera* was considered a junior synonym of *Spiniferites* by Duxbury 1983 (p. 54-55). However, beginning with Lentin & Williams 1989 (p. 3), many subsequent authors have preferred to retain *Achomosphaera*. The difference, perhaps best articulated by Stover & Evitt (1978, Appendix I, p. 283-284), is simply whether the gonal process bases are proximally linked by sutural features (*Spiniferites*) or not (*Achomosphaera*).

Whether two genera are maintained separately as a matter of convenience, or not, it seems inescapable that many of the species are closely related and some may even represent ecological variations of one another. Without a great deal of further analysis, the phylogenetic meaning of the *Achomosphaera* genus concept seems destined to remain unknown.

Achomosphaera ?alcicornu (Eisenack 1954b) Davey & Williams 1966a

Pl. 28, figs. 1-6

1954b *Hystrichosphaeridium alcicornu* Eisenack, p. 65-66, pl. 10, figs. 1-2, text-fig. 5

?1959 *Galea lychnea* Maier, p. 310, pl. 30, fig. 6

?1959 *Hystrichosphaeridium leptodermum* Maier, p. 321-322, pl. 33, figs. 5-6

1961 *Hystrichosphaeridium alcicornu* Eisenack 1954; Gerlach, p. 188-189, pl. 28, fig. 7

1965 *Hystrichosphaeridium alcicornu* Eisenack 1954; De Coninck, p. 26-27, pl. 6, figs. 9, 11

1966a *Achomosphaera alcicornu* (Eisenack) Davey & Williams, p. 50, pl. 5, fig. 3

1994 *Achomosphaera alcicornu* (Eisenack 1954) Davey and Williams *in* Davey *et al.* 1966; Stover & Hardenbol, p. 32, pl. 5, fig. 28

2005 *Achomosphaera alcicornu*; Schiøler, pl. 16, fig. 11

Original Description: [No translation available] Zentralkörper kugelförmig bis schwach oval, mit zahlreichen hohlen Anhängen versehen, die am Ende trichterartig erweitert sind. Diese Erweiterungen laufen in meist 3, gelegentlich weiter unterteilte Spitzen aus, die bogig verbunden sind, so daß eine entfernte Ähnlichkeit mit einer Elchschaufel entsteht ... (Eisenack 1954b, p. 65; ellipses replace figure references in the original).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type). Surface ornament lacking. Processes gonal; non-fibrous, branching, solid; not connected proximally, trifurcate distally. Tabulation weakly expressed by gonal processes, apparently gonyaulacacean. Sulcus indicated by a series of differentiated processes.

Size Range: Length excluding any processes = 45 (48) 50 µm (2 measurements). Width excluding any processes = 40 µm (one measured specimen). Length including any processes = 78 (86) 95 µm (2 measurements). Width including any processes = 75 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/44	Gerlach 1961

Age/Stage	Location	Sample	Sample Reference
middle Oligocene	north west Germany	Pr 1170/44	Davey & Williams 1966a
early Oligocene	Samland, Germany	Ph 4	Eisenack 1954b
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996
Ypresian	Merebeke, Belgium	Preparation 30	De Coninck 1965

Remarks: The forms encountered in the study were generally poor and seem to be at least somewhat transitional with *Achomosphaera ramulifera*.

Genus *Hafniasphaera* Hansen 1977

- 1977 *Hafniasphaera* Hansen, p. 13-14
 1982 *Rivernookia* Cookson & Eisenack, p. 56
 1987 *Hafniasphaera* Hansen 1977, p. 13; Stover & Williams, p. 117

Type Species: *Hafniasphaera hyalospinosa* Hansen 1977, p. 14, figs. 7-8, 18A [Paleocene (Danian)]

Original Description: Chorate cysts with a subspherical or ovoid central body composed of two layers, endophragm and periphragm. One or both of these layers contain numerous evenly distributed vesicles (vacuoles). The vesicles are spherical or, if interconnected, they may form a fine reticulum internal in the cyst wall. Processes intertabular [sic], formed by the periphragm, with or without vesicles, solid or hollow, closed or open distally. Simple processes trifurcate (gonal processes) or bifurcate (sutural processes). Composite processes ramifying in more complex ways. Tips of furcae bifid. Archeopyle type P, formed by loss of paraplate 3". Operculum becomes typically completely detached.

Paratabulation indicated by presence of sutural crests, weak bulges of the periphragm, by alignment of the vesicles, or by the arrangement of the processes only. Paratabulation of the plates 1'-3' (4'), 1"-6", 1c-6c, (1''') 2'''-6''', (ps), (1p), 1'''''. Paraplate 6" is triangular, 1''' very little if not absent. If present, paraplate 4' is situated between 1" and 5", above 6" and parasulcus. Suture between 3''' and 4''' is situated a little to the left of suture between 2" and 3", whereas suture between 4''' and 5''' is aligned with or slightly to the right of suture between 3" and 4". Paracingulum disposed in a laevorotary spiral (Hansen 1977, p. 13).

Remarks: Considered a junior synonym of *Spiniferites*, according to Stover & Williams (1987, p.117). Here, however, I have followed Edwards (1996, p.989) in retaining *Hafniasphaera*. The featureless, hyaline wall typical of most *Spiniferites* species, and the type species, *Spiniferites ramosus*, in particular, shows no signs of the "numerous evenly distributed vesicles" described by Hansen for *Hafniasphaera*, and nor does the type species of *Hafniasphaera*, *H. hyalospinosa*, at all resemble a typical species of *Spiniferites*.

***Hafniasphaera ?septata* (Cookson & Eisenack 1967b) Hansen 1977**

Pl. 28, figs. 7-9

- 1967b *Baltisphaeridium septatum* Cookson & Eisenack, p. 253-254, pl. 42, figs. 6-10, text-fig. 1
 1971 *Spiniferites septatus* (Cookson & Eisenack 1967b) McLean, p. 730, pl. 88, figs. 1-9
 1971 *Spiniferites septatus* (Cookson & Eisenack 1967b, p. 253-254, pl. 42, figs. 6-10; text-fig. 1) McLean, p. 730
 1977 *Hafniasphaera septata* (Cookson & Eisenack 1967b, p. 253-254, pl. 42, figs. 6-10; text-fig. 1) Hansen, p. 18
 1978 *Achomosphaera septata* (Cookson & Eisenack 1967b) Stover & Evitt, p. 139
 1982 *Rivernookia septata* (Cookson & Eisenack 1967) Cookson & Eisenack, p. 56
 1996 *Hafniasphaera septata*; Edwards, p. 993, pl. 1, figs. 2-3, text-fig. 12

Original Description: Shell spherical, thin-walled with a closely and rather coarsely, apparently granular surface and a variable number of radially arranged appendages which approximate in length to the radius of the shell. A 'marginal zone' often present, giving the impression that the shell is thick-walled, is, in fact, due to compression.

The appendages vary in size, shape and structure. The majority narrow somewhat from a broadened base and divide distally into two or three straight or curved tapering branches with closed, pointed or minutely bifurcate tips. The larger appendages are typically hollow and septate throughout ...; in the finer to thread-like ones, on the contrary ... the degree of septation is often difficult to determine and their distal portions, at least, appear be

solid. A few of the appendages are unbranched. A pylome has been seen in a few specimens ... (Cookson & Eisenack 1967b, p. 253-254; ellipses replace figure references in the original).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate; thin, about 1 µm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free. Surface ornament present, non-tabular, comprising granules; very low (about 1 µm or lower). Processes vacuolate, branching, solid; usually connected proximally, irregularly trifurcate distally. Tabulation weakly expressed, apparently gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 6"', 1ps, 1''', Xs; hyposome sexiform. Cingulum moderately expressed, indicated by surface ornament, about 6 µm wide. Sulcus weakly expressed, indicated by surface ornament.

Size Range: Length excluding any processes = 44 µm (one measured specimen). Width excluding any processes = 40 µm (one measured specimen). Length including any processes = 70 µm (one measured specimen). Width including any processes = 62 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan 1996
Porangan early Eocene	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	Edwards 1996
late Paleocene	Aquia Formation, Virginia-Maryland coastal plain, USA	SUPTC 10050-10051	McLean 1971

Genus *Hystrichostrogylon* Agelopoulos 1964 emend. Stover & Evitt 1978

1964 *Hystrichostrogylon* Agelopoulos, p. 673-674

1978 *Hystrichostrogylon* Agelopoulos 1964 emend. Stover & Evitt, p. 164-165

Type Species: *Hystrichostrogylon membraniphorum* Agelopoulos 1964, p. 674; text-figs. 1-2 [Late Eocene]

Original Description: Central shell spherical to oval, apparently slightly flattened, provided with forked spines, and enclosed by a delicate, transparent, only antapical developed, somewhat concentric outer shell that lies close to the inner shell ventrally and dorsally. Slender, long, hollow processes occur in the region of the apex which is indicated by a pylome, whereas wide, broad-surfaced processes are confined to the region of the antapex and therefore to the outer shell. The central shell within the outer shell possesses no processes (translated from Agelopoulos 1964, p. 673-674, by Stover & Evitt 1978, p. 164).

Emended Description of Stover & Evitt 1978: **Shape.** Endocyst subspherical; outline of periphragm varies in size and shape, consistent with degree of separation between endophragm and periphragm. **Wall Relationships.** Cysts camocavate; periphragm and endophragm always appressed dorsally, narrowly to widely separated elsewhere; size and shape of pericoel vary. **Wail Features.** Faint parasutural lines or ridges may be present on periphragm. Gonol and intergonal processes typically furcate, tips not interconnected; process shafts normally long where pericoel is least developed or not at all, short where pericoel is most developed. Endophragm and periphragm smooth or faintly ornamented. **Paratabulation.** Indicated by processes and additionally by faint parasutural lines or ridges; gonyaulacacean, formula: 3-4', 6", 6c, 5-6"', 0-1p, 1'''; rarely expressed completely. **Archeopyle.** Precingular, Type P (3" only); operculum free. **Paracingulum.** Position indicated by locations of processes and, additionally, by faint parasutural lines or ridges. **Parasulcus.** Not indicated, or outlined by parasutural features. **Size.** Intermediate (Stover & Evitt 1978, p. 164).

***Hystrichostrogylon membraniphorum* Agelopoulos 1964**

Pl. 28, figs. 10-12

1964 *Hystrichostrogylon membraniphorum* Agelopoulos, p. 674, text-fig. 1-Feb

1967 *Hystrichostrogylon membraniphorum* Agelopoulos 1964; Agelopoulos, p. 43, pl. 9, figs. 7-8, pl. 12, figs. 1-2, pl. 13, fig. 8

1976 *Achomosphaera membraniphora* (Agelopoulos 1964) Eaton, p. 237-238, pl. 1, figs. 8-10, text-fig. 5

1978 *Hystrichostrogylon membraniphorum* Agelopoulos 1964; Stover & Evitt, p. 165

1984b *Hystrichostrogylon membraniphorum* Agelopoulos, 1964; Helenes, p. 94, 104, pl. 5, figs. 13-14

2005 *Hystrichostrogylon membraniphorum*; Schiøler, pl. 1, fig. 12

Original Description: [As for the genus.] Central shell spherical to oval, apparently slightly flattened, provided with forked spines, and enclosed by a delicate, transparent, only antapical developed, somewhat concentric outer shell that lies close to the inner shell ventrally and dorsally. Slender, long, hollow processes occur in the region of the apex which is indicated by a pylome, whereas wide, broad-surfaced processes are confined to the region of the antapex and therefore to the outer shell. The central shell within the outer shell possesses no processes (translated from Agelopoulos 1964, p. 673-674, by Stover & Evitt 1978, p. 164).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; camocavate, with the characteristic ventral pericoel well-developed. Archeopyle precingular, type P (3"); pentagonal (standard Gonyaulax-type); operculum free. Surface ornament lacking. Non-fibrous, solid; proximally connected by sutural septa proximally, trifurcate distally. Gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 5-6"', 0 to 1ps, 1"', Xs; ventral organisation S-type; hyposome sexiform. Cingulum indicated by sutural septa, clearly expressed. Sulcus indicated by sutural septa, clearly expressed.

Size Range: Length excluding any processes = 57 (68) 88 µm (4 measurements). Width excluding any processes = 43 (50) 60 µm (4 measurements). Length including any processes = 72 (89) 122 µm (9 measurements). Width including any processes = 67 (87) 110 µm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
late Eocene	Kieselton von Heiligenhafen, Holstein	Prb. 23, nr. 258	Agelopoulos 1967
Kaiaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
middle Eocene-late Eocene	Bracklesham Beds, Isle of Wight, southern England	V57764-57797	Eaton 1976
Lutetian	Bateque Formation; Sebastian Vizcaino Basin, Baja California		Helenes 1984b

Genus *Nematosphaeropsis* Deflandre & Cookson 1955 emend. Wrenn 1988

1905 *Pterococcus* Lohmann, p. 47

1955 *Nematosphaeropsis* Deflandre & Cookson, p. 268

1966c *Nematosphaeropsis* Deflandre & Cookson 1955 [emend.] Williams & Downie, p. 222

1970 *Coccopterum* Silva, p. 942

1978 *Nematosphaeropsis* Deflandre & Cookson 1955 emended Williams & Downie in Davey *et al.* 1966; Stover & Evitt, p. 176

?1980 *Trabeculidium* Duxbury, p. 132-133

1988 *Nematosphaeropsis* Deflandre & Cookson 1955 emend. Wrenn, p. 137, 139

Type Species: *Nematosphaeropsis balcombiana* Deflandre & Cookson 1955, p. 268-269, pl. 8, fig. 5 [Middle Miocene]

Original Description: Shell globular, divided into fields by ridges, an equatorial series developed as in *Hystriochosphaera*. Branches of processes joined to one another by trabeculae or filaments as in the genus *Cannosphaeropsis* (Deflandre & Cookson, p. 268).

Remarks: The extant genera *Pterococcus* Lohmann 1905 (an illegitimate name) and *Coccopterum* Silva 1970, are treated as junior synonyms of *Nematosphaeropsis* by Reid 1974 (p. 592) and Fensome *et al.* 1993b (p. 93).

Stover & Williams (1987, p. 217) further regarded *Trabeculidium* Duxbury 1980 as a junior synonym, because they "could find no fundamental difference" between the description of *Trabeculidium* and *Nematosphaeropsis* as emended by Williams & Downie 1966c (p. 222). Subsequently, Sarjeant (1989, p. 93) retained *Trabeculidium*. In this matter I am inclined to side with Sarjeant: my own view is that it requires more persuasive evidence than failing to find a "fundamental" difference between two authors' circumscriptions to motivate synonymy between genera whose type species are separated in time by the best part of 100 million years.

Ectosphaeropsis differs in possessing an ectophragm supported on the trabeculae (Londeix & Jan du Chêne 1988, p. 252).

***Nematosphaeropsis balcombiana* Deflandre & Cookson 1955**

Pl. 29, figs. 1-6

1955 *Nematosphaeropsis balcombiana* Deflandre & Cookson, p. 268-269, pl. 8, fig. 5

1984 *Nematosphaeropsis balcombiana* Deflandre & Cookson 1955; Clowes & Morgans, pl. 2, fig. 12

1988 *Nematosphaeropsis balcombiana* Deflandre & Cookson 1955; Wrenn, p. 139-140, pl. 7, fig. 3

Original Description: Characters of the genus: shell slightly elliptical, with numerous processes of which the longest approaches half the diameter of the shell. Processes trifurcate, the extremities of the 3 branches joined to neighbouring processes by delicate filaments (Deflandre & Cookson 1955, p. 268).

Description of Study Material: Cysts small, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3^{''}); operculum free. Surface ornament lacking. Processes arising in gonal and intergonal positions; non-fibrous, solid; connected proximally by sutural septa, connected by well developed trabeculae distally. Tabulation clearly expressed, gonyaulaccean, inferred formula: 3 to 4', 0a, 5-6'', 6c, 5-6''', 1ps, 1''''', Xs; ventral organisation S-type; hyposome sexiform; torsion neutral. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length excluding processes = 22 (24) 27 μ m (2 measurements). Width excluding processes = 22 (22) 22 μ m (2 measurements). Length including processes = 32 (39) 47 μ m (18 measurements). Width including processes = 40 (43) 45 μ m (3 measurements).

Distribution: Generally uncommon, though it can be locally abundant in individual samples. The exact range in New Zealand requires more research, especially the upper boundary: I am not aware of any data to suggest that it doesn't extend well beyond the occurrences documented herein.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f172 (L11921)	
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f170 (L11919)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: *N. balcombiana* is treated as a junior synonym to *N. labyrinthus* (Ostenfeld 1903) by Reid 1974 (p. 592). However, as subsequently noted (see, for example, the discussion in Head & Wrenn 1992b, p. 10-18), *N. labyrinthus* is a highly problematic taxon and considerable uncertainty surrounds its application to extant cysts from the North Atlantic type area, let alone fossils from half a world away. Herein, I prefer to follow (e.g.) Wrenn 1988, p. 139, in retaining *N. balcombiana* (though not, obviously, his further recommendation that the name be restricted to the holotype, p. 129).

Nor can I discern in the original images (Deflandre & Cookson 1955, pl. 8, fig. 5) the "very broad-based, proximally branched processes" noted by Wrenn (1988, p. 136), at least not to the extent depicted by him (pl. 7, fig. 3). The proximal process attachments of the forms assigned herein to *N. balcombiana* are essentially typical of most any species of *Spiniferites* or *Achomosphaera*.

Genus *Rottnestia* Cookson & Eisenack 1961b

1961b *Rottnestia* Cookson & Eisenack, p. 40, 42

1978 *Rottnestia* Cookson & Eisenack 1961b; Stover & Evitt, p. 185

Type Species: *Rottnestia borussica* (Eisenack 1954b, p. 62, pl. 9, figs. 5-7) Cookson & Eisenack 1961b, p. 42 [Early Oligocene]

Original Description: The shells consist, like those of a number of fossil dinoflagellates, of an internal body and a thin outer membrane. The internal body is clearly defined and oval in shape. The outer membrane is in contact with the internal body in the central region but extends beyond it both apically and antapically. The apical expansion is surmounted by a median conical or cylindrical horn; the antapical expansion is squarish in shape with sharp or rounded angles. The shell is crossed by a median helicoid girdle and a relatively broad longitudinal furrow runs obliquely across the ventral surface. The surface of the outer membrane is divided into pre- and post-

equatorial fields the limits of which run into the edges supporting the apical and antapical expansions. Forked appendages may or may not be developed at the corners of the fields. A large elongate-trapezoid pylome develops on the dorsal side of the epitheca in both the internal body and outer membrane (Cookson & Eisenack 1961b, p. 40, 42).

Remarks: The appendages of the type species, *R. borussica*, described as “forked” in the original description (Eisenack 1954b, p. 62), are depicted in text-fig. 1c, and especially 1d, as trifurcate, suggesting a possible affinity with *Spiniferites*.

The genus *Hystrichosphaeropsis* Deflandre 1935 also exhibits this general range of morphologies, having an apical horn but lacking or having only weakly developed gonal processes. However, in some specimens of *R. borussica* the gonal spines are absent, or almost, which compromises the distinction: the morphological ranges of *Hystrichosphaeropsis ovum* and *R. borussica* appear to overlap. Notwithstanding that, their stratigraphic ranges are quite different (Senonian versus Eocene), which militates very strongly against any idea of synonymy.

A re-examination of the original (or fresh topotype) material seems to be indicated. If found to be synonyms, *Hystrichosphaeropsis* is senior.

***Rottnestia borussica* (Eisenack 1954b) Cookson & Eisenack 1961b**

Pl. 29, figs. 7-12

- 1954b *Hystrichosphaera borussica* Eisenack, p. 62, pl. 9, figs. 5-7
 ?1961 *Hystrichosphaera ovum* Deflandre 1937; Gerlach, p. 176-177, pl. 27, fig. 4
 1961b *Rottnestia borussica* (Eisenack 1954b, p. 62, pl. 9, figs. 5-7) Cookson & Eisenack, p. 42, pl. 1, figs. 8-10
 1965 *Rottnestia borussica* (Eisenack) Cookson et Eisenack 1961; De Coninck, p. 19-20, pl. 3, fig. 9
 1966a *Triblastula borussica* (Eisenack 1954b, p. 62, pl. 9, figs. 5-7) Morgenroth, p. 15-16, pl. 7, figs. 9-10
 1966b *Hystrichosphaeropsis borussica* (Eisenack 1954b, p. 62, pl. 9, figs. 5-7) Sarjeant, p. 139
 1967 *Rottnestia borussica* (Eisenack 1954); Agelopoulos, p. 24-25, pl. 7, figs. 2-4
 1969a *Rottnestia borussica* (Eisenack 1954) Cookson & Eisenack 1961; Eisenack, p. 105-108
 1986a *Rottnestia borussica* (Eisenack 1954) Cookson & Eisenack 1961; Jan du Chêne et al., p. 309

Original Description: The central body is oval, tabulated similarly to *H. speciosa* Defl. or *H. wetzeli* Defl., the lower pole is furnished with an extended system of membranous ridges that extends as far as the equatorial zone; however, in contrast to *H. wetzeli*, an upper pole is generally not present (Eisenack 1954b, p. 63).

Size Range: Length excluding any processes = 88 µm (one measured specimen). Width excluding any processes = 45 µm (one measured specimen). Length including any processes = 90 µm (one measured specimen). Width including any processes = 54 µm (one measured specimen).

Distribution: Very rare.

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/31	Gerlach 1961
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: Cookson & Eisenack 1961b (p. 42 and in the caption to text-fig. 1) allude to variation which they consider to lie within their concept of *Rottnestia borussica*, embracing forms both with gonal processes and without, and both with an apical horn and without. This view seems at odds with modern fossil dinoflagellate taxonomic practice, at the species level, and, in particular, it is unlikely that the form illustrated in Cookson & Eisenack 1961b, text-fig. 1a-b, would ordinarily be considered conspecific with that of text-fig. 1c-d.

Intermediate forms may have been present, though there is no explicit comment to this effect. Even if true, as noted elsewhere herein, the presence of intermediates does not necessarily imply conspecificity. There appear to be two distinct forms – or end-members – represented:

- The first is illustrated in Cookson & Eisenack 1961b, pl. 1, figs. 8-10, and text-fig. 1c-d. This form possesses an apical horn and trifurcating gonal processes, and appears most like the original German type material. The specimen photographed for pl. 1, fig. 8 is “one of the original specimens from the Amber Formation, East Prussia” although those of pl. 1 figs. 9-10 are from the Rottnest Bore and similarly ornamented. The few specimens encountered in the present study (see Pl. 29, figs. 7-12), are of this type.
- The second is illustrated in Cookson & Eisenack 1961b, pl. 2, figs. 1-2, and text-fig. 1a-b. This form lacks an apical horn, possessing instead a convex though more or less smooth apical profile, and lacks gonal

processes although the periphragm does appear to “peak” into sharp points at the gonal positions and one, at the left hand side of pl. 2, fig. 1, appears to be minutely ornamented (or it may be birefringence). This form has not been observed in the present study.

Genus *Cannosphaeropsis* O. Wetzel 1933b

1933b *Cannosphaeropsis* O. Wetzel

1978 *Cannosphaeropsis* O. Wetzel 1933b emended Williams & Downie in Davey *et al.* 1966; Stover & Evitt, p. 143-144

Type Species: Cannosphaeropsis utinensis O. Wetzel 1933b, p. 6, pl. 3, figs. 9-17, text-fig. 12 [Cretaceous (Senonian)]

Original Description: Similar to the radiolarian *Cannosphaera*, from which it differs (also from *Coelacantha*) externally by the lack of a true pylome, by the number and arrangement of radial rods, as well as by the construction of the meshwork (translation from O. Wetzel 1933b, p. 6, by Stover & Evitt 1978, p. 143).

?*Cannosphaeropsis* sp. 1

Pl. 30, figs. 1-3

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); operculum free. Surface ornament lacking. Processes gonal; non-fibrous, solid; connected proximally by sutural septa, and distally by well developed trabeculae. Tabulation clearly expressed, gonyaulacacean, inferred formula: ?4', 0a, ?6", ?6c, ?5"', 1ps, 1"', Xs; ventral organisation S-type; hyposome sexiform; torsion neutral. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 38 µm (one measured specimen). Width excluding any processes = 28 µm (one measured specimen). Length including any processes = 59 µm (one measured specimen). Width including any processes = 53 µm (one measured specimen).

Distribution: Extremely rare. Only a single specimen has been encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: The specimen is very faint (having taken up no stain) but otherwise looks perfect. It is fully inflated (3-dimensional) rather than flattened. Although it may be reworked, there is no physical evidence to indicate that is the case.

Genus *Corrudinium* Stover & Evitt 1978

1978 *Corrudinium* Stover & Evitt, p. 148-149

1993b *Corrudinium* Stover & Evitt 1978; Fensome *et al.*, p. 92

2004 *Corrudinium* Stover & Evitt, 1978, p. 148-149; Fensome & Williams, p. 159

2006 *Corrudinium* Stover & Evitt 1978; Clowes & Wilson, p. 400-401

Type Species: Corrudinium incompositum (Drugg 1970b, p. 810-811, figs. 1E-O, 2A) Stover & Evitt 1978, p. 149 [Oligocene]

Original Description: Cysts proximate to proximochorate, subspherical, and without an apical horn or protrusion; paratabulation gonyaulacacean, indicated by parasutural ridges or septa; the accessory ridges or septa present on most paraplates tend to obscure paratabulation; archeopyle precingular, Type P (Stover & Evitt 1978, p. 148).

Remarks: *Corrudinium* was separated from *Impagidinium* and *Leptodinium* in a revision of the latter by Stover & Evitt (1978) on the basis of possessing accessory ridges or septa.

More significantly, as we now know, *Corrudinium* is distinguished from *Leptodinium* by the possession of a S-type ventral topology: *Leptodinium* and its allies have L-type ventral topology.

Impagidinium and *Corrudinium* share the S-type ventral topology common to the Gonyaulacoideae. *Corrudinium* differs consistently only in the possession of accessory ridges or septa. *Impagidinium* species may sometimes also exhibit a more prolate shape than *Corrudinium*. However, few would regard these features alone as defining anything more than a grouping of convenience for forms having a gross morphological similarity, but no seriously

implied phylogenetic relationship; it seems likely there is considerably more work still to be completed before the phylogeny of these groups is in any way settled.

Ochetodinium Damassa 1979a is also broadly similar in outward appearance to some species of *Corrudinium*, especially *Corrudinium otagoense*, but can be readily distinguished by its characteristically perforate sutural ridges.

Corrudinium has been widely reported, both geographically and stratigraphically. However, I am of the view that the phylogenetically related "core" of species are confined to the Eocene and early Oligocene, or not much beyond it. A range chart for New Zealand occurrences of *Corrudinium* is provided in Appendix 2, chart 2.

Key to selected species:

0.	Septa very high (~8 µm high)....	1.
	Septa prominent (~6 µm high)....	2.
	Septa generally very low (<< 5 µm)	3.
1.	<i>Corrudinium otagoense</i>	
2.	Sutural septa consistently higher than intratabular septa	2.1.
2.	Sutural and intratabular septa of approximately similar height	2.2.
2.1.	<i>Corrudinium eyrense</i>	
2.2.	<i>Corrudinium obscurum</i>	
3.	Surface ornament vermiculate; no evidence of tabulation	3.1.
	Surface ornament includes low sutural septa, indicating a gonyaulaccean tabulation	3.2.
3.1	? <i>Corrudinium vermiculatum</i>	
3.2.	Cysts small (< ~50 µm); thin-walled and frequently deformed	3.2.1.
3.2.	Cysts small (< ~40 µm); walls relatively robust	3.2.2.
3.2.	Cysts larger (~50 µm and greater); walls relatively robust	3.2.3.
3.2.1.	<i>Corrudinium incompositum</i>	
3.2.2.	<i>Corrudinium bujackii</i>	
3.2.3.	<i>Corrudinium regulare</i>	

***Corrudinium incompositum* (Drugg 1970b) Stover & Evitt 1978**

Pl. 30, figs. 4-6

- 1970b *Gonyaulacysta incomposita* Drugg, p. 810-811, fig. 1E-O, 2A
- 1973 *Leptodinium incompositum* (Drugg 1970) Lentin & Williams, p. 87
- 1978 *Corrudinium incompositum* (Drugg 1970) Stover & Evitt, p. 148-149
- 1980 *Corrudinium incompositum* (Drugg 1970) L.E. Stover, W.R. Evitt 1978; Châteauneuf, p. 135, pl. 21, figs. 5-6
- 1983 *Corrudinium incompositum* (Drugg, 1970) Stover and Evitt, 1978; Goodman & Ford, p. 865, pl. 5, figs. 1-2
- 1992 *Corrudinium incompositum* (Drugg) Stover and Evitt, 1978; Brinkhuis, pl. 2, figs. 11-12
- 1993 *Corrudinium incompositum* (Drugg) Stover and Evitt, 1978; Brinkhuis & Biffi, p. 173, pl. 2, figs. 11-12
- 1994 *Corrudinium incompositum* (Drugg 1970) Stover and Evitt 1978; Stover & Hardenbol, p. 32
- ?2003 *Corrudinium incompositum*; Brinkhuis, Munsterman, et al., p. 22
- ?2003 *Corrudinium incompositum*; Brinkhuis, Sengers, et al., fig. 155
- 2006 *Corrudinium incompositum* (Drugg 1970) Stover & Evitt 1978; Clowes & Wilson, p. 401, fig. 3A-F

Original Description: Tract small, ovoidal to spherical in shape. The tabulation ... is 3', 6", 6-7c, 6"', 1 p. pl, 1p, 1'''. The archeopyle is formed by the loss of plate 3". The sulcus contains several small platelets. The cingulum is helicoidal and consists of six to seven cingular plates, some examples seemingly having six plates and some having seven plates. The sutures are in the form of low ridges. The wall is thin and often bears scattered grana. The ornamentation consists of random low ridges, which are often branched, and occasional small tubercles. The ridges usually originate from the sutures and project into the intratabular areas.... These ornamental ridges mimic sutural ridges and make the determination of the tabulation somewhat difficult. The tract diameter ranges from 25

to 36 μ , most specimens being about 30 μ . (Drugg 1970, p. 810-811; ellipses replace figure references in the original.)

Description of Study Material: Cysts small, proximate, subspherical, lacking horns; the episome and hyposome roughly equal. Cyst wall single layered; thin and delicate, so that distorted and broken cysts are common. Archeopyle precingular, type P (3"); operculum free. Processes lacking; ornament comprising low parasutural and intratabular septa and often isolated granules; the cyst wall appearing smooth between these features. Parasutural septa low, forming a well-defined gonyaulacacean paratabulation, ?4', 0a, 6", 6c, 6"', 1p, 1'''; hyposome sexiform, S-type ventral organisation, torsion neutral. Paracingulum and parasulcus clearly expressed by the parasutural septa; paracingulum with strong laevorotatory offset; parasulcus exhibiting considerable obliquity between contact with the cingular paraplates.

Size Range: Length including any processes = 30 (41) 51 μ m (8 measurements). Width including any processes = 42 μ m (one measured specimen).

Distribution: Infrequent. Ignoring the Bartonian occurrence reported by Bujak (see *C. bujakii*, below), *Corrudinium incompositum* is thought to range from the New Zealand Bartonian (Middle Eocene) through to at least the middle or late Rupelian (Stover & Hardenbol 1994; Brinkhuis, Munsterman, et al. 2003). Its occurrence in the Gippsland Basin, Australia, appears to be somewhat earlier, from latest Bartonian up to, but not crossing, the Eocene-Oligocene boundary (e.g. Partridge & Dettmann 2003, table 22.12).

Age/Stage	Location	Sample	Sample Reference
C10r (Rupelian)	ODP Site 1168, offshore western Tasmania, Tasman Sea	189-1168A-73X-3, 57-59 cm.	Brinkhuis, Munsterman, et al. 2003
middle Rupelian	Boom Clay Formation, northwest Belgium	47-1 and SN-22	Stover & Hardenbol 1994
Oligocene	Contessa Highway Section B, Italy	CH24	Brinkhuis & Biffi 1993
Oligocene	Glendon Limestone and Mint Spring Marl, Hinds County, Mississippi	2658-2(1)28-96 and 2649-1(3)34-103	Drugg 1970b
early Oligocene	DSDP Holes 511 and 513A, Falkland Plateau, southwest Atlantic Ocean	71-511-9-2, 102-104 cm.	Goodman & Ford 1983
early Oligocene	Red Bluff Clay, Wayne County, Mississippi	30223(S)28-100	Drugg 1970b
Rupelian	ODP Site 1168, offshore western Tasmania, Tasman Sea	189-1172A-39X-3, 138-149 cm.	Brinkhuis, Sengers, et al. 2003
Rupelian	Paris Basin		Châteauneuf 1980
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f182 (L11931)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f115 (L11051)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f176 (L11925)	
late Eocene-Oligocene	Massignano Section B, Italy	M8.70	Brinkhuis & Biffi 1993
late Eocene-Oligocene	Monte Cagnero Section A, Italy	CA111.6	Brinkhuis & Biffi 1993
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The oldest occurrences in the Puketeraki core are Bortonian, possibly early Bortonian. Although this seems to represent a slightly anomalous outlier to the more common occurrences in the very late Eocene-early Oligocene (e.g. at Cape Foulwind, this study, and at Falkland Plateau, Goodman & Ford 1983; the type is also early Oligocene) the Puketeraki specimens have been re-examined carefully and cannot be distinguished from younger material.

Corrudinium bujakii Clowes n. sp.

Pl. 30, figs. 7-9

1980 *Leptodinium incompositum* (Drugg, 1970) Lentin and Williams, 1973; Bujak, p. 72, pl. 19, figs. 1-2

?1986b *Corrudinium incompositum* (Drugg 1970); De Coninck, pl. 2, figs. 1-2

2005 *Corrudinium incompositum*; Schiøler, pl. 15, fig. 6-8

Derivation of Name: Named after Dr. Jonathan Bujak.

Holotype: Sample I43/f090, slide L16338/SM053; Burnside Formation, Puketeraki Core (Bortonian); Pl. 30, figs. 7-9

Description: Cysts small, proximate, not dorso-ventrally compressed. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type). Processes lacking; surface ornament present, sutural plus intratabular, comprising low septa, forming an incomplete reticulum; 2-3 µm high. Inferred formula: 3 to 4', 0a, 6", 6c, 5-6"', 0 to 1ps, 1"', ?s; ventral organisation S-type; hyposome sexiform; torsion neutral. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 30 (35) 40 µm (7 measurements). Width including any processes = 33 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Priabonian (Tongrien)	Sands of Asse, Woensdrecht borehole, southern Netherlands	263m	De Coninck 1986b
Bartonian-early Rupelian	Horda & Lark Formations, Alma-1X well, Danish North Sea	LVR24106 to 26013	Schiøler 2005
early Bartonian-middle Bartonian	Upper Barton Beds, Whitecliff Bay, Isle of Wight	V59992	Bujak 1980
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: *Corrudinium bujakii* is distinguished from *Corrudinium incompositum* by its more robust, thicker-walled, construction. On average it is also slightly smaller, although the ranges overlap considerably and are generally not diagnostic.

***Corrudinium eyrense* Clowes & Wilson 2006**

Pl. 30, figs. 10-12, Pl. 31, figs. 1-3

2006 *Corrudinium eyrense* Clowes & Wilson, p. 404, figs. 4J-L, 5A-C

Original Description: Cysts of intermediate size, proximate, spherical, lacking horns, with episome and hyposome of approximately equal size. Cyst wall single-layered and relatively thick (c. 3 µm). Archeopyle precingular, type P (3"), relatively large, pentagonal; operculum free. Processes lacking; ornament comprising fairly prominent parasutural septa (up to 6 µm in height) with smooth or undulating crests, and lower scattered intratabular septa. Parasutural septa define an apparent gonyaulacacean paratabulation which is difficult to fully determine. Secondary septa are often discontinuous but sometimes form small, somewhat circular, fields. Paracingulum and parasulcus expressed by parasutural septa; parasulcus often has somewhat reticulate appearance defined by secondary septa.

Size Range: Length including any processes = 53 µm (one measured specimen). Width including any processes = 53 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Mangaorapan	Upper Eyre River, Canterbury, New Zealand	L34/f7538 (L06997)	Wilson 1982c
Mangaorapan	Upper Eyre River, Canterbury, New Zealand	L35/f7539 (L06998)	Wilson 1982c

***Corrudinium obscurum* Wilson 1988**

Pl. 31, figs. 5-6, 8-9

1988 *Corrudinium obscurum* Wilson, p. 16, pl. 4, figs. 3, 6

2006 *Corrudinium obscurum* Clowes & Wilson, p. 404, 406, fig. 5D-E, G-H

Original Description: Cyst small to intermediate, subspherical, fairly thick-walled (c. 2 µm) without apical horn and apparently comprises autophragm only. Parasutural septa relatively low (up to 5 µm in height), irregular and indistinct, especially on ventral surface. Intratabular ornament very prominent, comprises both irregular, discontinuous septa, and solid slender spines, apparently randomly distributed; cyst has a somewhat spongy

reticulate pattern. Archeopyle relatively large, type P; operculum free. Paracingulum well defined on dorsal surface by relatively smooth, depressed area (width 3–4 μm). Paratabulation poorly defined but the second, third and fourth precingular and postcingular paraplates can usually be recognised. Ventral paratabulation and parasulcus indistinct (Wilson 1988, p. 16).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free. Processes lacking; surface ornament present, sutural plus intratabular, comprising membranous septa, forming an incomplete reticulum; about 6 μm high, sutural and intratabular septa approximately the same height. Inferred formula: 3 to 4', 0a, 6", 6c, 5-6"', 0 to 1ps, 1"', ?s; ventral organisation S-type; hyposome sexiform.

Size Range: Length including any processes = 55 (61) 67 μm (2 measurements). Width including any processes = 55 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Mangaorapan	Wanstead Formation, Waipawa, Hawkes Bay, New Zealand	V22/f8991	Wilson 1988

Comparison: *Corrudinium obscurum* is most similar to *Corrudinium eyrense*, but differs in having parasutural and intratabular septa of approximately similar height, whereas the parasutural septa of *C. eyrense* are consistently higher than the intratabular septa.

Remarks: The sutures of this species are difficult – often practically impossible – to discern, and in this respect it approaches a number of the Tertiary forms referred to *Pyxidinospis* (q.v.), suggesting there is more work to be done to fully understand these two groups.

***Corrudinium otagoense* Clowes & Wilson 2006**

Pl. 31, figs. 4, 7, 10-12, Pl. 32, figs. 1-3

- 1982a *Corrudinium* sp.; Wilson, pl. 3, fig. 12
- 1982c *Ochetodinium* cf. *romanum* Damassa; Wilson, p. 4, pl. 1, fig. 11
- 1985 *Pyxidinospis* sp.; Wilson, fig. 15
- 2006 *Corrudinium otagoense* Clowes & Wilson, p. 402, fig. 4D-I

Original Description: Cysts of intermediate size, proximate, spherical, lacking horns; the episome and hyposome roughly equal in size. Cyst wall single layered; thick (c. 2 μm) and robust, so that the cysts are typically found either fully spherical or else fractured rather than distorted. Archeopyle precingular, type P (3"), relatively large, pentagonal; operculum free. Processes lacking; ornament comprising prominent (up to 8 μm in height) parasutural and lower intratabular septa, with generally smooth crests. The paratabulation is apparently typical for the genus, though it is nearly impossible to discern among the multitude of folded septa. Paracingulum and parasulcus expressed by parasutural septa; parasulcus usually completely obscured by accessory ornament.

Description of Study Material: Cysts of intermediate size, proximate to proximochorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered; relatively robust, about 2 μm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, sutural plus intratabular, comprising membranous septa, forming a dense reticulum; about 8 μm high. Margins of crests more or less smooth. Tabulation obscured among the multitude of folded septa, apparently gonyaulacacean. Cingulum weakly expressed to moderately expressed, indicated by sutural septa. Sulcus usually completely obscured by accessory ornament, indicated by sutural septa.

Size Range: Length excluding any processes = 42 (44) 46 μm (2 measurements). Width excluding any processes = 43 (45) 47 μm (2 measurements). Length including any processes = 42 (56) 70 μm (39 measurements). Width including any processes = 50 (54) 60 μm (6 measurements).

Distribution: Frequent. Occurs widely in the late Heretaungan (Lutetian) to Kaiatan (early Priabonian) interval of New Zealand.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f064 (L09221)	Wilson 1985
Kaiatan	Waiareka Volcanic Formation, Jacksons Paddock, Otago,	J41/f8914	Wilson 1982a

Age/Stage	Location	Sample	Sample Reference
	New Zealand		
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: *Corrudinium otagoense* differs from *Corrudinium incompositum* in being distinctly larger, more spherical, and more robust; it differs from *C. incompositum* and *C. regulare* in having higher parasutural and intratabular septa, the latter obscuring the paratabulation. The surface ornament is distinctly denser than that of *C. eyrense*.

***Corrudinium regulare* Clowes & Wilson 2006**

Pl. 32, figs. 4-9

- 1975 *Leptodinium* sp.; Haskell & Wilson, pl. 2, fig. 7
 1983 *Corrudinium* sp.; Goodman & Ford, p. 865, pl. 10, figs. 6-10
 1996 *Impagidinium* sp.; Wilson & McMillan, fig. 4 (4)
 2006 *Corrudinium regulare* Clowes & Wilson, p. 402, fig. 3G-L, fig. 4A-C

Original Description: Cysts of intermediate size, proximate, spherical, lacking horns; the episome and hyposome roughly equal in size. Cyst wall single layered; thick and robust, so that the cysts are most commonly found either fully spherical or else fractured rather than distorted. Archeopyle precingular, type P (3"); operculum free. Processes lacking; ornament comprising low parasutural and intratabular septa, the latter forming an incomplete reticulum with features on a scale of ~3 microns; the cyst wall appears smooth within the lacunae. Parasutural septa low, rarely very low, forming a well-defined gonyaulacacean paratabulation, ?4', 0a, 6", 6c, 6"', 1p, 1''''; hyposome sexiform, S-type ventral organisation ..., torsion neutral ... Paracingulum and parasulcus clearly expressed by the parasutural septa; paracingulum with strong laevorotatory offset; parasulcus exhibiting considerable obliquity between contact with the cingular paraplates (Clowes & Wilson 2006, p. 402; ellipses replace figure references in the original).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered; relatively robust. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, sutural plus intratabular, comprising low septa, forming an incomplete reticulum; with features on a scale of 14-18 sculptural elements across the diameter; very low (about 1 µm or lower) to slightly elevated (2-3 µm). Margins of crests more or less smooth. Tabulation clearly expressed, gonyaulacacean, inferred formula: ?4', 0a, 6", 6c, 6"', 1ps, 1''''; Xs; ventral organisation S-type; hyposome sexiform; torsion neutral. Cingulum clearly expressed, indicated by sutural septa; offset strongly, by 2-3 widths. Sulcus clearly expressed, indicated by sutural septa; exhibiting considerable obliquity.

Corrudinium regulare exhibits a range of variation from relatively smooth (Pl. 32, fig. 7) to deeply sculptured, almost comparable to *C. otagoense* (Pl. 32, figs. 8-9).

Size Range: Length including any processes = 48 (54) 75 µm (26 measurements). Width including any processes = 51 (53) 55 µm (2 measurements).

Distribution: Frequent. *Corrudinium regulare* occurs widely throughout the middle Eocene to early Oligocene interval in the southern hemisphere.

Age/Stage	Location	Sample	Sample Reference
Rupelian	DSDP Hole 511, Falkland Plateau, southwest Atlantic Ocean	71-511-15-1, 38-40 cm.	Goodman & Ford 1983
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f101 (L11037)	
Runangan	Caversham Sandstone, Burnside Quarry, Otago, New Zealand	I44/f274	Wilson & McMillan 1996
?Kaiatan-Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	

Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f063 (L09220)	Wilson 1985
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
middle Eocene	DSDP Leg 29, Site 283, Tasman Sea, east of Tasmania	283-7, CC	Haskell & Wilson 1975
Lutetian	DSDP Hole 512, Falkland Plateau, southwest Atlantic Ocean	71-512-19-3, 29-31 cm.	Goodman & Ford 1983

Comparison: *Corrudinium regulare* is distinctly larger, more spherical, more robust, the intratabular areas more densely ornamented, and the intratabular septa distinctly lower than the parasutural features on *Corrudinium incompositum* or *Corrudinium bujakii*. It differs from *Corrudinium otagoense*, typically, in possessing lower septa, and consistently in displaying a distinct paratabulation, even in variants where the intratabular ornament is abnormally high.

Genus *Impagidinium* Stover & Evitt 1978

1978 *Impagidinium* Stover & Evitt, p. 165-166

Type Species: *Impagidinium dispertitum* (Cookson & Eisenack 1965a, p. 122-123, pl. 12, figs. 5-7) Stover & Evitt 1978, p. 165 [Late Eocene]

Original Description: Cysts proximochorate, acavate, subspherical to ellipsoidal, and typically without an apical projection or horn; paratabulation gonyaulacacean, indicated by parasutural septa only; paraplate 4' characteristically about as long as 1' and contact with subtriangular paraplate 6" very short; archeopyle precingular, Type P (Stover & Evitt 1978, p. 165).

Comparison: In a revision of the genus *Leptodinium*, Stover & Evitt (1978) separated the new genus *Impagidinium* on the basis of having "the first and fourth apical paraplates of similar shape, of about equal length, and often imperfectly separated" (p. 165) and in the shapes and contacts of plate 6" which are today recognised as topological consequences of the L-type (*Leptodinium*) and S-type (*Impagidinium*) ventral patterns of the two genera.

Impagidinium and *Corrudinium* share the S-type ventral topology common to the Gonyaulacoideae. *Corrudinium* differs consistently only in the possession of accessory ridges or septa. *Impagidinium* species may sometimes also exhibit a more prolate shape than *Corrudinium*.

In overall appearance, *Pterodinium* is also similar, and is potentially a senior synonym. However, the detailed plate topology of the type remains uncertain and the genus is less commonly used than *Impagidinium*.

Remarks: A range chart for species of *Impagidinium* identified in this study is provided in Appendix 2, chart 4.

Key to selected species:

0.	Cysts proximochorate....	1.
	Cysts proximate....	2.
1.	Overall shape more or less spherical....	1.1.
	Overall shape noticeably prolate....	1.2.
1.1.	Margins of sutural septa smooth....	1.1.1.
	Margins of sutural septa lacerate to irregularly incised....	1.1.2.
1.1.1.	<i>Impagidinium aculeatum</i>	
1.1.2.	<i>Impagidinium elegans</i>	
1.2.	Sutural septa extended into spinose 'tails' in the gonal positions....	1.2.1.
	Sutural septa lacking gonal extensions....	1.2.2.
1.2.1.	<i>Impagidinium aculeatum</i>	
1.2.2.	<i>Impagidinium waipawaense</i>	
2.	Surface ornament sutural....	2.1.

	Surface ornament intratabular....	2.2.
2.1.	Crests – margins smooth....	2.1.1.
	Crests – margins more or less smooth....	2.1.2.
2.1.1.	Sulcus divided by transverse septa into two or more plates longitudinally....	2.1.1.1.
	Sulcus not divided by transverse septa....	2.1.1.2.
2.1.1.1.	<i>Impagidinium dispertitum</i>	
2.1.1.2.	<i>Impagidinium victorianum</i>	
2.1.2.	<i>Impagidinium waipawaense</i>	
2.2.	Sutural septa entire; ornament comprising light 'dotting'....	2.2.1.
	Sutural septa entire; ornament distinctly scabrate....	2.2.2.
	Sutural septa distinctively perforate....	2.2.3.
2.2.1.	<i>Impagidinium maculatum</i>	
2.2.2.	<i>Impagidinium cf. maculatum</i> ;	
2.2.3.	<i>Impagidinium waipawaense</i>	

Impagidinium dispertitum (Cookson & Eisenack 1965a) Stover & Evitt 1978

Pl. 32, figs. 10-12

- 1965a *Leptodinium dispertitum* Cookson & Eisenack, p. 122-123, pl. 12, figs. 5-7
1977 *Leptodinium dispertitum?* Cookson & Eisenack 1965; De Coninck, p. 42, pl. 4, fig. 10
1978 *Impagidinium dispertitum* (Cookson & Eisenack 1965a, p. 122-123, pl. 12, figs. 5-7) Stover & Evitt, p. 165
1988 *Impagidinium dispertitum* (Cookson & Eisenack, 1965a) Stover & Evitt, 1978; Wilson, p. 23-24, pl. 12, fig. 4
1994 *Impagidinium dispertitum* (Cookson and Eisenack 1965) Stover and Evitt 1978; Stover & Hardenbol, p. 32, pl. 8, fig. 50

Original Description: Shell small, oval, without a horn, tabulated, and divided equally by a relatively broad, helicoid girdle consisting of six plates. Plates smooth or faintly granular, bordered by transparent ledges. The longitudinal field on the ventral surface (representative of a longitudinal furrow), which extends from the apical plates to the antapical plate, is typically marked by three large plates; very occasionally the transverse wall between the two upper ones is incomplete. Archeopyle formed by the removal of plate 3" (Cookson & Eisenack 1965a, p. 122-123).

Description of Study Material: Cysts small to intermediate, proximate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free to attached. Processes lacking; surface ornament present, sutural, comprising low septa. Septa sutural, with smooth margins. Tabulation clearly expressed, gonyaulaccean, inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1"', 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 35 (48) 85 µm (8 measurements). Width including any processes = 36 µm (one measured specimen).

Distribution: Infrequent. There are many described species having a generally similar morphology to *Impagidinium dispertitum*, and a thorough overhaul of *Impagidinium* would be a useful contribution to the field.

Age/Stage	Location	Sample	Sample Reference
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Porangan	Waipawa Section, Hawkes Bay, New Zealand	V22/f7401	Wilson 1988
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Eocene	Woensdrecht borehole, southern Netherlands	369m	De Coninck 1977

Remarks: In their comparison with *Impagidinium maculatum*, Cookson & Eisenack (1965a, p. 123) note that the "longitudinal field is usually divided, not continuous and furrow-like".

Impagidinium victorianum (Cookson & Eisenack 1965a) Stover & Evitt 1978

Pl. 33, figs. 1-9

- 1965a *Leptodinium victorianum* Cookson & Eisenack, p. 123, pl. 12, figs. 8-9
1978 *Impagidinium victorianum* (Cookson & Eisenack 1965a) Stover & Evitt, p. 166
1983 *Impagidinium victorianum* Cookson and Eisenack, 1965) Stover and Evitt, 1978; Goodman & Ford, p. 866, pl. 6, figs. 1-6
1984 *Impagidinium victorianum* (Cookson & Eisenack 1965); Clowes & Morgans, p. 32, pl. 2, figs. 5-7

Original Description: Shell nearly spherical, clearly tabulated, borders of plates, including those of girdle distinct, thin and transparent. Girdle strongly helicoid, represented by six plates, the lower borders of the two plates adjacent to the longitudinal field usually missing. Longitudinal field partially divided into three plates, the two upper ones always incompletely separated, the third adjacent to plate 1^{'''} clearly delimited. Archeopyle formed by the detachment of plate 3^{''} (Cookson & Eisenack 1965a, p. 123).

Description of Study Material: Cysts small to intermediate, proximate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3^{''}); pentagonal (standard *Gonyaulax*-type); operculum free to attached. Processes lacking; surface ornament present, sutural, comprising low septa. Crests sutural, margins of crests smooth. Tabulation clearly expressed, gonyaulaccean, inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6^{'''}, 0 to 1ps, 1^{''''}, 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 43 (69) 82 μ m (4 measurements). Width including any processes = 68 (73) 78 μ m (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f180 (L11929)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f169 (L11918)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: *Impagidinium victorianum* differs from *I. dispertitum* in being larger and in "the constant absence of the transverse dividing [septum] between the upper two plates of the ventral field [sulcus]" (Cookson & Eisenack 1965a, p. 123).

Impagidinium aculeatum (Wall 1967a) Lentin & Williams 1981

Pl. 33, figs. 10-12, Pl. 34, figs. 1-3

- 1967a *Leptodinium aculeatum* Wall, p. 104-105, pl. 14, figs. 18-19, text-fig. 3C-D
1981 *Impagidinium aculeatum* (Wall 1967, p. 104-105, pl. 14, figs. 18-19; text-figs. 3C-D) Lentin & Williams, p. 153
?1982 *Spiniferites cingulatus* var. *intermedius* zu *Sp. cingulatus cingulatus*; Cookson & Eisenack, p. 48, pl. 7, figs. 4-5
2003 *Impagidinium aculeatum*; Brinkhuis, Munsterman, et al., pl. 1, figs. 69-70
2005 *Impagidinium aculeatum*; Schiøler, pl. 9, fig. 15

Original Description: A relatively small, ovoid species with a relatively wide girdle zone and extensive ventral area; test hyaline with sutural septa most strongly developed in the posterior intercalary area; precingular plate-area 6^{''} very narrow (Wall 1967, p. 104).

Description of Study Material: Cysts small to intermediate, proximochorate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3^{''}); pentagonal (standard *Gonyaulax*-type); operculum free to attached. Surface ornament lacking. Processes gonial; non-fibrous, unbranched, solid; proximally connected by sutural

septa proximally, tapering to a more or less acute point distally. Crests sutural, margins of crests smooth. Inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1''', 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 28 (29) 30 μ m (2 measurements). Width excluding any processes = 27 (28) 28 μ m (2 measurements). Length including any processes = 40 (45) 52 μ m (9 measurements). Width including any processes = 43 (46) 49 μ m (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: *Impagidinium aculeatum* is a small taxon; Wall (1967a) records the type material at around 28-38 μ m.

***Impagidinium elegans* (Cookson & Eisenack 1965a) Stover & Evitt 1978**

Pl. 34, figs. 4-12, Pl. 35, figs. 1-3

1965a *Leptodinium elegans* Cookson & Eisenack, p. 123-124, pl. 12, 10-13

1978 *Impagidinium elegans* (Cookson & Eisenack 1965a, p. 123-124, pl. 12, figs. 10-13) Stover & Evitt, p. 165

1982b *Impagidinium elegans* (Cookson & Eisenack); Wilson, p. 8, pl. 3, fig. 11

Original Description: Shell spherical, thick walled (c. 3-5 μ), girdle equatorial, strongly helicoid, clearly defined and plated on the dorsal surface, only slightly so on the ventral surface. Borders of plates including those of girdle, high, transparent, and granular with wavy or dotted edges. The longitudinal field wide and only partially plated and bordered. The plate adjacent to the antapex is always present as is the right-hand border of the field; the left-hand border is restricted to the hypotheca. The archeopyle is formed by the detachment of a portion of plate 3" (Cookson & Eisenack 1965a, p. 123).

Description of Study Material: Cysts intermediate to large, proximochorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free to attached. Surface ornament present, sutural, comprising membranous septa. Crests sutural, margins of crests lacerate to irregularly incised. Tabulation clearly expressed, gonyaulacacean, inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1''', 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 63 (75) 82 μ m (6 measurements). Width excluding any processes = 68 (74) 79 μ m (6 measurements). Length including any processes = 65 (96) 122 μ m (45 measurements). Width including any processes = 88 (98) 112 μ m (7 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan 1996
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f115 (L11051)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f259 (L13545)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f262 (L13546)	
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The type illustrations show a strongly granulate surface to the periplasm. Whereas this may well be an artefact of preservation or processing, the present study has encountered both granulate and smooth-walled forms, otherwise attributable to *Impagidinium elegans*, which appear to be genuine differences in the taxa. Pending re-examination of the type material, both forms are referred to *Impagidinium elegans* for the present.

A second morphological variable is evident in the edges of the sutural crests, which in some specimens are almost smooth (Pl. 35, figs. 1-3) and in others are quite deeply and narrowly notched (Pl. 34, figs. 4-6). However, as above, no attempt has been made to distinguish a separate taxon in the course of the present study.

Inconspicuous, slender, trifurcating processes can be discerned at the gonal positions on the margins of the cingulum of some specimens (e.g. Pl. 34, figs. 4-6).

***Impagidinium maculatum* (Cookson & Eisenack 1961b) Stover & Evitt 1978**

Pl. 35, figs. 4-12

1961b *Leptodinium maculatum* Cookson & Eisenack, p. 40, pl. 2, figs. 5-6

Original Description: Shell oval to nearly spherical, without a horn. Girdle equatorial, strongly helicoid and rather broad with low borders. Longitudinal furrow broad, elongate-rectangular, bounded antapically by a large plate. Plates strongly outlined, bordered by low, thin, hyaline ledges. Surface of the plates distinctly dotted. Pylome formed by removal of plate 3". Tabulation 4', 6", 5"', 1p, 1''''.

Description of Study Material: Cysts small to intermediate, proximate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free. Ornament intratabular, comprising minute granules. Crests sutural, margins of crests smooth. Inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1''''; 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 40 (53) 83 µm (11 measurements). Width including any processes = 37 (41) 45 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Remarks: The dimensions of the type are recorded as 52 µm x 50 µm. The type specimens occur with *R. borussica* in the Rottneest Island bore.

Impagidinium cf. maculatum

Pl. 36, figs. 1-6

1978 *Impagidinium maculatum* (Cookson & Eisenack 1961b, p. 40, pl. 2, figs. 5-6) Stover & Evitt, p. 167

1988 *Impagidinium maculatum* (Cookson & Eisenack, 1961) Stover & Evitt, 1978; Wilson, p. 24, pl. 12, fig. 3

Description: Cysts small to intermediate, proximate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free. Ornament intratabular, comprising granules. Crests sutural, margins of crests smooth. Inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1''''; 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 45 (60) 70 µm (5 measurements). Width including any processes = 42 (49) 63 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Mangaorapan	Waipawa Section, Hawkes Bay, New Zealand	V22/f8993	Wilson 1988

Remarks: Differs from *Impagidinium maculatum* in possessing markedly coarser ornament: it is definitely scabrate as opposed to "maculate" although intermediates can be difficult to allocate to one or other form (e.g. Pl. 35, figs. 4-9).

***Impagidinium waipawaense* Wilson 1988**

Pl. 36, figs. 7-9

1988 *Impagidinium waipawaense* Wilson, p. 24, pl. 13, figs. 1a-b; pl. 14, figs. 1a-c, 2a-b

Original Description: Cyst subspherical, of intermediate size; autophragm characterised by perforate parasutural septa and smooth intratabular areas. Septa fairly prominent (height up to 4 µm) perforate (perforations 1-3 µm) and generally smooth crested; base of septa relatively broad (up to 3 µm) and may be bordered by narrow perforate zone. Horn short (length 6-11 µm) broad based (breadth up to 10 µm), somewhat perforate, with an irregular blunt apex. Paratabulation well defined by septa, gonyaulaccean, formula 4', 6", 6c, 1p, 1"', 2-3s [sic]. Archeopyle relatively small (length 14 µm, breadth 17 µm on holotype) Type P; operculum free. Paracingulum indicated by parallel, transverse ridges (breadth up to 8 µm) and usually comprises 6 paraplates. Parasulcus extends to epicyst and is somewhat broader on the hypocyst; up to three small sulcal paraplates present (Wilson 1988, p. 24).

Description of Study Material: Cysts intermediate to large, proximate to proximochorate, not dorso-ventrally compressed, prolate, with one apical horn; episome and hyposome more or less equal in length. Apical horn well developed, apex bluntly terminated; antapical horns lacking. Cyst wall single-layered. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type); operculum free. Crests sutural, perforate, up to about 4 µm, margins of crests more or less smooth. Inferred formula: 3 to 4', 0a, 5-6", 4-6c, 5-6"', 0 to 1ps, 1"', 0-3s; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length including any processes = 75 (89) 107 µm (4 measurements). Width including any processes = 60 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Genus Pentadinium Gerlach 1961

1961 *Pentadinium* Gerlach, p. 164-165

1978 *Pentadinium* Gerlach 1961; Stover & Evitt, p. 179-180

1982 *Pentadinium* Gerlach 1961; Edwards, p. 105-106, 108

Type Species: Pentadinium laticinctum Gerlach 1961, p. 165-166, pl. 26, figs. 5-6; text-figs. 6-7 [Mid Oligocene-Mid Miocene]

Original Description: Theca spherical to polyhedral. Shell always with an oval or spherical inner body, wall tabulate: 5", 5''' and 1'''. Number of apical plates 1' (?). Girdle helicoidal; longitudinal furrow between the displaced extremities of the girdle. External shell delicate, inner capsule robust (translated from Gerlach 1961, p. 164, by Stover & Evitt 1978, p. 179).

***Pentadinium* sp. 1**

Pl. 36, figs. 10-12, Pl. 37, figs. 1-3

?1986b *Impagidinium?* sp. cf. *I. multiplexum* (Wall & Dale 1968); De Coninck, pl. 4, figs. 19-20, 23-24

Description: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; suturocavate. Archeopyle precingular, type P (3"); operculum free to attached. Processes lacking; surface ornament lacking. Tabulation clearly expressed, gonyaulacacean, inferred formula: 4', 0a, 5-6", ?5c, 4-6''', 1ps, 1''', Xs; ventral organisation S-type; hyposome sexiform. Cingulum clearly expressed, indicated by the sutural pericoels..

Size Range: Length = 62 (68) 75 µm (5 measurements). Width = 65 (68) 70 µm (2 measurements).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
Priabonian (Tongrien)	Sands of Asse, Woensdrecht borehole, southern Netherlands	263m	De Coninck 1986b
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	

Genus *Tectatodinium* Wall 1967a emend. Head 1994a

1967a *Tectatodinium* Wall, p. 112-113

1978 *Tectatodinium* Wall 1967; Stover & Evitt, p. 193-194

1994a *Tectatodinium* Wall 1967 emend. Head, p. 306, 308

Type Species: Tectatodinium pellitum Wall 1967, p. 113, pl. 16, figs. 11-12 [Miocene-Holocene]

Original Description: Spherical to ovoid dinoflagellate cysts without apical, antapical, or any other form of projections. Test wall double (resembling tectate pollen), the outer layer being thicker and less compact or homogeneous than the inner. Test penetrated by a large dorsal precingular archeopyle representing the loss of one plate. A girdle or ventral sulcus rarely present (Wall 1967, p. 113).

***Tectatodinium pellitum* Wall 1967a emend. Head 1994a**

Pl. 37, figs. 4-9

1967a *Tectatodinium pellitum* Wall, p. 113, pl. 16, figs. 11-12

?1972 Kugelige kapsel unbekannter zuordnung 2 Benedek, p. 56, pl. 12, figs. 10a-c

1977 *Tectatodinium pellitum* Wall 1967; Jan du Chêne, p. 105-106, pl. 1, figs. 5-6

?1982b *Tectatodinium* cf. *pellitum* Wall; Wilson, pl. 4, fig. 7

1984 *Tectatodinium pellitum* Wall 1967; Clowes & Morgans, p. 32, pl. 2, fig. 9

1993 *Tectatodinium grande* Williams et al., p. 57

1994 *Tectatodinium pellitum* Wall 1967; Stover & Hardenbol, p. 33, pl. 9, fig. 60

1994a *Tectatodinium pellitum* Wall 1967 emend. Head, p. 308-314, pl. 1-4, pl. 11, figs. 1-9

2005 *Tectatodinium pellitum*; Schiøler, pl. 6, fig. 11

Original Description: The test is ovoid and thick-walled. The latter is double-layered, the inner [pedium] being thin and homogeneous, the outer [luxuria] thicker and spongy; apparently it is formed by numerous, finely interwoven fibrils so that in optical section the focus is indistinct. In surface view the test appears microgranular. There is a large, dorsal, trapezoidal archeopyle but no girdle or ventral sulcus (Wall 1967a, p. 113).

Size Range: Length = 35 (49) 75 μm (10 measurements). Width = 40 (52) 68 μm (5 measurements).

Distribution: Frequent.

Age/Stage	Location	Sample	Sample Reference
late Miocene	southern Spain		Jan du Chêne 1977
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f183 (L11932)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f170 (L11919)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f259 (L13545)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The upper margin to the archeopyle in Wall's (1967a) fig. 11 is quite distinctly pointed. The specimens encountered in this study, notably from the Kakanui River site, differ very slightly from Wall's fig. 11 in having a rounded upper margin to the archeopyle.

***Tectatodinium* sp. 1**

Pl. 37, figs. 10-12

1984 *Tectatodinium* sp.; Clowes & Morgans, p. 32, pl. 2, fig. 10

Description: Wall layers appressed, endophragm of constant thickness (about 1.5 μm) and homogeneous, periphragm varying in thickness (from less than 1 μm up to about 4 μm) and spongy. Tabulation indicated by large precingular archeopyle and variably developed, undivided cingulum. Operculum free. Overall size range: 57-73 μm (Clowes & Morgans 1984, p. 32).

Size Range: Length = 34 (61) 75 μm (4 measurements). Width = 34 (62) 80 μm (4 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f172 (L11921)	
Runangan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f098 (L10953)	Clowes & Morgans 1984

Remarks: This form is distinguished by the comparatively (for the genus) well-developed cingulum.

***Tectatodinium* sp. 2**

Pl. 38, figs. 1-6

?1993 *Tectatodinium* sp. A Martin, p. 115-116, figs. 11A-D

Description: Cysts small, generally markedly prolate, sometimes showing sign of a slight apical bulge but lacking true horns. Walls two-layered, closely appressed, lacking a prominent texture. Surface minutely scabrate. Lacking any indications of tabulation other than the type P (3'') precingular archeopyle.

Size Range: Length = 38 (40) 41 µm (2 measurements). Width = 30 (31) 32 µm (2 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f182 (L11931)	
Runangan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f098 (L10953)	Clowes & Morgans 1984
late Eocene	Mallee Cliffs bore 36465, 201-206 m., central Murray Basin, New South Wales, Australia	Slide 2829-1	Martin 1993
late Eocene	Mallee Cliffs bore 36465, 210-216 m., central Murray Basin, New South Wales, Australia	Slide 2830-1	Martin 1993

Remarks: This form can resemble a thin-walled *T. pellitum* but is usually readily distinguishable by a markedly prolate shape.

Genus *Filisphaera* Bujak 1984 emend. Head 1994b

1984 *Filisphaera* Bujak, p. 185

1989b *Muraticysta* Head et al., p.458

1994b *Filisphaera* Bujak 1984 emend. Head, p. 234-235

Type Species: *Filisphaera filifera* Bujak 1984, p. 185, pl. 1, figs. 7-12 emend. Head 1994b, p. 235-236 [Late Miocene-Early Pleistocene]

Original Description: Spherical to ovoidal dinoflagellate cysts, sometimes with small apical lobe. Cyst with thin inner wall and thicker outer wall composed of radiating fibers. Spines and other projections absent. Cingulum and sulcus absent. Archeopyle precingular, formed by loss or displacement of one or more plates (Bujak 1984, p. 185).

Emended Description of Head 1994b: Cysts spherical to ovoidal, sometimes with small apical lobe. Cyst wall formed of two closely appressed layers, a thin solid endophragm inner thicker periphragm of narrow, principally radiating, nontabular septa that form a microreticulum. Other projections absent or weakly expressed. Paracingulum and parasulcus absent or weakly expressed. Archeopyle precingular, with well developed angles, and formed by loss or displacement of one or more plates (Head 1994b, p. 235).

Filisphaera sp. 3

Pl. 38, figs. 7-9

Description: Cysts small, more or less spherical, lacking horns. Walls two-layered, closely appressed, characterised by a prominent texture of radial fibrils. Surface minutely and densely maculate, where the fibrils are seen end-on. Lacking any indications of tabulation other than the large, square, type P (3'') precingular archeopyle.

Size Range: Length including any processes = 38 µm (one measured specimen). Width including any processes = 36 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f183 (L11932)	
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Runangan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f098 (L10953)	Clowes & Morgans 1984

Remarks: This form is distinguished by the distinctive radially fibrous wall.

Subfamily Cribroperidinioideae Fensome et al. 1993b

Genus *Apteodinium* Eisenack 1958a

1958a *Apteodinium* Eisenack, p. 385

1978 *Apteodinium* Eisenack 1958; Stover & Evitt, p. 141-142

Type Species: Apteodinium granulatum Eisenack 1958a, p. 386-387, pl. 23, figs. 8-14 [Cretaceous (Aptian)]

Original Description: Shell globular, oval to ovoid, sometimes rounded diamond shaped, with a short pointed apical horn; without tabulation, without ornamentation (spines, crests). Epi- and hypovalve separated by a narrow, scarcely depressed (and then often visible with difficulty or not visible at all) unspiraled girdle. Longitudinal furrow not present. Pylome frequent, on dorsal side of epivalve below apical horn. Occasionally a small antapical horn occurs (translated from Eisenack 1958, p. 385, by Stover & Evitt 1978, p. 141).

Remarks: *Apteodinium* is morphologically similar to *Cribroperidinium*. The genotypes of both genera are Cretaceous, though their ranges are not close in time. The principal distinction previously recognised between *Cribroperidinium* and *Apteodinium* is that *Apteodinium* lacks the sutural features which are a prominent characteristic of *Cribroperidinium*. It is not unusual, however, for subtle sutural features to be variably expressed within a single species or subspecies, so that a number of taxa have sat between the two genera, and some have been shuttled back and forth between them to no particular effect. There may be a case to be made for synonymy (*Apteodinium* would be the senior synonym) although the wall structures of the two genera seem to me to be significantly different. Further investigation of this issue, however, is beyond the scope of this paper.

Helenes 1984a recommends the reassignment of species from *Apteodinium* to *Cribroperidinium* as tabulation is discovered, and this advice has been appropriately adopted (for example, by Crouch 2001, in the generic assignment of her "*Cribroperidinium* sp. A"). This is a perfectly orthodox form-taxonomic approach. However, if we adopt a more phylogenetic perspective, we should be doing something different.

The Eocene forms assigned to *Apteodinium* in the present study, together with *Apteodinium spiridoides* Benedek 1972 and *Apteodinium tectatum* Piasecki 1980, are not considered likely to be phylogenetically related (at least not closely) to the Cretaceous genotype species, *Apteodinium granulatum* Eisenack 1958a. Nor does reassigning them to *Cribroperidinium* effect any improvement over the status quo. A new genus – "*Neopteodinium*" perhaps – may be the way to solve the taxonomic problem, but will entail more investigation than I am able to include within the present study.

'*Apteodinium*' *australiense* (Deflandre & Cookson 1955) Williams 1978

Pl. 38, figs. 10-12

1955 *Gymnodinium australiense* Deflandre & Cookson, p. 248-249, pl. 5, fig. 1

1965a *Scriniodinium australiense* (Deflandre & Cookson 1955) Cookson & Eisenack, p. 122, pl. 13, fig. 15

1967 *Scriniodinium australiense* (Deflandre & Cookson 1955) Eisenack, p. 195

?1972 *Gonyaulacysta* cf. *giuseppi* (Morgenroth 1966); Benedek, p. 18-19, pl. 4, figs. 7a-b

?1972 *Apteodinium conjunctum* Eisenack & Cookson 1960; Benedek, p. 4, pl. 1, fig. 2

?1976 *Apteodinium* cf. *spiridoides* Benedek, 1972; Manum, pl. 1, fig. 6

1977 *Apteodinium australiense* (Deflandre & Cookson) Edwards, p. 114-115, pl. 1, figs. 2a-d, 4a-b

1978 *Apteodinium australiense* (Deflandre & Cookson 1955) Williams, p. 794

1984 *Apteodinium australiense* (Deflandre & Cookson 1955); Clowes & Morgans, pl. 2, fig. 11

1994 *Apteodinium australiense* (Deflandre and Cookson 1955) Williams 1978; Stover & Hardenbol, p. 32, pl. 8, fig. 51

?2005 *Apteodinium australiense*; Schiøler, pl. 1, fig. 5

Original Description: Cell globular, divided into 2 approximately equal parts by a narrow, rather shallow, strongly helicoidal girdle. A longitudinal furrow is visible on the hypotheca. The epitheca is surmounted by a short truncate process, the centre of which is frequently depressed. Usually the base of the process is distinctly mamillate. Hypotheca widely rounded; both parts or only the epitheca are bell-shaped. The membrane is finely punctate and sometimes indistinct lines suggestive of plates are apparent. The cell is generally encysted with a more or less quadrangular opening on the dorsal face of the epitheca (Deflandre & Cookson 1955, p. 248).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, with one apical horn; episome and hyposome more or less equal in length. Apical horn moderately

well-developed, apex bluntly terminated; antapical horns lacking. Cyst wall single-layered. Archeopyle precingular, type P (3"); operculum free. Processes lacking. Tabulation not expressed; hyposome sexiform; torsion dextral. Cingulum moderately expressed, indicated by folds in the autophragm. Sulcus generally not evident.

Size Range: Length = 65 (76) 94 μm (4 measurements). Width = 70 (80) 91 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f180 (L11929)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f123 (L11934)	
late Eocene	Browns Creek Clays, southwest Victoria, Australia		Cookson & Eisenack 1965a
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996

'Aptodinium' ?tenuitabulatum (Gerlach 1961) Clowes n. comb.

Pl. 39, figs. 1-9

- 1961 *Gonyaulax tenuitabulata* Gerlach, p. 159-161, pl. 25, figs. 10-11, text-fig. 1-3
- ?1963 *Gonyaulax* cf. *tenuitabulatum* Gerlach 1961; Brosius, p. 37, pl. 1, fig. 5
- ?1969 *Gonyaulacysta tenuitabulata* (Gerlach, 1961) De Coninck, p. 23, pl. 5, figs. 9-10, 13-16
- 1978 *Millioudodinium tenuitabulatum* (Gerlach 1961) Stover & Evitt, p. 174
- 1984a *Cribooperidinium tenuitabulatum* (Gerlach 1961) Helenes, p. 124
- 1984b *Rhynchodiniopsis tenuitabulata* (Gerlach, 1961) Sarjeant, p. 76
- 1985 *Cribooperidinium tenuitabulatum* (Gerlach 1961, p. 159, pl. 25, figs. 10-11; text-figs. 1-3) Helenes 1984, p. 124; Lentin & Williams, p. 81
- 1994 *Cribooperidinium tenuitabulatum* (Gerlach 1961) Helenes 1984; Stover & Hardenbol, p. 32, pl. 8, fig. 53
- ?2000 *Cribooperidinium giuseppi*; Levy & Harwood, p. 222, pl. 2, figs. f-i
- ?2001 *Cribooperidinium* sp. A; Crouch, p. 44, pl. 2, figs. 8-9
- ?2003 *Aptodinium australiense*; Brinkhuis, Munsterman, et al., pl. 1, figs. 4-8

Original Description: Casing thin-walled, compactly spheroidal, with a short, blunt apical horn. Tabulation scheme: 4", 6", 6"', 1p, 1ppl, 1'''''. Plates are bound by low, narrow straps. Girdle furrow spiral with an offset of approximately 1½ furrow widths. Membrane is finely granular (translation from Gerlach 1961, p. 159-160).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, with one apical horn; episome and hyposome more or less equal in length. Apical horn moderately well-developed, apex bluntly terminated; antapical horns lacking. Cyst wall single-layered; about 1.5 μm , increasing towards the cingulum to about 2 μm in thickness; sutural thickenings above and below the cingulum bring the combined thickness (wall plus sutural thickening) to about 4 μm . Archeopyle precingular, type P (3"); operculum free. Processes lacking; comprising low septa; very low (about 1 μm or lower). Tabulation weakly expressed; hyposome sexiform; torsion dextral. Cingulum clearly expressed, indicated by sutural septa. Sulcus weakly expressed.

Size Range: Length = 58 (73) 95 μm (44 measurements). Width = 63 (69) 74 μm (8 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle	north west Germany	Pr 1170/10-12	Gerlach 1961

Miocene			
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: Owing to the kind assistance of Jörg Pross, the writer was able to examine the holotype at Tübingen, on 21 May 2003. The material at the antapex of the specimen is an unrelated piece of debris, draped over the specimen: the antapex is rounded and entire. The specimen may have deteriorated, because the plates are not at all discernable. The only indications of tabulation I was able to observe were the archeopyle and cingulum. The wall is quite thick, as illustrated by Gerlach though in contrast to her description; ~1.5 µm on average increasing to 3 µm or more at the cingulum. The apical horn is partly obscured, the overall length is ~88 µm. The archeopyle is very large, 18.5 µm high x 31 µm wide at the cingular margin.

I have not had the opportunity to investigate the type material of *Cribopteridium giuseppei* (Morgenroth 1966a, p. 5, pl. 2, figs. 3-6) Helenes 1984a, p. 121, but any distinctions between that and the present taxon are not clear to me from the illustrations alone.

Genus *Achilleodinium* Eaton 1976

1976 *Achilleodinium* Eaton, p. 234

1978 *Achilleodinium* Eaton 1976; Stover & Evitt, p. 137-138

Type Species: *Achilleodinium biformoides* (Eisenack 1954b, p. 68, pl. 11, figs. 16-20) Eaton 1976, p. 234 [Late Eocene-Early Oligocene]

Original Description: Dinoflagellate cysts having a spherical or subspherical body bearing two types of intratabular processes: cylindrical processes, one per reflected plate area, hollow, circular to polygonal in cross-section, distally open or closed, variable in size; the larger processes occurring on the precingular and postcingular and antapical zones, the smaller on the apical zone. Slender processes, simple or bifurcate, distally open, restricted to the cingular and sulcal zones. Reflected tabulation 4', 6", 6c, 5"', 1p, 1''''; archeopyle precingular, formed by displacement of plate 3" (Eaton 1976, p. 234).

Remarks: Several species of *Achilleodinium* occur in the older part of the studied interval, from Heretaungan through to early Bortonian.

In overall appearance, *Achilleodinium* closely resembles *Hystrichokolpoma*. It differs, however, in possessing a precingular as opposed to an apical archeopyle. *Florentinia*, which is also somewhat similar, possesses a combination type tA+P archeopyle.

A range chart for New Zealand occurrences of *Achilleodinium* is provided in Appendix 2, chart 1.

Achilleodinium biformoides (Eisenack 1954b) Eaton 1976

Pl. 39, figs. 10-12, Pl. 40, figs. 1-6

1954b *Hystrichosphaeridium biformoides* Eisenack, p. 68, pl. 11, figs. 16-20

1965 *Baltisphaeridium biformoides* (Eisenack 1954b, p. 68-69, pl. 11, figs. 16-20) Downie & Sarjeant, p. 87

1965 *Hystrichokolpoma biformoides* (Eisenack 1954b, p. 68-69, pl. 11, figs. 16-20) Rozen, p. 308

1976 *Achilleodinium biformoides* (Eisenack 1954b, p. 68-69, pl. 11, figs. 16-20) Eaton, p. 234

1980 *Florentinia biformoides* (Eisenack 1954b, p. 68-69, pl. 11, figs. 16-20) Duxbury, p. 121

1984b *Achilleodinium biformoides* (Eisenack, 1954) Eaton 1976; Helenes, p. 94, 104, pl. 5, fig. 11-12

1994 *Achilleodinium biformoides* (Eisenack 1954) Eaton 1976; Stover & Hardenbol, p. 32, pl. 5, fig. 29

Original Description: Central body spheroid to slightly ovoid with dispersed, short and wide appendages furnished with secondary cusps. In between these appendages are irregularly distributed, thin, occasionally pointed, occasionally furcate or even outward-splaying appendages of approximately the same length as the first ones. Excystment holes are usually present (translation from Eisenack 1954b, p. 68-69).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome somewhat shorter than hyposome. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament lacking. Processes intratabular; non-fibrous, inflated, hollow, closed, variable in length, sometimes broader than high; not connected proximally, with distal, secondary cusps. Tabulation clearly expressed by the processes, gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 5"', 1ps, 1''', 3-5s; ventral organisation L-type; hyposome sexiform; torsion dextral. Cingulum clearly expressed, indicated by a series of differentiated processes. Sulcus clearly expressed, indicated by a series of differentiated processes.

Size Range: Length excluding any processes = 53 (68) 88 µm (3 measurements). Width excluding any processes = 46 (51) 55 µm (3 measurements). Length including any processes = 80 (95) 112 µm (11 measurements). Width including any processes = 63 (78) 88 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Remarks: New Zealand forms assigned to this species are somewhat variable, although the illustrated specimens compare very closely with the holotype and other types illustrated in Eisenack 1954b (pl. 11, figs. 16-20). The primary criterion used in this study for making specific distinctions within *Achilleodinium* is the relative length and degree of inflation of the large pre- and post-cingular processes, and the development of any secondary sculpturing on the distal parts of the large processes.

Achilleodinium cf. biformoides

Pl. 40, figs. 7-9

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome somewhat shorter than hyposome. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament lacking. Processes intratabular; non-fibrous, inflated, hollow, closed, variable in length, sometimes broader than high; not connected proximally, with distal, secondary cusps distally. Tabulation clearly expressed, gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 5"', 1ps, 1''', 3-5s; ventral organisation L-type; hyposome sexiform; torsion dextral. Cingulum clearly expressed, indicated by a series of differentiated processes. Sulcus clearly expressed, indicated by a series of differentiated processes.

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome somewhat shorter than hyposome. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament lacking. Processes intratabular; non-fibrous, inflated, hollow, closed, variable in length, sometimes broader than high; not connected proximally, with distal, secondary cusps. Tabulation clearly expressed by the processes, gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 5"', 1ps, 1''', 3-5s; ventral organisation L-type; hyposome sexiform; torsion dextral. Cingulum clearly expressed, indicated by a series of differentiated processes. Sulcus clearly expressed, indicated by a series of differentiated processes.

Size Range: Length excluding any processes = 86 µm (one measured specimen). Width excluding any processes = 50 µm (one measured specimen). Length including any processes = 107 µm (one measured specimen). Width including any processes = 96 µm (one measured specimen).

Distribution: Infrequent. Apparently co-occurring with *A. biformoides* s.s. though only in the older part of its range.

Age/Stage	Location	Sample	Sample Reference
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan-Bortonian	M26 Core, Oamaru-Dunedin, New Zealand	I44/f240 (L15506)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Remarks: This form is close to the type species, *A. biformoides* but differs in possessing longer, and generally broader processes.

***Achilleodinium echinatum* Wilson & Clowes n. sp.**

Pl. 40, figs. 10-12, Pl. 41, figs. 1-3

Derivation of Name: Latin, *echinatus*, prickly; originally from Greek, εχινοζ, meaning hedgehog; with reference to the spiny projections on the processes.

Holotype: Sample J42/f485, slide L23120/SM026; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); Pl. 40, figs. 10-12, Pl. 41, figs. 1-3

Description: Cysts intermediate to large, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Ornament intratabular, comprising differentiated inflated hollow processes and simple spines. Non-fibrous, hollow, closed, up to about 30 µm; not connected proximally, with a small number of thin solid spines along the distal margins distally, sometimes joined by rare, thin trabeculae; apical process relatively short, up to 15 µm and flat; antapical process up to 30 µm and club-shaped to sub-ovoid; cingular and sulcal processes simple or bifurcate, simple spines. Tabulation clearly expressed, gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 5"', 1p, 1''', 5-6s; ventral organisation L-type; hyposome sexiform; torsion dextral. Cingulum clearly expressed, indicated by up to 12 simple or bifurcate processes. Sulcus clearly expressed, indicated by a series of differentiated processes.

Size Range: Length excluding any processes = 57 µm (one measured specimen). Width excluding any processes = 50 µm (one measured specimen). Length including any processes = 97 µm (one measured specimen). Width including any processes = 100 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	

Comparison: The species is distinguished by the distal process spines, generally smooth surface and by having some of the processes joined by trabeculae. It superficially resembles *Hystrichokolpoma spinosum* from the New Zealand Early-Mid Eocene but is readily distinguished from that species by having a precingular rather than apical archeopyle.

Remarks: A provisional description for this taxon appears in an unpublished manuscript prepared by Dr. Graeme Wilson shortly prior to his retirement from GNS Science (formerly the New Zealand Geological Survey), under the name *Achilleodinium echinatum*. Although the description has been amended somewhat to bring it into conformity with the other descriptions provided herein, and observations from additional material incorporated, Dr. Wilson's fundamental contribution is recognised in the authorship of the proposed name.

***Achilleodinium improcerum* Wilson & Clowes n. sp.**

Pl. 41, figs. 4-12, Pl. 42, figs. 1-6

?1993 *Achilleodinium biformoides* (Eisenack) Eaton, 1976; Brinkhuis & Biffi, p. 173, pl. 5, fig. 9

Derivation of Name: Latin, *improcerus*, short; with reference to the processes.

Holotype: Sample J42/f484, slide L23119/SM020; Kurinui Formation, Hampden Beach Section (Heretaungan); Pl. 41, figs. 4-6

Description: Cyst of intermediate size, subspherical to ellipsoidal, two-layered, bearing short hollow, box-like intratabular processes. Precingular and postcingular processes broad, polygonal, short (length to breadth ratio less than 1:2) with a narrower distal margin. Polar processes not well-developed. Cingular processes generally short and narrow, occasionally spinose, sometimes absent. Sulcal processes generally short, spinose. Tabulation apparently 1-4', 6", 6c, 5"', 1p, 1''', 3-5s. Periphragm surface between processes usually has widely dispersed granules. Archeopyle precingular, type P (3"); operculum free. *Size Range:* Holotype – overall length 91 microns, breadth 86 microns, length of endocyst 78 microns, length of processes up to 11 microns; range of 6 specimens – overall length 78-108 microns, breadth 68-87 microns.

Size Range: Length excluding any processes = 60 (77) 94 μm (4 measurements). Width excluding any processes = 47 (67) 83 μm (4 measurements). Length including any processes = 72 (94) 126 μm (8 measurements). Width including any processes = 55 (88) 112 μm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Priabonian	Massignano Section, northeast Italy	MS 7.20-01	Brinkhuis & Biffi 1993
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: The species is distinguished by its short, generally broad precingular and postcingular processes, and in lacking a distinctive antapical process. Wilson 1985 further notes the more polygonal in cross-section of the processes as a point of difference from the genotype, *A. biformoides*. It superficially resembles *Hystrichokolpoma wilsonii* (Wilson) Williams et al. 1998, but differs in having a precingular rather than an apical archeopyle. It also resembles *Aireiana* species, but differs in having two distinct process types.

Remarks: A provisional description for this taxon appears in an unpublished manuscript prepared by Dr. Graeme Wilson shortly prior to his retirement from GNS Science (formerly the New Zealand Geological Survey), under the name *Achilleodinium improcerum*. Although the description has been amended somewhat to bring it into conformity with the other descriptions provided herein, and observations from additional material incorporated, Dr. Wilson's fundamental contribution is recognised in the authorship of the proposed name.

Genus *Araneosphaera* Eaton 1976

1976 *Araneosphaera* Eaton

Type Species: *Araneosphaera araneosa* Eaton 1976, p. 240, 242, pl. 2, figs. 5-8, text-figs. 6A-D [Mid-Late Eocene]

Original Description: Dinoflagellate cysts having a spherical or subspherical body with a smooth or finely fibro-reticulate surface. Processes intratabular, fibrous, simple or branched. A variable proportion of the processes are distally united by fibrous membrane. Processes invariably present on the apical, pre- and postcingular and antapical zones. Typically each reflected plate area has one process, sometimes more than one. Cingular zone usually, but not invariably, devoid of processes. Basic reflected tabulation 4', 6'', 5-6''', 0-1p, 1''''; archeopyle precingular, formed by displacement of plate 3'' (Eaton 1976, p. 240).

'*Araneosphaera*' *stephanophora* (Benedek 1972) Benedek & Sarjeant 1981

Pl. 42, figs. 7-12, Pl. 43, figs. 1-6

1972 *Cordosphaeridium minimum* (Morgenroth 1966) Benedek, pl. 9, fig. 3

1972 *Hystrichosphaeridium stephanophorum* Benedek, p. 30-31, pl. 9, fig. 6, text-fig. 10

1981 *Araneosphaera stephanophora* (Benedek, 1972) Benedek & Sarjeant, p. 349-351, fig. 10 (3, 6)

Original Description: [No translation available] Eine Art der Gattung *Hystrichosphaeridium* mit kleiner kugelförmiger Kapsel. Diese ist dünnwandig und hat eine glatte, ungefelderte Oberfläche. Sie wird locker von hohlen kurzen Fortsätzen besetzt, deren distale Erweiterungen verwaschen sein können (Benedek 1972, p. 30).

Size Range: Length excluding any processes = 20 (22) 27 μm (6 measurements). Width excluding any processes = 18 (22) 27 μm (4 measurements). Length including any processes = 29 (38) 47 μm (8 measurements). Width including any processes = 32 (37) 40 μm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)

Remarks: ‘*Araneosphaera*’ *stephanophora* was first described (Benedek 1972) as a species of *Hystrichosphaeridium*. Included among the types were some specimens subsequently reattributed to *Cordosphaeridium minimum* in Benedek & Sarjeant 1981, p. 350. (The comment that the reattributed specimens possess apical archeopyles is assumed to be an error since *Cordosphaeridium* has a precingular archeopyle.)

Strauss & Lund 1992, p. 161-162, advances the proposition that this species is a member of super-specific group of forms they term the “aff. *Cordosphaeridium minimum* (Morgenroth) Benedek 1972-cyst complex” which is characterised by a small, subspherical, hollow central body with “probably” a type P (3”) archeopyle and fibrous, distally expanded processes. These authors cite a continuous range of variation between typical *Cordosphaeridium minimum* types having no distal connections between processes, to others which are completely enveloped by an ectophragmal membrane. The continuous range of variation is somewhat supported in the present study. The abandonment of taxonomic duty by simply dumping the problem into a “complex”, however, is not.

The generic assignment is here regarded as highly dubious because the archeopyle type of ‘A.’ *stephanophora* is quite uncertain (the reassurances in Benedek & Sarjeant 1981 notwithstanding) and, even if it does prove to be precingular, the resemblance to the type species of *Araneosphaera*, *A. araneosa* Eaton 1976, remains slight. My own view is that by including all of these forms in *Cordosphaeridium*, Strauss & Lund were closer to the mark.

Genus *Cordosphaeridium* Eisenack 1963b emend. Davey 1969c

1963b *Cordosphaeridium* Eisenack, p. 261

1969c *Cordosphaeridium* Eisenack 1963 emend. Davey, p. 35

1978 *Cordosphaeridium* Eisenack 1963b emended Davey 1969c; Stover & Evitt, p. 146-147

Type Species: *Cordosphaeridium inodes* (Klumpp 1953, p. 391, pl. 18, figs. 1-2) Eisenack 1963b, p. 261 [Late Eocene]

Original Description: Hystrichospheres with spherical to (generally weakly) ellipsoidal shells, which are covered with approximately homogeneous and rather regularly distributed radial appendages, which appear cord-like, i.e., are formed of numerous thin, closely set fibres. A hollow space is, in general, not discernible; however, in some cases it can be present in relict fashion. Commonly the shell consists of two layers, of which the outer has a fibrous structure and (in all probability) the converging fibres constitute the processes. At the tips the fibres diverge in paintbrush-like fashion; however, they may also unite together in net like fashion (translated from Eisenack 1963b, p. 261, by Stover & Evitt 1978, p. 146).

Cordosphaeridium inodes (Klumpp 1953) Eisenack 1963b

Pl. 43, figs. 7-12, Pl. 44, figs. 1-3

1953 *Hystrichosphaeridium truncigerum* Deflandre; Cookson, p. 114, pl. 2, figs. 21-23

1953 *Hystrichosphaeridium inodes* Klumpp, p. 391, pl. 18, figs. 1-2

1955 *Hystrichosphaeridium inodes* Klumpp; Deflandre & Cookson, p. 277-278, pl. 8, fig. 7

1963 *Hystrichosphaeridium inodes* Klumpp 1953; Brosius, p. 40, pl. 5, fig. 5

1963b *C. (Hystrichosphaeridium) inodes* (Klumpp 1953) Eisenack, p. 261

1965 *Cordosphaeridium inodes* (Klumpp 1953); De Coninck, p. 31, pl. 8, figs. 1-7, pl. 9, figs. 1, 2, 5

1966b *Cordosphaeridium gracilis* (Klumpp) Davey & Williams, p. 83-84, pl. 3, fig. 9, text-fig. 18

1969 *Cordosphaeridium inodes inodes* (Klumpp 1953) Gocht, p. 41, pl. 1, figs. 11-12, pl. 4, fig. 14

1972 *Cordosphaeridium inodes inodes* (Klumpp 1953) Gocht 1969; Benedek, p. 25, pl. 7, fig. 10

1985 *Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963; Jan du Chêne & Adediran, p. 12, pl. 12, fig. 7

2004 *Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963b emend. Morgenroth 1968 emend. Sarjeant 1981; Ramirez, p. 45, pl. 2, fig. 6

Original Description: A species of the genus *Hystrichosphaeridium* with the following characteristics: the enclosing membrane is double layered, the outer layer consists of short fibres vertically aligned with the surface. The processes are formed from this fibre layer and ravel out irregularly at the ends (Klumpp 1953, p. 391).

Size Range: Length excluding any processes = 50 (56) 60 μm (3 measurements). Width excluding any processes = 50 (50) 50 μm (2 measurements). Length including any processes = 68 (119) 173 μm (18 measurements). Width including any processes = 84 (128) 165 μm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
middle Eocene-late Eocene	north west Venezuela	Pica-1X, 3818 ft.	Ramírez 2004
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	
late Paleocene-early Eocene	Lokoja, Nigeria		Jan du Chêne & Adediran 1985

Remarks: The holotype of *C. inodes* appears in a poor photograph (pl. 18, fig. 1) and a sketch (pl. 18, fig. 2) in Klumpp's original publication (Klumpp 1953). Unsurprisingly, given the date of the work, there is little useful diagnostic detail in these depictions, nor in the description.

A somewhat more recent sketch is provided in Jux 1968, text-fig. 1. Jux's sketch depicts the holotype in the identical orientation but, unlike Klumpp's, shows the outline of a fairly typical precingular archeopyle on the upper surface.

Sarjeant 1981, pl.1, fig. 1, provides a photograph of the holotype, "in oblique ventral view." In this figure, the specimen is recognisably the same, but the orientation is rotated approximately 90° clockwise with respect to the earlier illustrations. The area shown as an archeopyle in Jux's illustration, is out of focus in Sarjeant's photograph. It could be anything, and there is no way for the reader to assess the orientation for themselves. Sarjeant's sketches (text-fig. 1) illustrate his interpretation of the archeopyle shape and position. Even allowing for the rotation and left-to-right reflection in his depiction of the dorsal surface, Sarjeant's sketch of the archeopyle cannot be reconciled with Jux's, and the shape of Sarjeant's archeopyle is unconvincing.

***Cordosphaeridium gracile* (Eisenack 1954b) Davey & Williams 1966b**

Pl. 44, figs. 4-6

1954b *Hystrichosphaeridium inodes* subsp. *gracile* Eisenack, p. 66, pl. 8, fig. 17; pl. 10, figs. 3-8; pl. 12, figs. 7, 21

1966b *Cordosphaeridium gracilis* (Eisenack) Davey & Williams, p. 84-86, pl. 3, fig. 8, pl. 11, figs. 4, 6, 7, text-fig. 19

1969 *Cordosphaeridium inodes gracilis* (Eisenack 1954) Gocht, p. 41-42, pl. 1, figs. 1-9, 15

Original Description: A subspecies of *H. inodes* Klumpp 1953 with the following characteristics: The central body is spherical to oval, generally larger than the primary type, the appendages longer, significantly narrower and of even length (translation from Eisenack 1954b, p. 66).

Size Range: Length excluding any processes = 64 (74) 85 μm (2 measurements). Width excluding any processes = 60 (70) 80 μm (2 measurements). Length including any processes = 47 (149) 175 μm (13 measurements). Width including any processes = 117 (148) 163 μm (8 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985

Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	

***Cordosphaeridium fibrospinosum* Davey & Williams 1966b**

Pl. 44, figs. 7-12

- 1966b *Cordosphaeridium fibrospinosum* Davey & Williams, p. 86, pl. 5, fig. 5
- ?1969c *Cordosphaeridium fibrospinosum* Davey & Williams 1966b emend. Davey, p. 36, pl. 3, fig. 4, pl. 4, fig. 5, text-fig. 1 (5)
- 1980a *Cordosphaeridium fibrospinosum* Davey and Williams; Bujak et al., pl. 7, figs. 3, 6
- 1981 *Emmetrocysta? fibrospinosa* (Davey & Williams 1966b, p. 86, pl. 5, fig. 5) Sarjeant, p. 123
- 1986 *Tityrosphaeridium? fibrospinosum* (Davey & Williams 1966b, p. 86, pl. 5, fig. 5) Jain and Garg, p. 121

Original Description: Ovoidal central body with wall up to 0.5 μ thick, composed of smooth endophragm and fibrous periphragm. Processes fibrous, often very broad and ovoidal in cross-section, walls perforate. Processes open distally, with entire or undulose margin. One process per plate reflecting a tabulation typical of the genus. Archeopyle apical haplotabular [sic] (Davey & Williams 1966b, p. 86).

Description of Study Material: Cysts large, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Processes intratabular; fibrous, often perforate, variable, sometimes broader than high; not connected proximally, flaring distally. Inferred formula: 3 to 4', 0a, 6", 6c, 5-6"', 0 to 1ps, 1''', 0-3s; hyposome sexiform; torsion dextral.

Size Range: Length excluding any processes = 75 (78) 81 μ m (2 measurements). Width excluding any processes = 73 (74) 75 μ m (2 measurements). Length including any processes = 37 (101) 157 μ m (23 measurements). Width including any processes = 90 (104) 120 μ m (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	

Cordosphaeridium aff. funiculatum

Pl. 45, figs. 1-12

- 1988 *Cordosphaeridium cf. funiculatum* Morgenroth 1966; Biffi & Manum, pl. 10, figs. 13, 17
- 1989 *Cordosphaeridium cf. funiculatum* Morgenroth, 1966; Head & Norris, pl. 8, figs. 13-14
- 1992 *Cordosphaeridium funiculatum* Morgenroth, 1966a emend. Brinkhuis, p. 97, pl. 1, fig. 6
- 1993 *Cordosphaeridium funiculatum* Morgenroth, 1966a Brinkhuis & Biffi, p. 173, pl. 1, fig. 6
- 1993 *Cordosphaeridium funiculatum* Morgenroth, 1966a; Brinkhuis & Biffi, p. 173, pl. 1, fig. 6
- 1994 *Cordosphaeridium funiculatum* Morgenroth, 1966a; Brinkhuis, pl. 4, figs. 1-3

Description: Cysts more or less spherical with an indistinct equatorial cingulum. Two wall layers; a very thick (~4 to 5 μ m) endocyst and thin, hyaline, minutely perforate (?) pericyst. Archeopyle precingular, Type P (3"), with a flat bottom margin and semicircular upper margin; operculum free, possessing one central process complex. Ornament comprises intratabular (and possibly some accessory features in gonal positions) process complexes of variable morphology, including fibrous or at least striated, hollow, essentially "closed" though variably perforate processes which range from thick spines to blunt and sometimes inflated cones. Sometimes the antapical process appears broader than the others. The processes are joined proximally by an irregular, coarse reticulum which appears minutely maculate, possibly perforate. Indistinct indications of a cingulum may be provided by intratabular or possibly gonal processes on the cingular plates, and possibly an extremely faint and erratic alignment of the reticulum. The sulcus is not discernible at all on most specimens; only one from the present collection shows a very faint indication (Pl. 45, figs. 1-6). Tabulation is indicated by the archeopyle and process

placement, unambiguously by the archeopyle only; presumed to be gonyaulacacean; formula 4', 6", ?5-6c, 5"', ?0-1p, 1''''.

Size Range: Length excluding any processes = 80 (102) 127 µm (3 measurements). Width excluding any processes = 82 (98) 120 µm (3 measurements). Length including any processes = 43 (116) 175 µm (6 measurements). Width including any processes = 112 (137) 177 µm (3 measurements).

Distribution: Infrequent. Occurs in only a few samples, possibly indicating a narrow stratigraphic range, but can be locally abundant when it does occur.

Previous reports of this taxon have been from the Tethys; the present report provides a significant extension to the known geographic range of this taxon.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f115 (L11051)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f183 (L11932)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
latest Eocene	Monte Cagnero Section A, Italy		Brinkhuis & Biffi 1993
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f128 (L11939)	
late Eocene	Contessa Highway Section B, Italy		Brinkhuis & Biffi 1993
late Eocene	Massignano Section, northeast Italy	MS 18.00-01	Brinkhuis & Biffi 1993
late Eocene	Massignano Section, northeast Italy	MS 18.00-01	Brinkhuis 1992
late Eocene	Priabona Section, northeast Italy	PB24-02	Brinkhuis 1994
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996

Remarks: Brinkhuis (1992, p. 97) considered this form to be a variant of *Cordosphaeridium funiculatum* Morgenroth 1966a and emended the original description "to include forms that possess shorter and broader processes, such as those figured by e.g., Biffi and Manum (1988) and Head and Norris (1989)."

Brinkhuis 1992, p. 97, further notes that "representatives of the species exhibiting relatively short and broad processes are restricted to lower (paleo-) latitudes", though this is clearly not the case for the New Zealand material. Moreover, the forms with shorter and broader processes appear generally to be younger than Morgenroth's early Eocene type material from Katharinenhof on Fehmarn Island (northern Germany). Thus it is plausible to suggest that the reported occurrences trace the southward migration of a variant, or descendent, of *Cordosphaeridium funiculatum* sensu stricto.

C. aff. funiculatum appears to possess some characteristics which are closer to *Aireiana* than to the type species of *Cordosphaeridium*, *C. inodes*.

***Cordosphaeridium minimum* (Morgenroth 1966a) Benedek 1972**

Pl. 46, figs. 1-9

1966a *Cordosphaeridium inodes* Klumpp *minimum* Morgenroth, p. 24-25, pl. 5, figs. 6-7

1969 ?*Cordosphaeridium inodes* subsp. *minimum* Morgenroth, 1966; De Coninck, p. 31, pl. 8, figs. 20-22

1972 *Cordosphaeridium minimum* (Morgenroth 1966) Benedek, p. 25-26

1994 *Cordosphaeridium minimum* (Morgenroth 1966) Benedek 1972; Stover & Hardenbol, p. 32, pl. 7, fig. 39

Original Description: [No translation available] Eine Art der Gattung *Cordosphaeridium* mit einem "inodes"-ähnlichen Fortsatztyp. Fortsätze erweitern sich distal trompetenförmig und fasn auf. Keine Fortsatzverzweigungen. Kapseldurchmesser ca. 20µ kleiner als bei *Cordosphaeridium inodes* (Morgenroth 1966a, p. 24).

Description of Study Material: Cysts small, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free to attached. Processes intratabular, straight or gently curved; ?fibrous, unbranched; not connected proximally, irregularly flaring distally. Inferred formula: 3 to 4', 0a, 6", 6c, 5-6"', 0 to 1ps, 1'''' , 0-3s.

Size Range: Length excluding any processes = 17 (21) 25 µm (10 measurements). Width excluding any processes = 18 (21) 23 µm (4 measurements). Length including any processes = 30 (38) 45 µm (13 measurements). Width including any processes = 33 (37) 40 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan-Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f298 (L23128)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Remarks: There has been some confusion concerning the distinction between *Cordosphaeridium minimum* and 'Araneosphaera' *stephanophora*, presumably because they are both very small, occur together, and the ectophragm of 'A.' *stephanophora* is often incomplete, and possibly sometimes lacking. Refer to 'A.' *stephanophora* for further discussion.

The precingular archeopyle is clearly evident in the studied specimens of the present form (e.g. see Pl. 46, fig. 1).

Genus *Turbiosphaera* Archangelsky 1969a

- 1969a *Turbiosphaera* Archangelsky, p. 408
 1978 *Turbiosphaera* Archangelsky 1969a; Stover & Evitt, p. 198
 1984 *Turbiosphaera*; Damassa, p. 61-62

Type Species: *Turbiosphaera filosa* (Wilson 1967a, p. 66, figs. 2b, 31-32, 34) Archangelsky 1969a, p. 408-411 [Paleocene-Oligocene]

Original Description: Subspherical to suboval chorate cysts, with two-layered central body. Periphragm forming typically taeniate processes reflecting a tabulation 1', 6", 6c, 6"', (1p), 1'''. Apical and antapical processes bigger than the others; cingular processes smaller than the others. Archeopyle precingular with entire margins, formed by detachment of plate 3" (translated from Archangelsky 1969a, p. 408, by Stover & Evitt 1978, p. 198).

Turbiosphaera filosa (Wilson 1967a) Archangelsky 1969a

Pl. 46, figs. 10-12, Pl. 47, figs. 1-3

- 1961 Forma F Evitt, p. 392
 1967a *Cordosphaeridium filosum* Wilson, p. 66, figs. 2b, 31-32, 34
 1969a *Turbiosphaera filosa* (Wilson 1967a, p. 66, figs. 2b, 31-32, 34) Archangelsky, p. 408-411
 1982b *Turbiosphaera filosa* (Wilson); Wilson, pl. 2, figs. 14-15
 1984 *Turbiosphaera filosa*; Damassa, p. 61-62, pl. 6, figs. 1-3
 1989 *Turbiosphaera filosa* (Wilson) Archangelsky Wilson, pl. 1, fig. 18
 2000 *Turbiosphaera filosa* (Wilson, 1967) Archangelsky, 1969a; Levy & Harwood, p. 228, 230, pl. 10, figs. d-l

Original Description: Test bi-layered comprising fibrous outer cyst and smooth oval inner cyst. Outer cyst extended radially to form 20-24 broad, flat, non-tubular fibrous processes ($l = 8-26 \mu$) the longest and broadest being at the poles; processes of equatorial region about one half as long as polar processes; polar processes usually pointed, the others flat-tipped; ventral processes much smaller than those on dorsal surface. Laevo-rotatory transverse girdle clearly defined by whorl of 6-8 processes whose long, narrow bases are aligned parallel to the equator. Archeopyle large, subrounded, precingular, located on dorsal epitheca ... (Wilson 1967a, p. 66; ellipses replace figure references in the original).

Size Range: Length excluding any processes = 92 μ m (one measured specimen). Width excluding any processes = 73 μ m (one measured specimen). Length including any processes = 137 μ m (one measured specimen). Width including any processes = 110 μ m (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	L13177/1	Wilson 1989
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4737	Wilson 1967a
Eocene	erratics, McMurdo Sound, Antarctica	MB 245	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 1B	Levy & Harwood 2000

***Turbiosphaera* sp. 1**

Pl. 47, figs. 4-12

Description: Cysts intermediate to large, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate; fibrous. Archeopyle precingular, type P (3"); large; operculum free. Surface ornament present, non-tabular, comprising texture arising from the fibrous composition of the periphragm, forming an irregular reticulum. Processes intratabular; fibrous, unbranched, solid; flaring distally; sometimes separating into a small number of divisions, though not true branches, distally. Tabulation clearly expressed, gonyaulacacean, inferred formula: 1-4', 0a, 6", X-6c, 5-6"', 1ps, 1"', Xs; hyposome sexiform; torsion dextral. Cingulum clearly expressed, a differentiated, flattened, process series; offset only slightly. Sulcus moderately expressed, a few differentiated, spine-like processes.

Size Range: Length excluding any processes = 67 µm (one measured specimen). Width excluding any processes = 54 µm (one measured specimen). Length including any processes = 102 µm (one measured specimen). Width including any processes = 97 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	

Remarks: A form which differs from *Turbiosphaera filosa* and *T. sagena* in possessing relatively long, thin, processes, like some species of *Cordosphaeridium*, but retaining the "shelf-like" cingular process cross-sections characteristic of *Turbiosphaera*.

Genus *Disphaerogena* O. Wetzel 1933b emend. Sarjeant 1985b

- 1933b *Disphaerogena* O. Wetzel, p. 51
- 1976 *Cyclapophysis* Benson, p. 182
- 1978 *Cyclapophysis* Benson 1976; Stover & Evitt, p. 150-151
- 1981 *Plethysyrinx* Sarjeant, p. 106

Type Species: *Disphaerogena carposphaeropsis* O. Wetzel 1933b, p. 51, pl. 4, fig. 34 [Late Cretaceous]

Original Description: Shell with irregular outer trelliswork round the central sphere (translation from O. Wetzel 1933b, p. 51, by Norris & Sarjeant 1965, p. 26).

Emended Description of Sarjeant 1985b: Proximochorate to chorate, skolochorate cysts, of spheroidal to ovoidal or subpolygonal ambitus. Distinct apical and antapical processes are present, of variable absolute and relative length; these are surrounded by fibrous processes. The precingular and postcingular processes bend towards the cingulum, their tips linked by short trabeculae or fusing to form an equatorial tunnel round the cyst, though this may be interrupted at the sulcus. Paratabulation 4', 6", ?0c, 6—?7"', ?1p, 1'''. Archeopyle single-plate precingular, type P, formed by loss of paraplate 3" (Sarjeant 1985b, p. 141).

Remarks: Effectively emended by Sarjeant 1985b, p. 140-141, in which *Cyclapophysis* is considered a junior synonym.

?Disphaerogena morgansii Clowes n. sp.

Pl. 48, figs. 1-12

Derivation of Name: Named after the micropaleontologist and occasional field-mate, who supplied numerous samples and foraminifera age controls for the present study, Hugh Morgans.

Holotype: Sample J42/f486, slide L23121/SM015; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); Pl. 48, figs. 1-6

Description: Cysts of intermediate size, chorate, subspherical to slightly prolate, epicyst considerably shorter than the hypocyst, lacking horns. Surface ornament present, comprising non-tabular, scattered small granules. Processes arising from precingular and postcingular plates generally more or less tubular, hollow, and open, but very variable, and connected by distal trabeculae. The cingular series is represented by shorter, flat or spinose processes, which are not connected distally, arising from the upper margin only. The antapical plate supports a large tubular process, apparently hollow and open though constricted distally, which is not joined by trabeculae. A thinner, less regular process arises from the ?posterior intercalary plate. Tabulation appears to be completely represented by the processes, gonyaulaccean, inferred formula 4', 6'', 6c, 6''', 1p, 1''', xs; archeopyle precingular, type P (3'').

Size Range: Length excluding any processes = 60 (64) 68 μ m (3 measurements). Width excluding any processes = 42 (53) 63 μ m (3 measurements). Length including any processes = 103 (105) 110 μ m (3 measurements). Width including any processes = 85 (94) 99 μ m (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	

Comparison: *Disphaerogena morgansii* differs *D. carposphaeropsis* (a senior synonym of *D. monmouthensis*, according to Sarjeant 1985b) in lacking an apical horn and in possessing a much longer antapical process; and from *D. irregularis* and *D. lemniscata* in possessing cingular processes.

Genus Hystrichokolpoma Klumpp 1953

1953 *Hystrichokolpoma* Klumpp, p. 388

1978 *Hystrichokolpoma* Klumpp 1953 emended Williams & Downie in Davey et al. 1966; Stover & Evitt, p. 54-55

Type Species: *Hystrichokolpoma cinctum* Klumpp 1953, p. 389, pl. 17, figs. 3-4, 5a-d [Late Eocene]

Original Description: A genus possessing the characters of the family Hystrichosphaeridae and the following peculiarities: horn shaped appendices raised up from large plates between which are thin spines from a girdle and a particular field arrangement (translated from Klumpp 1953, p. 388).

Additionally, Stover & Evitt (1978) provides the following translation of Klumpp's description: The shell is almost round, divided by a girdle-like zone into two separate halves. The lower [but note that the taxon is being described upside-down] consists of six plates with inflated processes, between which in the middle there is an opening. The upper part carries four humped plates adjacent to the girdle and one field with thin spines as on the girdle. A smaller plate with a hollow process, longer than the bags [i.e., bag-like inflated processes], forms the apical field (translated from Klumpp 1953, p. 388, in Stover & Evitt 1978, p. 54).

***Hystrichokolpoma cinctum* Klumpp 1953**

Pl. 49, figs. 1-3

1953 *Hystrichokolpoma cincta* Klumpp, p. 389, pl. 17, figs. 3-4, 5a-d

?1954b *Hystrichokolpoma cinctum* Klumpp 1953; Eisenack, p. 64-65, pl. 10, figs. 11-14, text-fig. 4

1956 *Hystrichokolpoma cinctum* Klumpp; Cookson, p. 187-188, pl. 2, figs. 7-9

1961 *Hystrichokolpoma cinctum* Klumpp 1953; Gerlach, p. 182-183, pl. 28, fig. 1

1963 *Hystrichokolpoma cinctum* Klumpp 1953; Brosius, p. 43, pl. 2, fig. 4

1966a *Hystrichokolpoma eisenackii* Williams & Downie, p. 176-178, pl. 17, figs. 1-3, text-fig. 46

Original Description: [Given for the genus] A genus possessing the characters of the family Hystrichosphaeridae and the following peculiarities: horn shaped appendices raised up from large plates between which are thin spines from a girdle and a particular field arrangement (translated from Klumpp 1953, p. 388).

Additionally, Stover & Evitt (1978) provides the following translation of Klumpp's description: The shell is almost round, divided by a girdle-like zone into two separate halves. The lower [but note that the taxon is being described upside-down] consists of six plates with inflated processes, between which in the middle there is an opening. The upper part carries four humped plates adjacent to the girdle and one field with thin spines as on the girdle. A smaller plate with a hollow process, longer than the bags [i.e., bag-like inflated processes], forms the apical field (translated from Klumpp 1953, p. 388, in Stover & Evitt 1978, p. 54).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/38	Gerlach 1961
?Oligocene	Nelson Bore, Australia	730 ft.	Cookson 1956
early Oligocene	Samland, East Prussia		Eisenack 1954b
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f184 (L11933)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f101 (L11037)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f125 (L11936)	
late Eocene	Wohrden Bore, Holstein, Germany		Klumpp 1953
Eocene	Nelson Bore, Australia	992 ft.	Cookson 1956

***Hystrichokolpoma rigaudiae* Deflandre & Cookson 1955**

Pl. 49, figs. 4-9

- 1954 *Hystrichokolpoma rigaudae* Deflandre & Cookson, p. 1237 (1236?), text-fig. 15
- 1955 *Hystrichokolpoma rigaudae* Deflandre & Cookson, p. 279-281, pl. 6, figs. 6, 10, text-fig. 42
- 1961 *Hystrichokolpoma rigaudae* Deflandre & Cookson 1954; Gerlach, p. 183-184, pl. 27, fig. 8-9
- 1963 *Hystrichokolpoma rigaudae* Deflandre & Cookson 1954; Brosius, p. 43, pl. 2, fig. 6
- 1973 *Hystrichokolpoma rigaudae* Deflandre and Cookson, 1955, p. 279-281, pl. 6, fig. 6, 10; text-fig. 42; Lentin & Williams, p. 71
- 1975 *Hystrichokolpoma rigaudae* Deflandre and Cookson; Haskell & Wilson, pl. 2, fig. 12
- 1977b *Hystrichokolpoma rigaudiae* Deflandre and Cookson, 1955, p. 279-281, pl. 6, fig. 6, 10; text-fig. 42; Lentin & Williams, p. 78
- 1983 *Hystrichokolpoma rigaudiae* Deflandre and Cookson, 1955; Goodman & Ford, p. 866, pl. 8, fig. 9
- 1994 *Hystrichokolpoma rigaudiae* Deflandre and Cookson 1955; Stover & Hardenbol, p. 32, pl. 3, fig. 18

Original Description: Shell globular, more or less ellipsoidal, with approximately axial symmetry and processes of 2 kinds not communicating with the interior, disposed in parallel series starting from 1 pole considered as apical [in fact, though, the taxon is being described upside-down]. Antapical pole with a large aperture having a straight or angular margin. Bases of the large processes marked by lines forming quadrangular areas that give the impression of plates. Large processes always closed at their distal extremities, generally widened and provided with more or less numerous and sometimes relatively long horns. The large process situated at the apical pole is often longer than the others and is sometimes prolonged into a hollow horn.

The narrow tubular processes are slightly widened or divided at their extremities, which are either open or closed. Certain filiform processes seem to be solid throughout.

The narrow processes forming the equatorial series are about 10 in number, of which some may be paired. Between the equatorial series and the apex there is a circle of 4 large appendages and a space occupied by a small number (3-5) of narrow processes similar to those of the equatorial belt.

Below the equator there is a circle of 6 large processes, or in certain specimens 1 of these processes may, perhaps, be duplicated or replaced by several thinner appendages. Membrane of the shell smooth or indistinctly granular (Deflandre & Cookson 1955, p. 280).

Size Range: Length excluding any processes = 42 (47) 55 μm (4 measurements). Width excluding any processes = 30 (41) 50 μm (4 measurements). Length including any processes = 63 (90) 124 μm (5 measurements). Width including any processes = 48 (68) 83 μm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/39	Gerlach 1961
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	

Remarks: The initial published appearance of the name, in Deflandre & Cookson 1954, p. 1236 or 1237, did not validly establish the name, because the authors did not provide a description.

Deflandre & Cookson's original spelling, *rigaudae*, without the second 'i', is an orthographic error (Voss et al. 1983, article 73.10). The error was overlooked in Lentin & Williams 1973 (p. 71; -dae) but introduced in Lentin & Williams 1977b (p. 78; -diae) in which the entry is annotated "O.C." indicating an orthographic change, though no further explanation is provided.

Hystrichokolpoma rigaudiae is apparently distinguishable from *Hystrichokolpoma cinctum* by the presence of secondary projections on the larger processes (Cookson 1956, p. 187-188).

***Hystrichokolpoma* sp. 3**

Pl. 49, figs. 10-12, Pl. 50, figs. 1-3

?1965 *Hystrichokolpoma rigaudae* Deflandre et Cookson 1955; De Coninck, p. 27-28, pl. 7, figs. 7-16

Description: Cysts of intermediate size, proximate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle apical, type tA; operculum free. Surface ornament present, non-tabular, comprising granules; very low (about 1 μm or lower); minute. Processes intratabular; non-fibrous, hollow, closed; with distal, secondary cusps distally; apparently formed by the coalescence of hollow spines, some of which may continue to project beyond the end of the processes. Tabulation clearly expressed, gonyaulacacean, inferred formula: ?4', 0a, 6", ?6c, 6"', ?1ps, 1''', Xs. Cingulum clearly expressed, indicated by a series of differentiated processes. Sulcus clearly expressed, a few differentiated, spine-like processes.

Size Range: Length excluding any processes = 31 (34) 37 μm (2 measurements). Width excluding any processes = 31 (36) 40 μm (2 measurements). Length including any processes = 55 (56) 58 μm (2 measurements). Width including any processes = 56 (75) 94 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: A few specimens of ?*Hystrichokolpoma* with digitate extensions to the pre- and postcingular processes closely resemble the most extreme cases of the *Diphyes colligerum* variant in which the pre- and postcingular processes are conjoined at their bases into intratabular process complexes. The decision (acknowledged as somewhat arbitrary) to assign the present forms to *Hystrichokolpoma*, is motivated by the amalgamation of thin processes into large hollow, intratabular, processes not just at their bases, but almost to their distal ends.

The two forms may indeed intergrade. If substantiated, this observation suggests a connection between *Diphyes* and *Hystrichokolpoma* which cannot be readily explained by anagenesis or divergence of lineages, since it does not occur early in the stratigraphic range of either genus. An eventual explanation will have to consider possibilities such as whether *Diphyes* and *Hystrichokolpoma* are ecoforms of one another, or whether one or both genera are actually polyphyletic groups of species, and our current classification in fact disguises a true phylogenetic link between natural, but unrecognised, clades.

***Hystrichokolpoma spinosum* Wilson 1988**

Pl. 50, figs. 4-12, Pl. 51, figs. 1-3

1988 *Hystrichokolpoma spinosum* Wilson, p. 22, pl. 10, figs. 7a-b, 8

Original Description: Cyst of intermediate size, bi-layered, with thin smooth endophragm and periphragm; both layers in close contact except at base of intratabular processes. Precingular and postcingular processes fairly short, conical to polygonal, hollow with closed tips and adorned with thin solid spines (length up to 11 µm) at the distal extremity. Antapical process relatively large, conical, and adorned with numerous short spinules (length 2-3 µm). Paracingular and parasulcal processes simple or bifurcate, relatively long and thin. Apical process relatively long and spiny. Paratabulation 1-4', 6", 6c, 5-6"', 1p, 1"', 5-6s. Archeopyle with zig-zag margin and deep parasulcal notch. Paracingulum indicated by up to 12 single or bifurcate processes, interrupted by parasulcus on ventral surface (Wilson 1988, p. 22).

Size Range: Length excluding any processes = 39 (43) 48 µm (3 measurements). Width excluding any processes = 37 (39) 41 µm (3 measurements). Length including any processes = 50 (59) 70 µm (3 measurements). Width including any processes = 60 (65) 71 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Remarks: The present forms appear slightly less spinose than Wilson's (1988) type material, and may be closer to *Hystrichokolpoma torquata* Damassa 1984, p. 825-826, pl. 3, figs. 1-8, pl. 4, figs. 9-11, text-fig. 7, from the Eocene of northern California.

Genus *Diphyes* Cookson 1965a emend. Goodman & Witmer 1985

1965a *Diphyes* Cookson, p. 85

1966b *Diphyes* Cookson 1965: 85 emend. Davey & Williams, p. 95-96

1970b *Lingulaspheera* Drugg, p. 817

1978 *Diphyes* Cookson 1965a emended Davey & Williams in Davey *et al.* 1966; Stover & Evitt, p. 38-39

1985 *Diphyes* Cookson 1965 emend. Goodman & Witmer, p. 76-77

Type Species: *Diphyes colligerum* (Deflandre & Cookson 1955, p. 278-279, pl. 7, fig. 3) Cookson 1965a, p. 86-87 [Early Eocene]

Original Description: Shell composed of two parts, more or less unequal in size. The anterior part circular in outline with or without appendages. Archeopyle apical. The posterior part roughly bell-shaped to spherical with a small circular antapical opening and without typical appendages (Cookson 1965a, p.85).

Remarks: Many New Zealand examples of *Diphyes* species, especially *Diphyes colligerum*, exhibit proximally conjoined pre- and postcingular processes, clearly demonstrating a tabulation (though the exact formula may be obscure) and strongly suggestive of a close affinity with *Hystrichokolpoma* (notably *Hystrichokolpoma* sp. 3).

***Diphyes colligerum* (Deflandre & Cookson 1955) Cookson 1965a**

Pl. 51, figs. 4-9

1955 *Hystrichosphaeridium colligerum* Deflandre & Cookson, p. 278-279, pl. 7, fig. 3

1965a *Diphyes colligerum* (Deflandre & Cookson 1955, p. 278-279, pl. 7, fig. 3) Cookson, p. 86-87

1970b *Lingulaspheera spinula* Drugg, p. 817-818, figs. 10G, 11D-E, 12A-B

1978 *Diphyes spinulum* (Drugg 1970b) Stover & Evitt, p. 39

1982c *Diphyes* cf. *colligerum* (Deflandre & Cookson); Wilson, p. 4, pl. 2, figs. 1-3

1984b *Diphyes colligerum* (Deflandre and Cookson, 1955) Cookson, 1965; Helenes, p. 94, 104, pl. 3, fig. 16

Original Description: Shell globular, almost spherical; processes numerous, tubular, straight or slightly flexuous, with a conical base and a closed capitate or slightly furcate apex. At 1 pole of the shell there is a large, hollow, cylindro-conical outgrowth closed by a rounded conical apex. This outgrowth, like the small processes, does not communicate with the interior of the shell. It is frequently ornamented distally with a circle of short, blunt, hollow, conical knobs. Membrane of shell finely granular (Deflandre & Cookson 1955, p. 278).

Emended Description of Goodman & Witmer 1985: Skolochorate cysts with subspheroidal body bearing numerous nontabular or intratabular processes of nearly uniform size and a single large antapical process. Paratabulation gonyaulacacean; indicated by archeopyle, shape of the antapical process base, and rarely by the tendency of adjacent process bases to fuse into clusters apparently within the limits of individual paraplates. Archeopyle variable: Type (4A), (4A)P, 2P or P (Goodman & Witmer 1985, p. 76).

Size Range: Length excluding any processes = 25 (31) 35 μm (4 measurements). Width excluding any processes = 30 (36) 40 μm (4 measurements). Length including any processes = 38 (55) 64 μm (11 measurements). Width including any processes = 40 (62) 73 μm (7 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f487 (L23122)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Diphyes* aff. *colligerum

Pl. 51, figs. 10-12, Pl. 52, figs. 1-9

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate. Archeopyle apical, type tA; operculum free. Surface ornament lacking. Processes intratabular; non-fibrous, unbranched, hollow, closed; variably coalescent into intratabular groups proximally; the antapex carries a differentiated, large, variably inflated process; often with secondary cusps; and which may have a constricted distal opening. Hyposome sexiform; torsion dextral.

Size Range: Length excluding any processes = 39 (46) 52 μm (2 measurements). Width excluding any processes = 38 (39) 40 μm (2 measurements). Length including any processes = 52 (57) 62 μm (2 measurements). Width including any processes = 58 (67) 75 μm (3 measurements).

Distribution: Frequent.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: Distinguished from *D. colligerum* s.s. by having pre- and postcingular processes which are proximally conjoined into process complexes. In extreme cases, this taxon more closely resembles *Hystrichokolpoma* than *Diphyes*, particularly *Hystrichokolpoma* sp. 3.

***Diphyes ficusoides* Islam 1983b**

Pl. 52, figs. 10-12

1982b *Diphyes* aff. *colligerum* Cooks. & Eis.; Wilson, p. 7, pl. 3, fig. 1

1983b *Diphyes ficusoides* Islam, p. 338, pl. 2, figs. 8-9

1994 *Diphyes ficusoides* Islam 1983; Bujak, pl. 2, fig. 1

Original Description: Cyst subspherical, skolochorate and biphragmal; phragma adpressed; periphragm chagrinata or reticulate; many nontabular tubular processes tapering from broad circular bases to narrow necks before ending in distal aculeation or wider rims, proximally closed, distally open but rarely a few processes closed, a few neighbouring pairs sometimes proximally joined; antapical process inflated, distinctively broad with biconvex ambitus in all lateral views with figlike appearance. Antapical process rises from a circular base, proximally closed, distally open but constricted with maximum width at base or mid-length; archeopyle apical type (tA) (Islam 1983, p. 338).

Size Range: Length excluding any processes = 38 μm (one measured specimen). Width excluding any processes = 43 μm (one measured specimen). Length including any processes = 69 μm (one measured specimen). Width including any processes = 75 μm (one measured specimen).

Distribution: Rare; reported from only a single location in New Zealand.

Age/Stage	Location	Sample	Sample Reference
Kaiatan-Runangan	Jacksons Paddock, Oamaru-Dunedin, New Zealand	J41/f8914 (L04979)	Wilson 1982b

***Diphyes brevispinum* Bujak 1994**

Pl. 53, figs. 1-3

1994 *Diphyes brevispinum* Bujak, p. 121-123, pl. 2, figs. 4-6

Original Description: Cyst subspherical, skolochorate and biphragmal, endophragm and periphragm adpressed except beneath the processes. Periphragm smooth to chagrinata, forming numerous nontabular processes. Processes other than the antapical process less than 5 μm in length, tubular, tapering from broader circular bases to narrow, open or closed terminations. Antapical process large, inflated, ovoidal to subspherical, with a closed circular base, and a constricted distal opening. Archeopyle apical; operculum tetraplacoid, contiguous (Bujak 1994, p. 123).

Size Range: Length excluding any processes = 40 μm (one measured specimen). Width excluding any processes = 43 μm (one measured specimen). Length including any processes = 60 μm (one measured specimen). Width including any processes = 55 μm (one measured specimen).

Distribution: This taxon is known from a single specimen in the present study.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996

Remarks: The pre- and postcingular processes are at the long end of the published range (~5 μm) but it is otherwise apparently identical to Bujak's (1994) type material. It is, however, considerably younger: Kaiatan (early Priabonian) rather than Ypresian.

Genus *Lingulodinium* Wall 1967a

1967a *Lingulodinium* Wall, p. 109

Type Species: *Lingulodinium machaerophorum* (Deflandre & Cookson 1955, p. 274, pl. 9, figs. 4, 8) Wall 1967, p. 109 [Miocene]

Original Description: Spherical to ovoid dinoflagellate cysts which, after dehiscence, possess a large, compound epithelial archeopyle representing the loss of either four or five precingular plate-areas. The remainder of the epitheca forms an elongate angular projection or lingula; this corresponds to several (apical, intercalary, and one precingular) plate-areas. The test wall is micro-granular to microreticulate and ornamented with numerous intratabular spines (Wall 1967, p. 109).

Remarks: The genus was subsequently emended by Wall & Dale 1973, p. 24, to accommodate the observation that *Lingulodinium* species exhibit archeopyle types ranging from P to 5P and sometimes, though more rarely, incorporating the apical plates as well. This recommendation appears to have been widely adopted and is also used herein.

What is less clear, however, is their suggestion that the archeopyle sometimes includes intercalary plates, or that the genus even possesses intercalary plates. As noted in Stover & Evitt 1978 (p. 172) for example, "the presence of anterior intercalary paraplates on the epicyst of *Lingulodinium* has not been documented. We have not, therefore, included this type of archeopyle in our analysis of the genus." Small plates occupying a dorsal "intercalary" position are known to occur in some gonyaulacaceans, however, and a large "supernumary" climactal plate possessed by *Lingulodinium* "may be homologous with one of the small intercalary plates, Ci, of

Mesozoic genera" although there is "no obvious stratigraphic connection" between them (Fensome et al. 1993b, p. 85).

Lingulodinium ?machaerophorum (Deflandre & Cookson 1955) Wall 1967

Pl. 53, figs. 4-9

1955 *Hystrichosphaeridium machaerophorum* Deflandre & Cookson 1955, p. 274, pl. 9, figs. 4, 8

1967a *Lingulodinium machaerophorum* (Deflandre and Cookson 1955) Wall, p.109

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate. Archeopyle precingular, type ?A+3P; operculum free. Surface ornament lacking. Processes non-tabular; non-fibrous, unbranched, apparently hollow, closed; somewhat sinuous. Tabulation not expressed.

Size Range: Length excluding any processes = 47 µm (one measured specimen). Width excluding any processes = 48 µm (one measured specimen). Length including any processes = 78 µm (one measured specimen). Width including any processes = 73 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: May be conspecific with *Lingulodinium machaerophorum*. Although considerably older than the type, *L. machaerophorum* is known to extend back to the Eocene (Rob Fensome, *pers. comm.*)

Genus *Operculodinium* Wall 1967a emend. Matsuoka et al. 1997

1967a *Operculodinium* Wall, p. 110-111

1978 *Operculodinium* Wall 1967; Stover & Evitt, p. 178-179

1997 *Operculodinium* Wall 1967 emend. Matsuoka et al., p. 22

Type Species: *Operculodinium centrocarpum* (Deflandre & Cookson 1955, p. 272-273, pl. 8, figs. 3-4) Wall 1967, p. 111 [Miocene]

Original Description: Spherical to ovoid cysts possessing simple, dorsal precingular archeopyles (reflecting plate 3"), and lacking polar structures. A weakly defined girdle and ventral sulcal depression often present. Cell wall double, the inner thin and outer thicker and microgranular or microreticulate. Elements of ornamentation variable, from small cones to long spines, but all with circular, minutely striated bases and often capitate extremities. Spine arrangement intratabular with several spines to each plate area, commonly arranged immediately within the reflected plate-area margins (Wall 1967, p. 110).

Emended Description of Matsuoka et al. 1997: Spherical to ovoid cysts possessing a 3" precingular archeopyle and lacking polar structures. A weakly defined girdle and ventral sulcal depression may or may not be present. Cell wall composed of a thin smooth endophragm and a thicker microgranular or microreticulate periphragm. Positive sculpturing varies from small cones to long processes with circular bases. Process bases may be striate or microreticulate. A variety of distal process shaft terminations may be present, including capitate, recurved, truncated or patulate, though usually one type per species. Processes distribution [sic] nontabular and/or intratabular, with several processes per paraplate area (Matsuoka et al. 1997, p. 22).

Remarks: The emended generic diagnosis provided by Matsuoka et al. (1997, p. 22), following their restudy of the genoholotype, expands the wording of the original, but adds little to either broaden or restrict the circumscription. The inclusion of non-tabular (as opposed to only intratabular) processes is moot: the plate boundaries are unknown, so there is no practical means to distinguish between the two kinds. The emendation adds "recurved, truncated or patulate" to the original capitate, as recognised process endings.

A range chart for species of *Operculodinium* is provided in Appendix 2, chart 5.

Operculodinium ?centrocarpum (Deflandre & Cookson 1955) Wall 1967

Pl. 53, figs. 10-12, Pl. 54, figs. 1-3

1955 *Hystrichosphaeridium centrocarpum* Deflandre & Cookson, p. 272-274, pl. 8, figs. 3-5

- 1961 *Baltisphaeridium centrocarpum* (Deflandre & Cookson 1955, p. 272-273, pl. 8, figs. 3-4) Gerlach, p. 192-193
- 1965 *Cordosphaeridium centrocarpum* (Deflandre & Cookson 1955, p. 272-273, pl. 8, figs. 3-4) De Coninck, p. 33
- 1966a *Cordosphaeridium tiara* (Klumpp 1953) *centrocarpum* (Deflandre & Cookson 1955) Morgenroth, p. 26, pl. 5, fig. 12, pl. 6, fig. 1
- 1967a *Operculodinium centrocarpum* (Deflandre and Cookson 1955) Wall, p. 111, pl. 16, figs. 1-2, 5
- 1969 *Cordosphaeridium microtriainum* subsp. *centrocarpum* (Deflandre & Cookson 1955, p. 272-273, pl. 8, figs. 3-4) De Coninck, p. 32
- 1978 *Cleistosphaeridium centrocarpum* (Deflandre & Cookson 1955, p. 272-273, pl. 8, figs. 3-4) Jiabo, p. 61
- 1983 *Operculodinium centrocarpum* (Deflandre & Cookson, 1955) Wall, 1967; Goodman & Ford, p. 866, pl. 8, fig. 8
- 1997 *Operculodinium centrocarpum* (Deflandre & Cookson) Wall 1967; Matsuoka et al., p. 22-23, pl. 1, figs. 1-6, pl. 2, figs. 1-9
- 2005 *Operculodinium centrocarpum*; Schiøler, pl. 3, fig. 3

Original Description: Shell globular, more or less ellipsoidal (probably by deformation), covered with numerous straight, slender processes placed irregularly or with a certain alignment. Processes solid, showing radiating fibrils at their point of insertion on the shell, which is clearly ornamented with a fine reticulum. The slightly widened apices of the processes are fringed with 10 or more small curved spines (this structure is only visible with a high-powered objective) (Deflandre & Cookson 1955, p. 273).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate; thin, about 1 µm in thickness. Archeopyle precingular, type P (3"); large. Surface ornament present, non-tabular, comprising spines. Capitata distally. Nature of spines short, sinuous, expanding proximally, length of spines 5-10 µm. Cingulum lacking.

Size Range: Length excluding any processes = 35 (43) 47 µm (3 measurements). Width excluding any processes = 35 (44) 50 µm (3 measurements). Length including any processes = 54 (57) 60 µm (5 measurements). Width including any processes = 54 (60) 63 µm (3 measurements).

Distribution: Frequent. Noted by Goodman & Ford (1983, p. 866) as having "little stratigraphic value."

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany		Gerlach 1961
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f178 (L11927)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f171 (L11920)	
late Eocene-early Oligocene	DSDP Leg 71, Hole 511, Falkland Plateau, southwest Atlantic Ocean		Goodman & Ford 1983
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	

Remarks: The form encountered in this study quite closely resembles the type species of *Operculodinium*, *O. centrocarpum*, especially those specimens (e.g. Pl. 54, figs. 1-3) with slightly longer processes.

Jux (1976) reports morphological variation in a Holocene population of *O. centrocarpum* ranging from proximate to chorate. Leaving aside the specific identity of Jux's Holocene material with Deflandre & Cookson's (1955) Miocene type material, it is clear that real dinoflagellate populations exhibit considerable morphological variation, so it seems reasonable not to accord too much significance to the exact length of the processes alone.

Some Quaternary forms attributed to *Operculodinium centrocarpum* by Wall 1967b are further analysed in Matsuoka et al. 1997, which concludes they are a different species owing, principally, to a consistently smaller central body diameter and process lengths. [The "cyst diameter" referred to frequently in Matsuoka et al. 1997 is the diameter of the central body, excluding processes, though this important point is not made explicit.] The ratio between the dimensions they report, however, is very close to constant (0.23 versus 0.25) so it is evident that the dimensions of central body and processes scale in proportion to the overall size. If preservational artefacts (e.g. greater compression, which would tend to squash a spherical object into a flattened disc with a greater diameter) cannot be ruled out, then the case for separating these forms reduces to process length, again, and appears very weak indeed.

The extant dinoflagellate, *Protoceratium reticulatum* (Claparède & Lachmann) Bütschli, forms cysts which apparently are virtually indistinguishable from *Operculodinium centrocarpum*.

Operculodinium schioleri Clowes n. sp.

Pl. 54, figs. 4-12

?2005 *Operculodinium piaseckii*; Schiøler, pl. 2, fig. 7

Derivation of Name: Named after the dinoflagellate palynologist, Poul Schiøler.

Holotype: Sample K29/f097, slide L10914/SM031; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); Pl. 54, figs. 4-9

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, subspherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate; quite thin, about 1 µm in thickness. Archeopyle precingular, type P (3"). Processes ?gonal, spinose; ?fibrous, unbranched, apparently solid, generally less than about 12-13 µm; broadening proximally, capitate distally. Cingulum weakly expressed, indicated by the alignment of processes.

Size Range: Length excluding any processes = 60 (88) 108 µm (3 measurements). Width excluding any processes = 102 (106) 110 µm (2 measurements). Length including any processes = 80 (112) 133 µm (5 measurements). Width including any processes = 110 (118) 127 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f180 (L11929)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f173 (L11922)	
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996

Comparison: This form bears a slight resemblance to *Operculodinium piaseckii* Strauss and Lund 1992 but is distinguished by being markedly larger and in possessing fewer processes, which appear to be confined to the gonal areas.

***Operculodinium* sp. 10**

Pl. 55, figs. 1-3

Description: Cysts large, chorate, not dorso-ventrally compressed, subspherical, lacking horns; episome somewhat shorter than hyposome. Cyst wall two-layered; acavate; quite thin, about 1 µm in thickness. Archeopyle precingular, type P (3"); large. Processes ?gonal, spinose, somewhat sinuous; ?fibrous, unbranched, apparently solid, 20-30 µm; broadening proximally, capitate distally. Cingulum weakly expressed to moderately expressed, indicated by the alignment of processes.

Size Range: Length excluding any processes = 92 µm (one measured specimen). Width excluding any processes = 87 µm (one measured specimen). Length including any processes = 117 (121) 125 µm (2 measurements). Width including any processes = 122 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985

Remarks: *Operculodinium* sp. 10 differs from the type species, *O. centrocarpum*, in possessing fewer, relatively longer, spines, which appear to occupy (or at least cluster towards) the gonal positions. It differs from the form described here as *O. vulgare* in possessing relatively shorter spines, though it is possible that the two forms represent members of the same population. The stratigraphic range of *O. sp. 10* lies within that of *O. vulgare*.

***Operculodinium vulgare* Clowes n. sp.**

Pl. 55, figs. 4-9

?1982a *Operculodinium* sp.; Wilson, pl. 1, fig. 7

Derivation of Name: Latin, *vulgaris*, usual, commonplace, everyday; with reference to the taxon's ubiquity.

Holotype: Sample I43/f093, slide L16341/SM066; Burnside Formation, Puketeraki Core (Bortonian); Pl. 55, figs. 4-6

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate; quite thin, about 1 µm in thickness. Archeopyle precingular, type P (3"); large; operculum free. Processes ?gonal, spinose, somewhat sinuous; non-fibrous, unbranched, apparently solid, 30-40 µm; broadening proximally, capitate distally. Cingulum weakly expressed, indicated by the alignment of processes.

Size Range: Length excluding any processes = 52 (71) 95 µm (5 measurements). Width excluding any processes = 50 (61) 87 µm (4 measurements). Length including any processes = 40 (93) 170 µm (25 measurements). Width including any processes = 80 (98) 135 µm (9 measurements).

Distribution: Common. Widely found throughout a lengthy time range, from Bortonian (Bartonian) to early Whaingaroan (early Rupelian).

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f116 (L11052)	Clowes & Wilson 2006
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f184 (L11933)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f125 (L11936)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f262 (L13546)	
late Eocene-early Oligocene	Chalky Island, Fiordland, New Zealand	SM1319	Wilson 1982a
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: *Operculodinium vulgare* somewhat resembles ?*Hystrichosphaeridium paucifurcatum* Cookson & Eisenack 1961b in overall appearance. An implication of the generic placement of ?*H. paucifurcatum* is that it has an apical archeopyle (clearly different from the precingular archeopyle of *O. vulgare*) although the brief species description makes no specific mention of the archeopyle and the single illustration (Cookson & Eisenack 1961b, pl. 2, fig. 15) shows a pale area near the apex which looks as if it *might* be a distorted precingular archeopyle. Pending some further work on the Australian material, I have elected to follow the recommendation in Stover & Evitt 1978, p. 56, that the specific name *H. paucifurcatum* be restricted to the holotype.

Operculodinium vulgare differs from the type species, *O. centrocarpum* in possessing fewer, relatively longer, spines, which appear to occupy (or at least cluster towards) the gonial positions. It differs from the form informally listed here as *O. sp. 10* in possessing relatively longer spines.

***Operculodinium ?janduchenei* Head et al. 1989b**

Pl. 55, figs. 10-12, Pl. 56, figs. 1-2

?1977 *Operculodinium* sp. Jan du Chêne, p. 106, pl. 1, figs. 7-8

?1989b *Operculodinium janduchenei* Head et al., p. 459, pl. 4, figs. 7, 8, 12

?1993 *Operculodinium janduchenei* Head et al., 1989b Martin, p. 115, figs. 10A-F

Original Description: [Diagnosis] Cysts small, proximochorate, with subspherical or broadly ellipsoidal body having a granulate wall surface. Processes are short conical and hollow, and may be distally closed or truncated and open. Distribution is apparently nontabular. Archeopyle precingular Type P (presumably Type P3). Operculum free. There is no other indication of paratabulation.

[Description] Wall surface varies from coarsely to faintly granulate, and some specimens may have short, solid, conical granules interspersed between processes, as described by Mudie (1987, p. 805). Processes are variable but most are open distally, although some specimens were observed with predominantly distally closed processes, and often specimens were found to possess a range of process morphologies. On the holotype, most processes are distally open, although some appear to be closed distally. Processes have a fairly regular distribution and appear to be nontabular. The archeopyle is presumably formed by loss of paraplate 3" (Head et al. 1989b, p. 459).

Description of Study Material: Cysts small, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament present, non-tabular, comprising small clavae; densely covering the surface. Processes non-tabular, comprising short clavae; apparently solid, about 5 µm long. Tabulation not expressed. Cingulum lacking to weakly expressed, indicated by the alignment of processes. Not expressed.

Size Range: Length excluding any processes = 44 µm (one measured specimen). Width excluding any processes = 43 µm (one measured specimen). Length including any processes = 48 µm (one measured specimen). Width including any processes = 49 µm (one measured specimen).

Distribution: Very rare in the present study.

Age/Stage	Location	Sample	Sample Reference
late Miocene	ODP Leg 105, Site 646, Labrador Sea	105-646B-78X-CC, 1-3 cm.	Head et al. 1989b
Miocene			Jan du Chêne 1977
late Eocene	Mallee Cliffs bore 36465, 183-187 m., central Murray Basin, New South Wales, Australia	Slide 2806-1	Martin 1993
late Eocene	Mallee Cliffs bore 36465, 192-197 m., central Murray Basin, New South Wales, Australia	Slide 2828-3	Martin 1993
late Eocene	Mallee Cliffs bore 36465, 201-206 m., central Murray Basin, New South Wales, Australia	Slide 2829-1	Martin 1993
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	

Remarks: The identification is provisional because forms encountered in this study appear to possess granules which are slightly larger and more clavate than the type material. However, insufficient material has been recovered to give a reasonable indication of any variability within the population.

***Operculodinium pulcher* Clowes n. sp.**

Pl. 56, figs. 3-12

?1993 *Operculodinium longispinigerum* Matsuoka 1983; Martin, p. 115, figs. 10G-I

Derivation of Name: Latin, *pulcher*, beautiful, handsome; with reference to the delicate elegance of the processes.

Holotype: Sample I43/f093, slide L16341/SM042; Burnside Formation, Puketeraki Core (Bortonian); Pl. 56, figs. 4-6

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate; quite thin, about 1 µm in thickness. Archeopyle precingular, type P (3"); large. Processes non-tabular, spinose, straight; non-fibrous, unbranched, apparently solid, 10-15 µm in length; typically capitate distally; slender; process tips quite variable; from more or less acuminate to almost furcate. Cingulum not expressed.

Size Range: Length excluding any processes = 28 (29) 30 µm (6 measurements). Width excluding any processes = 28 (29) 30 µm (5 measurements). Length including any processes = 38 (52) 58 µm (9 measurements). Width including any processes = 45 (57) 75 µm (14 measurements).

Distribution: Locally common but encountered in only a few samples.

Age/Stage	Location	Sample	Sample Reference
late Eocene	Mallee Cliffs bore 36465, 183-187 m., central Murray Basin, New South Wales, Australia	Slide 2806-1	Martin 1993
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	

Comparison: Holistically, this taxon has a very similar appearance to *Melitasphaeridium pseudorecurvatum* (Morgenroth 1966a), but differs in possessing many more processes (approximately twice the number). Additionally, the processes of *Melitasphaeridium* are said to be hollow and open, whereas these do not seem to be so, although some specimens do appear to possess a minute sinus at the very base of the processes.

Remarks: The process tips exhibit quite a variety of development, from almost none (e.g. Pl. 56, fig. 7) to very well-developed radial spinules (e.g. Pl. 56, fig. 10). A specimen from the late Eocene of south-eastern Australia illustrated in Martin 1993 (fig. 10G-I) resembles the former (Pl. 56, fig. 7).

***Operculodinium* sp. 5**

Pl. 57, figs. 1-6

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); large. Processes non-tabular, spinose, somewhat sinuous; non-fibrous, unbranched, apparently solid, 10-15 μm in length; capitate distally; slender. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 30 (32) 34 μm (2 measurements). Width excluding any processes = 30 (30) 31 μm (2 measurements). Length including any processes = 51 (53) 55 μm (2 measurements). Width including any processes = 45 (48) 52 μm (2 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	

***Operculodinium* sp. 7**

Pl. 57, figs. 7-12

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament present, non-tabular, comprising a reticulum with angular lacunae. Processes ?gonal, spinose, straight or gently curved; non-fibrous, unbranched, apparently solid, highly variable, from about 5 to 15 μm in length; acuminate distally. Tabulation not clearly expressed. Cingulum weakly expressed, indicated by a differentiated series of generally longer processes. Sulcus weakly expressed, alignment of processes; more or less vertical.

Size Range: Length excluding any processes = 33 μm (one measured specimen). Width excluding any processes = 29 μm (one measured specimen). Length including any processes = 44 μm (one measured specimen). Width including any processes = 48 μm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

***Operculodinium ?xanthium* (Benedek 1972) Stover & Evitt 1978**

Pl. 58, figs. 1-3

1972 *Cordosphaeridium xanthium* Benedek, p. 27-28, pl. 9, fig. 8, text-fig. 9

1978 *Operculodinium xanthium* (Benedek 1972) Stover & Evitt, p. 179

Original Description: [No translation available] Eine Art der Gattung *Operculodinium*, deren Kapseloberfläche eine von derben Fasern aufgebaute netzartige Struktur aufweist, aus der zahlreiche kleine und zugespitzte Fortsätze entspringen (Benedek 1972, p. 27).

Description of Study Material: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"). Surface ornament present, non-tabular, comprising a dense reticulum. Processes non-tabular, comprising short spines, straight or gently curved; non-fibrous, unbranched, apparently solid, about 5 µm long. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 45 µm (one measured specimen). Width excluding any processes = 45 µm (one measured specimen). Length including any processes = 47 (60) 78 µm (3 measurements). Width including any processes = 54 (68) 83 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Nine Mile Bluff, Westland, New Zealand	J31/f9186 (L08325)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985

Remarks: This species appears very similar to, and may be conspecific with, *Operculodinium xanthium* (Benedek 1972) Stover & Evitt 1978. A SEM image appearing in Brinkhuis, Sengers, et al. 2003 (pl. 1, fig. 196) appears similar, also.

Operculodinium ?xanthium differs from the type species, *O. centrocarpum* in possessing relatively shorter spines. The spines appear stiffer and less sinuous than those of the form informally described here as *O. sp. 3*, though it is possible that the two forms represent members of the same population.

Operculodinium sp. 3

Pl. 58, figs. 4-6

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"); large. Processes non-tabular, comprising short spines, usually curved; unbranched, apparently solid, 5-10 µ in length. Cingulum lacking to weakly expressed.

Size Range: Length excluding any processes = 55 µm (one measured specimen). Width excluding any processes = 55 µm (one measured specimen). Length including any processes = 53 (62) 70 µm (2 measurements). Width including any processes = 65 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: *Operculodinium sp. 3* differs from the type species, *O. centrocarpum* in possessing relatively shorter spines. The spines appear more flexible and sinuous than those of the form tentatively attributed to *O. ?xanthium*, though it is possible that the two forms represent members of the same population.

Operculodinium sp. 6

Pl. 58, figs. 7-9

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"). Surface ornament lacking. Processes non-tabular, spinose, straight or gently curved; non-fibrous, unbranched, apparently solid, 10-15 µm in length. Tabulation not expressed. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 44 µm (one measured specimen). Width excluding any processes = 40 (44) 47 µm (2 measurements). Length including any processes = 60 (68) 80 µm (5 measurements). Width including any processes = 60 (64) 67 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f057 (L09214)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985

Remarks: *Operculodinium* sp. 3 differs from the type species, *O. centrocarpum* in possessing relatively longer spines. Although it is possible that the two forms represent end members of the same population, *O. Sp. 6* appears to be confined to the older part of their aggregate stratigraphic range.

Operculodinium crouchii Clowes n. sp.

Pl. 58, figs. 10-12, Pl. 59, figs. 1-12

?1982a *Operculodinium tiara* (Klumpp); Wilson, p. 8, pl. 1, fig. 8

Derivation of Name: Named after the dinoflagellate palynologist, Dr. Erica Crouch.

Holotype: Sample J42/f302, slide L23132/SM019; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); Pl. 58, figs. 10-12

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns; episome and hyposome more or less equal in length. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"); operculum free. Surface ornament present, non-tabular, comprising a dense reticulum. Processes non-tabular, spinose, somewhat sinuous; non-fibrous, unbranched, apparently solid, 10-15 µm in length; dolabrate distally. Tabulation not expressed. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 42 (51) 59 µm (7 measurements). Width excluding any processes = 40 (48) 57 µm (7 measurements). Length including any processes = 55 (71) 82 µm (7 measurements). Width including any processes = 50 (67) 85 µm (7 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
late Eocene-early Oligocene	Chalky Island, Fiordland, New Zealand	L6893	Wilson 1982a
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	

Comparison: Insofar as it is a thick-walled chorate cyst with a precingular archeopyle and reticulate surface ornament, *Operculodinium crouchii* resembles *O. tiara* (Klumpp 1953) Stover & Evitt 1978. Klumpp's illustrations comprise a somewhat inferior photograph (pl. 17, fig. 8) and two line drawings (pl. 17, figs. 9-10) which depict a form with bluntly terminated processes (esp. pl. 17, fig. 9) but which reveal few diagnostic details.

Sarjeant (1981) redescribed a number of Klumpp's (1953) types held in the Kiel collections. For some reason, however, he failed to include "*Hystriosphæridium*" *tiara* among his redescrptions, and so there does not appear to be any more recent illustration of the holotype than Klumpp's own.

A few years later, Morgenroth (1966a), who presumably had access to Klumpp's types, provided an emended description for *tiara*. His illustrations (pl. 5, figs. 10-11), however, although seeming to portray a thick-walled chorate cyst of the *Operculodinium* type, are little more enlightening than Klumpp's line-drawings, and do not really convincingly resemble them.

In summary, although the present form is somewhat similar to *O. tiara* in overall appearance, the processes are typically acuminate, rather than truncated (albeit somewhat 'kinked' near the distal ends in the manner named dolabrate by Eaton et al. 2001). Unless or until the Kiel types are reassessed, the present material is treated separately.

***Operculodinium* sp. 11**

Pl. 60, figs. 1-6

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"). Surface ornament lacking. Processes non-tabular, spinose, straight or gently curved; non-fibrous, unbranched, apparently solid, 10-15 µm in length. Tabulation not expressed. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 45 (51) 57 µm (2 measurements). Width excluding any processes = 40 (46) 53 µm (2 measurements). Length including any processes = 62 (72) 82 µm (2 measurements). Width including any processes = 60 (70) 80 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: Compared with *O. crouchii*, this is a more robust form in which the spines appear more prominent. However, the two forms occur in the same area and with consistent stratigraphic ranges; it is possible they represent end members of the same population.

***Operculodinium* sp. 12**

Pl. 60, figs. 7-12

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall two-layered; acavate. Archeopyle precingular, type P (3"). Surface ornament lacking. Processes non-tabular, spinose, straight or gently curved; non-fibrous, unbranched, apparently solid, 10-15 µm in length. Tabulation not expressed. Cingulum not expressed. Sulcus not expressed.

Size Range: Length excluding any processes = 42 (44) 47 µm (2 measurements). Width excluding any processes = 32 (38) 45 µm (2 measurements). Length including any processes = 65 (68) 70 µm (2 measurements). Width including any processes = 50 (59) 68 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	

Remarks: Compared with *O. crouchii*, this is a more gracile form in which the spines appear less prominent. However, the two forms are broadly similar and have overlapping geographic and stratigraphic ranges; it is possible they represent end members of the same population.

Genus *Samlandia* Eisenack 1954b

- 1954b *Palmnickia* Eisenack, p. 69
- 1954b *Samlandia* Eisenack, p. 76
- 1978 *Samlandia* Eisenack 1954; Stover & Evitt, p. 185-186
- 1984 *Samlandia*; Damassa, p. 61

Type Species: *Samlandia chlamydophora* Eisenack 1954b, p. 76, pl. 11, figs. 12-15 [Early Oligocene]

Original Description: Central body spherical to slightly elliptical, surrounded by a thin second membrane which is connected to the inner shell by supports, whose cross sections form irregularly curved (vermiform) lines. Pylome at pole of the ellipsoid (translated from Eisenack 1954b, p. 76, by Stover & Evitt 1978, p. 185).

***Samlandia reticulifera* Cookson & Eisenack 1965a**

Pl. 61, figs. 1-6

1965a *Samlandia reticulifera* Cookson & Eisenack, p. 126-127, pl. 15, figs. 10-15

1982b *Samlandia reticulifera* C. & E.; Wilson, p. 8, pl. 3, figs. 14-16

Original Description: Shell oval with a short, conical, apical and antapical projection and two lower, broader and less clearly defined projections in an equatorial position, one on each side. Wall of shell 2-layered, the inner ornamented by a complete or incomplete reticulum. The relatively thick muri support short, thin, closely and vertically arranged appendages with broadened apices (Pl. 15, fig. 15) which, by their close approximation and possible coalescence, form the closely opposed outer thin layer of the wall. The archeopyle is sub-apical and the operculum approximately quadrangular or rectangular in outline (Cookson & Eisenack 1965a, p. 126-127).

Size Range: Length including any processes = 102 (104) 106 μm (2 measurements). Width including any processes = 77 (78) 78 μm (2 measurements).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Runangan	Waiareka Volcanics formation, Jacksons Paddock, Oamaru, Otago, New Zealand	J41/f8914	Wilson 1982b
late Eocene	Browns Creek Clays, southwest Victoria, Australia		Cookson & Eisenack 1965a
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Remarks: *Samlandia reticulifera* Cookson & Eisenack 1965a apparently differs from *S. chlamydophora* in "in the prominent reticulation of the inner layer of the wall and the close approximation of the enclosing membrane. In *S. chlamydophora* the outer membrane is widely separated from the inner wall and is supported by long unbranched laminae" (Cookson & Eisenack 1965a, p. 127).

Although not stated by Cookson & Eisenack (1965a), it is also apparent that the endophragm is very much thinner in *S. reticulifera* than in *S. chlamydophora*. In this respect, it is very much closer to *S. tenuis*.

***Samlandia tenuis* Clowes n. sp.**

Pl. 61, figs. 7-12, Pl. 62, figs. 1-3

?1961 *Palmnickia lobifera* Eisenack 1954; Gerlach, p. 207-208, pl. 29, fig. 10

1982b *Samlandia* cf. *chlamydophora* Eis.; Wilson, p. 7, pl. 2, fig. 16, pl. 4, fig. 8

1984 *Samlandia* cf. *chlamydophora*; Damassa, p. 61, pl. 5, figs. 10-11

1993 *Samlandia chlamydophora* Eisenack, 1954; Brinkhuis & Biffi, p. 177, pl. 9, fig. 7

1994 *Samlandia chlamydophora* Eisenack 1954; Stover & Hardenbol, p. 33, pl. 8, fig. 54

2002 *Samlandia chlamydophora* Eisenack, 1954; De Coninck, pl. 13, figs. 3-5

Derivation of Name: Latin, *tenuis*, thin, slender, slight; with reference to the cyst walls which are much thinner than the otherwise similar species, *Samlandia chlamydophora*.

Holotype: Sample K29/f097, slide L10914/SM019; Port Elizabeth Member, Cape Foulwind Section, Westland, New Zealand (early Whaingaroan); Pl. 61, figs. 7-12

Description: Cysts intermediate to large, proximate, not dorso-ventrally compressed, prolate, with one apical horn; episome and hyposome more or less equal in length. Apical horn well developed, apex rounded to subconical; antapical horns lacking. Cyst wall single-layered, with an ectophragm; the more or less continuous ectophragm is supported on numerous processes arising from the autophragm. Archeopyle precingular, type P (3"); operculum free. Surface ornament present, non-tabular, comprising coarse reticulum. Processes non-tabular, arising from the muri of the reticulum, irregular; non-fibrous, apparently solid. Tabulation weakly expressed, apparently gonyaulacacean. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 50 (96) 139 μm (33 measurements). Width = 65 (87) 100 μm (9 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/73	Gerlach 1961
late Rupelian	Monte Cagnero Section A, Italy	CA 114-01	Brinkhuis & Biffi 1993
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f180 (L11929)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f108 (L11044)	
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f170 (L11919)	
Runangan	Totara Limestone formation, mouth of Kakanui River, Oamaru, Otago, New Zealand	J42/6837	Wilson 1982b
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	
late Eocene-early Oligocene	Grimmerten section, eastern Belgium	-3.3 m.	De Coninck 2002
Kaiatan	Raki Siltstone, Rakis Table, Oamaru, Otago, New Zealand	J41/f8841	Wilson 1982b
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: This form has often been illustrated in the past (see synonymy) as *Samlandia chlamydophora*. Note, however, that *S. chlamydophora* possesses an extremely thick endophragm+periphragm: more than 4 µm, see Eisenack 1954b, especially pl. 11, figs. 12 and 13, and Text-Fig. 21 herein.

The present form possesses a very much thinner endophragm+periphragm; typically 2-3 µm, which serves to distinguish it readily. Moreover, other than the archeopyle, there are no indications of tabulation on *S. chlamydophora* whereas occasional discontinuities in the ectophragm of *S. tenuis* may indicate plate boundaries (e.g. see Williams et al. 1973, fig. 1, Damassa 1984, p. 61, pl. 6, figs. 4, 5).

Samlandia tenuis combines the wide spacing between endophragm+periphragm and ectophragm of *Samlandia chlamydophora* with the thin endophragm of *Samlandia reticulifera*.



Text-Fig. 21: Specimen of *Samlandia chlamydophora* from the type slide; possibly the holotype itself but, if so, it has been 'rolled' since being imaged in Eisenack 1954b (pl. 11, fig. 12).

Genus *Stoveracysta* Clowes 1985

1985 *Stoveracysta* Clowes, p. 29-30

1987 *Stoveracysta* Clowes 1985, p. 29; Stover & Williams, p. 205-206

Type Species: Stoveracysta kakanuiensis Clowes 1985, p. 32, 34, pl. 1, figs. 1-12; pl. 2, figs. 1-12; text-figs. 4a-b [Early Oligocene]

Original Description: Proximate to proximochorate single layered cysts, subspherical in shape, lacking horns, ornamented by sutural to penitabular ridges or septa delineating a gonyaulacacean tabulation, formula: 4', 6", X to 6c, 6"', 1p, 1"', X to 4s. The four plates of the apical series are developed subequally. The sulcal notch is not deep. Plate 1"' is very small, poorly delimited, and intimately associated with the sulcus. Plates 1p and ps are large. The antapical plate is clearly sexiform; it is in contact with plates 1p, 3"' through 6"', and ps. Archeopyle apical, type tA; operculum free (Clowes 1985, p. 29).

***Stoveracysta kakanuiensis* Clowes 1985**

Pl. 62, figs. 4-6

- 1984 *Stoveracysta kakanuiensis* Clowes (in prep.); Clowes & Morgans, pl. 2, fig. 4
 1985 *Stoveracysta kakanuiensis* Clowes, p. 32-34, pl. 1, figs. 1-12; pl. 2, figs. 1-12, text-fig. text-figs. 4a-b
 2003 *Stoveracysta kakanuiensis*; Brinkhuis, Sengers, et al., p. 21, figs. 137-138
 2003 *Stoveracysta kakanuiensis*; Sluijs et al., p. 23, figs. 19-20
 2004 *Stoveracysta kakanuiensis* Clowes 1985; Williams et al., pl. 9, figs. 17-18

Original Description: Proximate gonyaulacoid cysts, not dorso-ventrally compressed, prolate, lacking horns, consisting of a single wall layer. The ornament comprises low, incomplete, essentially sutural, septa which typically fail to develop on the upper margin of the cingulum, and minor intratabular granules. The archeopyle is apical, type tA; the operculum is free and ornamented with septa similar to those of the cyst body. These septa terminate a short distance from the absolute apex, thus leaving a small granular area at the pole. The full tabulation as defined by the ornament is gonyaulacacean, sexiform, formula: ?pr, 4', 6", X to 6c, 6"', 1p, 1"', ?4s.

Size Range: Length = 65 µm (one measured specimen). Width = 60 µm (one measured specimen).

Distribution: Locally abundant although apparently confined to a narrow stratigraphic interval.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f180 (L11929)	
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f176 (L11925)	
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f112 (L11048)	

Remarks: *S. kakanuiensis* occurs in an apparently narrow stratigraphic interval, close to the Eocene-Oligocene boundary in New Zealand.

It was correlated with Chron C13r at ODP Site 1172 by Sluijs et al. (2003) who go on to note that it "potentially provides an excellent regional correlation, conspicuously appearing at the time of the deepening of the Tasmanian Gateway" (p. 10).

***Stoveracysta ?ornata* (Cookson & Eisenack 1965a) Clowes 1985**

Pl. 62, figs. 7-9

- 1965a *Eisenackia ornata* Cookson & Eisenack, p. 124, pl. 13, figs. 1-8
 1975 *Eisenackia ornata* Cookson & Eisenack 1965; Stover, p. 40-41, pl. 2, figs. 6-11, text-fig. 5
 1983 *Alisocysta ornata* (Cookson and Eisenack, 1965) Stover and Evitt, 1978; Goodman & Ford, p. 865, pl. 7, figs. 10-11
 1985 *Stoveracysta ornata* (Cookson & Eisenack 1965a, p. 124, pl. 13, figs. 1-8) Clowes, p. 34

Original Description: Shell oval, apex slightly pointed, antapex with two short projections, girdle equatorial, broad, strongly helicoid, divided into six plates. Dorsal surface clearly tabulated, the plates which are outlined by low,

transparent ledges ... being separated by distinct furrows. The ventral field, corresponding to the longitudinal furrow, is broadly oval and crossed by a varying number of irregularly arranged straight or curved low, narrow ridges of different lengths. The two antapical projections are situated at the ventral corners of the antapical plate. The surface of the shell is rather finely and closely granular. The shell opens by the detachment of a slightly hexagonal apical operculum ... (Cookson & Eisenack 1965a, p. 124).

Size Range: Length = 43 (46) 49 μm (2 measurements). Width = 60 μm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Runangan late Eocene	Cape Foulwind Section, Westland, New Zealand	K29/f104 (L11040)	Stover 1975
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

Genus *Thalassiphora* Eisenack & Gocht 1960

1960 *Thalassiphora* Eisenack & Gocht, p. 513

1978 *Thalassiphora* Eisenack & Gocht 1960 emended Gocht 1968; Stover & Evitt, p. 194-195

Type Species: *Thalassiphora pelagica* (Eisenack 1954b, p. 71, pl. 12, figs. 17-18) Eisenack & Gocht 1960, p. 513-514 [Late Eocene-Early Oligocene]

Original Description: Central body spherical to ellipsoidal, hollow, firm-walled, surrounded by an equatorially placed helmet to bowl-shaped, wide, flexible membranous wing that never the less is double walled. The central body commonly has circular to horseshoe-shaped pylome (translated from Eisenack & Gocht 1960, p. 153, by Stover & Evitt 1978, p. 194).

Remarks: A supposed 1a intercalary plate was postulated by Gocht (1968). I am sceptical.

***Thalassiphora pelagica* (Eisenack 1954b) Eisenack & Gocht 1960 emend. Benedek & Gocht, 1981**

Pl. 62, figs. 10-12, Pl. 63, figs. 1-12

1954b *Pterospermopsis pelagica* Eisenack, p. 71, pl. 12, figs. 17-18

1960 *Thalassiphora pelagica* (Eisenack 1954b, p. 71, pl. 12, figs. 17-19) Eisenack & Gocht, p. 513-514

1961 *Pterospermopsis pelagica* Eisenack 1954; Gerlach, p. 209-210, pl. 28, fig. 15

1982a *Thalassiphora pelagica* (Eisenack); Wilson, pl. 1, fig. 2

1982b *Thalassiphora pelagica* Eis; Wilson, p. 7, pl. 4, fig. 6

1988 *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht, 1960 emend. Benedek & Gocht, 1981 Biffi & Manum, pl. 15, fig. 11

2000 *Thalassiphora pelagica* (Eisenack, 1954) Eisenack & Gocht, 1960; Levy & Harwood, p. 228, pl. 10, figs. a-c

2007 *Thalassiphora pelagica* (Eisenack, 1954) Eisenack & Gocht, 1960; Landman et al., fig. 17 (D-E)

Original Description: A mostly ellipsoidal (rarely spherical) central body with fairly solid walls is suspended from or adheres to the middle of a double-walled helmet-shaped, flat shell-shaped or bell-shaped membranous wing in such a way that the longitudinal axis of the ellipsoid proceeds into the membrane. Usually a low, \pm sharp-edged wedge extends over the convex side of this membrane towards the longitudinal axis and ends in a short point at the rear edge of the membrane. Often an excystment hole has developed in the shape of a horseshoe in the front half of the outer (upper) side of the central body (Eisenack 1954b, p.71).

Size Range: Length = 98 (144) 200 μm (5 measurements). Width = 112 (153) 225 μm (5 measurements).

Distribution: *Thalassiphora pelagica* appears to be a long-ranging taxon, reported from (for example) the Maastrichtian of northeast USA (Landman et al. 2007) to the Miocene of Italy (Biffi & Manum 1988) and New Zealand (herein).

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany	Pr 1170/75	Gerlach 1961
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan

Age/Stage	Location	Sample	Sample Reference
			1996
Oligocene-early Miocene	Marche region, central Italy	slide 29456	Biffi & Manum 1988
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f174 (L11923)	
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f169 (L11918)	
late Eocene-early Oligocene	Chalky Island, Fiordland, New Zealand	SM1320	Wilson 1982a
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000
Maastrichtian	Manasquan River Basin, Monmouth County, New Jersey, USA		Landman et al. 2007

Remarks: The long (and biostratigraphically unhelpful) range of *Thalassiphora pelagica* may be due in part to “lumping” of multiple taxa into the species. Nevertheless, it has proved difficult to discern any systematic differences between the oldest and youngest representatives in the present study. Perhaps this particular morphology is, indeed, exceptionally conservative.

Genus *Tityrosphaeridium* Sarjeant 1981

1981 *Tityrosphaeridium* Sarjeant, p. 120

1987 *Tityrosphaeridium* Sarjeant 1981, p. 120-121 Stover & Williams, p. 213-214

Type Species: *Tityrosphaeridium cantharellus* (Brosius 1963, p. 40-41, pl. 6, fig. 1; text-fig. 2, nos. 11a-c) Sarjeant 1981, p. 120

Original Description: Cyst spheroidal to broadly ellipsoidal, skolochorate. Phragma two-layered, with processes typically or constantly formed by the periphragm only. Processes intratabular, essentially cylindrical in shape (solid or hollow), yet of very variable form – they may be bifid or branched and expanded distally, but are not linked by an enclosing membrane, partial or complete, or by trabeculae. The process walls are fibrous, with or without rootlike proximal extensions: parasutural or penitabular features are inconspicuous or lacking. Paratabulation gonyaulacacean, with the formula 3-4', 6", 5-7c, 5-6"', 0-1p, 0-?5s. The cingular processes may be slender or conspicuously elongate. The antapical processes may be larger and more conspicuous than the others. Archeopyle precingular: operculum free (Sarjeant 1981, p. 120).

Remarks: *Tityrosphaeridium* is considered a junior synonym of *Cordosphaeridium*, by to Lentin & Williams 1985, Stover & Williams 1987, and Fensome & Williams 2004. Quattrocchio & Sarjeant 1996, retained the genus, and it is provisionally recognised here, thought there exists considerable doubt over its validity.

?*Tityrosphaeridium cantharellus* (Brosius 1963) Sarjeant 1981

Pl. 64, figs. 1-12, Pl. 65, figs. 1-3

1963 *Hystrichosphaeridium cantharellus* Brosius, p. 40-41, pl. 6, fig. 1, text-fig. 2

1981 *Tityrosphaeridium cantharellus* (Brosius 1963, p. 40-41, pl. 6, fig.1; text-fig. 2, nos. 11a-c) Sarjeant, p. 120

1994 *Cordosphaeridium cantharellum* (Brosius 1963) Gocht 1969; Stover & Hardenbol, p. 32, pl. 7, fig. 38

2005 *Tityrosphaeridium cantharellus*; Schiøler, pl. 5, fig. 5

Original Description: A species of the genus *Hystrichosphaeridium* with the following characteristics: The spherical to egg-shaped smooth central body supports about 15-20 hollow tree-like processes. These are mainly

broadly cylindrical, narrowing in the middle somewhat and gently widening towards the end. They consist of fibres that are distally split and curled far back. Isolated reticulated protrusions also appear. The process ends always appear matted and only with strong magnification can the branching fibres be seen. Both narrow and wide processes can be found on the same specimen. A calotte can be separated to form an excystment hole (Brosius 1963, p. 40-41).

Size Range: Length excluding any processes = 20 (29) 35 µm (6 measurements). Width excluding any processes = 20 (27) 35 µm (6 measurements). Length including any processes = 35 (55) 70 µm (7 measurements). Width including any processes = 40 (54) 70 µm (6 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f055 (L09212)	Wilson 1985
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	

Subfamily Leptodinioideae Fensome et al. 1993b

Genus *Areosphaeridium* Eaton 1971

1971 *Areosphaeridium* Eaton, p. 357

1978 *Areosphaeridium* Eaton 1971; Stover & Evitt, p. 19-20

1995 *Areosphaeridium* Eaton 1971 emend. Stover & Williams, p. 100, 102

1995 *Enneadocysta* Stover & Williams, p. 108-109

2006 *Enneadocysta* Stover and Williams 1995 emend. Fensome et al., p. 394, 396

Type Species: *Areosphaeridium diktyoplokum* (Klumpp 1953, p. 392, pl. 18, figs. 3-7) Eaton 1971, p. 358-359 [Eocene]

Original Description: Dinoflagellate cyst having a central body which is sub-circular to sub-quadrate in outline, with a finely granular surface, bearing solid, fibrous, intratabular processes. The process stems may be simple or branched, and frequently show fenestration. Distally the process stems are expanded and they terminate either as a distal bifurcation or a broad distal platform. Processes are invariably present on the apical, pre- and postcingular, and apical zones. Processes may or may not be present on the cingular zone. There is typically one process per plate, although some plates may be devoid of processes, and others may have two or three processes. The reflected paratabulation is 4', 5-6", 5-6"', 0-1 p, 1'''. The archeopyle is apical tetratabular (Eaton 1971, p. 357).

Comparison: *Areosphaeridium* differs from *Hystrichosphaeridium* and *Oligosphaeridium* in having solid, generally fibrous processes rather than tubular, nonfibrous processes (Stover & Evitt 1978, p. 19-20). It is noteworthy, however, that *Hystrichosphaeridium* and *Oligosphaeridium* differ from one another in the respective presence and absence of cingular processes, which *Areosphaeridium* may or may not have.

The body and processes of *Eatonicysta* and *Areosphaeridium* are essentially identical, but *Eatonicysta* is readily distinguished by the ectophragm supported on the process tips.

Surculosphaeridium differs from *Areosphaeridium* in lacking fenestrate platform-like or arcuate features at the ends of the processes (Stover & Evitt 1978, p. 20). *Surculosphaeridium* does have complex process tips, so this seems like a somewhat artificial distinction to me. However, the type species of *Surculosphaeridium*, *S. cribrrotubiferum*, is ancient (Oxfordian; early Late Jurassic), so it is unlikely that the two genera are closely related.

A similar state of affairs pertains to *Stiphrosphaeridium*: it is morphologically quite similar to *Areosphaeridium* but the type species (*Stiphrosphaeridium dictyophorum*) ranges from Late Jurassic to Early Cretaceous and so seems unlikely to be a close relative. (Oddly, none of Davey 1982b, Stover & Williams 1987, or Stover & Williams 1995 provides a comparison between *Stiphrosphaeridium* and *Areosphaeridium*, despite the obvious morphological similarities.)

Remarks: *Areosphaeridium* was revised, and many *Areosphaeridium* species moved to a new genus, *Enneadocysta*, by Stover & Williams (1995). The division into two genera is widely recognised today (e.g. Fensome & Williams 2004, Fensome et al. 2006). However, as earlier noted by Brinkhuis, Sengers, et al.

2003, p. 19, some and perhaps all species of *Enneadocysta* are “gonyaulacoid sexiform rather than partiform as suggested by Stover & Williams (1995).” The supposed partiform hypocystal organisation of *Enneadocysta* is here regarded as “reading too much” into a slight dorso-ventral compression, and, accordingly, *Enneadocysta* is misplaced among the Cladopyxiaceae and belongs instead with *Areosphaeridium* (within the Leptodinioideae, as placed here, although Fensome et al. 2006 presents a good case for placing both close to *Cleistosphaeridium*, within the Areoligeraceae). Indeed, the validity of *Enneadocysta* must now stand in some doubt and it is simply treated as a junior synonym of *Areosphaeridium* herein.

The current conventional deployment of species variously allocated between these two genera is summarised in the following table, together with the significantly different treatment adopted herein.

Original Epithet	Stover & Williams 1995	Herein
<i>Cleistosphaeridium actinocoronatum</i>	–	<i>Reticulosphaera actinocoronata</i>
<i>Areosphaeridium arcuatum</i>	<i>Enneadocysta arcuata</i>	<i>Areosphaeridium arcuatum</i> Possibly a jnr. syn. of <i>A. pectiniforme</i>
<i>Areosphaeridium argentinense</i>	<i>Surculosphaeridium?</i> <i>argentiniense</i>	–
<i>Areosphaeridium calcigerum</i>	<i>Surculosphaeridium?</i> <i>calcigerum</i>	–
<i>Areosphaeridium capricornum</i>	<i>Cooksonidium capricornum</i>	<i>Cooksonidium capricornum</i>
–	<i>Enneadocysta deconinckii</i>	? <i>Areosphaeridium deconinckii</i> n. comb. = <i>Enneadocysta deconinckii</i> Stover & Williams 1995, p. 110
<i>Areosphaeridium diktyoplokus</i>	<i>Areosphaeridium diktyoplokus</i>	<i>Areosphaeridium diktyoplokum</i>
<i>Areosphaeridium dictyostilum</i>	<i>Enneadocysta?</i> <i>dictyostila</i>	<i>Areosphaeridium dictyostilum</i>
<i>Areosphaeridium ebdonii</i>	–	<i>Areosphaeridium ebdonii</i>
<i>Areosphaeridium fenestratum</i>	<i>Enneadocysta fenestrata</i>	<i>Areosphaeridium fenestratum</i>
–	<i>Enneadocysta harrisii</i>	? <i>Areosphaeridium harrisii</i> n. comb. = <i>Enneadocysta harrisii</i> Stover & Williams 1995, p. 111-112
<i>Areosphaeridium michoudii</i>	–	<i>Areosphaeridium michoudii</i>
<i>Areosphaeridium multicornutum</i>	<i>Enneadocysta multicornuta</i>	<i>Areosphaeridium multicornutum</i>
–	<i>Enneadocysta partridgei</i>	Jnr. syn. of <i>A. dictyostilum</i>
<i>Baltisphaeridium pectiniforme</i>	<i>Enneadocysta pectiniformis</i>	<i>Areosphaeridium pectiniforme</i>
<i>Areosphaeridium polypetellum</i>	<i>Cleistosphaeridium polypetellum</i>	–
–	<i>Enneadocysta robusta</i>	? <i>Areosphaeridium robustum</i> n. comb. = <i>Enneadocysta robusta</i> Stover & Williams 1995, p. 115
<i>Areosphaeridium suggestium</i>	<i>Surculosphaeridium suggestium</i>	–

A key to understanding the genus *Areosphaeridium* is, of course, the nature and relationships of the type species, *A. diktyoplokum*. One myth that has grown up around this species is that the process fenestrae mostly or always exhibit smooth margins (“entire clypeate”; e.g. Goodman & Ford 1983, p. 865; Fensome et al. 2006, p. 397, but not Stover & Williams 1995, which notes variability of this feature on p. 102). However, the most casual glance at Klumpp’s original illustrations (1953, pl. 18, figs. 3-7) shows four specimens, including the holotype, all with ragged margins.

There are certainly some southern hemisphere occurrences of cysts which, but for the lack of an entire margin, would be identified as *A. diktyoplokum* by almost anyone (e.g. Text-Fig. 22, from the Tasman Sea). Specimens from mainland/near-shore New Zealand, however, generally have less well-developed process tips, and have been assigned to *Areosphaeridium dictyostilum* in this study (e.g. Pl. 65, figs. 4-9). There is little evidence to support a view that these are species of different genera, and the idea that they represent separate families – unless perhaps caught in the act of divergence – is unsustainable.

[Note that the Gonyaulacaceae (*Areosphaeridium*) and the Cladopyxiaceae (the usual resting place for *Enneadocysta*, although the Areoligeraceae has also been suggested; see Eaton et al. 2001) diverged during the Mesozoic.]



Text-Fig. 22: A probable specimen of *Areosphaeridium diktyoplokum* from the Tasman Sea, DSDP Leg 29, hole 280A, 20-3-38 cm (L6370/SM002).

Areosphaeridium dictyostilum (Menéndez 1965) Sarjeant 1981 emend. Fensome et al. 2006

Pl. 65, figs. 4-12, Pl. 66, figs. 1-3

- 1965 *Hystrichosphaeridium dictyostilum* Menéndez, p. 11-12, pl. 2, fig. 6; pl. 3, figs. 18-22
- 1967a *Cordosphaeridium dictyoplokus* (Klumpp) Eisenack; Wilson, p. 67, figs. 33, 35
- 1972 *Oligosphaeridium?* *dictyostilum* (Menéndez 1965, p. 11, 12, pl. 2, fig. 6; pl. 3, figs. 18-22) Eisenack & Kjellström, p. 845
- 1975 *Areosphaeridium diktyoplokus* (Klumpp); Haskell & Wilson, pl. 1, fig. 1
- 1981 *Areosphaeridium dictyostilum* (Menéndez 1965, p. 11, 12, pl. 2, fig. 6; pl. 3, figs. 18-22) Sarjeant, p. 115
- 1983 *Areosphaeridium* sp. cf. *A. diktyoplokus* (Klumpp, 1953) Eaton, 1971; Goodman & Ford, p. 865, pl. 8, fig. 4
- 1988 *Areosphaeridium diktyoplokum* (Klumpp 1953) Eaton 1971; Wrenn & Hart, p. 346-347, fig. 15, 6
- 1989 *Areosphaeridium* cf. *dictyoplokus* (Klumpp) Eaton; Wilson, pl. 1, fig. 16
- 1995 *Enneadocysta?* *dictyostila* (Menéndez 1965) Stover & Williams, p. 109
- 1995 *Enneadocysta partridgei* Stover & Williams, p. 113-114, pl. 4, figs. 4a-e, 5, pl. 5, figs. 1a-c, 2a-c, 3a-c, 4, 5a-b, text-fig. 1D, J
- 2000 *Enneadocysta partridgei* Stover & Williams, 1995; Levy & Harwood, p. 222, 224, pl. 4, fig. h
- 2006 *Enneadocysta?* *dictyostila* (Menéndez 1965) Stover and Williams 1995, emend. Fensome et al., p. 396-397, pl. 3, figs. 1-20, text-fig. 7 A-F, 8 A-R

Original Description: Body ellipsoid or ovoid, membrane almost smooth, tubular processes (17 or 18) distributed more or less radially, widened at the base, the free end broadly funnel-shaped with irregular branches or forming a reticulum (translation from Menéndez 1965, p. 11).

Emended Description of Fensome et al. 2006: [Diagnosis] A species of *Enneadocysta* with 6 precingular and 3-5 cingular processes and ragged clypeate to lirate process terminations.

[Description] **Shape:** Cyst chorate with a slightly dorsoventrally flattened, subspherical central body that may be symmetrical or slightly asymmetrical in outline. **Wall relationships:** Autophragm up to 1.5µm thick. **Wall features:** Autophragm smooth to faintly granulate, occasionally pitted. The central body bears 22 to 23 processes, mostly mesotabular but at least three (two antapical and the posterior sulcal) apparently obtabular to

penitabular, with 10 epicystal, 9 hypocystal, and 3-5 (usually 4) cingular. Processes predominantly simple, but may occasionally be branched or form a linear complex. Process stems are solid, occasionally faintly fibrous and may be perforate or fenestrate; they vary in width, cingulars being the narrowest. One of the dorsal apical processes (on the operculum) may have a wider stem or may be twinned. Occasionally, cingular processes are minute protuberances without distal expansions. Processes vary distally from bifid to most commonly ragged clypeate.... **Archeopyle:** Apical, type (tA), tetratabular, operculum simple, free. **Tabulation.** Indicated by processes and archeopyle margin. Each precingular plate has a mesotabular process, with first and sixth precingular processes and plates being of equal size. The anterior sulcal plate never has a process. Three to four, occasionally five, cingular plates have processes, which are located towards the ambitus. On the hypocyst, there are six postcingular processes, one per plate, a process that we interpret as the postcingular sulcal, and two antapical processes. The two antapical processes are interpreted as penitabular, located close to the lateral boundaries. Process formula: 4', 6", 3-5c, 6"', ps, 2'''' (interpreted as representing a single 1'''' plate, as discussed above). **Dimensions.** Range of 36 specimens except where noted: central body width 50 (54) 67µm; central body length without operculum 40 (44) 58µm (30 specimens); central body length with operculum 57 (66) 75µm (2 specimens); processes length up to 17-30µm; width at midlength of processes stems (excluding cingular processes) 2-5µm; width of distal terminations 14 (22) 32µm (Fensome et al. 2006, p. 396-397).

Size Range: Length excluding any processes = 45 (57) 72 µm (5 measurements). Width excluding any processes = 47 (55) 62 µm (6 measurements). Length including any processes = 77 (97) 120 µm (13 measurements). Width including any processes = 80 (103) 125 µm (7 measurements).

Distribution: Common.

Age/Stage	Location	Sample	Sample Reference
Whaingaroan	Akitio River, Hawkes Bay, New Zealand	U24/f201 (L12144)	
late Eocene-early Oligocene	DSDP Hole 511		Goodman & Ford 1983
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Kaiatan	Nine Mile Bluff, Westland, New Zealand	J31/f9186 (L08325)	
Kaiatan	Nine Mile Bluff, Westland, New Zealand	J31/f9185 (L08324)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
late early Eocene	northern Seymour Island, West Antarctica	8476	Wrenn & Hart 1988
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	L13259/1	Wilson 1989
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4737	Wilson 1967a
Eocene	erratics, McMurdo Sound, Antarctica	MB 181(2)	Levy & Harwood 2000

Remarks: "*Enneadocysta*" *partridgei* is allegedly smooth or faintly granulate; 21 to 23 processes which are vasiform, simply branched or expanded distally; stems single, moderately wide and long; length about 1/3 body diameter; 6" process present; as process absent; usually 4 cingular processes; medial or offset sulcal notch; 1" = 6" (same size, presumably); 88-128 µm overall diameter. I fully concur with Fensome et al. 2006 that it is a junior synonym of *dictyostilum*, whether it be called *Areosphaeridium* or *Enneadocysta*.

The holotype of "*E.*" *partridgei* is from DSDP leg 29, site 283, core sample 11-3 (119-121 cm) (refer Haskell & Wilson 1975).

***Areosphaeridium ebdonii* Bujak 1994**

Pl. 66, figs. 4-9

1994 *Areosphaeridium ebdonii* Bujak, p. 119-121, pl. 2, figs. 8-9

Original Description: Cysts skolochorate with subspherical bodies comprising an autophragm. Body typically with 17 intratabular processes, ten on the epicyst and seven on the hypocyst; areas between process bases smooth, or indistinctly ornamented, or finely and irregularly granulate. Processes less than 15 µm in length. Process stems solid, with proximal fibrous ends expanded slightly and merging smoothly with the autophragm surface. Process stems expanded distally into vasiform or infundibular, fenestrate to reticulate process platforms with irregular to circular outlines. On some specimens the vasiform or infundibular distal terminations have irregular or entire margins. The processes reflect a paratabulation of 4', 6", 0c, 5"', 1p, 1''', 0s, with the hypocystal paratabulation following the standard sexiform pattern. Paracingulum typically expressed by the absence of

processes, but one or two narrow paracingular processes may be present. Parasulcal processes absent although a medial parasutural notch is frequently discernible. Archeopyle apical; operculum tetraplacoid, contiguous (Bujak 1994, p. 119-120).

Size Range: Length excluding any processes = 55 μm (one measured specimen). Width excluding any processes = 55 (56) 57 μm (2 measurements). Length including any processes = 67 (83) 105 μm (4 measurements). Width including any processes = 72 (87) 102 μm (3 measurements).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

***Areosphaeridium multicornutum* Eaton 1971**

Pl. 66, figs. 10-12, Pl. 67, figs. 1-3

1971 *Areosphaeridium multicornutum* Eaton, p. 363-364, pl. 4, figs. 1-7, text-fig. 6

1995 *Enneadocysta multicornuta* (Eaton 1971, p. 363-364, pl. 4, figs. 1-7; text-fig. 6) Stover & Williams, p. 109

Original Description: The central body has a sub-circular to sub-quadrate outline and a finely granular surface. The processes are intratabular and have solid fibrous stems of variable length and breadth. Each process is distally expanded and bifurcate; the attitude of the bifurcations varies from patulate to recurved. The bifurcations are of variable length, and they vary in breadth from slender with a denticulate distal margin, to broad, typically net-like, with an irregular distal margin. Fenestration is sometimes present in a few of the process stems and produces stem branches. The tabulation of 4', 6", 6''', 1p, 1'''' is not fully reflected by the Intratabular processes. On the apical zone there are 4 processes (1' - 4'). On the precingular zone there are five processes (1'' - 5''), and plate 6'' is devoid of processes. There are between four and seven cingular processes which are situated on the lateral margins of the cingular zone. On the postcingular zone there are five processes (1''' - 5'''), and plate 6''' is devoid of processes. There is one process reflecting the posterior intercalary plate (1p). The antapex is typically offset to the right of the mid-ventral line and bears one process (1''''). Between the postcingular processes and the antapical process there are between one and five additional processes. The archeopyle is apical, tetratabular.

The variation in the form of the processes in *A. multicornutum* is similar to that shown by *A. arcuatum*, including the frequent occurrence of broader processes reflecting plates 2''' and 4''' (pl. 4 fig. 2). The cingular processes in *A. multicornutum* are typically slender. Although they are restricted to the margins of the cingular zone, the cingular processes are not randomly distributed, but are arranged in a line approximately parallel to the pre- and postcingular zones. As with *A. arcuatum* the additional processes are probably postcingular or antapical rather than reflecting distinct plate areas. The number of cingular and additional processes quoted in the diagnosis for *A. multicornutum* is based on specimens from the Bracklesham Beds; specimens with a greater number of processes may occur (Eaton 1971, p. 363-364).

Size Range: Length excluding any processes = 45 μm (one measured specimen). Width excluding any processes = 42 (46) 48 μm (3 measurements). Length including any processes = 65 (92) 107 μm (9 measurements). Width including any processes = 80 (82) 85 μm (4 measurements).

Distribution: Common.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	

***Areosphaeridium pectiniforme* (Gerlach 1961) Stover & Evitt 1978**

Pl. 67, figs. 4-12

1961 *Baltisphaeridium pectiniforme* Gerlach, p. 195-196, pl. 28, fig. 14, text-fig. 18

- 1963 *Baltisphaeridium pectiniforme* Gerlach 1961; Brosius, pp. 43-44, pl. 1, fig. 7, text-fig. 2 (9a-b)
- 1969 *Cleistosphaeridium pectiniforme* (Gerlach) Davey et al., p. 16
- ?1971 *Areosphaeridium arcuatum* Eaton, p. 360-363, pl. 3, figs. 1-9, text-fig. 4-5
- 1978 *Areosphaeridium? pectiniforme* (Gerlach 1961) Stover & Evitt, p. 20
- 1982b *Areosphaeridium arcuatum* Eaton; Wilson, p. 7, pl. 2, fig. 7
- 1984b *Areosphaeridium arcuatum* Eaton, 1971; Helenes, p. 94, 104, pl. 5, figs. 5-6
- ?1995 *Enneadocysta arcuata* (Eaton 1971, p. 360-363, pl. 3, figs. 1-9; text-figs. 4-5) Stover & Williams, p. 108, 109, text-figs. 1D, E
- 1995 *Enneadocysta pectiniformis* (Gerlach 1961) Stover & Williams, p. 108, 114-115, pl. 6, figs. 1-4, text-figs. 1D, F

Original Description: [No translation available] Eine Art der Gattung *Baltisphaeridium* mit schlanken massiven Anhängen, die nach beiden Seiten weit ausladen und mit zahlreichen kleinen Häkchen besetzt sind. Form der Kapsel kreisförmig bis oval. Membran granuliert (Gerlach 1961, p. 195).

[Eaton's (1971) description of *A. arcuatum*] The central body has a sub-circular to sub-quadrate outline and a finely granular surface. The processes are intratabular and they have solid fibrous stems of variable length and breadth. Each process is distally expanded and bifurcate; the attitude of the bifurcations varies from patulate to recurved. The bifurcations are of variable length, and they vary in breadth from slender with a denticulate distal margin, to broad frequently net-like, with an irregular distal margin. Fenestration may be developed in the process stems producing stem branches which are sometimes distally free. The tabulation of 4', 6", 6"', 1p, 1''' is not always fully reflected by the processes. The processes reflecting plates 6", 6"' and 1p are not always present. The cingular zone is typically devoid of processes although occasionally a process may occur on this zone. The antapex is typically offset to the right of the mid-ventral line and bears one process (1'''). Between the postcingular processes and the antapical process there may be one or occasionally two additional processes. The archeopyle is apical, tetratabular (Eaton 1971, p. 360-361).

Size Range: Length excluding processes = 45 (51) 55 µm (3 measurements). Width excluding processes = 42 (49) 58 µm (3 measurements). Length including processes = 55 (94) 110 µm (20 measurements). Width including processes = 75 (87) 112 µm (10 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Oligocene	Emsburen Borehole-7, northwest Germany	Pr. 1170/53	Gerlach 1961
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Lutetian	Bateque Formation; Sebastian Vizcaino Basin, Baja California		Helenes 1984b

Remarks: Stover & Evitt 1978, p. 20, notes that *Areosphaeridium actinocoronatum*, *A. arcuatum*, and *A. pectiniforme* might all be conspecific.

"*Areosphaeridium*" *actinocoronatum* is certainly different, many of the process tips being connected distally by a trabeculae. It has subsequently been reassigned to *Reticulosphaera*, by Bujak & Matsuoka 1986, p. 238, although this placement is contingent upon the assumption of a precingular archeopyle – refer to the discussion under that taxon.

Areosphaeridium pectiniforme allegedly differs from *Areosphaeridium arcuatum* in exhibiting 6 rather than 5-6 precingular processes, and in possessing an anterior sulcal process, for a total of 20 rather than 18-19 processes, and in having plate 1" smaller than plate 6", rather than larger as in *A. arcuatum* (Stover & Williams 1995, table 1). To be meaningful, these differences have to be real, consistent, and phylogenetically significant. I am sceptical on all three counts.

Areosphaeridium michoudii Bujak 1994 was distinguished from various species of "*Enneadocysta*" on the basis of its sexiform hypocystal topology. If the present treatment of *Enneadocysta* as a junior synonym of *Areosphaeridium* is accepted, that distinction vanishes and the possibility arises that *Areosphaeridium michoudii* is a junior synonym of *Areosphaeridium pectiniforme* (or *Areosphaeridium arcuatum*, if the latter is itself distinct).

Genus *Cooksonidium* Stover & Williams 1995

- 1995 *Cooksonidium* Stover & Williams, p. 106-107

Type Species: Cooksonidium capricornum (Cookson & Eisenack 1965a, p. 128-129, pl. 15, figs. 1-9) Stover & Williams 1995, p. 107 [Late Eocene]

Original Description: Cysts skolochorate, central body subspherical and bears 16 to 18 intratabular processes and process complexes; process stems solid, smooth to fibroid, tips expanded distally, arcuate or rarely licrate or heart-shaped, ends free or connected by trabeculae; epicyst with 10 or 11 processes, hypocyst with six or seven processes arranged in the standard sexiform pattern, paracingular processes absent; archeopyle apical, operculum tetratabular, simple and free (Stover & Williams 1995, p. 106).

Remarks: *Cooksonidium* appears to range from relatively late in the Bortonian through to the Kaiatan.

Cooksonidium capricornum (Cookson & Eisenack 1965a) Stover & Williams 1995

Pl. 68, figs. 1-3

- 1965a *Cordosphaeridium capricornum* Cookson & Eisenack, p. 128-129, pl. 15, figs. 1-9
1969a *Systematophora? capricorna* (Cookson & Eisenack 1965a, p. 128-129, pl. 15, figs. 1-9) Eisenack, p. 113
1978 *Areosphaeridium capricornum* (Cookson & Eisenack 1965a, p. 128-129, pl. 15, figs. 1-9) Stover & Evitt, p. 20
1982b *Areosphaeridium capricornum* (Cooks. & Eis.); Wilson, p. 7, pl. 3, figs. 2-3
1995 *Cooksonidium capricornum* (Cookson & Eisenack 1965a, p. 128-129, pl. 15, figs. 1-9) Stover & Williams, p. 107
2005 *Enneadocysta? aff. arcuata* (Eaton 1971) Stover & Williams 1995; Heilmann-Clausen & Van Simaey, p. 164, 166, pl. 4, figs. 15-16

Original Description: Shell approximately spherical with numerous radially arranged appendages of characteristic form which vary in number in individual specimens and in size, form, and structure in one and the same specimen. All are solid; some are simple with unbranched or slightly branched apices or with terminal bifurcations which extend laterally and are upwardly or downwardly curved; others are broadly flattened and perforated to varying degrees with broad apices which narrow gradually as they curve backwards towards the shell. The upper surface of the apices and their extensions are consistently finely denticulate.... The bases of the larger appendages are semicircular to, occasionally, almost circular, and similarly the tips of the apical prolongations sometimes appear to touch but, in reality, are never connected. The appendages are sometimes faintly and longitudinally striated; shorter and more pronounced striations may be evident at or near their points of origin. The surface of the shell is faintly granular.

The archeopyle is apical, the operculum bearing four appendages, two relatively large and two small....

At the antapex an approximately circular area, outlined either completely ... or incompletely by a ridge to which a few small simple appendages may or may not be attached, has been seen. Such an area is suggestive of an antapical field (Cookson & Eisenack 1965a, p. 128-129).

Description of Study Material: Forms encountered in this study exhibit less well-developed trabeculae than the Australian types.

Size Range: Length excluding any processes = 32 µm (one measured specimen). Width excluding any processes = 37 µm (one measured specimen). Length including any processes = 52 (74) 105 µm (17 measurements). Width including any processes = 57 (81) 105 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bartonian	Søvind Marl Formation, Kysing Research Borehole, eastern Jylland, central Danish Basin	2661	Heilmann-Clausen & Van Simaey 2005
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

Remarks: It is often difficult to place individual specimens within *Areosphaeridium pectiniforme* or *Cooksonidium capricornum*; the two taxa seem to intergrade in most samples, although the end points of the two populations are very clearly distinguishable. This intergradation may have been present in Cookson & Eisenack's original Browns Creek Clay material, too: the specimen illustrated in their pl. 15, fig. 1, bears a strong likeness to *Areosphaeridium pectiniforme* as used here.

Genus *Graptodinium* Clowes n. gen.

Derivation of Name: Greek, γραπτοζ, written; with reference to the intratabular ornament which bears a fanciful resemblance to pictographic writing.

Type Species: Graptodinium inconditum Clowes n. sp. [Bortonian]

Description: Cysts small, proximate, subspherical to distinctly prolate, lacking horns; the apical hemisphere slightly to considerably smaller than the antapical hemisphere. Cyst walls apparently single layered, ornamented by numerous short, sutural crests and characteristic intratabular accessory crests. Archeopyle apical, type tA; operculum free or attached; margin gently zig-zag; sulcal notch shallow and often inconspicuous. Processes lacking; ornament comprising low sutural and intratabular septa. Sutural septa clearly delineate a gonyaulacacean tabulation; formula ?4', 0a, 6", 6c, 5 to 6"', 1ap, 1''''; where only five postcingular plates are apparent, they are interpreted as representing plates 2''' to 6'''; torsion sinistral; ventral organisation L-type; antapical plate sexiform. Accessory septa forming an intratabular ornament, varying from discontinuous ridges and isolated granules to a fully developed reticulum. Cingulum and sulcus usually clearly expressed by the sutural septa; cingulum subdivided into transversely elongate plates; the ends of the cingulum not perceptibly offset but meeting the sulcus directly opposite one another.

Comparison: Directly opposite the apex of *Graptodinium* lies a single, large, six-sided antapical plate (the sexiform condition of Evitt 1985, p. 90), marking this form as a gonyaulacinean. The two genera with which *Graptodinium* cysts have commonly been identified in the past, *Histiocysta* and *Microdinium*, both exhibit a partiform hyposome and are thought to be Cladopyxiaceae. The hyposome condition, unfortunately, can be quite difficult to ascertain where specimens are few or inconveniently oriented, because the partiform and sexiform arrangements are topologically equivalent. They possess identical plate contacts and triple junctions. The only difference is the extent to which plate 1p extends towards the antapical pole, which can only be seen in certain orientations.

Further morphological comparison with *Histiocysta* is difficult because the detailed morphology, particularly the tabulation pattern, of *Histiocysta* is rather poorly known, although the late Jurassic to Cretaceous *Histiocysta* versus Eocene (*Graptodinium*) distribution is sufficient to avoid confusion for the practical purposes of daily identification.

Stover & Evitt 1978, p. 65, 66) notes the occurrence of anterior intercalary plates in *Microdinium*; there is no evidence of anterior intercalary plates in *Graptodinium*.

Characters determining placement within the Leptodinioideae are the number of apical plates, ventral organisation, and torsion. Other Leptodinioideae (or possible Leptodinioideae) sharing an apical archeopyle, single wall-layer, and lacking processes, include *Clathroctenocystis*, *Lanterna*, *Lithodinia*, and *Meiourogonyaulax*. None closely resembles *Graptodinium* except *Meiourogonyaulax*, which can be distinguished by the more strongly helicoid cingulum, deep sulcal notch, and very different stratigraphic range.

Remarks: *Graptodinium* exhibits a morphological range which is here recognised by two species and an informal morphotype. The last, although equally distinctive, cannot be formally described with the material currently available.

The two formally described species are observed to (?almost) intergrade in some samples. Some authorities have taken the presence of intermediates as cue to "lump" taxa into a single species. However, as noted repeatedly throughout this paper, this urge is not rational: The discovery or otherwise of intermediates between phylogenetically related organisms is a sampling artefact, and thus an inappropriate motive for splitting or lumping taxa. Divisions between fossil morphotaxa are necessarily arbitrary and the imprecision of gradational boundaries between taxa is unavoidable.

Graptodinium inconditum Clowes n. sp.

Pl. 68, figs. 4-12, Pl. 69, figs. 1-6

- cf. 1976 *Meiourogonyaulax* sp. l; Manum, pl. 3, figs. 20-21
- 1980 *Microdinium* sp. 1; Châteauneuf, p. 143, pl. 26, figs. 5-7
- ?1982a *Corrudinium* sp.; Wilson, pl. 1, fig. 6
- 1982b *Corrudinium* sp.; Wilson, pl. 1, figs. 2-3
- 1982b *Corrudinium* sp. Wilson, p. 7, pl. 1, figs. 2-3
- 1983 *Histiocysta* sp.; Goodman & Ford, pl. 9, figs. 7-8
- 1984 ?*Histiocysta* sp.; Clowes & Morgans, p. 32, pl. 2, fig. 3
- 1985 *Histiocysta* sp.; Wilson, p. 99, pl. 1, fig. 8
- 1986b *Microdinium reticulatum* Vozzhennikova 1967; De Coninck, p. 16, pl. 6, figs. 1-7, pl. 7, figs. 14-16
- 1989 *Histiocysta* sp. of Goodman & Ford 1983; Head & Norris, p. 530, pl. 3, figs. 5-9
- 1992 *Histiocysta* sp.; Brinkhuis, pl. XVII, figs. 12-14

- 1994 *Histiocysta* sp.; Stover & Hardenbol, pl. 2, figs. 13-14
 1994 *Histiocysta* sp.; Stover & Hardenbol, p. 32, pl. 2, fig. 13
 1995 *Stoveracysta* sp. cf. *S. ornata* Cookson & Eisenack 1974) Clowes 1985; Mao & Mohr, p. 255, pl. 5, fig. 13
 2005 *Microdinium* cf. *reticulatum*; Schiøler, pl. 13, fig. 11
 2005 *Microdinium* sp. 1 of Châteauneuf (1980); Schiøler, pl. 17, figs. 14-15

Derivation of Name: Latin, *inconditus*, irregular, with reference to the intratabular ornamentation.

Holotype: Sample I43/f090, slide L16338/SM060; Burnside Formation, Puketeraki Core (Bortonian); Pl. 68, figs. 4-9

Description: Cysts small, proximate, subspherical to slightly prolate, lacking horns; the apical hemisphere somewhat or, more usually, considerably smaller than the antapical hemisphere. Cyst walls apparently single-layered. Archeopyle apical, type tA; operculum free or, more commonly, attached. Processes lacking; ornament comprising low, solid sutural and intratabular septa. Sutural septa approximately 2.5 to 4.5 μ m high, particularly distinct in equatorial view, forming a well-defined gonyaulacacean tabulation, ?4', 0a, 6", 6c, 6"', 1ap, 1'''. Accessory septa comprising the irregular intratabular ornament forming an incomplete reticulum, sometimes continuous with the sutural septa, sometimes separated by a narrow clear area (Plate 1, figs. A, D). The floors of the muri appear smooth. Cingulum and sulcus clearly expressed by the sutural septa; cingulum broad (~5 μ m) and typically subdivided, though not always clearly.

Size Range: Length = 28 (36) 45 μ m (77 measurements). Width = 30 (35) 40 μ m (11 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
?late Whaingaroan	Chalky Island Formation, Chalky Island, Fiordland, New Zealand	A45/f9553 (al. S165/f553)	Wilson 1982a
Rupelian	Boom Clay Formation, north-western Belgium	0.50 to 52.35 m.	Stover & Hardenbol 1994
early Rupelian	Lark Formation; Alma-1X well, Danish North Sea	1825.8 to 1853.2 m.	Schiøler 2005
early Rupelian	Sands of Berg, Woensdrecht borehole, southern Netherlands	219m	De Coninck 1986b
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Runangan	Waiareka Volcanic Formation, Jacksons Paddock, Otago, New Zealand	J41/f8914	Wilson 1982b
late Eocene-early Oligocene	Chalky Island, Fiordland, New Zealand		Wilson 1982a
Priabonian-Rupelian	Falkland Plateau, DSDP Leg 71, Hole 511	511-17-1, 102-104 cm	Goodman & Ford 1983
?Kaiatan-Runangan ?Priabonian	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	Brinkhuis 1992
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
?Kaiatan	Hampden Beach section, Otago, New Zealand (LAD)	J42/f064	Wilson 1985
?Kaiatan	Waiareka Formation; highest recorded occurrence in Hampden Section, Otago, New Zealand	J42/f064	Wilson 1985
?late Bartonian	Horda Formation; Alma-1X well, Danish North Sea	1862.3 m.	Schiøler 2005
Bartonian	Clay of Asse, Woensdrecht borehole, southern Netherlands	278m	De Coninck 1986b
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Hampden Beach section, Otago, New Zealand	J42/f044	Wilson 1985
Bortonian	Hampden Formation, Hampden section, Otago, New Zealand	J42/f8690	Wilson 1982b
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985

Age/Stage	Location	Sample	Sample Reference
	Zealand		
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	

Comparison: The ornamentation of *G. inconditum* comprises discontinuous ridges and isolated granules, as opposed to the fully developed reticulum of *G. reticulatum*. Both taxa exhibit a range of morphologies which are quite distinct at their mid points in the samples examined as part of this study, though some intermediate specimens are less readily placed.

***Graptodinium reticulatum* Clowes n. sp.**

Pl. 69, figs. 7-12, Pl. 70, figs. 1-3

Derivation of Name: Latin, *reticulus*, a net or mesh; with reference to the surface texture.

Holotype: Sample I43/f093, slide L16341/SM071; Burnside Formation, Puketeraki Core (Bortonian); Pl. 69, figs. 7-12

Description: Cysts small, proximate, subspherical to slightly prolate, lacking horns; the apical hemisphere somewhat or, more usually, considerably smaller than the antapical hemisphere. Cyst walls apparently single-layered. Archeopyle apical, type tA; operculum free or, more commonly, attached. Processes lacking; ornament comprising low, solid sutural and intratabular septa. Sutural septa approximately 2 to 3 μ m high, particularly distinct in equatorial view, forming a fairly well-defined gonyaulacacean tabulation, ?4', 0a, 6", 6c, 5 to 6"', 1ap, 1'''. The dorsal postcingular series is particularly prominent. Accessory septa form an irregular intratabular reticulum, typically continuous with the sutural septa but more open and sometimes lacking immediately adjacent to sutures (Plate 1, fig. J). The floors of the muri appear smooth. Cingulum and sulcus clearly expressed by the sutural septa; cingulum broad (~5 μ m) and typically subdivided, though not always clearly.

Size Range: Length = 29 (35) 45 μ m (9 measurements). Width = 26 (32) 37 μ m (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
?Kaiatan-Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f099 (L11035)	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Comparison: See *G. inconditum*, above.

Genus *Kleithriasphaeridium* Davey 1974

1974 *Kleithriasphaeridium* Davey, p. 55-56

1976 *Diversispina* Benson, p. 184

1978 *Kleithriasphaeridium* Davey 1974; Stover & Evitt, p. 167-168

Type Species: *Kleithriasphaeridium corrugatum* Davey 1974, p. 56-57, pl. 5, figs. 1-5; text-fig. 3 [Cretaceous (Barremian)]

Original Description: The cysts are subspherical and bear one intratabular process per reflected plate area. The processes are hollow, open distally, and may be lightly striated; they vary in width with the smallest occupying the sulcal region (some of these may be solid). Rarely processes may be linked proximally by a membrane. The cyst wall beneath the processes is unusually thickened and granular. The reflected tabulation appears to be 3-4', 6", 6c, 5"', 1p?, 1'''' and 2 or more sulcal processes. The archeopyle is precingular formed by the loss of plate 3" (Davey 1974, p. 55).

Remarks: In overall appearance, *Kleithriasphaeridium* exhibits an immediate similarity to *Spiniferites*. It differs, however, in that the processes seem essentially round in cross-section, are hollow, open, and distally they flare

raggedly (somewhat similarly to *Hystrichosphaeridium tubiferum*) rather than being drawn into bi- or trifurcate points.

cf. *Kleithriasphaeridium* sp. 1

Pl. 70, figs. 4-9

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns; episome and hyposome more or less equal in length. Archeopyle precingular, type P (3"). Surface ornament lacking. Processes ?gonal, spinose, straight; non-fibrous, hollow, open; proximally connected by sutural septa proximally, irregularly flaring distally. Tabulation clearly expressed, gonyaulacacean. Cingulum clearly expressed, indicated by sutural septa. Sulcus clearly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 72 (72) 73 µm (2 measurements). Width excluding any processes = 72 (74) 75 µm (2 measurements). Length including any processes = 80 (101) 125 µm (9 measurements). Width including any processes = 98 (102) 107 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Runangan-early Whaingaroan	Old Mountain Road, Waikato, New Zealand	S14/f8599 (L10662)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996

Remarks: The processes of this form may be gonal, rather than intratabular, suggesting that placement in *Kleithriasphaeridium* is inappropriate. However, they also appear to be hollow and open distally, precluding placement in, say, *Spiniferites*.

The form identified as *Spiniferites* cf. *ovatus* Matsuoka 1983b by Ramirez (2004, pl. 4, figs. 11-12) from the Middle-Late Eocene of the east coast of the Maracaibo Lake, Venezuela, looks somewhat similar but seems to have shorter processes relative to the overall diameter.

Genus *Lophocysta* Manum 1979

1979 *Lophocysta* Manum, p. 238

1987 *Lophocysta* Manum 1979, p. 238; Stover & Williams, p. 151-152

Type Species: *Lophocysta sulcolimbata* Manum 1979, p. 238, 240-242, pl. 1, figs. 1-11; text-figs. 1A-E [Early Miocene]

Original Description: Dinoflagellate cysts with apparent gonyaulacacean paratabulation; archeopyle pentagonal, precingular. Prominent periphragm expansion restricted to mid-ventral area and with ribs indicating paratabulation. Dorsal face with inconspicuous processes in gonal positions (Manum 1979, p. 238).

***Lophocysta ?sulcolimbata* Manum 1979**

Pl. 70, figs. 10-12, Pl. 71, figs. 1-3

1979 *Lophocysta sulcolimbata* Manum, p. 238, 240-242, pl. 1, figs. 1-11, text-fig. 1A-E

Original Description: Dinoflagellate cysts with pentagonal, precingular archeopyle. Central body ovoid, with a prominent ventral crest formed by an expanded periphragm along the entire midventral zone, extending from anterior end of archeopyle to posterior end of parasulcus; maximum crest height about 2/3 equatorial diameter of central body. The crest has a finely reticulate to striate texture and more prominent parasutural ribs. The entire parasulcus plus paraplates 1' and 4', 6", 6c, 1''' and 6''', and ip are represented in the crest.

Three conspicuous openings are in constant positions at the base of the periphragm crest: one in either side at the intersections between crest and paracingulum, the third – and largest – opening immediately below the paracingular opening in the left hand side. Two further openings – inconspicuous and sometimes fused – occur in a position interpreted as the left accessory sulcal paraplate.

Inconspicuous processes, 1-3 µm high, occur in some – but not all – gonal positions of dorsal paraplates. Most consistent are two in posterior end of paraplate 4” and eight occupying gonal positions of cingular paraplates.

Dorsal cyst wall apparently unstratified and slightly under 2 µm thick, surface entirely smooth (Manum 1979, p. 238).

Size Range: Length = 54 (58) 62 µm (4 measurements). Width = 40 (45) 52 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Subfamily Uncertain

Genus *Aireiana* Cookson & Eisenack 1965a

- 1965a *Aireiana* Cookson & Eisenack, p. 127
- 1975 *Aireiana* Cookson & Eisenack 1965; Stover, p. 43
- 1978 *Aireiana* Cookson & Eisenack 1965a; Stover & Evitt, p. 139
- 1984 *Aireiana*; Damassa, p. 60-61

Type Species: *Aireiana verrucosa* Cookson & Eisenack 1965a, p. 127, pl. 14, figs. 11-13 [Late Eocene]

Original Description: Shell spherical, firm-walled, with an apical and antapical prominence and a number of irregularly distributed wart-like areas of variable size and construction. A smooth girdle-like zone and a similar unornamented longitudinal area may be indicated on the dorsal and ventral surfaces respectively. The shell opens by a sub-apical archeopyle (Cookson & Eisenack 1965, p. 127).

Remarks: *Aireiana* differs from *Cordosphaeridium* and *Kleithriasphaeridium* in lacking cingular processes, and in having distally closed and generally shorter processes (after Stover & Evitt 1978, p. 139).

Aireiana salicta Damassa 1979a

Pl. 71, figs. 4-9

- 1979a *Aireiana salicta* Damassa, p. 817-818, pl. 1, figs. 4-9

Original Description: [Diagnosis] Skolochorate cyst, ellipsoidal to spherical in shape, having fibrous intratabular processes formed by differentiation of outer part of autophragm. Processes tend to become fused in apical and sulcal regions. Paracingulum devoid of processes. Precingular archeopyle with rounded margin. (Description) Skolochorate cyst, ellipsoidal to spherical, overall diameter 54-60 microns, average 56 microns, of eight specimens. Diameter of holotype = 57 microns. Wall consists of autophragm only. Total wall thickness 2-3 microns. Twelve to fourteen fibrous intratabular processes, 13-35 microns in length, formed by differentiation of outer part of autophragm. Processes without a hollow interior. Processes tend to become fused in apical and sulcal regions. Longitudinal cross section of processes more or less rectangular; transverse cross section circular to irregular. Paracingulum devoid of processes; parasulcal processes variably distinct, but anterior and posterior sulcal processes generally can be distinguished. Precingular, postcingular and antapical processes large and generally well developed, although the first and second postcingular processes are fused with those of the parasulcus. Apex bears a single large process. Archeopyle Type P, formed by loss of the third precingular paraplate. Margin of archeopyle rounded; operculum free. Surface of cyst similar to processes in appearance, fibrous and highly perforate at the surface. Process formula – 1', 5-6", 0c, xs, 1p, 6"', 1'''''. Inferred thecal tabulation – 4', 6", 6c, xs, 1p, 6"', 1''''.

[Remarks] *Aireiana salictum* can be distinguished from *A. verrucosa*, the type species, by the length (13-35 vs. 6-10 microns, respectively) and fibrous nature of the processes (Stover 1975 [p. 43-44]). The number and shape of processes in the parasulcal region of *A. salictum* are highly variable. The sulcal paraplates are represented by an irregular mass from which several process tips arise. This group may include 1p, 1''', and 2''' as well. Clear indication of any paracingular processes is lacking in the specimens observed, although there is a possibility they may be represented as irregular thickenings on the adcingular side of the postcingular processes. The four apical paraplates are represented by a process complex which may have a divided tip, indicating fusion of several processes. The antapical process tends to be tapered and terminally rounded, a feature which aids in specimen orientation. In contrast, distal surfaces of the large precingular and postcingular processes are roughly parallel to the surface of the cyst (Damassa 1979, p. 817-818).

Size Range: Length excluding any processes = 73 (74) 75 μm (2 measurements). Width excluding any processes = 75 (76) 77 μm (2 measurements). Length including any processes = 95 (108) 122 μm (2 measurements). Width including any processes = 102 (115) 128 μm (2 measurements).

Distribution: Very rare. In the present study, two specimens, only, were observed in a single sample.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: *Aireiana salicta* can be distinguished from *A. verrucosa* by the length (13-35 vs. 6-10 μm , respectively) of the processes (Damassa 1979a, p. 818).

Genus *Fibrocysta* Stover & Evitt 1978

1978 *Fibrocysta* Stover & Evitt, p. 155

Type Species: *Fibrocysta bipolaris* (Cookson & Eisenack 1965b, p. 135, pl. 16, figs. 7-8) Stover & Evitt 1978, p. 155 [Early Eocene]

Original Description: Cysts skolochorate; body ellipsoidal with small to long hornlike protrusions, generally one at each pole; body also bears numerous solid or hollow, normally nontabular processes; paratabulation usually indicated by precingular, Type P, archeopyle only (Stover & Evitt 1978, p. 155).

Fibrocysta bipolaris (Cookson & Eisenack 1965b) Stover & Evitt 1978

Pl. 71, figs. 10-12, Pl. 72, figs. 1-3

- 1965b *Cordosphaeridium bipolare* Cookson & Eisenack, p. 135, pl. 16, figs. 7-8
- 1969 *Lantemosphaeridium bipolare* (Cookson & Eisenack 1965b, p. 135, pl. 16, figs. 7-8) De Coninck, p. 38
- 1969 *Lantemosphaeridium essentielle* De Coninck, p. 38, pl. 11, figs. 7-8
- 1969c *Amphorosphaeridium bipolare* (Cookson & Eisenack 1965b, p. 135, pl. 16, figs. 7-8) Davey, p. 35
- 1978 *Fibrocysta bipolaris* (Cookson & Eisenack 1965b, p. 135, pl. 16, figs. 7-8) Stover & Evitt, p. 155
- 1999a *Fibrocysta essentialis* (De Coninck, 1969); De Coninck, pl. 1, figs. 1-2
- 1999a *Fibrocysta* aff. *essentialis* (De Coninck, 1969); De Coninck, p. 150-151, pl. 1, figs. 3-4

Original Description: Shell typically oval, well-covered with narrow, solid, unbranched appendages of varying length and width. Usually the appendages narrow somewhat from broadish bases to widen distally to shallow funnel-shaped apices, the recurved edges of which may bear minute hair-like branches. In the larger appendages fine, longitudinal fibrils may be seen. The shell is bipolar, being characterized by the development of a distinctive apical and antapical appendage. The apical appendage is relatively short and broad, solid, densely granular and with a bluntish tip. It may be simple or with one or two short, slender, lateral branches. In the type specimen ... it appears to be connected with three broad, flattened, longitudinally striated appendages. The antapical appendage is longer than the neighbouring ones, unstriated, unbranched with approximately straight sides and a pointed tip.

The surface of the shell is densely granular with a linear arrangement evident near the bases of the appendages. A large archeopyle extends from close to the apical pole to the equatorial region of one surface (Cookson & Eisenack 1965b, p. 135; ellipses replace figure references in the original).

Size Range: Length excluding any processes = 70 (76) 83 μm (2 measurements). Width excluding any processes = 63 (65) 67 μm (2 measurements). Length including any processes = 108 (122) 137 μm (2 measurements). Width including any processes = 95 (96) 97 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Ypresian	Kallo borehole, Belgium	-374.5 m. - prep. 2	De Coninck 1969
late Paleocene-early Eocene	Kallo borehole, Belgium	-272.5 m. - lame 1; -272.5 m. - lame 2	De Coninck 1999a
late Paleocene-early	Knokke borehole, Belgium	-283 m. - lame 1; -284 m. - lame	De Coninck 1999a

Genus *Pyxidinospis* Habib 1976

- 1976 *Pyxidinospis* Habib, p. 382
 1978 *Pyxidinospis* Habib 1976; Stover & Evitt, p. 183-184
 1989c *Pyxidinospis* Habib, 1976; Head et al., p. 494

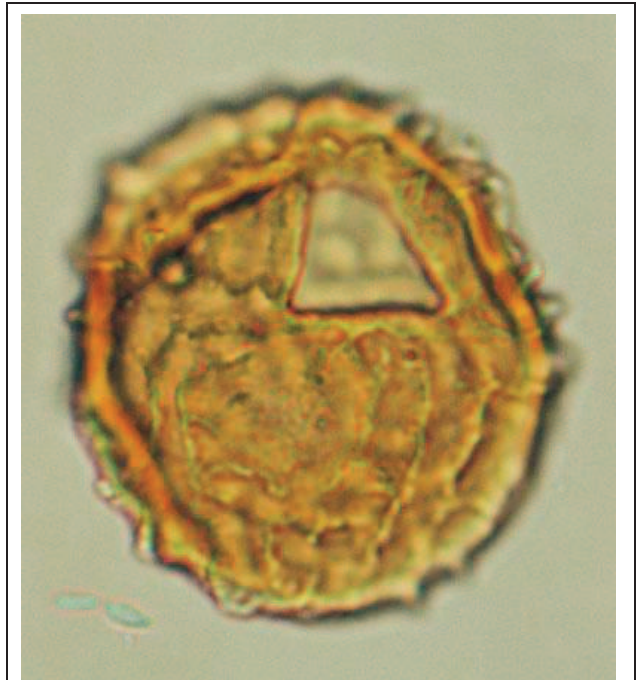
Type Species: Pyxidinospis challengerensis Habib 1976, p. 382, pl. 1, figs. 1a-b; pl. 3, figs. 1-2 [Cretaceous (Berriasian-Hauterivian)]

Original Description: Proximate dinoflagellate cysts. Outline in lateral, dorsal and ventral views oval to elliptical; longer than wide with rounded polar areas. Discrete apical and antapical horns lacking. Autoblast two-layered [sic] with periphragm and endophragm in contact. Evidence of cyst tabulation, cingulum or sulcus lacking. Archeopyle large and precingular, formed by loss of a single plate (Type P). Operculum simple and free. Periphragm texture variable, processes always wider or longer than high (Habib 1975, p. 382).

Remarks: *Pyxidinospis* exists today as a kind of catch-all for any essentially spherical, proximate cyst with a type P archeopyle, but lacking other indications of tabulation. Accordingly, it has accumulated an odd assortment of species, ranging in age from late Jurassic (*P. laminata* Davies 1983) to Recent (*P. psilata* Wall & Dale 1973; *P. reticulata* McMinn & Sun 1994) and geographically from arctic Canada and the north Atlantic to New Zealand. The type species, *P. challengerensis*, hails from the early Cretaceous (Berriasian-Hauterivian) of the north Atlantic, and is most unlikely to have any phylogenetic affinity with many – or possibly any – of the other species.

Unfortunately, the genus is difficult to split apart precisely because it is so featureless. It is already divided into species according to ornament, and to separate it into multiple genera on that basis leaves us no better off. Even the occasional hint of a cingulum offers little hope: nobody seriously doubts that the thing *has* a cingulum, so unless we can get a very good indication of its end points on the ventral surface (e.g. to state with confidence whether the topology is L- or S-type) these mere hints of its existence avail us not at all. The only morphological features which do seem to offer some insight are the (a) size and (b) shape of the archeopyle.

Among the New Zealand Paleogene dinoflagellate species with single plate precingular archeopyles and few indications of tabulation, two distinct groups may be assembled, depending upon the size and shape of the archeopyle. The forms most similar to the type species of *Pyxidinospis*, *P. challengerensis*, are those with large (“oversize”) archeopyles having the standard *Gonyaulax* shape. Within this group, it is possible the lightly constructed forms with an open reticulum, such as *P. delicata*, may form a natural clade. A second group, as first noted in Clowes & Wilson 2006, is denoted by a rather small (“undersize”) archeopyle with a characteristically narrow apex, which lends it a triangular shape. This group includes *P. waiapawaensis* and similar forms (Pl. 75, figs. 1-3, Pl. 75, figs. 4-5, Pl. 75, fig. 6) as well as the enigmatic *?Corrudinium vermiculatum* (Text-Fig. 23).



Text-Fig. 23: Holotype of *?Corrudinium vermiculatum* (Wilson 1988) Clowes & Wilson 2006, showing “undersized” sub-triangular precingular archeopyle.

Beyond morphology alone, there may be some phylogenetic validity in dividing the genus on the basis of clustering of the species in space and time. For example, the New Zealand Tertiary forms are almost certainly not closely related to the type species, yet they may very well be related to one another.

A range chart for species of *Pyxidinospis* is provided in Appendix 2, chart 8.

Key to selected species:

0.	Archeopyle small....	1.
	Archeopyle large....	2.
1.	Archeopyle shape is narrow/subtriangular....	1.1.

	Archeopyle is the standard <i>Gonyaulax</i> pentagonal shape....	1.2.
1.1.	Cingulum lacking....	1.1.1.
	Cingulum weakly expressed....	1.1.2.
1.1.1.	<i>Pyxidinospis</i> cf. <i>waipawaensis</i> (Pl. 75, fig. 6)	
1.1.2.	? <i>Corrudinium vermiculatum</i>	
1.2.	<i>Pyxidinospis waipawaensis</i>	
2.	Surface ornament comprising a reticulum with angular lacunae....	2.1.
	Surface ornament comprising irregular ridges/rugulae....	2.2.
2.1.	Surface ornament density 8-12 sculptural elements across the diameter....	2.1.1.
	Surface ornament density 10-15 sculptural elements across the diameter....	2.1.2.
	Surface ornament density 14-18 sculptural elements across the diameter....	2.1.3.
	Surface ornament density ~20 sculptural elements across the diameter....	2.1.4.
2.1.1.	<i>Pyxidinospis</i> cf. <i>delicata</i>	
2.1.2.	<i>Pyxidinospis</i> sp. 3	
2.1.3.	<i>Pyxidinospis delicata</i>	
2.1.4.	<i>Pyxidinospis mundus</i>	
2.2.	Walls very thick....	2.2.1.
	Walls relatively thinner ("normal" for the genus)....	2.2.2.
2.2.1.	<i>Pyxidinospis crassimurata</i>	
2.2.2.	<i>Pyxidinospis teuriensis</i>	

***Pyxidinospis crassimurata* Wilson 1988**

Pl. 72, figs. 4-6

1988 *Pyxidinospis crassimurata* Wilson, p. 27, pl. 17, figs. 1a-b, 2, 3a-c

Original Description: Cyst subspherical, of intermediate size, with a thick two layered wall (total thickness c. 4 µm) comprising a thin smooth inner layer and a thick spongy (tectate) microreticulate outer layer, both layers being in close contact. Surface ornament also comprises thin solid irregular ridges (height up to 3 µm) which are linked to form a coarse macroreticulum superimposed upon the microreticulate outer layer; ridges apparently not related to a paratabulation. Archeopyle precingular type P (3" only) relatively large, elongate, pentagonal; operculum free. Paratabulation indicated by archeopyle only, although the macroreticulation has a somewhat polygonal pattern which resembles paraplates. Paracingulum and parasulcus not generally indicated (Wilson 1988, p. 27).

Size Range: Length = 58 (76) 95 µm (2 measurements). Width = 58 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985

***Pyxidinospis teuriensis* Clowes n. sp.**

Pl. 72, figs. 7-12, Pl. 73, figs. 1-6

Derivation of Name: Named after the type locality, Te Uri Stream.

Holotype: Sample J42/f484, slide L23119/SM031; Kurinui Formation, Hampden Beach Section (Heretaungan);

Description: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, non-tabular, comprising irregular ridges/rugulae; with features on a scale of 14-18 sculptural elements across the diameter; 2-3 µm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 61 (72) 80 μm (5 measurements). Width = 62 (71) 77 μm (5 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: *Pyxidinospis teuriensis* is most similar to *P. crassimurata*, in possessing a coarse reticulum, but is readily distinguished because it lacks the fine microreticulum visible in the lumina of *crassimurata*, and in its thinner cyst wall.

Pyxidinospis cf. delicata

Pl. 73, figs. 7-12

?2005 *Cerebrocysta bartonensis*; Schiøler, pl. 19, figs. 10-11

Description: Cysts small to intermediate, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 μm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, non-tabular, comprising reticulum with angular lacunae; with features on a scale of 8-12 sculptural elements across the diameter; 2-3 μm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 40 (44) 47 μm (2 measurements). Width = 52 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: Compared with *Pyxidinospis delicata* s.s., this form has (1) a relatively more open reticulum, 8-12 sculptural elements across the diameter as opposed to 14-18, and (2) a younger age range, Bortonian as opposed to Heretaungan to Porangan. However, the two forms are otherwise very similar (pers. obs.; GJ Wilson pers. comm.) It remains to be seen if these differences are consistent and are not just sampling artefacts.

***Pyxidinospis delicata* Wilson 1988**

1988 *Pyxidinospis delicata* Wilson, p. 27-28, pl. 17, figs. 6, 7a-b

Original Description: Cyst subspherical, small to intermediate in size, fairly thick-walled (2-4 μm), apparently comprising autophragm only with thin smooth inner layer and slightly thicker reticulate outer layer. Reticulum somewhat irregular with thin delicate, smooth or crenulate muri (height 2-3 μm). Texture of lumina finely reticulate. Archeopyle small, polygonal (usually pentagonal or nearly square); operculum free or attached along posterior margin. Paratabulation indicated by archeopyle only. No trace of paracingulum or parasulcus (Wilson 1988, p. 28).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 μm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free to attached. Processes lacking; surface ornament present, non-tabular, comprising reticulum with angular lacunae; with features on a scale of 14-18 sculptural elements across the diameter; 2-3 μm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 40 (53) 72 μm (24 measurements). Width = 50 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f061 (L09218)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f039 (L09196)	Wilson 1985

Remarks: *Pyxidinopsis delicata* s.s. has a relatively fine reticulum and appears confined to the Porangan or older. A younger form (*P. cf. delicata*) has a relatively more open reticulum.

***Pyxidinopsis* sp. 3**

Pl. 74, figs. 1-3

Description: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, non-tabular, comprising reticulum with angular lacunae; with features on a scale of 10-15 sculptural elements across the diameter; 2-3 µm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 57 µm (one measured specimen). Width = 55 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	

***Pyxidinopsis mundus* Clowes n. sp.**

Pl. 74, figs. 4-12

Derivation of Name: Latin, *mundus*, elegant, tidy; with reference to the neat, even reticulum.

Holotype: Sample U24/f419, slide L23127/SM020; Wanstead, Te Uri Stream (Porangan); Pl. 74, fig. 4

Description: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), large; operculum free. Processes lacking; surface ornament present, non-tabular, comprising reticulum with angular lacunae; with features on a scale of 20 sculptural elements across the diameter; 2-3 µm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 42 (51) 55 µm (7 measurements). Width = 43 (49) 54 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f057 (L09214)	Wilson 1985
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f042 (L09199)	Wilson 1985
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: *Pyxidinopsis mundus* is most similar to *P. waipawaensis* but differs in possessing a larger archeopyle, which, as noted above, may possibly have generic significance, and in the finer reticulum.

Remarks: The alignment of ornamental features evident in Pl. 74, fig. 6, which appears to hint at a faint tabulation, is not an artefact of the photograph: the features are also visible under the microscope. However, it is well-known that the human eye is adept at discerning patterns, even where they may not exist. Without the corroboration at least another specimen with similar features, it is probably premature to think of claiming a tabulation for *Pyxidinospis* although most would agree it undoubtedly possesses one.

***Pyxidinospis waipawaensis* Wilson 1988**

Pl. 75, figs. 1-6

1988 *Pyxidinospis waipawaensis* Wilson, p. 28, pl. 17, figs. 4, 5a-b

Original Description: Cyst subspherical, small to intermediate in size, fairly thick walled (c. 2 µm), apparently comprising autophragm only, with a characteristically reticulate surface. Reticulation sharply defined by interconnected narrow muri (height c. 1-2 µm) defining polygonal smooth lumina of variable size (average breadth range 0.5 µm to 4 µm), but size of lumina rarely exceeding 5 µm. Occasional short non-interconnecting ridges project from muri. No other surface ornamentation present. Archeopyle relatively large, precingular, type P (3" only), somewhat rounded pentagonal, to almost quadrangular, typically bordered by low, narrow, ridge; operculum free. Paratabulation indicated by archeopyle only. No trace of paracingulum or parasulcus (Wilson 1988, p. 28).

Description of Study Material: Cysts of intermediate size, proximate, not dorso-ventrally compressed, more or less spherical, lacking horns. Cyst wall single-layered; relatively robust, about 2 µm in thickness. Archeopyle precingular, type P (3"); pentagonal (standard *Gonyaulax*-type), small; operculum free. Processes lacking; surface ornament present, non-tabular, comprising reticulum with angular lacunae; with features on a scale of 24-30 sculptural elements across the diameter; about 1-2 µm high. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 58 (69) 80 µm (2 measurements). Width = 56 (69) 82 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Heretaungan	Waipawa Section, Hawkes Bay, New Zealand	V22/f8994 (L12118)	Wilson 1988

Remarks: Note that the holotype of *Pyxidinospis waipawaensis* comes from sample V22/f8994, laboratory preparation number L12118, not preparation number L12121 as erroneously stated in Wilson 1988, p. 28. The paratype illustrated in Wilson 1988, pl. 17, fig. 4, is a single mount slide, registered as SM279, and comes from sample V22/f7401. This sample was prepared at least twice, the second time as laboratory preparation number L12121. Wilson 1988, Appendix 1 (p. 34) records the earlier preparation number as L976. However, that is incorrect according to the GNS Science L and SM catalogues, which attribute L976 to a different collection altogether, and do not record an L number for SM279. Notwithstanding the two clerical errors, which relate to the preparation numbers only, all accounts agree on the sample attribution, and the typification of the species is secure.

Family Areoligeraceae Evitt 1963b

Key to genera identified in this study:

0.	Cyst wall single-layered....	1.
	Cyst wall two-layered (endophragm + periphragm)....	2.
1.	Cysts chorate....	1.1.
	Cysts proximochorate....	1.2.
1.1.	Processes rarely connected distally....	1.1.1.
	Processes connected by well developed trabecula....	1.1.3.
1.1.1.	Processes dolabrate (see <i>Remarks</i> under <i>Cleistosphaeridium</i>)....	1.1.1.1.
	Processes not dolabrate....	1.1.1.2.
1.1.1.1.	<i>Cleistosphaeridium</i>	
1.1.1.2.	<i>Areoligera</i>	
1.1.3.	<i>Glaphyrocysta</i>	
1.2.	<i>Cyclonephelium</i>	
2.	<i>Chiropteridium</i> ; <i>Membranophoridium</i> ; <i>Senoniasphaera</i>	

Genus *Areoligera* Lejeune-Carpentier 1938a

- 1938a *Areoligera* Lejeune-Carpentier, p. B164
1978 *Areoligera* Lejeune-Carpentier 1938; Stover & Evitt, p. 17-19
2004 *Areoligera* Lejeune-Carpentier, 1938a, p. B164; Fensome & Williams, p. 58-61

Type Species: *Areoligera senonensis* Lejeune-Carpentier 1938a, p. B164-B166, text-figs. 1-3 [Cretaceous (Senonian)]

Original Description: The shell is more or less hemispherical, showing a large convex face and another more or less depressed face of more reduced dimensions. This latter does not show in itself any particular ornament; it is bordered by a fringe of spiny laminae. On the other face are located large areas, each one encircled by a collarette; these areas are divided into two main groups by a line of much smaller elements forming a girdle. From the small areas as well as from the collarettes arise numerous spines, most of them long and slender, which may unite together at their distal extremity (translated from Lejeune-Carpentier 1938, p. 164, by Stover & Evitt 1978, p. 17-18).

?*Areoligera hampdenensis* Clowes n. sp.

Pl. 75, figs. 7-12, Pl. 76, figs. 1-12

- 1988 *Systematophora placacantha* (Deflandre & Cookson, 1955) Davey et al., 1969, emend. May, 1980; Wilson, p. 31, pl. 22, figs. 1-4
2005 *Heterosphaeridium heteracanthum*; Schiøler, pl. 2, fig. 2

Derivation of Name: Named after the type locality, Hampden Beach.

Holotype: Sample J42/f483, slide L23118/SM005; Kurinui Formation, Hampden Beach Section (Heretaungan); Pl. 75, figs. 7-12

Description: Cysts of intermediate size, chorate, dorso-ventrally compressed, lenticular, lacking horns. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Processes penitabular, spinose, somewhat sinuous; non-fibrous, commonly bi- and trifurcating, apparently solid, highly variable, from about 10 to 20 µm in length; incompletely united into penitabular ridges proximally, capitate distally. Tabulation weakly expressed, apparently gonyaulacacean, inferred formula: 4', 0a, 6", X-6c, 5-6"', 1ps, 1"', Xs. Cingulum not expressed. Sulcus weakly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 47 (59) 72 µm (14 measurements). Width excluding any processes = 43 (58) 75 µm (17 measurements). Length including any processes = 75 (96) 125 µm (14 measurements). Width including any processes = 70 (89) 107 µm (17 measurements).

Distribution: Frequent. Although apparently of limited stratigraphic range, within that interval it occurs frequently, and is common in some samples.

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
Porangan	Waipawa standard section, Hawkes Bay, New Zealand	V22/f7401	Wilson 1988
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Heretaungan-Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f298 (L23128)	
Heretaungan	Waipawa standard section, Hawkes Bay, New Zealand	V22/f8994	Wilson 1988
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: This taxon is broadly similar to the *Cleistosphaeridium ancycra-placacanthum* group, but differs in possessing a more robust cyst, heterogeneous processes, and process tips which are not principally dolabrate.

The species described in Maier 1959 as *Galea* (now questionably assigned to *Hystrichosphaeridium* by Eisenack & Kjellström 1975b) *koryka* somewhat resembles the present taxon (see especially Maier's pl. 30, fig. 7) and would obviously be the senior synonym if they are indeed the same.

Remarks: As noted above, this taxon is broadly similar to the *Cleistosphaeridium ancyrea-placacanthum* group, but generic placement is tipped in favour of *Areoligera* by the heterogeneous processes, and nature of the process tips. The type of *Heterosphaeridium* differs from the present material in possessing a relatively straight margin to the archeopyle and “appendages of varying widths in one and the same specimen” (Cookson & Eisenack 1968, p. 115).

In the absence of any plausible intermediate taxa, however, it seems unlikely to be closely related to the Cretaceous genotype species, *Areoligera senonensis*, which, if one is to adopt the phylogenetic viewpoint, is a reason to question the generic assignment.

?*Areoligera* sp. 2

Pl. 77, figs. 1-9

Description: Cysts of intermediate size, chorate, dorso-ventrally compressed, lenticular, lacking horns; episome somewhat shorter than hyposome. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Processes penitabular, spinose, somewhat sinuous; non-fibrous, commonly bi- and trifurcating, apparently solid, highly variable, from about 10 to 20 μm in length; incompletely united into penitabular ridges proximally, capitate distally. Tabulation clearly expressed, gonyaulacacean, inferred formula: 4', 0a, 6", X-6c, 5-6"', 1ps, 1''', Xs. Cingulum moderately expressed, indicated by sutural septa. Sulcus weakly expressed, indicated by sutural septa.

Size Range: Length excluding any processes = 54 (61) 68 μm (2 measurements). Width excluding any processes = 62 (62) 62 μm (2 measurements). Length including any processes = 79 (83) 87 μm (2 measurements). Width including any processes = 77 (84) 91 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	

Remarks: A few specimens of ?*Areoligera* appear sufficiently dissimilar to those listed here as *Areoligera* sp. 1 to warrant separate consideration, but they are too few to merit formal description. Their processes are very heterogeneous, and some are more flattened.

Genus *Cleistosphaeridium* Davey et al. 1966 emend. Eaton et al. 2001

- 1966 *Cleistosphaeridium* Davey et al., p. 166
- 1978 *Cleistosphaeridium* Davey et al. in Davey et al. 1966; Stover & Evitt, p. 31-32
- 2001 *Cleistosphaeridium* Davey et al. 1966 emend. Eaton et al., p. 176-177
- 2004 *Cleistosphaeridium* Davey et al., 1966, p. 166; Fensome & Williams, p. 133-143
- 2006 *Cleistosphaeridium* Davey et al. 1966 emend. Eaton et al. 2001; Fensome et al., p. 410

Type Species: *Cleistosphaeridium diversispinosum* Davey et al. 1966, p. 167, pl. 10, fig. 7 emend. Eaton et al. 2001 [Early Eocene]

Original Description: Chorate dinoflagellate cysts having spherical to ovoidal central bodies bearing numerous processes, typically closed distally and without communication to endocoel. Number of processes typically exceeding 50; processes show no definite alignment, so that the tabulation is not determinable. Archeopyle apical, with zigzag margin (Davey et al. 1966, p. 166).

Remarks: The implication of the words “closed distally” in the original diagnosis is that the processes of *Cleistosphaeridium* are hollow, whereas, in fact, those of the type species, at least, are solid. This point is also noted in Islam 1993 (p. 82).

Islam 1993 (p. 88) further reports that the type species of *Cleistosphaeridium*, *C. diversispinosum*, sometimes has processes connected into penitabular areolae, and notes a partial tabulation, although no formula is derived. On the strength of this observation, Islam proposed *Cleistosphaeridium* to be a junior synonym of *Systematophora*, a recommendation which was adopted by a number of subsequent authors. However, as contended many times herein, the nature of the ornament – whether sutural, intratabular, subtly connected into areolae or not – has less phylogenetic significance at the generic level than the vast temporal gulf separating the type species of the two genera (Eocene in the case of *Cleistosphaeridium diversispinosum*, as opposed to Early Kimmeridgian for *Systematophora areolata*; a small matter of 100 million years). The only phylogenetically

important distinction between intratabular and non-tabular ornament, per se, is that the former permits the deduction of a tabulation pattern whereas the latter does not, allowing cysts possessing an intratabular ornament to be more readily classified.

Accordingly, *Cleistosphaeridium* is retained here, recognised as a valid genus.

These considerations are echoed in Eaton et al. 2001, which also comments upon the “very different stratigraphic ranges” of the taxa (p. 171), and explores an interesting interpretation of the “pick-like” process terminations of *Cleistosphaeridium*, for which the authors coin the term “dolabrate” (p. 174, fig. 7).

I accept with enthusiasm the idea that an asymmetrical process tip is evidence of asymmetrical process placement within the plate – obtabular, parasutural or intratabular – and may thus distinguish between, for example, intratabular and non-tabular ornament. But do notionally non-tabular processes ever actually straddle sutures? If one can't tell, then the distinction is moot, anyway.

Downiesphaeridium and *Polysphaeridium* differ from *Cleistosphaeridium* in possessing hollow processes. *Impletosphaeridium* has solid processes and may yet prove to be a (senior) synonym of *Cleistosphaeridium* (Eaton et al. 2001, p. 173), being nominally distinguished only because there is no record of the type material exhibiting penitabular ridges joining some processes into process complexes. I am unaware of any comparison of the process tips. (The type material for the genotype, *Impletosphaeridium transfodum* Morgenroth 1966a is apparently lost; see Islam 1993, p. 85.)

The formal placement of *Cleistosphaeridium* within the Areoligeraceae is effected in Fensome et al. 2006 although, in the present writer's view, the authors of that paper draw a rather long bow at times, and, as noted elsewhere, I cannot concur with maintaining the distinction between *Areosphaeridium* and *Enneadocysta* on such slim evidence as the symmetry of the process tips.

The present writer's decision to place *Cleistosphaeridium* within the Areoligeraceae was prompted by the evident similarity with the species described herein as *?Areoligera hampdenensis*, and further encouraged by the comment in Eaton et al. 2001, p. 173-174, that *Cleistosphaeridium* species generally show a preferred dorso-ventral orientation and that the archeopyle margin sometimes exhibits an offset sulcal notch. (It must, however, also be mentioned that the emended description of the type species, *Cleistosphaeridium diversispinosum*, given in Eaton et al. 2001, p. 177-189, describes any dorso-ventral flattening as “only limited”, p. 180.)

***Cleistosphaeridium diversispinosum* Davey et al. 1966 emend. Eaton et al. 2001**

Pl. 77, figs. 10-12

1966 *Cleistosphaeridium diversispinosum* Davey et al. 1966, p. 167, pl. 10, fig. 7

2001 *Cleistosphaeridium diversispinosum* Davey et al. 1966 emend Eaton et al., p. 177-188, figs. 1-7

Original Description: A *Cleistosphaeridium* with granular wall and polygonal archeopyle. Processes solid, taeniate or tubular, usually slender and proximally expanded. Distal end forked or expanded (Davey et al. 1966, p. 167).

Size Range: Length excluding any processes = 43 µm (one measured specimen). Width excluding any processes = 32 (38) 45 µm (2 measurements). Length including any processes = 72 µm (one measured specimen). Width including any processes = 52 (63) 74 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	

***Cleistosphaeridium ancyreum* (Cookson & Eisenack 1965a) Eaton et al. 2001**

Pl. 78, figs. 1-6

1965a *Systematophora ancyrea* Cookson & Eisenack, p. 126, pl. 14, figs. 1-3

1992 *Systematophora placacantha* var. *ancyrea* (Cookson & Eisenack 1965a, p. 126, pl. 14, figs. 1-3) Strauss & Lund, p. 173

2000 *Systematophora ancyrea* Cookson & Eisenack, 1965a; Levy & Harwood, p. 228, pl. 9, figs. j-l

Original Description: Shell spherical or slightly oval with a rather thick, densely granular wall and numerous slender, flexuous, simple or occasionally forked appendages with capitate or slightly bifurcate apices. The appendages arise, mainly, from raised ridges which completely or incompletely delimit circular or polygonal areas. These areas are variable in size and are either separate from one another or coalescent. On one surface such areas tend to bound a narrow longitudinal apparently appendage-free surface. The shell opens by an apical archeopyle, the angular rim of which is suggestive of plates (Cookson & Eisenack 1965a, p. 126).

Size Range: Length excluding any processes = 40 µm (one measured specimen). Width excluding any processes = 35 (39) 43 µm (2 measurements). Length including any processes = 65 µm (one measured specimen). Width including any processes = 41 (52) 62 µm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	
Eocene	erratics, McMurdo Sound, Antarctica	MB 188G	Levy & Harwood 2000
Eocene	erratics, McMurdo Sound, Antarctica	MTD 42	Levy & Harwood 2000

Remarks: *Cleistosphaeridium ancyreum* is a morphological intermediary between *C. diversispinosum*, in which penitabular ridges are developed only very weakly or not at all, and *C. placacanthum*, in which penitabular ridges are complete and pronounced. Ridges are developed, but they are not continuous and sometimes not evident on every plate (Eaton et al. 2001, p. 188).

***Cleistosphaeridium placacanthum* (Deflandre & Cookson 1955) Eaton et al. 2001**

Pl. 78, figs. 7-9

- 1955 *Hystriospheridium placacanthum* Deflandre & Cookson, p. 276-277, pl. 9, figs. 1-3
- 1965 *Baltisphaeridium placacanthum* (Deflandre & Cookson 1955) Downie & Sarjeant, p. 94
- 1965 *Baltisphaeridium placacanthum* (Deflandre & Cookson 1955, p. 276-277, pl. 9, figs. 1-3) Downie & Sarjeant, p. 94
- 1966a *Impletosphaeridium placacanthum* (Deflandre & Cookson 1955) Morgenroth, p. 35-36, pl. 9, figs. 10-11
- 1969 *Systematophora placacantha* (Deflandre & Cookson 1955, p. 276-277, pl. 9, figs. 1-3) Davey et al., p. 17
- 1972 *Impletosphaeridium placacanthum* (Deflandre and Cookson 1955) Morgenroth 1966; Benedek, p. 31, pl. 10, figs. 3a-c
- ?1983 *Systematophora placacantha* (Deflandre and Cookson, 1955) Davey et al., 1969; Goodman & Ford, p. 866, pl. 8, figs. 6-7
- 2001 *Cleistosphaeridium placacanthum* (Deflandre & Cookson 1955) Eaton et al., p. 190-191
- 2005 *Cleistosphaeridium placacanthum*; Schiøler, pl. 9, fig. 6

Original Description: Shell globular, circular or asymmetrical in outline, with a large number of processes that are aligned so as to divide the whole surface into more or less polygonal plate-like areas or fields. Each field is separated from its neighbours by an area devoid of appendages. Processes solid, of variable form, somewhat flexuous, simple or branched with pointed or hammer-shaped extremities, widening at the base. Sometimes the bases of 2 or more processes are connected by bridge-like strands; occasionally the apices may coalesce or be connected by a delicate thread as in *Cannosphaeropsis* (Deflandre & Cookson 1955, p. 277).

Size Range: Length excluding processes = 47 µm (one measured specimen). Width excluding processes = 56 µm (one measured specimen). Length including processes = 63 (74) 84 µm (2 measurements). Width including processes = 93 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Whaingaroan	Akitio River, Hawkes Bay, New Zealand	U24/f201 (L12144)	
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f106 (L11042)	
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f102 (L11038)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan

Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	1996
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)	
Eocene	northern Germany; Belgium		Morgenroth 1966a

Remarks: *Cleistosphaeridium placacantum* is distinguished from *Cleistosphaeridium ancyreum* by possessing penitabular ridges which are complete and pronounced, as opposed to discontinuous to lacking on some plates (*Cleistosphaeridium ancyreum*) or barely evident at all (*Cleistosphaeridium diversispinosum*) (Eaton et al. 2001, p. 188).

***Cleistosphaeridium* sp. 1**

Pl. 78, figs. 10-12

Description: Cysts of intermediate size; more or less spherical; apparently single layered; with numerous, evenly and densely distributed, similar non-tabulate spines; spines solid, non-fibrous, some possibly vacuolated at the base; capitate, generally straight, and fairly stubby. Cyst surface between spines minutely, evenly and densely maculate. No indications of cingulum or sulcus. Archeopyle apparently apical; type tA. Tabulation indeterminate.

Size Range: Length excluding processes = 47 (48) 50 μm (2 measurements). Width excluding processes = 40 μm (one measured specimen). Length including processes = 45 (59) 80 μm (12 measurements). Width including processes = 60 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Runangan	Cape Foulwind Section, Westland, New Zealand	K29/f261 (L13543)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The very straight, relatively short spines of this form are quite distinctive.

***Cleistosphaeridium* sp. 3**

Pl. 79, figs. 1-6

Description: Cysts small, chorate, dorso-ventrally compressed, lenticular, lacking horns; episome and hyposome more or less equal in length. Cyst wall single-layered. Archeopyle apical (?); operculum free. Surface ornament present, non-tabular, comprising a dense reticulum. Processes penitabular, spinose, somewhat sinuous; non-fibrous, occasionally branching, apparently solid; incompletely united into penitabular ridges proximally, dolabrate distally. Tabulation weakly expressed, apparently gonyaulacacean. Cingulum weakly expressed, indicated by the alignment of processes. Sulcus weakly expressed, indicated by the alignment of processes.

Size Range: Length excluding any processes = 40 μm (one measured specimen). Width excluding any processes = 45 μm (one measured specimen). Length including any processes = 52 (70) 102 μm (10 measurements). Width including any processes = 65 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f114 (L11050)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	

Remarks: I have to admit that I am far from confident that this taxon does not possess a large precingular archeopyle. There are many specimens, yet none show a precingular archeopyle face-on, yet, in the end, it was only the dolabrate processes which tipped me in favour of *Cleistosphaeridium*, with the implied apical archeopyle.

Genus *Cyclonephelium* Deflandre & Cookson 1955 emend. Stover & Evitt 1978

- 1955 *Cyclonephelium* Deflandre & Cookson, p. 285
1958a *Tenua* Eisenack, p. 410
1978 *Cyclonephelium* Cookson 1955 emend. Stover & Evitt, p. 35-36

Type Species: Cyclonephelium compactum Deflandre & Cookson 1955, p. 285, pl. 2, figs. 11-13; text-figs. 44-46 [Cretaceous (Albian-Santonian)]

Original Description: Shell spheroidal, flattened, with an equatorial ornamentation that extends for varying distances from the equator but never to the poles. The ornament is composed of processes that are either distinct or close and confluent and sometimes connected by more or less broad trabeculae. Shell often provided with large and ill-defined lateral opening (Deflandre & Cookson 1955, p. 258).

Cyclonephelium membranophorum Cookson & Eisenack 1962b

Pl. 79, figs. 7-9

- 1962b *Cyclonephelium membranophorum* Cookson & Eisenack, p. 495, pl. 6, figs. 8-14

Original Description: Shell apparently concavo-convex ..., circular to subcircular in outline. Circumferential border zone delimited by two thin membranes of equal width, each of which is supported by rather widely spaced, equidistant, radial fibres. These fibres arise from the peripheral surfaces of the shell, and their bases are connected with one another tangentially. They are simple or capitate and relatively stout. Sometimes fine radial striae cross the width of the membranes, in which cases the edges appear to be very finely toothed. Occasionally a union between opposing fibres may occur, with the formation of wide funnel-like structures. The sculpture of the shell varies from very finely to coarsely granular (Cookson & Eisenack 1962b, p. 495; ellipses replace figure references in the original).

Size Range: Length including processes = 87 µm (one measured specimen). Width including processes = 95 µm (one measured specimen).

Distribution: Extremely rare; known from a single specimen.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996

Remarks: The form encountered in this study superficially resembles *C. membranophorum*, although the age is quite wrong (*C. membranophorum* is supposedly Albian; the present specimen is Bortonian.)

Genus *Glaphyrocysta* Stover & Evitt 1978

- 1978 *Glaphyrocysta* Stover & Evitt, p. 49-50

Type Species: Glaphyrocysta retiintexta (Cookson 1965a, p. 88, pl. 11, fig. 4) Stover & Evitt 1978, p. 50 [Cretaceous (Senonian)]

Original Description: Cysts skolochorate, body lenticular with several annulate to arcuate penitabular process complexes; most complexes join to one another distally by a simple to intricate system of trabeculae; midventral and middorsal areas typically process-free or with reduced processes; archeopyle apical, Type tA; parasulcal notch offset (Stover & Evitt 1978, p. 49).

Glaphyrocysta cf. retiintexta

Pl. 79, figs. 10-12, Pl. 80, figs. 1-12, Pl. 81, figs. 1-9

- ?1965 *Cyclonephelium exuberans* Deflandre et Cookson 1955; De Coninck, p. 44-45, pl. 13, figs. 3-4, 6
cf. 1966b *Cyclonephelium incultum* Morgenroth, p. 9, pl. 2, fig. 5
1969b *Cyclonephelium [retiintextum]* Cookson; Archangelsky, p. 203-204, pl. 5, figs. 8-9
cf. 1978 *Glaphyrocysta inculta* (Morgenroth 1966b) Stover & Evitt, p. 50

Description: Cysts of intermediate size, chorate, dorso-ventrally compressed, lenticular, lacking horns. Cyst wall single-layered, with an ectophragm. Archeopyle apical, type tA; operculum free. Non-tabular, comprising minute granules; evenly covering the surface of the central body. Processes ?intratabular, straight or gently curved; non-fibrous, apparently solid, 20-30 µm; sometimes incompletely connected proximally, connected by a well developed trabeculum distally. Tabulation weak to lacking. Cingulum lacking. Sulcus sometimes weakly expressed, indicated by incomplete sutural ridges.

Size Range: Length excluding processes = 45 (53) 60 µm (3 measurements). Width excluding processes = 50 (53) 55 µm (3 measurements). Length including processes = 72 (85) 102 µm (4 measurements). Width including processes = 70 (94) 115 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Oligocene	Depold'sche Ziegelei, southern Helmstedt	H2/I	Morgenroth 1966b
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f486 (L23121)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f300 (L23130)	
Eocene	Rio Turbio Formation, Santa Cruz Province, Patagonia	720	Archangelsky 1969b
Ypresian	Merelbeke, Belgium	Preparation 17	De Coninck 1965

Remarks: *Glaphyrocysta* cf. *retiintexta* has processes which are comparable to the diameter of the central body, ranging from perhaps a third to three quarters or more, often on a single specimen. In this respect it differs from *G. retiintexta* (Cookson 1965a) Stover & Evitt 1978 s.s., and *Glaphyrocysta semitecta* (Bujak 1980), in which most processes appear to be relatively shorter.

It differs from the type illustrations of *G. exuberans* (Deflandre & Cookson 1955) Stover & Evitt 1978 in possessing fewer, less densely arranged processes, though it is quite similar to a number of reported specimens subsequently appearing under that name.

It resembles, at least superficially, the specimen illustrated as *Membranilarnax* cf. *liradisoides* in Pastiels 1948, pl. 5, fig. 15, subsequently (and unwisely, in my view, because the description and figures were inadequate by the day's standards) designated *Cyclonephelium* (now *Glaphyrocysta*) *pastielsi* by Deflandre & Cookson 1955. However, Sarjeant's (1986) re-illustrations of the holotype depict a cyst with considerably more numerous processes connecting the trabeculum with the central body. Additionally, his emended diagnosis indicates that the processes are probably relatively shorter as well: "less than 1/3 the equatorial diameter of the cyst" (Sarjeant 1986, p. 28).

In respect of the length and density of its processes, the published species which *Glaphyrocysta* cf. *retiintexta* most closely resembles is *Glaphyrocysta inculta* (Morgenroth 1966b). It differs, however, in having a minutely granulate central body wall, rather than the relatively coarse granulation described by Morgenroth.

Genus *Membranophoridium* Gerlach 1961 emend. Stover & Evitt 1978

1961 *Membranophoridium* Gerlach, p. 198

1978 *Membranophoridium* Gerlach 1961 emend. Stover & Evitt, p. 64-65

Type Species: *Membranophoridium aspinatum* Gerlach 1961, p. 199-201, pl. 29, figs. 7-8 [Mid Oligocene]

Original Description: A genus with the characteristics of the Family Hystrichosphaeridae and the following distinctions: thecal outline oval or circular; however, dominantly semicircular owing to the loss of the apical polar cap. Lower, in contrast to upper side, bordered by two, parallel, more or less low, meridionally trending, thorny fringes that may be interrupted repeatedly. Fringes not joined at antapex, often drawn out into two long lobes of unequal length. Lower side of the theca weakly depressed longitudinally (translated from Gerlach 1961, p. 198, in Stover & Evitt 1978, p. 64).

***Membranophoridium perforatum* Wilson 1988**

Pl. 81, figs. 10-12

1988 *Membranophoridium perforatum* Wilson, p. 26, pl. 16, figs. 5a-b, 6a-b

Original Description: Cyst lenticular, subspherical, bilayered, circumcavate, periphragm and endophragm in closest contact only in mid dorsal and mid ventral regions. Periphragm thin, generally folded, outline somewhat irregular to undulating, smooth with a sub-pointed apex and occasionally two poorly developed antapical lobations present. Perforations (diameter up to 10 µm) present in variable numbers, mainly around periphragm margin. Occasional solid slender processes (breadth up to 4 µm) sometimes connect periphragm to endophragm in antapical area. Endocyst thin walled, smooth, with a circular outline. Paratabulation indicated by archeopyle only, formula unknown. Archeopyle relatively broad, apical, type tA; principal archeopyle suture zig-zag, parasulcal notch indicating apical position of parasulcus. No indication of paracingulum (Wilson 1988, p. 26).

Size Range: Length = 83 µm (one measured specimen). Width = 102 µm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	

Genus *Riculacysta* Stover 1977

1977 *Riculacysta* Stover, p. 76-77

Type Species: *Riculacysta perforata* Stover 1977, p. 77-78, pl. 2, figs. 22-31 [Mid to Late Oligocene]

Original Description: Cysts are chorate with a subspherical body that bears solid, normally isolated processes which arise from the ventrolateral and lateral surfaces and are typically lacking on the midventral and middorsal surfaces. Ventrolateral processes are longer than the lateral ones; all are connected distally by irregularly perforate to trabecular ectophragm that is close or appressed dorsally to the autophragm. Paratabulation indicated by apical type A archeopyle, by paracingulum, and less conspicuously by processes (Stover 1977, p. 76).

Remarks: Stover (1977) contrasted *Riculacysta* with *Adnatosphaeridium*, noting the distinction that the trabecular ectophragm of *Riculacysta* is close or appressed dorsally to the autophragm, and *Cyclonephelium*, noting that the processes of *Riculacysta* are of more or less equal length, regardless of their position. Although Stover & Evitt (1978) did not contrast their new genus, *Glaphyrocysta*, with *Riculacysta*, the distinction with *Cyclonephelium* appears to hold true for *Glaphyrocysta* also.

?*Riculacysta* sp. 1

Pl. 82, figs. 1-12

Description: Archeopyle apparently apical. Central body single-layered, apparently more or less spherical, although one specimen (see Pl. 82, fig. 5) shows possible evidence for an antapical lobe-like structure. Surface ornamented with variable ridges and granules, forming a pattern which might approximately be called reticulate. A number of processes arise from ?intratabular areas, of variable width ranging from thin rod-like structures to (more commonly) broad, flattened, perforated-fenestrate sheets, often incorporating rod-like structures. The processes are connected distally by a perforate-fenestrate trabeculum, appearing essentially similar to the broader processes.

Size Range: Length excluding processes = 55 (60) 67 µm (4 measurements). Width excluding processes = 61 (68) 80 µm (4 measurements). Length including processes = 76 (86) 95 µm (4 measurements). Width including processes = 82 (92) 102 µm (4 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f488 (L23123)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)	

Remarks: The present form bears some superficial resemblance to *Glaphyrocysta* but differs significantly in appearing to be essentially spherical rather than dorso-ventrally compressed, which suggests it may not belong with the Areoligeraceae. On some specimens, processes can be observed arising from all plate series, and it is not clear whether they are confined to the ambital plates.

Placement in *Riculacysta* is provisional because, although the middle Eocene forms described here possess a morphology which broadly resembles *Riculacysta perforata*, I know of no evidence for any geographic or temporal intermediates which might suggest a phylogenetic relationship.

Suborder Goniodomineae Fensome et al. 1993b

Family Goniodomaceae Lindemann 1928

Subfamily Pyrodinioideae Fensome et al. 1993b

Genus *Eisenackia* Deflandre & Cookson 1955

- 1955 *Eisenackia* Deflandre & Cookson, p. 258
1978 *Alisocysta* Stover & Evitt, p. 15-16
1978 *Eisenackia* Deflandre & Cookson 1955 emended Sarjeant in Davey *et al.* 1966, Stover & Evitt, p. 42
2003 *Eisenackia* Deflandre and Cookson, 1955, emend. Quattrocchio and Sarjeant, p. 144, 146

Type Species: Eisenackia crassitabulata Deflandre & Cookson 1955, p. 258-261, pl. 5, fig. 2; text-figs. 6-16 [Paleocene-Early Eocene]

Original Description: Cell globular without appendages. Transverse girdle and longitudinal furrow not marked by a depression of the membrane which has a completely continuous outline. Transverse girdle delimited by the bases of the plates. Tabulation 2-3', 6'', ?6g, 6''', 2p, 1'''''. The epitheca has, amongst others, an elongated ventral plate and the hypotheca a ventral area consisting of several small plates (Deflandre & Cookson 1955, p. 258).

Remarks: *Alisocysta* is distinguished from *Schematophora* by the expression of intratabular ornament on the cingular series.

Alisocysta aff. *circumtabulata*

Pl. 83, figs. 1-11

- 1982c *Alisocysta* sp. Wilson, p. 4, pl. 2, figs. 5-7
1982c *Alisocysta* sp.; Wilson, p. 4, pl. 2, figs. 5-7
1988 *Alisocysta circumtabulata* (Drugg 1967) Stover and Evitt 1978; Wrenn & Hart, p. 345, fig. 15, 1-3

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome somewhat shorter than hyposome. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Ornament intratabular, comprising inflated, hollow processes. Processes intratabular, comprising high membranous septa; non-fibrous, open; somewhat ragged distally. Tabulation clearly expressed, gonyaulacacean. Cingulum clearly expressed, a differentiated, flattened, process series; offset only slightly. Sulcus clearly expressed, indicated by the alignment of processes; more or less vertical.

Size Range: Length excluding processes = 45 (47) 49 μm (3 measurements). Width excluding processes = 37 (39) 41 μm (3 measurements). Length including processes = 53 (59) 62 μm (6 measurements). Width including processes = 45 (52) 57 μm (6 measurements).

Distribution: Common.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996
Mangaorapan	Eyre River, Oxford area, central Canterbury, New Zealand	L34/f7538	Wilson 1982c
Mangaorapan	White Stream, Oxford area, central Canterbury, New Zealand	L34/f7539	Wilson 1982c
late early Paleocene	northern Seymour Island, West Antarctica	8497	Wrenn & Hart 1988

Remarks: *Alisocysta* aff. *circumtabulata* resembles *A. circumtabulata* quite closely, but seems to differ consistently in possessing higher penitabular septa, sometimes developed to the extent (e.g. Pl. 83, figs. 7-11) that they could fairly be called intratabular processes.

?*Alisocysta* cf. *circumtabulata*

Pl. 83, fig. 12, Pl. 84, figs. 1-3

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome somewhat shorter than hyposome. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Ornament intratabular, comprising inflated, hollow processes. Processes intratabular, comprising high membranous septa; non-fibrous, open; somewhat ragged distally. Tabulation clearly expressed, gonyaulacacean. Cingulum clearly expressed, a differentiated, flattened, process series; offset only slightly. Sulcus clearly expressed, indicated by the alignment of processes; more or less vertical.

Size Range: Length excluding processes = 52 µm (one measured specimen). Width excluding processes = 47 µm (one measured specimen). Length including processes = 70 µm (one measured specimen). Width including processes = 61 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f090 (L16338)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: *Alisocysta* cf. *circumtabulata* resembles *A. aff. circumtabulata* quite closely, and *A. circumtabulata* more distantly, but in this case the septa/processes are even longer and more constricted – more “process-like” – than either.

?*Alisocysta* sp. cf. *Hystrichokolpoma wilsonii*

Pl. 84, figs. 4-12, Pl. 85, figs. 1-3

1988 *Hystrichosphaeridium tubiferum* subsp. *brevispinum* (Davey and Williams 1966) Lentin and Williams 1973; Wrenn & Hart, p. 356, fig. 26, 7-9

?1995 *Hystrichokolpoma salacia* Eaton, 1976; Mao & Mohr, pl. 5, figs. 3, 7

Description: Cysts of intermediate size, chorate, not dorso-ventrally compressed, prolate, lacking horns; episome somewhat shorter than hyposome. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Ornament intratabular, comprising inflated, hollow processes. Processes intratabular, comprising high membranous septa; non-fibrous, open; somewhat ragged distally. Tabulation clearly expressed, gonyaulacacean, inferred formula: 4', 0a, 6", 6c, 6"', 1ps, 1''', 2-5s. Cingulum clearly expressed, a differentiated, flattened, process series; offset only slightly. Sulcus clearly expressed, indicated by the alignment of processes; more or less vertical.

Size Range: Length excluding processes = 28 (35) 43 µm (3 measurements). Width excluding processes = 33 (35) 36 µm (3 measurements). Length including processes = 45 (51) 57 µm (3 measurements). Width including processes = 45 (49) 51 µm (3 measurements).

Distribution: Frequent.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	
late early Eocene	northern Seymour Island, West Antarctica	8503	Wrenn & Hart 1988

Remarks: The processes are open and the cingular processes, although a strongly rectangular rather than square cross-section and, so, a different shape to the pre- and post-cingular processes, do not attain the thin, tubular form characteristic of *Hystrichokolpoma* s.s. The processes are of such a length as to fall outside the range normally attributed to *Alisocysta*, and the hyposomal topology has not been determined.

Genus *Homotryblium* Davey & Williams 1966b

1966b *Homotryblium* Davey & Williams, p. 100

1978 *Homotryblium* Davey & Williams in Davey *et al.* 1966; Stover & Evitt, p. 210

Type Species: *Homotryblium tenuispinosum* Davey & Williams 1966b, p. 101-102, pl. 4, fig. 11; pl. 12, figs. 1, 5, 7; text-fig. 21 [Early Eocene]

Original Description: Sub-spherical chorate cyst with central body composed of thin endophragm and surrounding periphragm which gives rise to processes. Processes intratabular, cylindrical to tubiform, open distally, reflecting a tabulation of 3', 6", 6c, 6"', 1p, 1"" and 1 to 5s. Processes not in communication with the cavity of the central body. Archeopyle epitrectal, suture running just above cingulum processes (Davey & Williams 1966b, p. 100).

Homotryblium sp. 2

Pl. 85, figs. 4-6

Description: Cysts small, apparently more or less spherical, lacking horns. Walls two-layered, acavate. Processes non-tabular, about 10 µm in length, hollow, tapering from broad bases then distally aculeate, apparently open. Surface smooth and hyaline. No evidence of tabulation could be observed.

Size Range: Length excluding any processes = 35 µm (one measured specimen). Width excluding any processes = 35 µm (one measured specimen). Length including any processes = 45 (51) 60 µm (6 measurements). Width including any processes = 45 µm (one measured specimen).

Distribution: Very rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Genus Hystrichosphaeridium Deflandre 1937b emend. Davey & Williams 1966

1937b *Hystrichosphaeridium* Deflandre, p. 68

1978 *Hystrichosphaeridium* Deflandre 1937b emended Davey & Williams in Davey *et al.* 1966; Stover & Evitt, p. 55-57

Type Species: *Hystrichosphaeridium tubiferum* (Ehrenberg 1838, pl. 1, fig. 16) Deflandre 1937b, p. 68 [?Late Cretaceous]

Original Description: This genus comprises all the hystrichospheres totally destitute of an equatorial system of elongate plates and whose shell, in general, does not bear fields or plates limited by sutures. The shell, of a dimension greater than 20µ, is most often spherical or spheroidal; some species, however, are more or less elongate (translated from Deflandre 1937b, p. 68, by Stover & Evitt 1978, p. 55).

***Hystrichosphaeridium tubiferum* (Ehrenberg 1838) Deflandre 1937b**

Pl. 85, figs. 7-12

1838 *Xanthidium tubiferum* Ehrenberg, pl. 1, fig. 16

1933b *Hystrichosphaera tubifera* Ehrbg.; O. Wetzel, p. 40

1937b *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre, p. 96

1961 *Hystrichosphaeridium tubiferum* (Ehrenberg); Gerlach, p. 184-185, pl. 28, fig. 2

1963 *Hystrichosphaeridium tubiferum* (Ehrenberg 1838); Brosius, p. 38-39, pl. 8, fig. 4, text-fig. 2 (6a-c)

1965 *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre 1937; De Coninck, p. 25-26, pl. 6, figs. 1-3, 6-7, text-fig. 11

1967a *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre; Wilson, p. 67, fig. 40

1982b *Hystrichosphaeridium tubiferum* (Her.); Wilson, p. 7, pl. 1, fig. 1

1983 *Hystrichosphaeridium tubiferum* (Ehrenberg, 1836) Deflandre, 1937; Goodman & Ford, p. 866, pl. 8, fig. 5

1989 *Hystrichosphaeridium tubiferum* (Ehr.) Deflandre; Wilson, pl. 1, fig. 14

Original Description: [No textual description provided.]

Size Range: Length excluding processes = 38 (42) 48 µm (4 measurements). Width excluding processes = 32 (34) 35 µm (3 measurements). Length including processes = 47 (88) 185 µm (42 measurements). Width including processes = 68 (83) 110 µm (13 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle	north west Germany	Pr 1170/40	Gerlach 1961

Miocene				
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f057 (L09214)	Wilson 1985	
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f489 (L23124)		
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f303 (L23133)		
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f040 (L09197)	Wilson 1985	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996	
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f418 (L23126)		
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f417 (L23125)		
middle Eocene-late Eocene	DSDP Holes 511 and 512		Goodman & Ford 1983	
Heretaungan-Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f298 (L23128)		
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)		
Eocene	CIROS-1 drillhole, McMurdo Sound, Antarctica	SM3799	Wilson 1989	
Eocene	erratics near Minna Bluff, McMurdo Sound, Antarctica	L4737	Wilson 1967a	
Ypresian	Merelbeke, Belgium	Preparation 20	De Coninck 1965	

***Hystrichosphaeridium salpingophorum* Deflandre 1935**

Pl. 86, figs. 1-6

1935 *Hystrichosphaeridium salpingophorum* Deflandre, p. 232, pl. 9, fig. 1

1937b *Hystrichosphaeridium salpingophorum* Deflandre 1935, p. 232, pl. 9, fig. 1 ex Deflandre, p. 71

1965 *Hystrichosphaeridium salpingophorum* Deflandre 1937; De Coninck, p. 24-25, pl. 5, figs. 2, 3, 5-8, 11-12, text-fig. 9-10

Original Description: ... *H. salpingophora* n. sp. ... body spherical or subspherical, ornamented with more or less flared tubular processes ... (translation from Deflandre 1935, p. 232).

Size Range: Length excluding processes = 40 (44) 47 μm (2 measurements). Width excluding processes = 38 (39) 40 μm (2 measurements). Length including processes = 73 (80) 87 μm (2 measurements). Width including processes = 70 (76) 81 μm (2 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Ypresian	Merelbeke, Belgium	Preparation 20	De Coninck 1965

Remarks: *Hystrichosphaeridium salpingophorum* supposedly differs from *H. tubiferum* in possessing processes which are more square in cross section than those of *H. tubiferum*. A few specimens encountered in the present study do have somewhat squarish cross sections, and are presented here. However, the distinction is not really convincingly supported by the present material.

***Hystrichosphaeridium brevispinum* (Davey & Williams 1966b) Clowes n. stat.**

Pl. 86, figs. 7-12, Pl. 87, figs. 1-3

1966b *Hystrichosphaeridium tubiferum* var. *brevispinum* Davey & Williams, p. 58, pl. 10, fig. 10

1973 *Hystrichosphaeridium tubiferum* subsp. *brevispinum* (Davey & Williams 1966b, p. 58, pl. 10, fig. 10) Lentin & Williams, p. 80

Original Description: A variety of *Hystrichosphaeridium tubiferum* with processes rarely exceeding one-third of the diameter of the central body (Davey & Williams 1966b, p. 58).

Size Range: Length excluding processes = 42 (44) 46 µm (4 measurements). Width excluding processes = 38 (41) 47 µm (5 measurements). Length including processes = 52 (70) 93 µm (17 measurements). Width including processes = 60 (71) 85 µm (12 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f057 (L09214)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f094 (L16342)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: *Hystrichosphaeridium brevispinum* is usually treated as a subspecies of *H. tubiferum*. However, there is no objective evidence to suggest it is more closely related or otherwise “similar” to *H. tubiferum* than other *Hystrichosphaeridium* species – notably *H. salpingophorum* – so it is herein considered as a species in its own right.

Suborder Uncertain

Family Uncertain

Genus *Batiacasphaera* Drugg 1970b

1970b *Batiacasphaera* Drugg, p. 813

1978 *Batiacasphaera* Drugg 1970b; Stover & Evitt, p. 20-21

Type Species: *Batiacasphaera compta* Drugg 1970b, p. 813-814, figs. 6A-E, 7A-B [Late Eocene]

Original Description: Tract spherical to subspherical with an angular apical archeopyle. The ornamentation consists of rod-shaped elements, either separated or arranged to form a reticulum. In the latter case they may be fused (Drugg 1970b, p. 813).

Batiacasphaera perforata Wilson & Clowes n. sp.

Pl. 87, figs. 4-12, Pl. 88, figs. 1-3

Derivation of Name: Latin, *perforatus*, perforated; with reference to the perforate autophragm.

Holotype: Sample I43/f089, slide L16337/SM102; Burnside Formation, Puketeraki Core (Bortonian); Pl. 87, figs. 4-9

Description: Cysts of intermediate size, proximate, dorso-ventrally compressed, lenticular, lacking horns. Cyst wall single-layered. Archeopyle apical, type tA; operculum free. Processes lacking; surface ornament present, non-tabular, comprising circular perforations (diameter about 1µm); with features on a scale of 20 sculptural elements across the diameter. Tabulation not expressed.

Size Range: Length including any processes = 53 (60) 68 µm (10 measurements). Width including any processes = 57 (62) 67 µm (2 measurements).

Distribution: Very rare.

Age/Stage	Location	Sample	Sample Reference
Kaiatan-Runangan	Jacksons Paddock, Oamaru-Dunedin, New Zealand	J41/f8914 (L04979)	Wilson 1982b
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: *Batiacasphaera perforata* is distinguished from all other similar species, known at this time, by its characteristic perforate autophragm.

Remarks: A provisional description for this taxon appears in an unpublished manuscript prepared by Dr. Graeme Wilson shortly prior to his retirement from GNS Science (formerly the New Zealand Geological Survey), under the name *Batiacasphaera perforata*. Although the description has been amended somewhat to bring it into conformity with the other descriptions provided herein, and observations from additional material incorporated, Dr. Wilson’s fundamental contribution is recognised in the authorship of the proposed name.

Genus *Cerebrocysta* Bujak 1980

1980 *Cerebrocysta* Bujak, p. 42

1987 *Cerebrocysta* Bujak in Bujak *et al.* 1980, p. 42; Stover & Williams, p. 57

Type Species: Cerebrocysta bartonensis Bujak 1980, p. 42, pl. 13, figs. 4-11 [Late Eocene]

Original Description: Autocyst spherical to ovoidal, without apical, antapical, or other projections, except for an apparently random ornament of low crests. The crests occasionally suggest a paratabular arrangement. The archeopyle is formed by the loss of one (3'') or more precingular paraplates (Bujak 1980, p. 42).

Remarks: According to Stover & Williams (1987, p. 57), *Cerebrocysta* differs from *Pyxidinospis* Habib 1976 in having discontinuous ridges and isolated granules rather than being reticulate, and in including forms having different archeopyle types whereas only forms with a simple precingular (type P) archeopyle are assigned to *Pyxidinospis*.

The distinction from *Pyxidinospis* on the basis of ornament is not considered significant; forms which possess a reticulum rather than discontinuous ridges may still be considered a "good" *Cerebrocysta*. If this view is accepted, *Cerebrocysta* primarily differs from *Pyxidinospis* in possessing a 2P (-3P) archeopyle, whereas *Pyxidinospis* possesses a 1P archeopyle.

Cerebrocysta sp. 1

Pl. 88, figs. 4-9

Description: Cysts small, proximate, not dorso-ventrally compressed, more or less spherical to prolate, lacking horns. Cyst wall single-layered. Archeopyle precingular, type ?P (3''); operculum free. Processes lacking; surface ornament present, non-tabular, comprising low membranous crests, forming an irregular reticulum; with features on a scale of 8-12 sculptural elements across the diameter; very low (about 1 µm or lower). Tabulation not expressed. Cingulum not expressed. Sulcus sometimes weakly expressed, indicated by surface ornament; more or less vertical.

Size Range: Length = 20 (28) 33 µm (17 measurements). Width = 22 (26) 29 µm (5 measurements).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Cerebrocysta ?sp. 2

Pl. 88, figs. 10-12

2001 *Spongodinium?* Sp. A; Crouch, p. 47, pl. 10, figs. 8-9

2003 *Cerebrocysta bartonensis* Brinkhuis, Munsterman, *et al.*, pl. 1, figs. 32-33

?2003 *Cerebrocysta bartonensis*; Brinkhuis, Sengers, *et al.*, pl. 1, fig. 24

Description: Cysts proximate, spherical, lacking horns; the apical and antapical hemispheres roughly equal. Cyst walls single layered (~1.5 µm thick); walls delicate and flexible so that distorted cysts are common. Archeopyle precingular, type 2 (-3?) P; operculum free and the plates typically separated. Processes lacking; ornament comprising a low (~0.5 µm) nontabular reticulum; the cyst wall appearing completely smooth within the reticulae. Tabulation indicated only by the archeopyle and cingulum; formula unknown. Cingulum poorly expressed by alignment of reticulae and sometimes by folding of the cyst wall.

Size Range: Length = 60 µm (one measured specimen). Width = 55 µm (one measured specimen).

Distribution: Infrequent.

Age/Stage	Location	Sample	Sample Reference
Otaian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f101 (L16349)	Wilson & McMillan 1996
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
Bortonian	Burnside Marl Pit, Oamaru-Dunedin, New Zealand	I44/f080 (L08947)	Clowes & Wilson 2006
Waipawan	Tawanui Section, Wairarapa, New Zealand		Crouch 2001

Remarks: *Cerebrocysta* ?sp. 2 differs from *Cerebrocysta bartonensis* in being considerably larger (~60 cf. ~25 µm), in having a reticulate ornament rather than discontinuous ridges and isolated granules, and in an apparently less variable archeopyle. Another species possessing a reticulum resembling *Cerebrocysta* ?sp. 2 is *Pyxidinosia waipawaensis*, which differs in being somewhat smaller (~50 µm), possessing a thicker, most robust wall (~2 µm), and in possessing a much smaller archeopyle which is quite clearly formed by the release of a single plate.

Genus *Chlamydophorella* Cookson & Eisenack 1958

1958 *Chlamydophorella* Cookson & Eisenack, p. 56

1978 *Chlamydophorella* Cookson & Eisenack 1958; Stover & Evitt, p. 27-28

Type Species: *Chlamydophorella nyei* Cookson & Eisenack 1958, p. 56, pl. 11, figs. 1-3 [Cretaceous (Aptian-Turonian)]

Original Description: Shell enclosed in a delicate membrane that is supported by closely arranged, slender bifurcate spines of approximately equal length (Cookson & Eisenack 1958, p. 56).

Cysts proximate, holocavate [sic], subspherical to elongate ellipsoidal, with or without an apical protrusion or horn; autophragm with numerous nontabular processes of essentially uniform height and covered by an ectophragm; archeopyle apical, Type tA (Stover & Evitt 1978, p. 28).

Remarks: Stover & Evitt 1978 (p. 28) applies the descriptor “holocavate” to *Chlamydophorella*. However, I am not convinced the term is correctly applied in this situation. Although it is frequent practice to treat the ectocoel as an analogue to the pericoel (e.g. Evitt 1985, p. 65), they are not homologous structures (in a developmental sense); personally, I restrict the cavation concept to spaces between the endophragm and periphragm of those two- or three-layered cysts possessing them.

Brideaux (1971, p. 98) remarked on the similarity between *Gardodinium* and *Chlamydophorella* and stated that “should both genera prove to have apical archeopyles [as is the case], it would be difficult to maintain two different names for the same concept.” Stover & Evitt 1978, however, regards *Gardodinium* as remaining distinct from *Chlamydophorella* “in always having a prominent apical horn, in having more slender, delicate, less densely distributed processes, and in showing faint indications of paratabulation other than the archeopyle” (p. 28). In any event, if the two are considered synonymous, *Chlamydophorella* is the senior name.

Chlamydophorella neopilata Clowes n. sp.

Pl. 89, figs. 1-12

1984 *Chlamydophorella* sp.; Clowes & Morgans, p. 32, pl. 2, figs. 1-2

Derivation of Name: Greek, νεοζ, new, + *pilata*; with reference to the younger range than the similar taxon, *Chlamydophorella pilata*.

Holotype: Sample J42/f096, slide L10951/SM2952; Totara Limestone, Kakanui River (early Whaingaroan); Pl. 89, figs. 1-4

Description: Cysts subspherical to prolate, lacking horns; two-layered, the wall layers typically separated by numerous short (~2 µm) non-tabular processes. Archeopyle apical, type tA or (tA); archeopyle margin quite ragged; operculum free though frequently adherent. Surface appearance granulate from the effect of seeing the non-tabular processes end-on. Other than the archeopyle there are no consistent indications of tabulation. However, it is occasionally possible to discern an imperfect alignment of the granulae suggesting a cingulum (e.g. Pl. 89, fig. 4).

Size Range: Length = 29 (35) 43 µm (15 measurements). Width = 28 (30) 34 µm (3 measurements).

Distribution: Ranges ?Bortonian to Whaingaroan, but commoner in the younger part of this range.

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f096 (L10951)	Clowes & Morgans 1984
?early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f097 (L10952)	Clowes & Morgans 1984
Runangan-early Whaingaroan	Kakanui River, Oamaru-Dunedin, New Zealand	J42/f125 (L11625)	
Runangan-early Whaingaroan	Kakanui River mouth		Clowes & Morgans 1984
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan

	Zealand		1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Comparison: Although some specimens of this taxon sometimes exhibit a very faint alignment of the pilae, suggesting sutural lineations, the lineations are both far less frequent and far less pronounced than in specimens of the older (Heretaungan to ?Bortonian) species, *Chlamydothorella pilata*.

***Chlamydothorella pilata* Clowes n. sp.**

Pl. 90, figs. 1-12

Derivation of Name: Latin, *pila*, pillar; with reference to the surface ornament which recalls a pilate pollen grain.

Holotype: Sample J42/f485, slide L23120/SM046; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); Pl. 90, figs. 1-6

Description: Cysts subspherical to prolate, lacking horns; two-layered, the wall layers typically separated by numerous short (~2 µm) non-tabular processes. Archeopyle apical, type tA or (tA); archeopyle margin quite ragged; operculum free though frequently adherent. Surface appearance granulate from the effect of seeing the non-tabular processes end-on. Tabulation is variably indicated by alignment or coarsening of the ornament into sutural lineations, especially along the margins of the cingulum.

Size Range: Length = 44 (48) 56 µm (3 measurements). Width = 33 (34) 35 µm (3 measurements).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f485 (L23120)	
Porangan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f299 (L23129)	
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f483 (L23118)	

Comparison: This species differs from *Chlamydothorella pilata* in the stronger and more consistent development of sutural lineations.

Genus *Dapsilidinium* Bujak et al. 1980b

1980b *Dapsilidinium* Bujak et al., p. 27-28

1987 *Dapsilidinium* Bujak in Bujak et al. 1980, p. 27; Stover & Williams, p. 69-71

Type Species: *Dapsilidinium pastielsii* (Davey & Williams 1966b, p. 92-93, pl. 4, fig. 10) Bujak et al. 1980, p. 28 [Early Eocene]

Original Description: Chorate cysts with a subspherical to ovoidal central body bearing numerous processes. Processes intratabular, generally exceeding one per paraplate, mostly uniform in length but sometimes varying slightly in width. Processes hollow, open distally, tubiform or tapering. Periphragm ornament smooth, chagrinated, granulate or spinate, often extending on to the processes. Archeopyle apical, tetratabular. Operculum detached (Bujak et al. 1980, p. 27).

Remarks: *Dapsilidinium* differs from *Cleistosphaeridium* most obviously in the possession of hollow processes.

***Dapsilidinium pseudocolligerum* (Stover 1977) Bujak et al. 1980**

Pl. 91, figs. 1-6

1961 *Hystrichosphaeridium simplex* (White 1842); Gerlach, p. 190, pl. 28, fig. 10, text-fig. 20-22

1971 *Hystrichosphaeridium simplex* (White 1842); Jux, pl. 26, figs. 7-14, text-fig. 1, 3d

1972 *Hystrichosphaeridium simplex* (White 1842) Gerlach 1961; Benedek, p. 29, pl. 9, fig. 11

1975 *Polysphaeridium pastielsii* Davey and Williams 1966; Williams & Brideaux, pl. 24, fig. 3

1977 *Polysphaeridium pseudocolligerum* Stover, p. 74-75, pl. 1, figs. 14-19

1980b *Dapsilidinium pseudocolligerum* (Stover 1977, p. 74-75, pl. 1, figs. 14-19) Bujak et al., p. 28

Original Description: Cysts are chorate with spherical to subspherical body from which arise 40 or more nontabular processes. Endophragm is typically thicker than the periphragm, and the wall layers are appressed between processes. Processes are nearly uniform in size and shape, hollow, generally slightly wider proximally than near their tips, more or less circular in cross-section, and expanded and open distally. Surface of processes is smooth, faintly granular or striate, and areas between processes are granular or punctoreticulate. Archeopyle is apical, type A, principal archeopyle suture only slightly angular and accessory sutures are rarely developed. Operculum is free and constituent apical plates are not delineated on its surface. Except for the archeopyle, indicators of paratabulation and parasulcus are lacking; paracingulum not expressed or indicated by equatorial alignment of processes. Overall size 60 to 92 µm; body 36 to 45 µm in diameter; processes 15 to 23 µm in length and 3 to 7 µm in basal diameter (Stover 1977, p. 75).

Size Range: Length excluding processes = 30 (39) 50 µm (5 measurements). Width excluding processes = 38 (40) 43 µm (4 measurements). Length including processes = 45 (61) 77 µm (19 measurements). Width including processes = 25 (64) 75 µm (18 measurements).

Distribution: Common.

Age/Stage	Location	Sample	Sample Reference
middle Oligocene-middle Miocene	north west Germany		Gerlach 1961
?Kaiatan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f062 (L09219)	Wilson 1985
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f048 (L09205)	Wilson 1985
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f302 (L23132)	
Porangan-Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f301 (L23131)	

Genus *Distatodinium* Eaton 1976

1976 *Distatodinium* Eaton, p. 262-263

1978 *Distatodinium* Eaton 1976; Stover & Evitt, p. 39

Type Species: *Distatodinium craterum* Eaton 1976, p. 263-264, pl. 9, figs. 1-5 [Late Eocene]

Original Description: Dinoflagellate cysts in which the cyst body has an oval or elongate oval outline. Processes simple or branched, variable in breadth, flattened and blade-like in cross section, proximally expanded and frequently united by a membrane, distally expanded and ramified. Ramifications typically, but not invariably, complex. Occasionally, slender tubular processes are present. The number of processes varies from about 14 (in some specimens without an operculum) to about 60 or more. Processes aligned into rows parallel to the long axis of the cyst body, and apparently situated on or close to reflected plate boundaries; many are also arranged in a more or less circular manner around the cyst body. Archeopyle apical (Eaton 1976, p. 262).

***Distatodinium apennanicum* Brinkhuis et al. 1992**

Pl. 91, figs. 7-9

1992 *Distatodinium apennanicum* Brinkhuis et al., p. 237-238, pl. 1, figs. 1-9; pl. 8, figs. 1-4

Original Description: A species of *Distatodinium* that is characterized by the presence of 15 to 18 (including those on the operculum) intratabular, short, broad, tubular, hollow processes. Distally, the processes are closed and terminate in a complexly ramified, platform-like structure that may be recurved around its margin, or may be modified with interconnections developed between adjacent processes to produce an incomplete ectophragm. Proximally, the processes are flared and united by low ridges. Two apical processes may be united. A reflected gonyaulacean paratabulation of 4', 6", xc, 5"', 0-2p, 1''' is inferred. The surface ornament is smooth to scabrate or lightly reticulate. The apical archeopyle, which is invariably evident with a detached operculum, reflects the loss of all the apical paraplates (Brinkhuis et al. 1992, p. 237-238).

Size Range: Length excluding processes = 68 µm (one measured specimen). Width excluding processes = 46 µm (one measured specimen). Length including processes = 110 µm (one measured specimen). Width including processes = 77 µm (one measured specimen).

Distribution: Extremely rare; only one poor specimen was encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f091 (L16339)	Wilson & McMillan 1996

Genus *Labyrinthodinium* Piasecki 1980

1980 *Labyrinthodinium* Piasecki

Type Species: *Labyrinthodinium truncatum* Piasecki 1980, p. 67, 70, pl. 2, figs. 9-11, pl. 3, fig. 2, pl. 6, figs. 3-4 [Mid Miocene]

Original Description: Small chorate cysts with spherical main body and apical archeopyle. The cyst wall is two layered, and periphragma forms a closed or open reticulum of anastomosing crests. The smaller crests support the larger ones, which form membraneous processes of equal length (Piasecki 1980, p. 67).

?*Labyrinthodinium* sp. 1

Pl. 91, figs. 10-12, Pl. 92, figs. 1-3

Description: Cysts small, proximochorate, not dorso-ventrally compressed, prolate, lacking horns. Cyst wall single-layered, with an ectophragm. Archeopyle apical (?); operculum free. Processes non-tabular; variable in length, sometimes broader than high; connected by an irregularly developed trabeculum distally. Tabulation not expressed. Cingulum not expressed. Sulcus not expressed.

Size Range: Length = 35 (37) 38 µm (3 measurements). Width = 31 (34) 37 µm (2 measurements).

Distribution: Rare: known from only a single sample, within which it occurs infrequently.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Remarks: The archeopyle could not be confidently discerned in the handful of specimens available; thus, generic placement remains provisional.

Genus *Paucisphaeridium* Bujak et al. 1980b

1980b *Paucisphaeridium* Bujak et al., p. 32

1987 *Paucisphaeridium* Bujak in Bujak et al. 1980, p. 30, 32; Stover & Williams, p. 173

Type Species: *Paucisphaeridium inversibuccinum* (Davey & Williams 1966b, p. 82, pl. 12, fig. 3) Bujak et al. 1980, p. 32 [Early Eocene]

Original Description: Chorate cysts with a spherical to subspherical body. The processes are proximally expanded, hollow, and constricted near the distal end. Process formula ?4', 6'', 0c, 6''', 0''''', xs. When present, the sulcal processes are slender. Archeopyle apical, presumably tetratabular. Operculum not observed (Bujak et al. 1980, p. 30).

?*Paucisphaeridium inversibuccinum* (Davey & Williams 1966b) Bujak et al. 1980b

Pl. 92, figs. 4-6

1966b *Paucisphaeridium inversibuccinum* Davey & Williams, p. 82, pl. 12, fig. 3

Original Description: The wall of the central body is usually thin, but thick walled specimens have occasionally been encountered. The processes are not in connection with the interior of the central body and seldom exceed 15 [sic]. The larger processes are sub-conical and may be up to 10µ wide at the base, rapidly decreasing in width to approximately 1.5-2µ, before expanding distally into a denticulate or aculeate margin. In addition to these stout processes there are usually one or two slender ones which are possibly closed distally. The latter are probably

sulcal processes. An apical tetragonal archeopyle was seen in one specimen, the archeopyle being surrounded by 6 precingular processes. However the remaining tabulation is obscure (Davey & Williams 1966b, p. 82).

Size Range: Length excluding processes = 33 μ m (one measured specimen). Width excluding processes = 30 μ m (one measured specimen). Length including processes = 58 μ m (one measured specimen). Width including processes = 53 μ m (one measured specimen).

Distribution: Extremely rare.

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f093 (L16341)	Wilson & McMillan 1996

Subfamily Uncertain

Genus *Indet 3*

Indet 3 sp. 1

Pl. 92, figs. 7-12

Description: Cysts small, comprising a more or less spherical central body, which lacks surface ornament and from which arises numerous ?intratabular (though possibly gonal) processes. The processes are united distally by thin trabeculae which appear to be more numerous in the apical, cingular, and antapical regions, leaving the pre- and postcingular areas comparatively free. A projection, assumed to be antapical, which has no discernable analogue on the central body, is developed by the trabeculae, and there appears to exist a thin membrane covering parts of the trabeculae in this area (recalling *Ectosphaeropsis*).

Size Range: Length excluding processes = 33 (36) 38 μ m (2 measurements). Width excluding processes = 29 (32) 35 μ m (2 measurements). Length including processes = 68 (72) 76 μ m (2 measurements). Width including processes = 64 (67) 70 μ m (2 measurements).

Distribution: Very rare; only two specimens encountered in the present study.

Age/Stage	Location	Sample	Sample Reference
Heretaungan	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f484 (L23119)	

Remarks: If the archeopyle could be demonstrated to be precingular, this form would be a candidate for inclusion within *Cannosphearopsis*.

Genus *Indet 4*

Description: Proximate, tabulate cysts, with a distinctively tuberculate surface sculpturing.

Remarks: The rare specimens encountered in this study are invariably fragmented (suggesting a compound archeopyle?) making a more detailed description impossible at this time. However, the distinctive surface ornamentation makes the form easy to recognise when encountered, even in an extremely crushed or fragmentary state.

Indet 4 sp. 1

Pl. 93, figs. 1-12, Pl. 94, figs. 1-3

Description: [Refer genus].

Size Range: Length = 55 (65) 75 μ m (3 measurements). Width = 50 (55) 60 μ m (3 measurements).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996
Bortonian	Hampden Beach Section, Oamaru-Dunedin, New Zealand	J42/f487 (L23122)	
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996

Order Pterospermales

Family Cymatiosphaeraceae

[No translation available] Die hierhergehörigen Formen zeichnen sich meistens durch den Besitz lamellöser Außenhäute aus, die durch unregelmäßig verteilte, doch etwa radial angeordnete "Stäbchen" (= Verdickungen der Feldergrenzen?) gestützt werden. Mit ihrem Maschenwerk erinnern sie z. T. an die seinerzeit von Rüst im englischen Feuerstein gefundene Radiolarie *Dictyospyris anglica* Rüst 1885. Zugleich finden sich bei den vorliegenden Fossilien, ähnlich wie bei der vorigen Gruppe, Anklänge an die rezenten Pterospermacean Lohmann's (1904) bzw. an die Trochiscien Lemmermann's (1903), aber auch an rundliche Peridineen, insbesondere an solche mit Gürtellamelle und ohne große apikale Vorsprünge (O. Wetzel 1933b, p. 27).

Genus *Cymatiosphaera* O. Wetzel 1933b

1933b *Cymatiosphaera* O. Wetzel, p. 27

Type Species: Cymatiosphaera radiata O. Wetzel 1933b, p. 27, pl. 4, fig. 8

Original Description: The characteristics of the group [envelopes with less numerous and less uniform fields finer lines] also apply to the genus (translation from O. Wetzel 1933b, p. 27).

?*Cymatiosphaera* sp. 1

Pl. 94, figs. 4-6

2000 *Cymatiosphaera* sp. E; Levy & Harwood, p. 235, pl. 14, figs. a-c

2003 *Cerebrocysta poulsenii*; Brinkhuis, Munsterman, et al., p. 15, pl. 1, figs. 23-27

Description: Cysts small, tabulate though showing no apparently dinoflagellate tabulation, ornamented by low, smooth-edged crests in "sutural" positions on an otherwise smooth, hyaline surface. Viewed from above, the crests are characteristically sinuous.

Size Range: Length = 27 (29) 30 μm (3 measurements). Width = 29 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f092 (L16340)	Wilson & McMillan 1996
Bortonian	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f089 (L16337)	Wilson & McMillan 1996
Eocene	erratics, McMurdo Sound, Antarctica	MB 188B	Levy & Harwood 2000

?*Cymatiosphaera* sp. 2

Pl. 94, figs. 7-9

?2005 *Cymatiosphaera* sp. 1; Schiøler, pl. 4, fig. 9-10

Description: Cysts small, ornamented by high (~15% of the overall diameter), smooth-edged crests in "sutural" positions on an otherwise smooth, hyaline surface. The crests delimit areas which might be called tabulae; the tabulation so defined is apparently not a dinoflagellate tabulation, although a narrow band on one specimen resembles a cingulum.

Size Range: Length = 27 (29) 30 μm (3 measurements). Width = 29 μm (one measured specimen).

Distribution:

Age/Stage	Location	Sample	Sample Reference
early Whaingaroan	Cape Foulwind Section, Westland, New Zealand	K29/f097 (L10914)	
Kaiatan	Puketeraki Core, Oamaru-Dunedin, New Zealand	I43/f096 (L16344)	Wilson & McMillan 1996

Family Pterospermellaceae

Genus *Pterospermella* Eisenack 1972

1972 *Pterospermella* Eisenack, p. 597

Type Species: Pterospermella aureolata (Cookson & Eisenack 1958, p. 49, pl. 9, figs. 10-12) Eisenack 1972, p. 597

Original Description: Microfossils in organic matter that consist of a central body, which appears circular when viewed from above, eccentrically ovoid or occasionally circular in transverse section and has a concentrically and equatorially placed annular, double-walled and either smooth or jagged marginal wing. This can be flat or contain radial folds.

Its method of opening is still unknown (translation from Eisenack 1972, p. 597).

***Pterospermella* sp. 1**

Pl. 94, figs. 10-12

Description: Cysts large, flattened, ovoidal; comprising an oval inner body supporting a large annular flange, marked by radial folds.

Size Range: Length including any processes = 110 µm (one measured specimen). Width including any processes = 87 µm (one measured specimen).

Distribution: Rare.

Age/Stage	Location	Sample	Sample Reference
Porangan	Te Uri Stream, Hawkes Bay, New Zealand	U24/f419 (L23127)	

Biostratigraphy

Introduction

A number of important biostratigraphic works, including Hornibrook 1961, Hoskins 1982, Wilson 1984a, Wilson 1988, and Cooper 2004, provide a solid foundation to move ahead towards a better understanding of the middle Eocene to early Oligocene interval in New Zealand.

In the following biostratigraphic analysis, homotaxial biostratigraphic events are preferred for correlations; first appearances are preferred to extinctions (ignoring contamination, an occurrence proves existence; absence proves nothing); acmes have not been used. Despite these precautions, however, many – or all – of the biostratigraphic data discussed below could, in principle, be diachronous, and in most cases we simply do not yet know.

I have persisted with a conventional zonal scheme, in the tradition of Wilson (e.g. 1984d; see more below) rather than adopting the increasingly common practise of simply listing key FADs and LADs. To some extent the distinction is moot, insofar as the zones I have adopted from Wilson's earlier work, and the new divisions proposed below, are based on single FADs or LADs, anyway.

However, I have considerable misgivings at the extent to which single events are being used today. We all know from our daily experience that FADs and LADs occur in different order in different sections, and various techniques, such as Shaw's graphic correlation, are employed to address precisely this problem. When choosing an event to define a zone, at least some thought goes into resolving these matters, and supporting assemblage data are available to assist our interpretations.

In the future, it will be better to tie local biostratigraphic events back to the only practically testable isochronous units available, the magnetostratigraphic chrons. This will not be completely straight-forward, of course. Pending fuller paleomagnetic or radiometric surveys of the sediments discussed herein, both local and international chronostratigraphic interpretations must be extrapolated from potentially diachronous biotic events.

Zonal Scheme for the Mid-Late Eocene to Early Oligocene

The earliest practical dinoflagellate zonal scheme for New Zealand sediments, of any age, was that of Wilson 1967c, an informal eight- or nine-fold division based upon *Wetzelielloideae* species. Extending this early work, Wilson later published a formal biozonation (Wilson 1984d) which proposed a sequence of thirteen zones extending from the Cretaceous-Tertiary boundary to the top of the Eocene. Subsequently, more detailed revisions were undertaken of the Cretaceous-Tertiary boundary (Wilson 1987) and of the mid-Paleocene to Middle Eocene interval (Wilson 1988, Morgans et al. 2004).

To this extent, a dinoflagellate zonation exists for the New Zealand Eocene. Its resolution is similar to, or slightly better than, that of the New Zealand marine stages (eleven dinoflagellate zones; seven stages) which are defined on foraminifera data. In the Eocene interval, the majority of dinoflagellate data are first and last appearances of *Wetzeliella*-group taxa. Unfortunately, these taxa are seldom common and may be ecologically constrained.

The zonation presented below for the late Middle Eocene (approximately middle Lutetian) to earliest Oligocene, is loosely based upon Wilson's (Wilson 1967c, 1984d, 1988, Morgans et al. 2004) with the following departures:

- a. By analogy with best geochronologic practice, only the base of each zone is defined, the top being determined by the base of the next higher zone. Some of Wilson's (1984d) zones were separated by gaps where no zone was defined; the approach adopted here does not permit gaps.
- b. The *Wilsonidium echinosuturatum* Zone is generally accounted in the literature to be of considerable duration, as much as 5 Ma according to Cooper 2004. However, at its type section, Waipawa, it is represented by a single sample. Nor is the situation any better at Hampden, where Wilson 1985 again records only a single sample. Both it, and the following *Wilsonidium lineidentatum* Zone are further compromised by the scarcity of the index fossils defining their boundaries. Accordingly, they are herein replaced with three new zones: *Deflandrea convexa*, *Graptodinium inconditum*, and *Impagidinium elegans*.
- c. The *Wilsonidium tabulatum* Zone is replaced by an approximate equivalent defined by a more commonly found taxon, *Rhombodinium glabrum*.
- d. A new zone (marked by the FAD of *Stoveracysta kakanuiensis*) is introduced at the Eocene-Oligocene boundary.

The upper boundary of the last zone in the present scheme, the *Stoveracysta kakanuiensis* Zone, is not defined. This will require further study.

The relationships between Wilson's earlier (1984d, 1988, Morgans et al. 2004) zones, and those recognised below, are summarised in the following table.

Ma	NZ Stage	Wilson 1984	Wilson 1988	Morgans et al. 2004	This Study	Correlation (Cooper 2004)	
						Intl Stage	Chron
33						Rupelian	C13n
34					<i>Stoveracysta kakanuiensis</i>		C13r
35	Runangan (Ar)	<i>Deflandrea phosphoritica</i>		<i>Deflandrea phosphoritica</i>	<i>Deflandrea phosphoritica</i>	Priabonian	C15r
36	Kaiatan (Ak)						C16n
37		<i>Wilsonidium tabulatum</i>		<i>Wilsonidium tabulatum</i>	<i>Rhombodinium glabrum</i>		C17n
38		<i>Wetzeliella hampdenensis</i>		<i>Wetzeliella hampdenensis</i>	<i>Wetzeliella hampdenensis</i>	Bartonian	C18n
39							C18r
40	Bortonian (Ab)	<i>Wilsonidium lineidentatum</i>		<i>Wilsonidium lineidentatum</i>	<i>Impagidinium elegans</i>		C19r
41						Lutetian	C20n
42					<i>Graptodinium inconditum</i>		C20r
43		<i>Wilsonidium echinosuturatum</i>	<i>Wilsonidium echinosuturatum</i>	<i>Wilsonidium echinosuturatum</i>	<i>Deflandrea convexa</i>		C21n
44	Porangan (Dp)				<i>Membranophoridium perforatum</i>	C21r	
45			<i>Membranophoridium perforatum</i>	<i>Membranophoridium perforatum</i>	<i>Membranophoridium perforatum</i>		
46			<i>Kisselovia edwardsii</i>	<i>Kisselovia edwardsii</i>	<i>Charlesdowniea edwardsii</i>		
47	Heretaungan (Dh)	<i>Kisselovia edwardsii</i>		<i>Charlesdowniea edwardsii</i>	<i>Charlesdowniea edwardsii</i>		
48							

Table 2: Summary of stratigraphic relationships between several earlier New Zealand dioflagellate zonal schemes and those recognised herein. The darker markers between some zones indicate uncertain boundaries where there was a known hiatus or where different criteria were used to define the top of one zone and the base of next higher zone.

Summary of Zones

Charlesdowniea edwardsii Zone (middle Heretaungan)

The base of this zone is defined by LAD of *Charlesdowniea coleothrypta*.

It was originally described from the Waipawa Section, Hawkes Bay, where it is restricted to part of the Heretaungan Stage (Wilson 1984d, 1988) although the top of the zone is obscured by an unexposed interval at its type locality.

The zone correlates with part of the *Globorotalia crater crater* foraminiferal zone and the upper part of the *Reticulofenestra dictyoda* nannofossil zone (Wilson 1988).

Typical dinoflagellate species associated with the zone include *Charlesdowniea edwardsii*, *Deflandrea scabrata*, *Damassadinium crassimuratum*, *Pyxidinopsis waipawaensis*, *Pyxidinopsis delicata*, *Cleistosphaeridium placanthum* sensu Wilson 1988 (= *Areoligera hampdenensis*, as used here), *Impagidinium parvireticulatum*, and *Impagidinium waipawaense*.

The zone has been widely recorded from throughout New Zealand and the zone index has also been reported from the Gippsland Basin in Australia (Partridge 1976).

Membranophoridium perforatum Zone (late Heretaungan – earliest Porangan?)

The zone base is defined by the LAD of *Charlesdowniea edwardsii*.

It was originally recognised in the Waipawa Section, Hawkes Bay (Wilson 1988). Both the base and the top of the zone are obscured by unexposed intervals at the type locality and the zone includes upper Heretaungan and possibly lower Porangan Stages (Wilson 1988).

The *Membranophoridium perforatum* Zone correlates with the upper part of the *Globorotalia crater crater* foraminiferal zone and with the *Discoaster elegans* nannofossil zone (Wilson 1988).

Dinoflagellate species associated with the zone include *Membranophoridium perforatum*, *Deflandrea scabrata*, *Damassadinium crassimuratum*, *Impagidinium waipawaense*, *Pyxidinopsis waipawaensis*, *Pyxidinopsis delicata*, and *Areoligera hampdenensis* (see note above). *Wetzeliella*-group taxa are unknown from this zone (Wilson, pers. comm.).

Deflandrea convexa Zone n. zone (early Porangan – late Porangan)

The zone base is defined by the FAD of *Deflandrea convexa*.

The type locality is Te Uri Stream section, Hawkes Bay, where the lower boundary has been observed at U24/2803190 6095920 (New Zealand Map Grid; sample U24/f418).

Characteristic associated species include *Paucilobimorpha tricornus*, *Deflandrea* aff. *antarctica*, *Pyxidinoopsis crassimurata*, and *Turbiosphaera filosa*.

This zone replaces the lower part of the *Wilsonidium echinosuturatum* Zone (Wilson 1984d, 1988, Cooper 2004).

Graptodinium inconditum Zone n. zone (late Porangan – early Bortonian)

The zone base is defined by the FAD of *Graptodinium inconditum*.

The type locality is Hampden Beach section, Otago, where the lower boundary has been observed at J42/2339920 5542600 (New Zealand Map Grid; sample J42/f301).

Characteristic associated species include *Paucilobimorpha tripa*, *Corrudinium otagoense*, *Glaphyrocysta* cf. *retiintexta*, *Impagidinium maculatum* and *I.* cf. *maculatum*.

This zone replaces the middle to upper part of the *Wilsonidium echinosuturatum* Zone (Wilson 1984d, 1988, Cooper 2004).

Impagidinium elegans Zone n. zone (early Bortonian – late Bortonian)

The zone base is defined by the FAD of *impagidinium elegans* s.s.; it is noted that similar though recognisably different forms occur slightly earlier.

The type locality is Hampden Beach section, Otago, where the lower boundary has been observed at J42/2339920 5542610 (New Zealand Map Grid; sample J42/f302).

Characteristic associated species include *Areosphaeridium pectiniforme*, *Hystrichosphaeridium brevispinum*, *Cordosphaeridium fibrospinum* and *Cordosphaeridium gracile*.

This zone replaces the uppermost part of the *Wilsonidium echinosuturatum* Zone (Wilson 1984d, 1988, Cooper 2004) and the *Wilsonidium lineidentatum* Zone (Wilson 1984d, Cooper 2004).

Wetzeliella hampdenensis Zone (late Bortonian)

The zone base is defined by the FAD of *Wetzeliella hampdenensis*.

The type locality for the zone is the Hampden section, North Otago (Wilson 1984, 1985).

The zone is correlated with the upper part of the *Globigerapsis index index* foraminiferal zone (Wilson 1984d).

Both *Wetzeliella hampdenensis* and *Palaeocystodinium hampdenensis* are restricted to this zone. Other characteristic species include *Phthanoperidinium dentatum*, *Corrudinium otagoense*, and an undescribed new species of *Deflandrea*.

The zone has been frequently reported throughout New Zealand.

Rhombodinium glabrum Zone n. zone (late Bortonian – Kaiatan)

The zone base is defined by the FAD of *Rhombodinium glabrum*.

The type locality is the Hampden section, North Otago (Wilson 1985).

The zone apparently lies mainly within the lower part of the *Globorotalia inconspicua inconspicua* foraminiferal zone, but further work needs to be completed to confirm this.

Typical dinoflagellate species associated with the zone include *Rhombodinium glabrum*, *Dracodinium granulatum*, *Cooksonidium capricornum*, and *Wilsonidium tabulatum*.

The *Rhombodinium glabrum* Zone is introduced to replace Wilson's (1984d) slightly shorter *Wilsonidium tabulatum* Zone because the index fossil, *Rhombodinium glabrum*, is far more common than *W. tabulatum*.

Deflandrea phosphoritica Zone (late Kaiatan – latest Runangan)

The zone base is re-defined by the LAD of *Rhombodinium glabrum*; Wilson's original concept of the zone was defined by the LAD of *Wilsonidium tabulatum* (see above).

The type locality is the Kakanui River mouth section, Otago.

The zone lies mainly within the *Globigerina linaperta* and *G. brevis* foraminiferal zones (Wilson 1984d).

Deflandrea phosphoritica is abundant throughout the zone (Wilson 1984d), although the actual FAD for *D. phosphoritica* occurs much earlier, in the mid Bartonian (or possibly earlier; refer discussion in the systematic section). Other distinctive species include *Impagidinium elegans*, and several *Phthanoperidinium* species. Abundant *Operculodinium* species also occur near the top of the *Deflandrea phosphoritica* Zone; seemingly earlier in New Zealand than in southeastern Australia (cf. Partridge & Dettmann 2003).

The zone is very common throughout New Zealand.

Stoveracysta kakanuiensis Zone n. zone (latest Runangan – early Whaingaroan)

The zone base is defined by the FAD of *Stoveracysta kakanuiensis*.

The type locality is the Kakanui River mouth section, Otago, where the age is basal Whaingaroan, very close to the Eocene-Oligocene boundary. The lower boundary has been observed at J42/2344600 5555800 (New Zealand Map Grid; sample J42/f096)

The zone appears to lie completely within the *Globigerina brevis* foraminiferal zone of Jenkins 1966.

It is associated with the last, or near last, appearances of the typically Paleogene species, including *Chlamydochorella neopilata*, *Corrudinium incompositum*, *Deflandrea phosphoritica*, *Impagidinium victorianum*, and *Graptodinium inconditum*. Additionally, species such as *Nematosphaeropsis balcombiana*, *Operculodinium* spp. and *Spiniferites* spp. become more prevalent.

The incoming of *Stoveracysta kakanuiensis* has been widely recognised in the Australasian region as appearing at or just below the Eocene-Oligocene boundary (e.g. Clowes & Morgans 1984, Partridge & Dettmann 2003, Sluijs et al. 2003). However, the event is probably diachronous, occurring first at lower paleolatitudes then migrating south. The initial work on mainland New Zealand, reported in Clowes & Morgans 1984, indicates a FAD that is essentially indistinguishable from the Eocene-Oligocene boundary.

Eocene-Oligocene Boundary

The Runangan-Whaingaroan boundary is currently defined by the LAD of *Globigerapsis index* (Foraminifera, Orbulinidae) (Cooper 2004, p. 154). For the sake of convenience, this datum is generally assumed to be isochronous throughout New Zealand. (However, also see Hornibrook 1965, p. 1195 and Scott 1971, pp. 705-706.) For example, Srinivasan & Vella 1975 (p. 30) placed the Runangan-Whaingaroan boundary at Cape Foulwind, at the horizon where *Globigerapsis index* disappears.

The Eocene-Oligocene (Priabonian-Rupelian) boundary in New Zealand had earlier been assumed to coincide with the local Runangan-Whaingaroan boundary (e.g. Srinivasan 1965, Hornibrook & Edwards 1978, Hoskins 1982). Jenkins, however, often contended that the Eocene-Oligocene boundary lies within the lower part of the Whaingaroan stage, although he also noted that the planktonic Foraminifera upon which he based his conclusions had not been described from the Eocene and Oligocene type sections (e.g. Jenkins 1971, p. 18; also 1963, p. 707 and 1974, p. 164).

The latter view has been increasingly adopted by subsequent writers (e.g. Clowes & Morgans 1984, Clowes 1985) and prevails today. For example, Cooper 2004 places the Runangan-Whaingaroan boundary between 34.0 and 34.5 Ma and the Eocene-Oligocene boundary between 33.5 and 34.0 Ma (fig. 11.2). The absolute age of the Eocene-Oligocene GSSP has since been refined (to 33.9 ± 0.1 Ma, Gradstein et al. 2004), and no doubt the ages of both data will be visited again, but the important recognition is that the Eocene-Oligocene boundary occurs some way – in the order of a million years – into the Early Whaingaroan.

Younger Assemblages

The upper boundary of the *Stoveracysta kakanuiensis* Zone is not defined, the dinoflagellates of the Whaingaroan being poorly studied, even after the present endeavour. It is expected that further research will define younger zones in such a way that the *Stoveracysta kakanuiensis* Zone will remain very short.

A significant reduction in diversity across the Eocene-Oligocene boundary is noticeable in both taxonomically and geographically dispersed groups of microplankton. It is observed in, for example, Carpathian foraminifera (Sotak et al. 2005) and it is certainly the case for New Zealand dinoflagellates. With few exceptions, the morphological diversity typical of the Eocene rapidly declines near the top of this zone, leaving impoverished assemblages dominated by a few species representing various chorate forms, notably *Spiniferites* and *Operculodinium*.

Conclusion

The principal goal of this study has been to assess the utility of the phylogenetic approach to workaday fossil dinoflagellate cyst biostratigraphy and taxonomy. Difficulties were expected: The first comprehensive synthesis of fossil and neontological dinoflagellate data to be more or less universally adopted, Fensome et al. 1993b, is still quite new, compared with (to take one example) trilobite taxonomy, which has been phylogenetically based at least since Barande's publications of around 150 years ago (Barande 1852, 1872).

The suprageneric classification of Fensome et al. (1993b) is firmly based, as it should be, upon phylogenetic principles, whereas most fossil dinoflagellate cyst genera are form-taxonomic constructs and, to some extent, inevitably so. Notwithstanding that Fensome et al. provide morphological definitions for all of the suprageneric taxa which they recognise, we are left with a discontinuity in the underlying principles by which we define taxa when we "get down" to the generic level. It carries the potential to produce absurdities, such as genera which overlap two or more subfamilies. The only solution, if we are not to abandon phylogeny entirely, is to define, or redefine, where necessary, form-genera along phylogenetic lines.

How might we attempt this? Fossil taxa are characterised – indeed, could almost be defined – by the absence of genetic data. Morphological information is most of what we have left. Yet the richness of morphological data available to the palynologist, working with the ordinary tools we employ routinely, is poor indeed compared to one of Barande's trilobites.

If we are going to adopt a phylogenetic approach, we will almost certainly have to abandon our idea of genera which are uniquely defined by mutually exclusive morphological criteria. The Neocomian, Maastrichtian and Eocene member species of *Pyxidinosia*, for example, are almost certainly not closely related, yet they are difficult to separate on morphology alone.

Ideally, we might reconstruct whole lineages thereby defining clades. As more fossil dinoflagellates are found and described, such an approach becomes more realistic and several well-known studies along these lines have been referenced already. At present, however, most lineages are too poorly known, so we must adopt other clues to phylogeny.

Stratigraphic and regional occurrence data are two possible indicators. Earlier reports of the taxon *Graptodinium*, to take another example, had usually attributed it to either *Histiocysta* or *Microdinium*. However, the genotype of *Histiocysta*, *H. palla*, is apparently confined to the early Cretaceous. The likelihood of any close phylogenetic relationship between *H. palla* and *Graptodinium* is small. *Microdinium ornatum*, the genotype of *Microdinium*, is a more likely relative but, again, the type and most other valid species of *Microdinium* occur in much older rocks: middle to late Cretaceous, although a few range into the Danian. Again, the likelihood of any close phylogenetic relationship with forms from the Cenozoic of New Zealand seems remote.

These were the clues which led to the hypothesis that *Graptodinium inconditum* was distinct from *Histiocysta* or *Microdinium*, at the generic level or higher, prompting a conscious search for new material to elucidate the detailed plate topology. I am confident that the new material described above amply confirms the hypothesis, and that the creation of a new genus is well-supported.

But this is still a morphological distinction. I have not (yet) been brave enough to suggest a new taxon based wholly on geographical and temporal criteria. However, this is clearly a rational extension to the present ideas, and is advocated as worthy of serious further investigation. There is a danger of tautology, of course, but this can be avoided with care.

My conclusion is that the difficulties of an explicitly phylogenetic approach do not seem insurmountable, and the rewards are profound.

A secondary goal of this study was to further refine the younger part of the dinoflagellate biozonation for New Zealand, as it is presently known. The current zonation is primarily based upon Wilson's (1984d, 1987, 1988; Morgans et al. 2004) work, which in turn had its origins in an earlier analysis of a succession of Wetzelielloideae species (Wilson 1967c).

Specific biostratigraphic objectives of the present study were:

- To improve the resolution of existing dinoflagellate zonal schemes, if possible.

This has been progressed by two measures. First, the long *Wilsonidium echinosuturatum* Zone and the following *Wilsonidium lineidentatum* Zone are herein replaced with three new zones. Second, a new zone (marked by the FAD of *Stoveracysta kakanuiensis*) is introduced at the Eocene-Oligocene boundary. The upper boundary of the *Stoveracysta kakanuiensis* Zone, is not defined. This will require further study.

- To clarify an ambiguous boundary remaining in the literature, between the *Wetzeliella hampdenensis* and *Wilsonidium tabulatum* zones.

To eliminate this (or any other) possibility for a gap or an overlap to occur between zones, only the base of each zone is defined in the scheme proposed here. The top of each zone is implicitly determined by the base of the next higher zone.

- To incorporate more common taxa, which may be expected in more diverse ecological settings, than have been employed in the past.

Some progress was made here: the *Wilsonidium tabulatum* Zone is replaced by an approximate equivalent defined by a more commonly found taxon, *Rhombodinium glabrum*. It remains true that many of the New Zealand Eocene dinoflagellate zones are defined by quite rare, and perhaps ecologically constrained, index taxa. However, this was the only change thought to be well-supported by the present study.

It is hoped that further research will continue to improve both the resolution and the practical utility of the zonation. Further analysis of the range charts provided in the appendices may prove fruitful, perhaps by suggesting additional index taxa. However, I feel that the charts should be bolstered by the addition of sampling from many more sections, and ideally more granular sampling within sections, before such steps may be taken with surety.

Glossary

aculeate	The tip of a tubular process which flares into pointed serrations of constant or variable length. [Williams et al. 1973]
archeopyle	The excystment aperture formed by the loss or displacement of one or a group of plates along pre-formed lines of weakness, usually the sutures surrounding the affected plates.
climactal	The plates anterior to the precingular series, excluding those of the sulcus and apical pore complex.
dextral torsion	The condition in which the hyposome is rotated so that the boundary between plates 4''' and 5''' lies middorsally and usually close to the boundary between 3'' and 4''.
dinocyst	A contraction of "dinoflagellate cyst", avoided herein
dolabrate	"Pick" shaped bifurcating process terminations in which one bifurcation is clearly longer than the other. In extreme cases, the shorter bifurcation may be completely reduced, so that the process is apparently not bifurcate, but has a distinct angular bend at its extremity. [Eaton et al. 2001]
eurydeltaform	Peridinioid archeopyle in which the archeopyle ration is less than 1 and the archeopyle signum is less than 1. [Evitt 1985]
fundital	The plates posterior to the postcingular series, excluding those of the sulcus.
homotaxial	occurring in the same order at diverse locations
isodeltaform	Peridinioid archeopyle in which the archeopyle ration is approximately 1 and the archeopyle signum is less than 1. [Evitt 1985]
latideltaform	Peridinioid archeopyle in which the archeopyle ration is less than 1 and the archeopyle signum is less than 1 (= eurydeltaform). [Evitt 1985]
L-type	A term so named because of the longitudinal nature of the sulcus. The sulcus is more or less straight. The sixth precingular plate (1i) is bounded to left and right by almost parallel sutures and anteriorly by a gabled margin due to its contact with both the fourth and first apical plates or their homologues (A, 1u). The fourth apical plate or its homologue (A) is typically not long and narrow, and does not contact the anterior sulcal plate (ai). There is commonly a broad contact between the last precingular plate and the first apical plate or its homologue (1i/1u). See also S-type ventral organization. [Fensome et al. 1998]
Q1	The anterior edge of a quadra-style 2a plate, adjoining plate 3'. [Lentin & Williams 1976]
S-type	A term so named because of the sigmoidal nature of the sulcus. The sixth precingular plate (1i) tends to have a triangular shape, with anteriorly converging lateral margins and a narrow, typically planate anterior margin. The fourth apical plate or its homologue (A) tends to be (but is not always) long and predominantly ventral, and contacts the anterior sulcal plate (ai). See also L-type ventral organization. [Fensome et al. 1998]
sinistral torsion	The condition in which the hyposome is rotated so that the boundary between plates 4''' and 5''' is distant to the boundary between 3'' and 4'' (refer dextral torsion).
topology	The "layout" of the plates, including both consideration of the number of plates in each series, and also which vertices contact which edges of which plates.
transverse archeopyle index	The maximum width of the archeopyle divided by the width of the epicyst measured along the same line. [Evitt 1985]
transverse archeopyle ratio	The width of a hexa 2a archeopyle at the widest point divided by the width of the epicyst less the archeopyle width. [Lentin & Williams 1976]

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Appendix 1. List of Samples and Preparations

The following table lists collection data for all illustrated specimens.

Sample	Preparation	Provenance	Age
I43/f089	L16337	Puketeraki Core	Bortonian
I43/f090	L16338	Puketeraki Core	Bortonian
I43/f091	L16339	Puketeraki Core	Bortonian
I43/f092	L16340	Puketeraki Core	Bortonian
I43/f093	L16341	Puketeraki Core	Bortonian
I43/f094	L16342	Puketeraki Core	Bortonian
I43/f096	L16344	Puketeraki Core	Kaiatan
I43/f101	L16349	Puketeraki Core	Otaian
I43/f108	L16358	Tumai	Runangan
I44/f080	L08947	Burnside Marl Pit	Bortonian
I44/f240	L15506	M26 Core	Heretaungan-Bortonian
J31/f9185	L08324	Nine Mile Bluff	Kaiatan
J31/f9186	L08325	Nine Mile Bluff	Kaiatan
J41/f8914	L04979	Jacksons Paddock	Kaiatan-Runangan
J42/f039	L09196	Hampden Beach Section	Heretaungan
J42/f040	L09197	Hampden Beach Section	Bortonian
J42/f041	L09198	Hampden Beach Section	Bortonian
J42/f042	L09199	Hampden Beach Section	Bortonian
J42/f048	L09205	Hampden Beach Section	Bortonian
J42/f055	L09212	Hampden Beach Section	Bortonian
J42/f057	L09214	Hampden Beach Section	Bortonian
J42/f061	L09218	Hampden Beach Section	Bortonian
J42/f062	L09219	Hampden Beach Section	?Kaiatan
J42/f063	L09220	Hampden Beach Section	Kaiatan
J42/f064	L09221	Hampden Beach Section	Kaiatan
J42/f096	L10951	Kakanui River	early Whaingaroan
J42/f097	L10952	Kakanui River	?early Whaingaroan
J42/f098	L10953	Kakanui River	Runangan
J42/f125	L11625	Kakanui River	Runangan-early Whaingaroan
J42/f298	L23128	Hampden Beach Section	Heretaungan-Porangan
J42/f299	L23129	Hampden Beach Section	Porangan
J42/f300	L23130	Hampden Beach Section	Porangan
J42/f301	L23131	Hampden Beach Section	Porangan-Bortonian
J42/f302	L23132	Hampden Beach Section	Porangan-Bortonian
J42/f303	L23133	Hampden Beach Section	Bortonian
J42/f483	L23118	Hampden Beach Section	Heretaungan
J42/f484	L23119	Hampden Beach Section	Heretaungan
J42/f485	L23120	Hampden Beach Section	Porangan-Bortonian
J42/f486	L23121	Hampden Beach Section	Porangan-Bortonian
J42/f487	L23122	Hampden Beach Section	Bortonian
J42/f488	L23123	Hampden Beach Section	Bortonian
J42/f489	L23124	Hampden Beach Section	Bortonian
J42/f8690	L06958	Hampden Beach Section	Bortonian
K29/f097	L10914	Cape Foulwind Section	early Whaingaroan
K29/f099	L11035	Cape Foulwind Section	?Kaiatan-Runangan
K29/f101	L11037	Cape Foulwind Section	Runangan

K29/f102	L11038	Cape Foulwind Section	Runangan
K29/f104	L11040	Cape Foulwind Section	Runangan
K29/f106	L11042	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f108	L11044	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f112	L11048	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f114	L11050	Cape Foulwind Section	early Whaingaroan
K29/f115	L11051	Cape Foulwind Section	early Whaingaroan
K29/f116	L11052	Cape Foulwind Section	early Whaingaroan
K29/f123	L11934	Cape Foulwind Section	Runangan
K29/f125	L11936	Cape Foulwind Section	Runangan
K29/f128	L11939	Cape Foulwind Section	Runangan
K29/f169	L11918	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f170	L11919	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f171	L11920	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f172	L11921	Cape Foulwind Section	Runangan-early Whaingaroan
K29/f173	L11922	Cape Foulwind Section	early Whaingaroan
K29/f174	L11923	Cape Foulwind Section	early Whaingaroan
K29/f176	L11925	Cape Foulwind Section	early Whaingaroan
K29/f178	L11927	Cape Foulwind Section	early Whaingaroan
K29/f180	L11929	Cape Foulwind Section	early Whaingaroan
K29/f182	L11931	Cape Foulwind Section	early Whaingaroan
K29/f183	L11932	Cape Foulwind Section	early Whaingaroan
K29/f184	L11933	Cape Foulwind Section	early Whaingaroan
K29/f259	L13545	Cape Foulwind Section	Runangan
K29/f261	L13543	Cape Foulwind Section	Runangan
K29/f262	L13546	Cape Foulwind Section	Runangan
L34/f7538	L06997	Upper Eyre River	Mangaorapan
L35/f7539	L06998	Upper Eyre River	Mangaorapan
S14/f8599	L10662	Old Mountain Road	Runangan-early Whaingaroan
U24/f201	L12144	Akitio River	Whaingaroan
U24/f417	L23125	Te Uri Stream	Porangan
U24/f418	L23126	Te Uri Stream	Porangan
U24/f419	L23127	Te Uri Stream	Porangan
V22/f8994	L12118	Waipawa Section	Heretaungan

Appendix 2. Range Charts

Range Chart for *Achilleodinium*

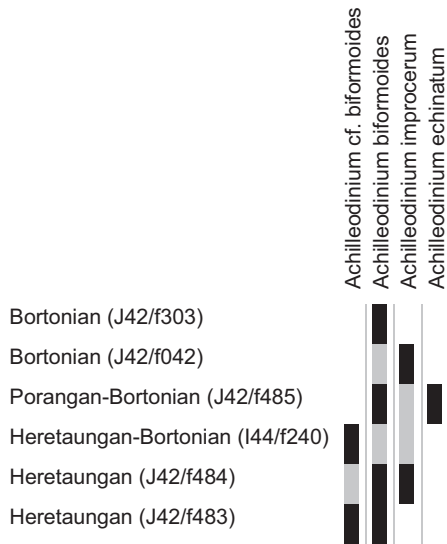


Chart 1: Range Chart for *Achilleodinium*.

Range Chart for *Corrudinium*

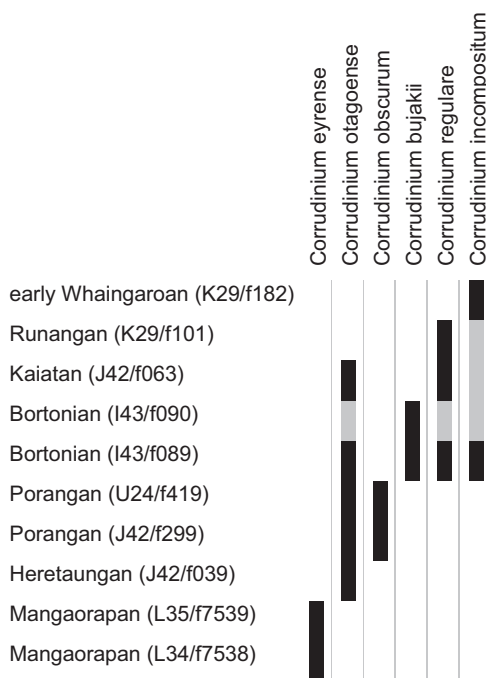


Chart 2: Range Chart for *Corrudinium*.

Range Chart for *Deflandrea*

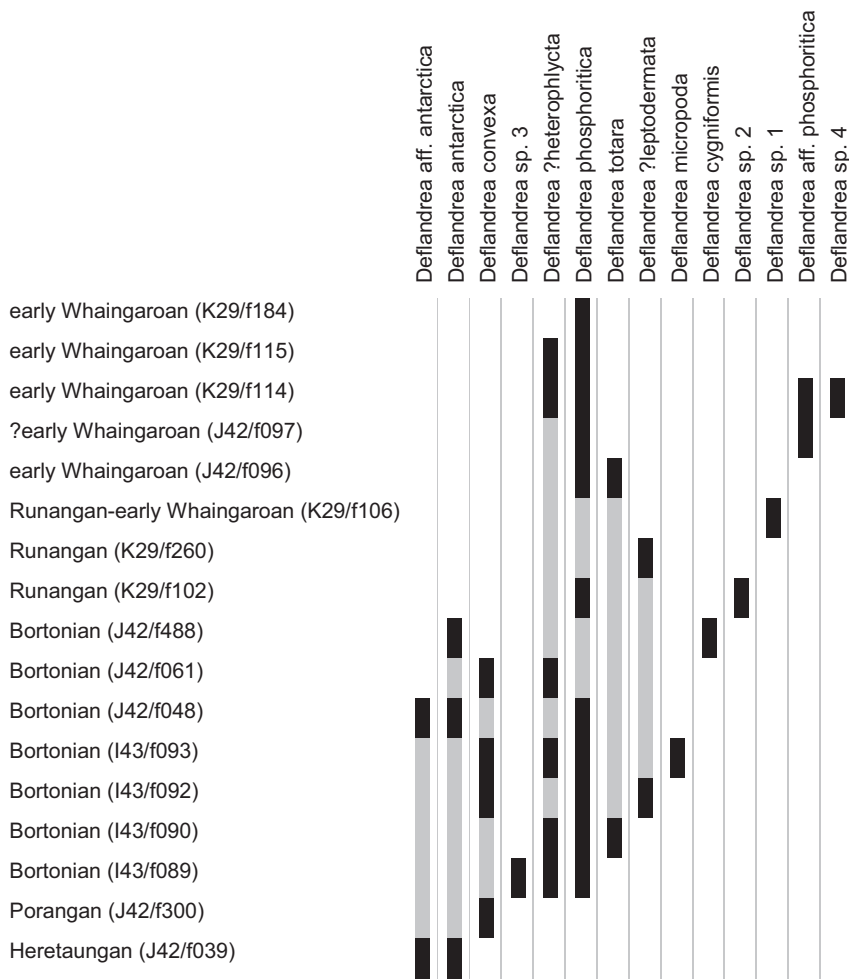


Chart 3: Range Chart for *Deflandrea*.

Range Chart for *Impagidinium*

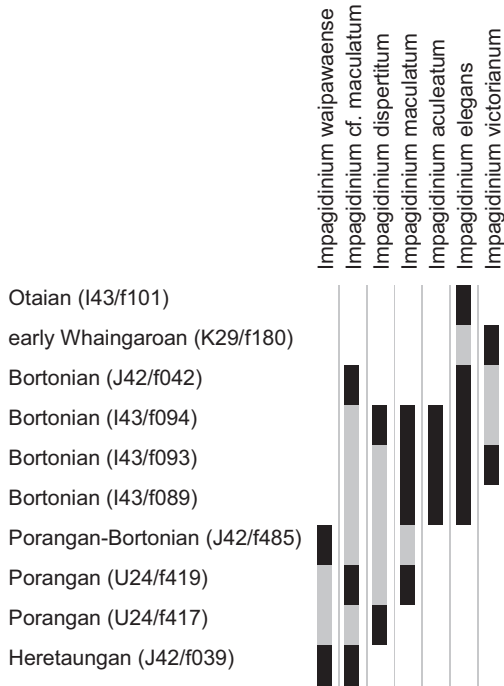


Chart 4: Range Chart for *Impagidinium*.

Range Chart for *Operculodinium*

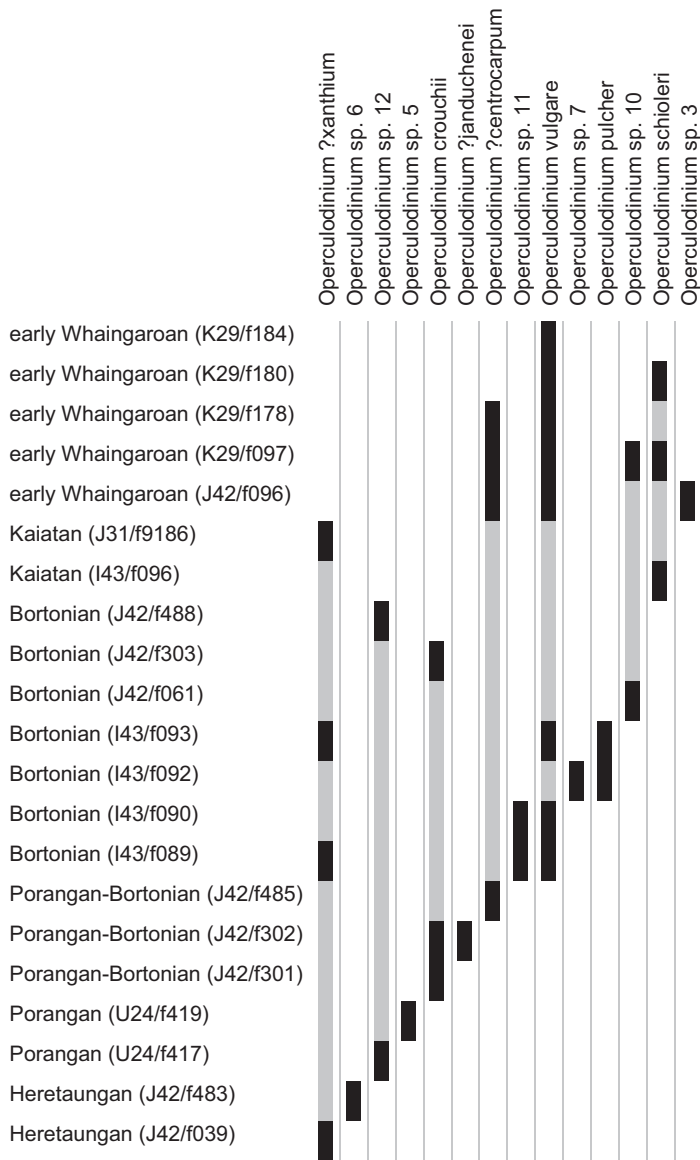


Chart 5: Range Chart for *Operculodinium*.

Range Chart for *Paucilobimorpha*

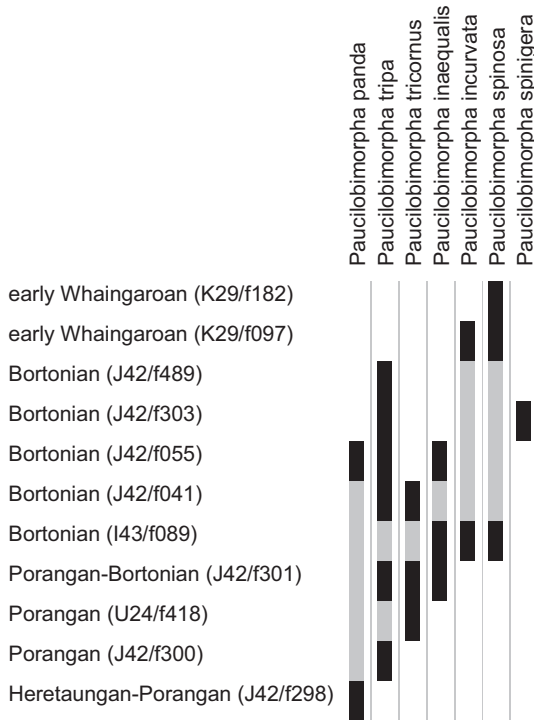


Chart 6: Range Chart for *Paucilobimorpha*.

Range Chart for *Phthanoperidinium*

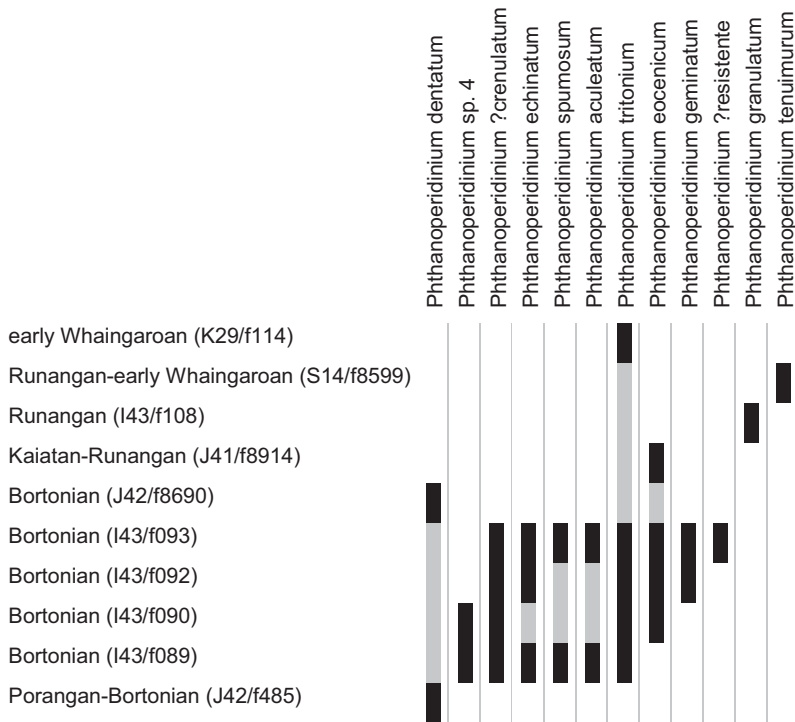


Chart 7: Range Chart for *Phthanoperidinium*.

Range Chart for *Pyxidinospis*

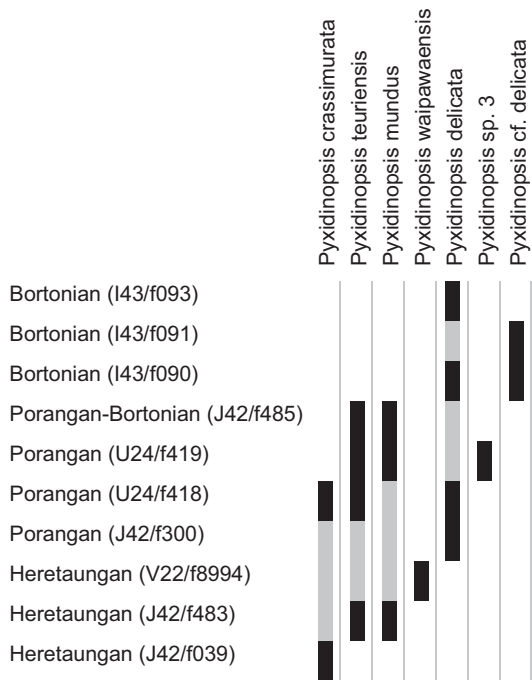
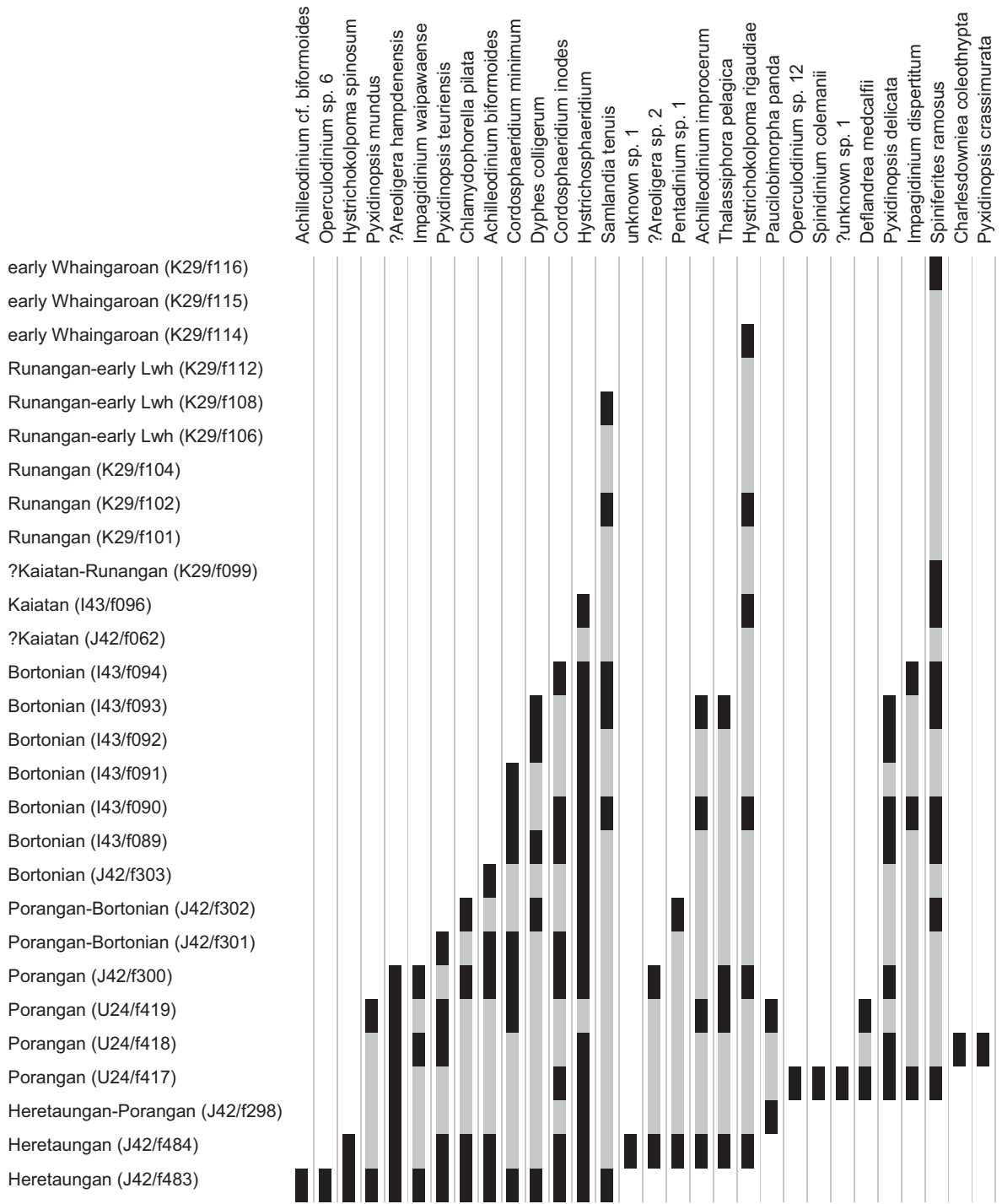
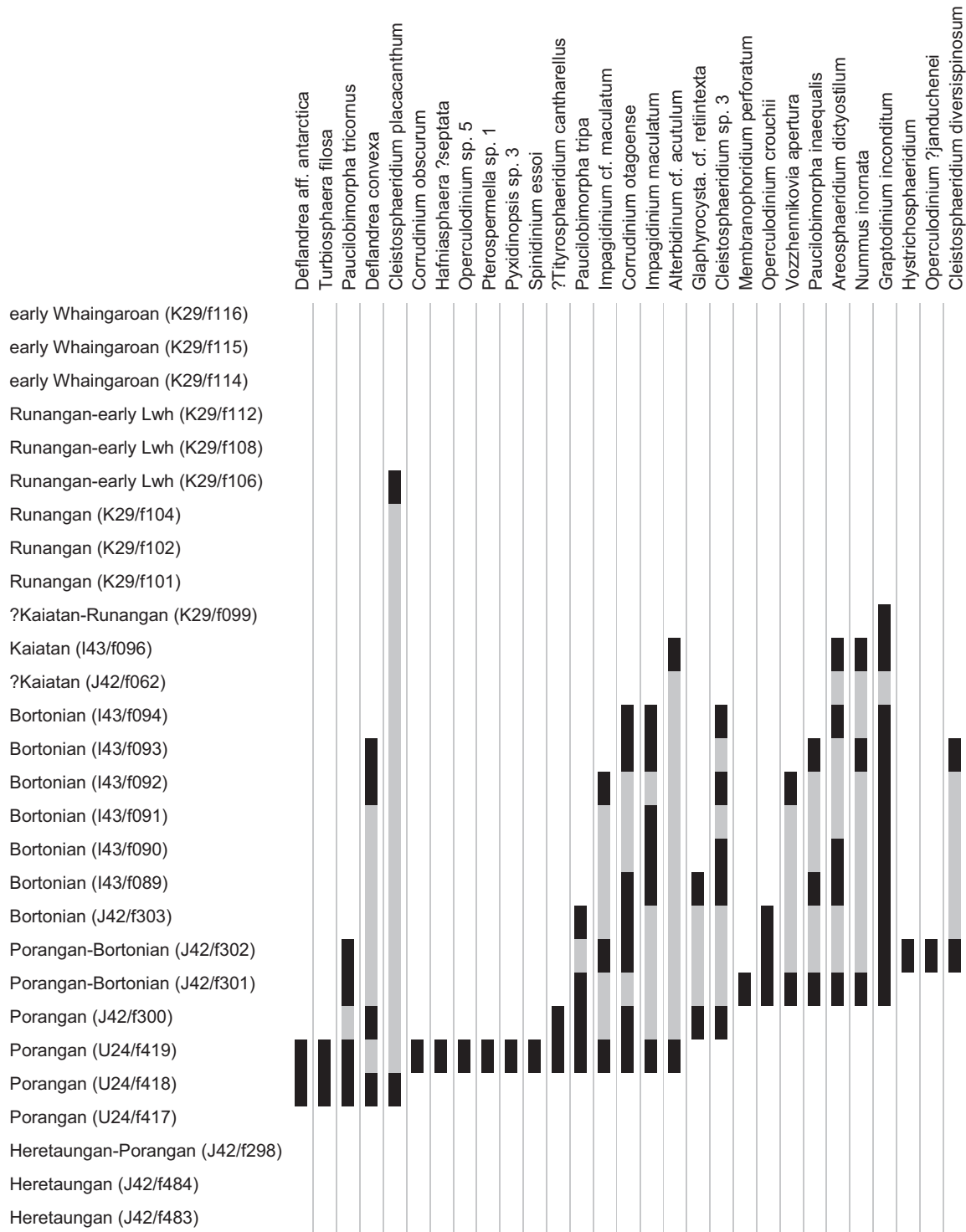
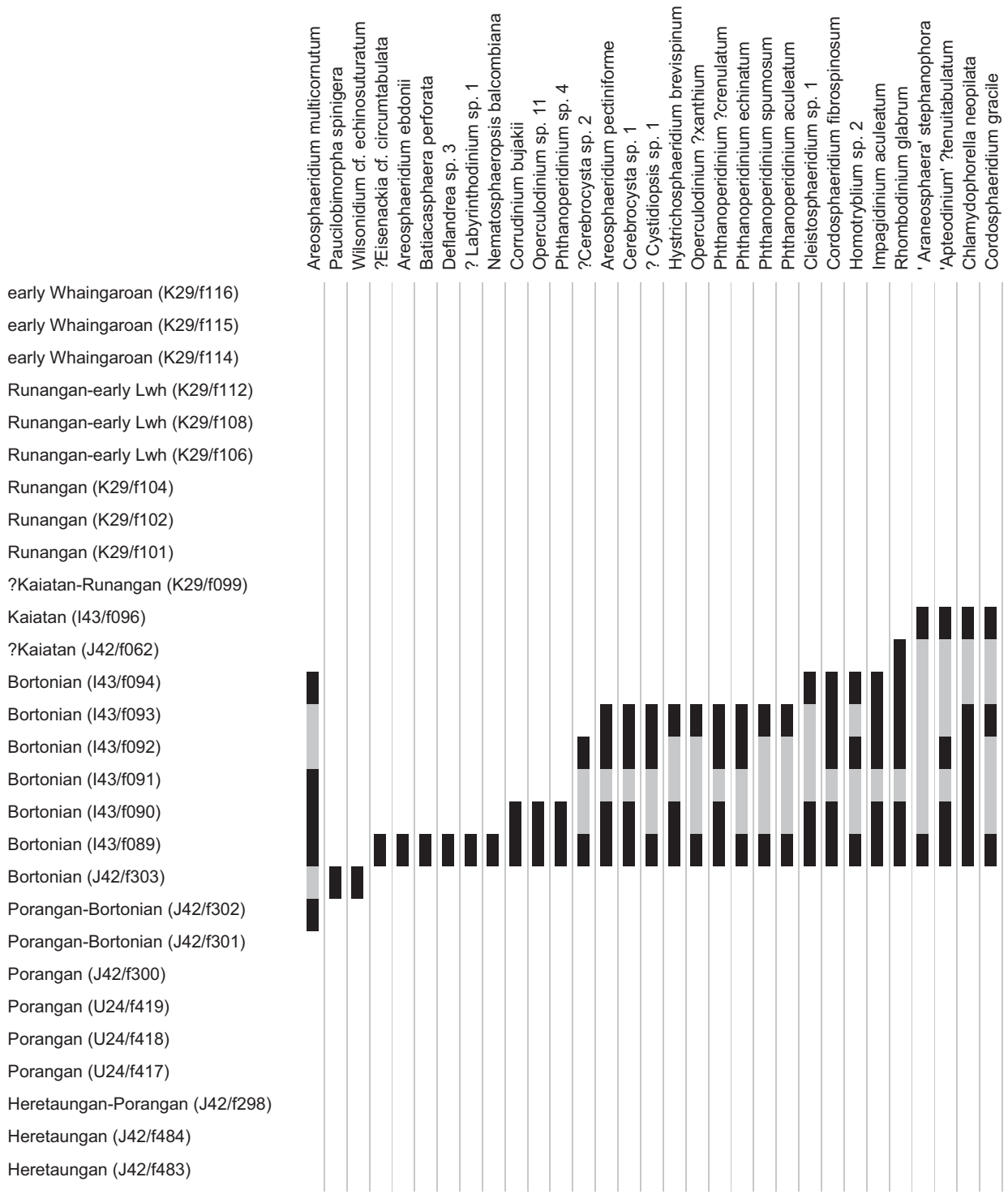


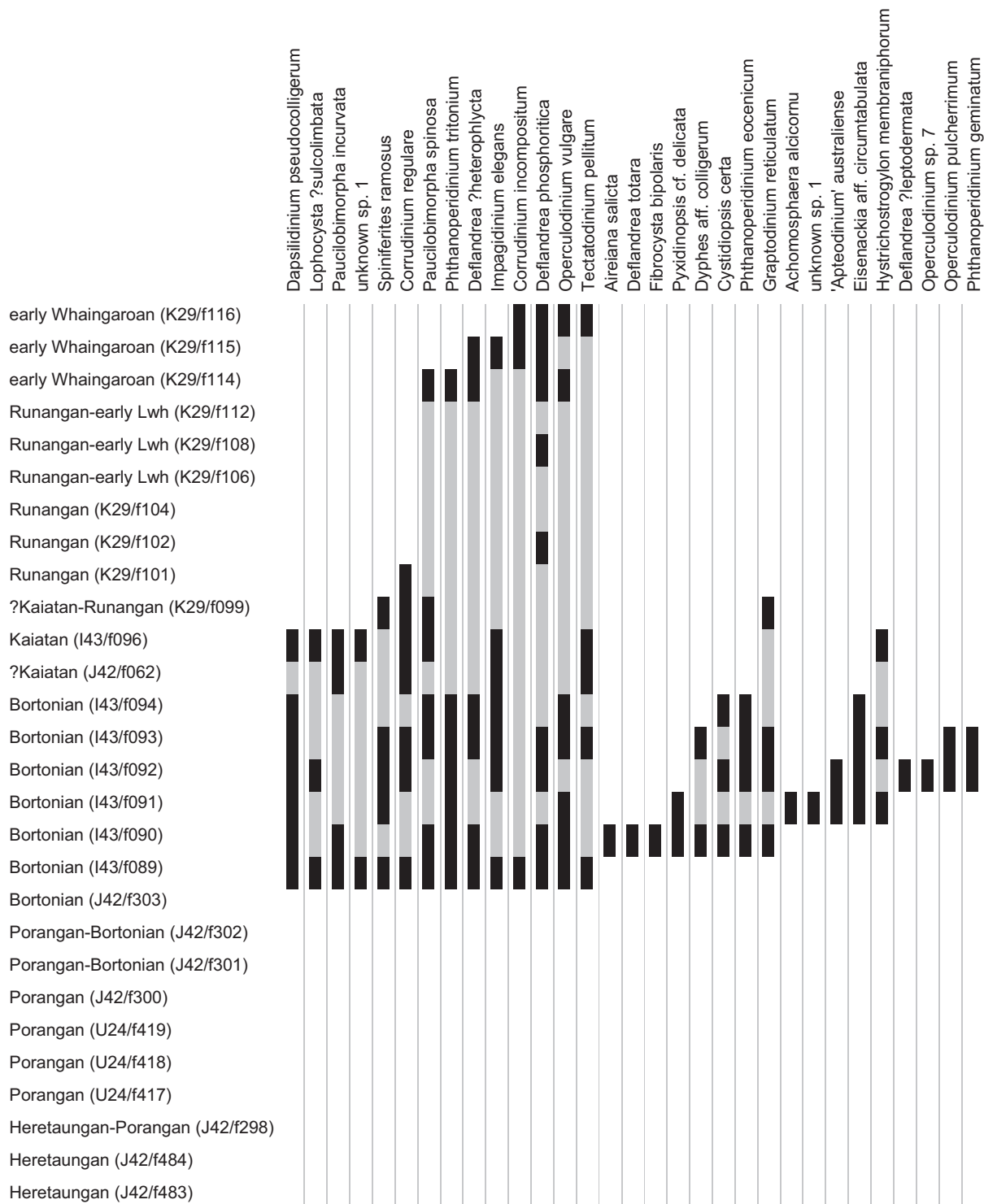
Chart 8: Range Chart for *Pyxidinospis*.

Composite Range Chart









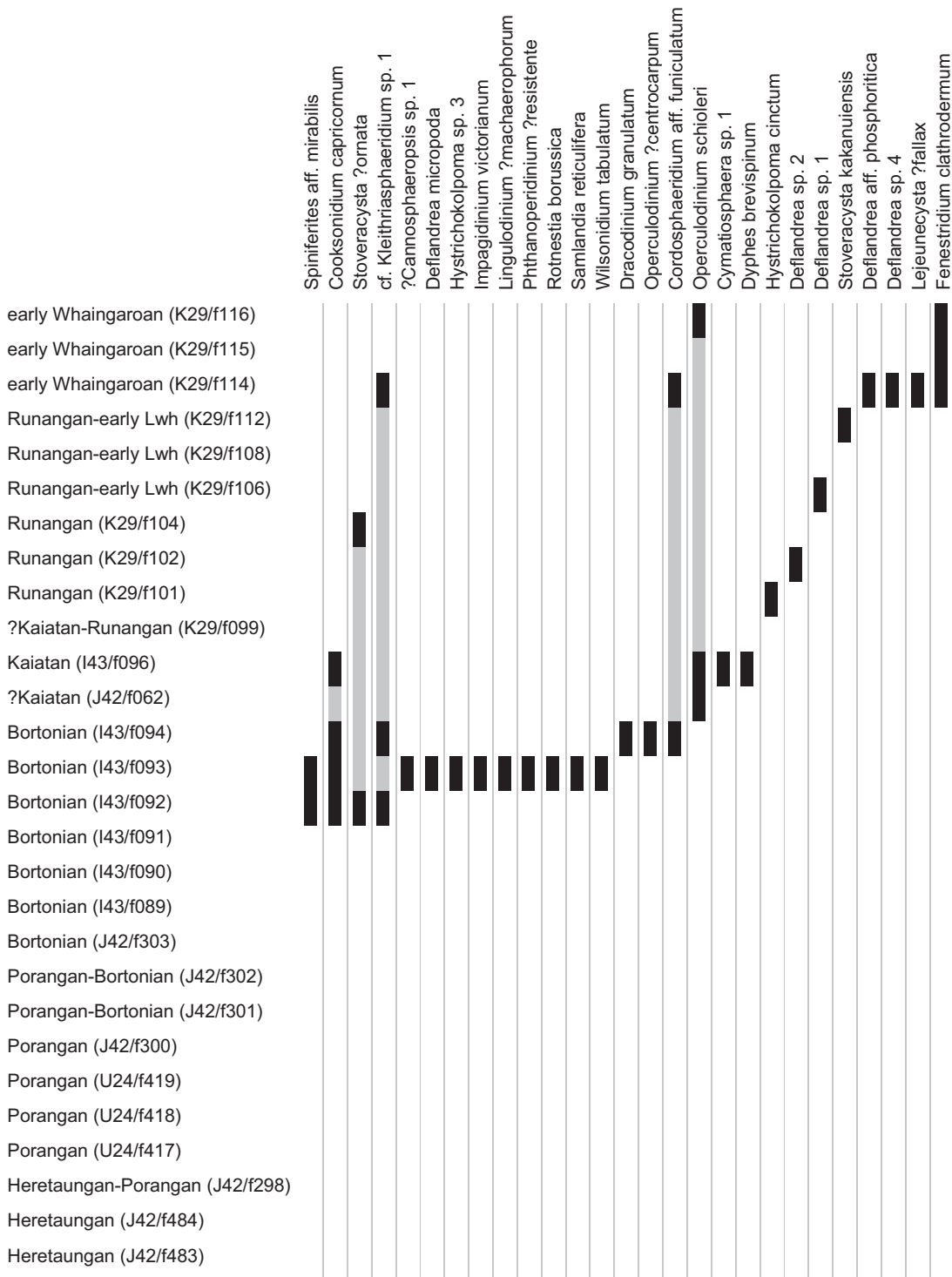


Chart 9: Range chart for composite stratigraphic section.

Appendix 3. The TransAntarctic Flora Assemblage

The name “TransAntarctic Flora” (TAF) is due to Wrenn & Beckman 1982 (p. 189), but, while some of us might believe we can recognise the TAF when we see it, there is no universally accepted “definition” of exactly which species comprise the flora, in the sense of which must essentially be present before we are sure we have it.

Perhaps the most straight-forward approach to this issue is to begin by listing who has found what. The species published in Wilson’s (1967a) seminal account of the assemblage together with those species reported (or indicated to be characteristic of the TAF) by various subsequent authors are shown in the following table, excluding such cosmopolitan taxa as *Hystrichosphaeridium tubiferum*, *Thalassiphora pelagica*, etc. The tinted columns indicate studies from continental Antarctica or close islands (e.g. Seymour Island).

Taxon	Wilson 1967	Archangel'sky 1969a, b	Haskell & Wilson 1975	Kemp 1975	Wrenn & Beckman 1982	Goodman & Ford 1983	Wrenn & Hart 1988 (table 5)	Wilson 1989	Cocozza & Clarke 1992	Mao & Mohr 1995	Levy & Harwood 2000	this study
<i>Alterbidinium asymmetricum</i> ³	Y	Y	Y	Y				Y	Y	Y	Y	✘
<i>Alterbidinium ?distinctum</i>	Y					Y	Y	Y			Y	✘
<i>Arachnodinium antarcticum</i>	Y	Y	Y	Y			Y	Y	Y	Y	Y	✘
<i>Areosphaeridium dictyostilum</i>	Y	Y	Y	Y		Y		Y	Y	Y	Y	✓
<i>Deflandrea antarctica</i>	Y		Y		Y	Y	Y	Y	Y	Y	Y	✓
<i>Deflandrea oebisfeldensis</i> sensu Cookson & Cranwell 1967				Y			Y					✘
<i>Deflandrea cygniformis</i>			Y				Y			Y	Y	✓
<i>Deflandrea granulata</i>		Y		cf.			Y	cf.				✘
<i>Graptodinium inconditum</i>						Y		?		Y	?	✓
<i>Spinidinium macmurdoense</i>	Y	Y		Y	Y	Y	Y	Y	Y		Y	✓
<i>Turbiosphaera filosa</i>	Y	Y	Y	Y				Y			Y	✓
<i>Vozzhennikovia apertura</i>	Y		Y	Y	Y	Y	Y	Y	Y	Y	Y	✓
<i>Vozzhennikovia rotunda</i>	Y	Y	Y		Y			Y				✘
<i>Wilsonidium echinosuturatum</i>			Y				Y					✓

The species having the broadest support among the reports, especially those from Antarctica itself, appear to be *Alterbidinium asymmetricum*, *Alterbidinium ?distinctum*, *Arachnodinium antarcticum*, *Areosphaeridium dictyostilum* (recorded under various aliases; refer to the systematic section), *Deflandrea antarctica*, which, at least in some cases, appears to be the same as the form reported as *D. oebisfeldensis* sensu Cookson & Cranwell 1967, *Spinidinium macmurdoense*, and *Vozzhennikovia apertura*.

Age control over the Antarctic material itself has typically been weak. Instead, we have had to rely upon correlations with other high-latitude southern localities.

Although some elements of the TAF have been reported from the New Zealand mainland, others, including perhaps the most distinctive member, *Arachnodinium antarcticum*, have not. Of those which have, most are long-ranging, and of limited use in fixing a date to the assemblage. Only *Wilsonidium echinosuturatum* is useful, indicating an interval of Porangan to early Bortonian (middle to late Lutetian). However, it is open to debate whether this species really ought to be considered a fully paid up member of the TAF: it is not mentioned by the great majority of publications reporting occurrences of the assemblage.

Goodman & Ford 1983 reports elements of the Trans-Antarctic Flora, including *Vozzhennikovia apertura*, *Deflandrea antarctica* and *Spinidinium macmurdoense*, ranging up into the Oligocene – indeed, beyond the local LAD of *Deflandrea phosphoritica* (fig. 2, occurrence data for DSDP Hole 511, on the eastern margin of the Falklands Plateau). In the present study, *Vozzhennikovia apertura* appears to be the TAF taxon exhibiting the youngest LAD, ranging into the later part of the Middle Eocene (Bortonian). However, the Falklands Plateau material of Goodman & Ford 1983 conspicuously excludes *Arachnodinium antarcticum*; another hint that it is perhaps this species which most usefully characterises the TAF as a whole.

³ *Alterbidinium asymmetricum* comb. nov., basionym = *Deflandrea asymmetrica* Wilson 1967a, p. 62-63, figs. 17-21.

Appendix 4. Other Species of *Phthanoperidinium*

Other species assigned at various times to *Phthanoperidinium* include the following, none of which has been reported from New Zealand at this time:

Other Accepted Species

Phthanoperidinium comatum (Morgenroth 1966b) Eisenack & Kjellström 1972 — The plate topology of the ventral [or maybe the whole?] episome is not described, nor visible in the illustrations provided by the original description. However, on the assumption that it is the same as that of *P. tritonium*, *P. comatum* is retained in *Phthanoperidinium* until evidence emerges to the contrary.

Phthanoperidinium coreoides (Benedek 1972) Lentin and Williams, 1976 — this taxon was originally described with a perplexing yet distinctly gonyaulacacean tabulation formula, 4', ?1a, 6'', 6c, 5-6'', 1p, 0-1, 1'''''. However, Benedek & Sarjeant 1981, pp. 327-330, provides a reinterpretation which is more or less consistent with conventional *Phthanoperidinium*, despite the plate 1' contacting plate 3a where 4' is expected (text-fig. 5).

Phthanoperidinium delicatum Michoux 1985

Phthanoperidinium filigranum (Benedek 1972) Benedek and Sarjeant 1981

Phthanoperidinium multispinum Bujak 1980

Phthanoperidinium obscurum Harland & Sharp 1980

Phthanoperidinium pseudoechinatum Bujak 1980 — A junior synonym of *P. stockmansii/echinatum* according to Islam 1982, p. 309.

Phthanoperidinium stockmansii (De Coninck 1975) Lentin & Williams 1977b

Provisionally Accepted Species

I have been unable to discern important diagnostic characters from published descriptions of the following species, and do not have material readily available to study at first hand. Pending future determinations, they are here regarded as provisionally accepted.

Phthanoperidinium alectrolophum Eaton 1976

Phthanoperidinium amiculum Liengjarern et al. 1980

Phthanoperidinium antarcticum Mao & Mohr 1995

Phthanoperidinium bennettii Matsuoka & Bujak 1988

Phthanoperidinium chalossense Michoux 1985

Phthanoperidinium clithridium Bujak 1994

Phthanoperidinium cornutum Heilman-Clausen & van Simaey 2005 — The photographs accompanying the original description depict a cyst which appears to possess a pericoel, which would place *P. cornutum* outside of our concept of *Phthanoperidinium*. However, the original description makes no mention of pericoels, so the species is provisionally retained in *Phthanoperidinium* for the present.

Phthanoperidinium crenulatum (De Coninck 1975) Lentin & Williams 1977b

Phthanoperidinium distinctum Bujak 1994 — The holotype (Bujak 1994, pl. 4, figs. 7-8) appears to possess well developed pericoels, which is unlike the typically developed wall structure in *Phthanoperidinium*.

Phthanoperidinium flebile Liengjarern et al. 1980

Phthanoperidinium indistinctum Islam 1982 — The ventral view shown by Islam 1982, fig. 2, depicts a 1' plate which (ignoring any preapical contacts) is five-sided but not in any significant contact with plate 7''. Although such an arrangement does not correspond exactly with the ortho-style of organisation, the species is provisionally retained in *Phthanoperidinium*, pending further research.

Phthanoperidinium levimurum Bujak 1980 — Published photographs of this species, particularly Bujak 1980, pl. 19, fig. 13 (of the holotype) depict a cyst which appears to possess an epipericoel, which would place *P. levimurum* outside of our concept of *Phthanoperidinium*. However, the original description makes no mention of pericoels, so the species is provisionally retained in *Phthanoperidinium* for the present.

Phthanoperidinium ovoideum He 1991

Phthanoperidinium paleocenicum Lucas-Clark 2006 — As noted above, the holotype of this species is also more strongly cornucavate and has more distinctly developed antapical horns than are ordinarily seen in *Phthanoperidinium*.

Phthanoperidinium polytrix (Benedek 1972) Lentin & Williams 1976 — Possibly conspecific with *P. tritonium*, in which case *polytrix* would be the senior synonym.

Phthanoperidinium regale Bujak 1994

Phthanoperidinium rhomboidale He 1991

Phthanoperidinium schizokeras (De Coninck 1975) Lentin & Williams 1977 [b] — Note, however, that the principal diagnostic feature of this form, namely the “short [apical] horn which, starting from the base, is divided into two” (De Coninck 1975, p. 97), seems unlikely to have much diagnostic significance. The author’s tiny illustrations of a single individual are unhelpful. Pending a modern redescription of the type material, it seems best to avoid using this name.

Phthanoperidinium stoveri (Lienjareem et al. 1980) Islam 1982

Phthanoperidinium tenellum Jin et al. 1989 [in He et al.]

Not Accepted Species

Phthanoperidinium brooksii Edwards & Bebout 1981 — Possesses the meta-style of ventral epicyst topology and a cancellous pericoel filling, neither of which are typical *Phthanoperidinium* characteristics. This species may be better placed in another genus, possibly new.

Phthanoperidinium campoense Caro 1973 — Described from one specimen, refer Edwards & Bebout 1981, table 1; additionally, the tabulation formula given in the description is not that of *Phthanoperidinium*, refer Stover & Evitt 1978, p. 119; it is recommended the foregoing name be applied to the holotype specimen alone.

Phthanoperidinium coriciterium Islam 1982 — This species does not exhibit the diagnostic ortho-hexa arrangement of the epicyst; see Islam 1982, fig. 1.

Phthanoperidinium illustrans (O. Wetzel 1933a) Lentin & Williams 1973 — Described from one specimen, refer Stover & Evitt 1978, p. 119; it is recommended the foregoing name be applied to the holotype specimen alone.

Phthanoperidinium lambdoideum (E. Nagy 1966) Eisenack & Kjellström 1972 — Considered unidentifiable, refer Stover & Evitt 1978, p. 119; it is recommended the foregoing name be applied to the holotype specimen alone.

Phthanoperidinium powellii Bujak 1994 — The very wide pericoel and lack of clear differentiation into plates by either sutural or penitabular features suggest that it would be more appropriately placed in another genus such as *Luxadinium*.

Appendix 5. Alphabetical Listing of Genera

Genus	Page
<i>Achilleodinium</i> Eaton 1976	100
<i>Achomosphaera</i> Evitt 1963a	77
<i>Aireiana</i> Cookson & Eisenack 1965a	141
<i>Alterbidinium</i> Lentin & Williams 1985 emend. Khowaja-Ateequzzaman et al. 1991	46
<i>Apteodinium</i> Eisenack 1958a	98
<i>Araneosphaera</i> Eaton 1976	103
<i>Areoligera</i> Lejeune-Carpentier 1938a	148
<i>Areosphaeridium</i> Eaton 1971	130
<i>Batiacasphaera</i> Drugg 1970b	160
<i>Cannosphaeropsis</i> O. Wetzel 1933b	83
<i>Cerebrocysta</i> Bujak 1980	161
<i>Cerodinium</i> Vozzhennikova 1963 emend. Lentin & Williams 1987	47
<i>Charlesdowniea</i> Lentin & Vozzhennikova 1989	66
<i>Chlamydophorella</i> Cookson & Eisenack 1958	162
<i>Cleistosphaeridium</i> Davey et al. 1966 emend. Eaton et al. 2001	149
<i>Cooksonidium</i> Stover & Williams 1995	135
<i>Cordosphaeridium</i> Eisenack 1963b emend. Davey 1969c	104
<i>Corrudinium</i> Stover & Evitt 1978	83
<i>Cyclonephelium</i> Deflandre & Cookson 1955 emend. Stover & Evitt 1978	153
<i>Cymatiosphaera</i> O. Wetzel 1933b	167
<i>Cystidiopsis</i> Nagy 1965	22
<i>Dapsilidium</i> Bujak et al. 1980b	163
<i>Deflandrea</i> Eisenack 1938b emend. Lentin & Williams 1976	34
<i>Diphyes</i> Cookson 1965a emend. Goodman & Witmer 1985	113
<i>Disphaerogena</i> O. Wetzel 1933b emend. Sarjeant 1985b	109
<i>Distatodinium</i> Eaton 1976	164
<i>Dracodinium</i> Gocht 1955 emend. Bujak et al. 1980	67
<i>Eisenackia</i> Deflandre & Cookson 1955	156
<i>Fenestridium</i> Clowes n. gen.	30
<i>Fibrocyta</i> Stover & Evitt 1978	142
<i>Filisphaera</i> Bujak 1984 emend. Head 1994b	97
<i>Glaphyrocysta</i> Stover & Evitt 1978	153
<i>Graptodinium</i> Clowes n. gen.	136
<i>Hafniasphaera</i> Hansen 1977	78
<i>Homotryblium</i> Davey & Williams 1966b	157
<i>Hystrichokolpoma</i> Klumpp 1953	110
<i>Hystrichosphaeridium</i> Deflandre 1937b emend. Davey & Williams 1966	158
<i>Hystrichostrogylon</i> Agelopoulos 1964 emend. Stover & Evitt 1978	79
<i>Impagidinium</i> Stover & Evitt 1978	89
Indet 2	22
Indet 3	166
Indet 4	166
<i>Isabelidium</i> Lentin & Williams 1977a	48
<i>Kleithriasphaeridium</i> Davey 1974	139
<i>Labyrinthodinium</i> Piasecki 1980	165

Genus	Page
<i>Lejeunecysta</i> Artzner & Dörhöfer 1978	72
<i>Lingulodinium</i> Wall 1967a	115
<i>Lophocysta</i> Manum 1979	140
<i>Membranoporphidium</i> Gerlach 1961 emend. Stover & Evitt 1978	154
<i>Nematosphaeropsis</i> Deflandre & Cookson 1955 emend. Wrenn 1988	80
<i>Nummus</i> Morgan 1975	24
<i>Operculodinium</i> Wall 1967a emend. Matsuoka et al. 1997	116
<i>Paucilobimorpha</i> De Coninck 1986b emend. Prössl 1994	25
<i>Paucisphaeridium</i> Bujak et al. 1980b	165
<i>Pentadinium</i> Gerlach 1961	94
<i>Phthanoperidinium</i> Drugg & Loeblich Jr. 1967 emend. Clowes	55
<i>Planoperidinium</i> De Coninck 1986b	49
<i>Pterospermella</i> Eisenack 1972	168
<i>Pyxidinopsis</i> Habib 1976	143
<i>Rhombodinium</i> Gocht 1955 emend. Bujak, 1979	68
<i>Riculacysta</i> Stover 1977	155
<i>Rottnestia</i> Cookson & Eisenack 1961b	81
<i>Samlandia</i> Eisenack 1954b	124
<i>Spinidinium</i> Cookson & Eisenack 1962b	50
<i>Spiniferites</i> Mantell 1850 emend. Sarjeant 1970	74
<i>Stoveracysta</i> Clowes 1985	126
<i>Tectatodinium</i> Wall 1967a emend. Head 1994a	95
<i>Thalassiphora</i> Eisenack & Gocht 1960	128
<i>Tityrosphaeridium</i> Sarjeant 1981	129
<i>Turbiosphaera</i> Archangelsky 1969a	108
<i>Vozzhennikovia</i> Lentin & Williams 1976	53
<i>Wetzeliella</i> Eisenack 1938b emend. Lentin & Williams 1976	66
<i>Wilsonidium</i> Lentin & Williams 1976	70

Plates

Plates

Plate 1

Indet 2 sp. 1

Figure 1-3 Sample J42/f096, slide L10951/SM070; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 23 x 21 μm

Indet 2 sp. 2

Figure 4-6 Sample J42/f096, slide L10951/SM105; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 20 x 20 μm

Cystidiopsis certa

Figure 7-9 Sample I43/f094, slide L16342/1-1439-183; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 25 x 25 μm

?*Cystidiopsis sp. 1*

Figure 10-12 Sample I43/f089, slide L16337/SM071; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 30 x 28 μm

Plate 1

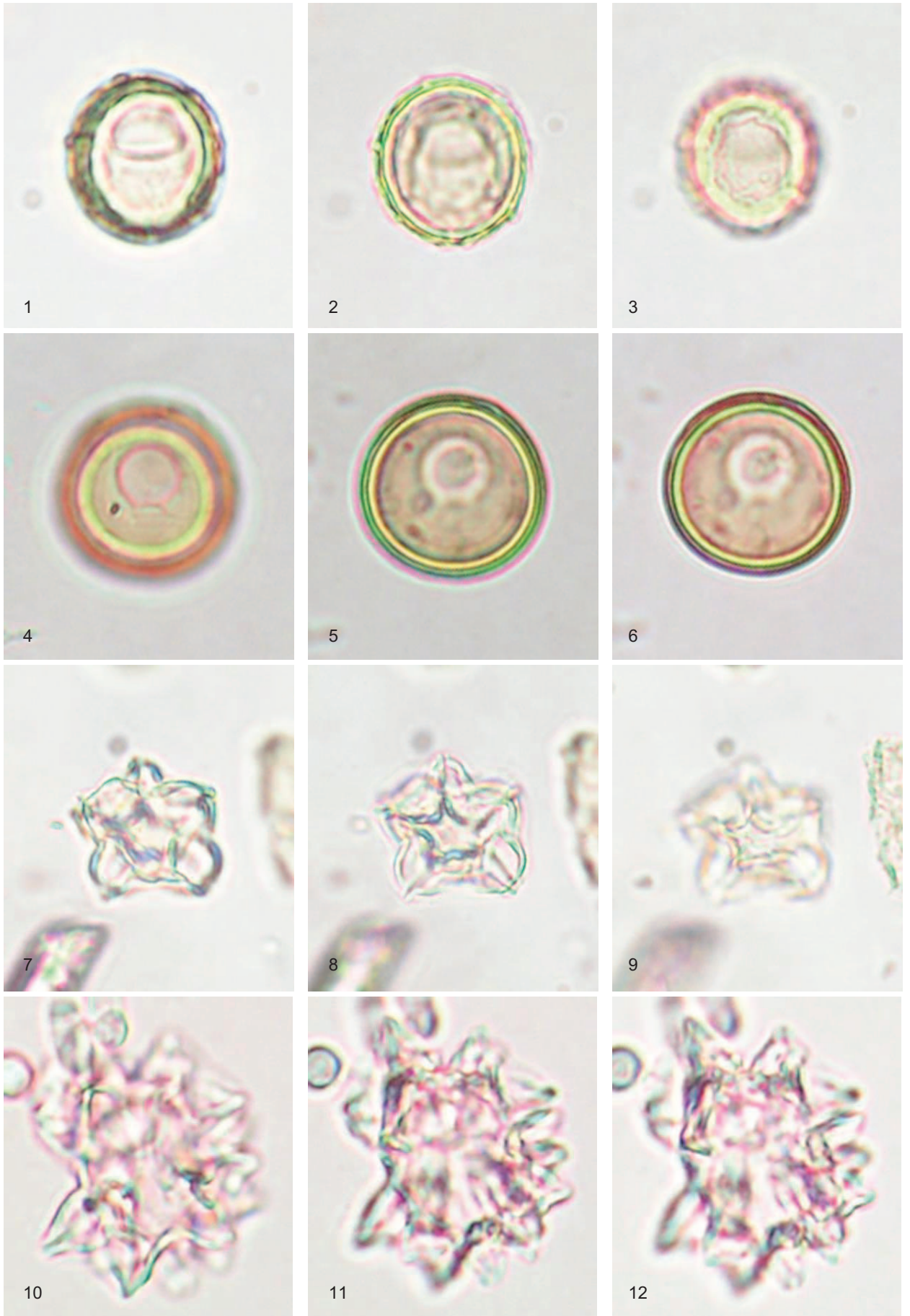


Plate 2

Nummus inornatus

Figure 1-3 Sample I43/f093, slide L16341/SM100; Burnside Formation, Puketeraki Core (Bortonian); x 475; specimen measures 96 x 87 μm

Figure 4-6 Sample I43/f093, slide L16341/SM122; Burnside Formation, Puketeraki Core (Bortonian); x 350; specimen measures 120 x 122 μm

Paucilobomorpha inaequalis

Figure 7-9 Sample J42/f301, slide L23131/SM003; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); specimen measures 23 x 22 μm

Figure 10-12 Sample I43/f089, slide L16337/SM072A; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 27 x 26 μm

Plate 2

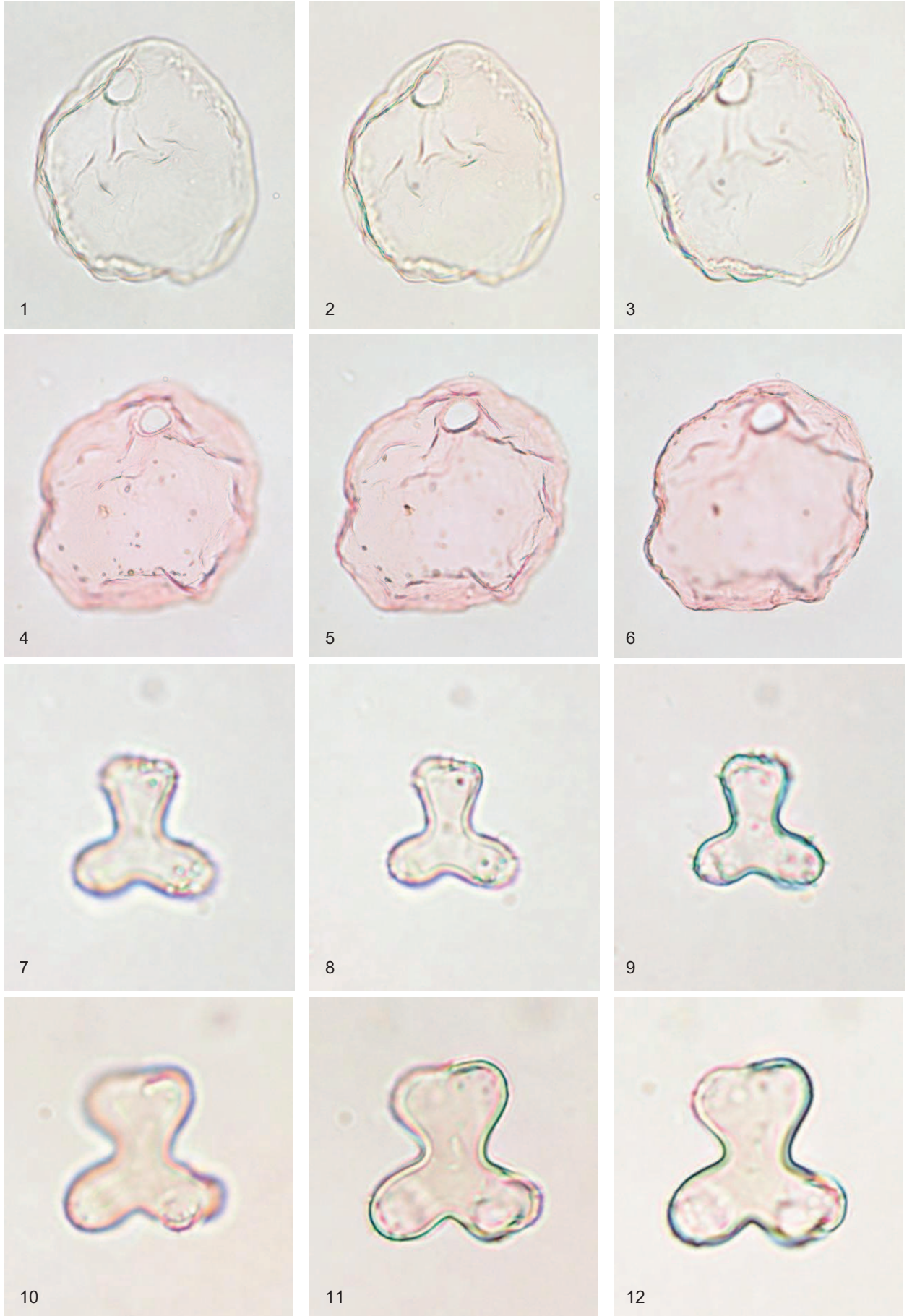


Plate 3

Paucilobimorpha inaequalis

Figure 1-3 Sample I43/f093, slide L16341/SM124; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 30 x 27 μm

Paucilobimorpha incurvata

Figure 4 Sample I44/f080, slide L08947/SM009B; Burnside Formation, Burnside Marl Pit (Bortonian); specimen measures 27 x 23 μm

Figure 5 Sample J42/f062, slide L09219/2-1431-032; Hampden Formation, Hampden Beach Section (?Kaiatan); specimen measures 13 x 13 μm

Figure 6 Sample J42/f064, slide L09221/1-1341-164; Waiareka Volcanics, Hampden Beach Section (Kaiatan); specimen measures 15 x 14 μm

Paucilobimorpha panda

Figure 7-8 Sample J42/f298, slide L23128/SM001; Kurinui Formation, Hampden Beach Section (Heretaungan-Porangan); specimen measures 17 x 20 μm

Figure 9 Sample J42/f489, slide L23124/SM001; Hampden Formation, Hampden Beach Section (Bortonian); specimen measures 20 x 21 μm

Figure 10 Sample U24/f419, slide L23127/SM097; Wanstead, Te Uri Stream (Porangan); specimen measures 19 x 17 μm

Figure 11-12 Sample U24/f419, slide L23127/SM004; Wanstead, Te Uri Stream (Porangan); specimen measures 20 x 17 μm

Plate 3

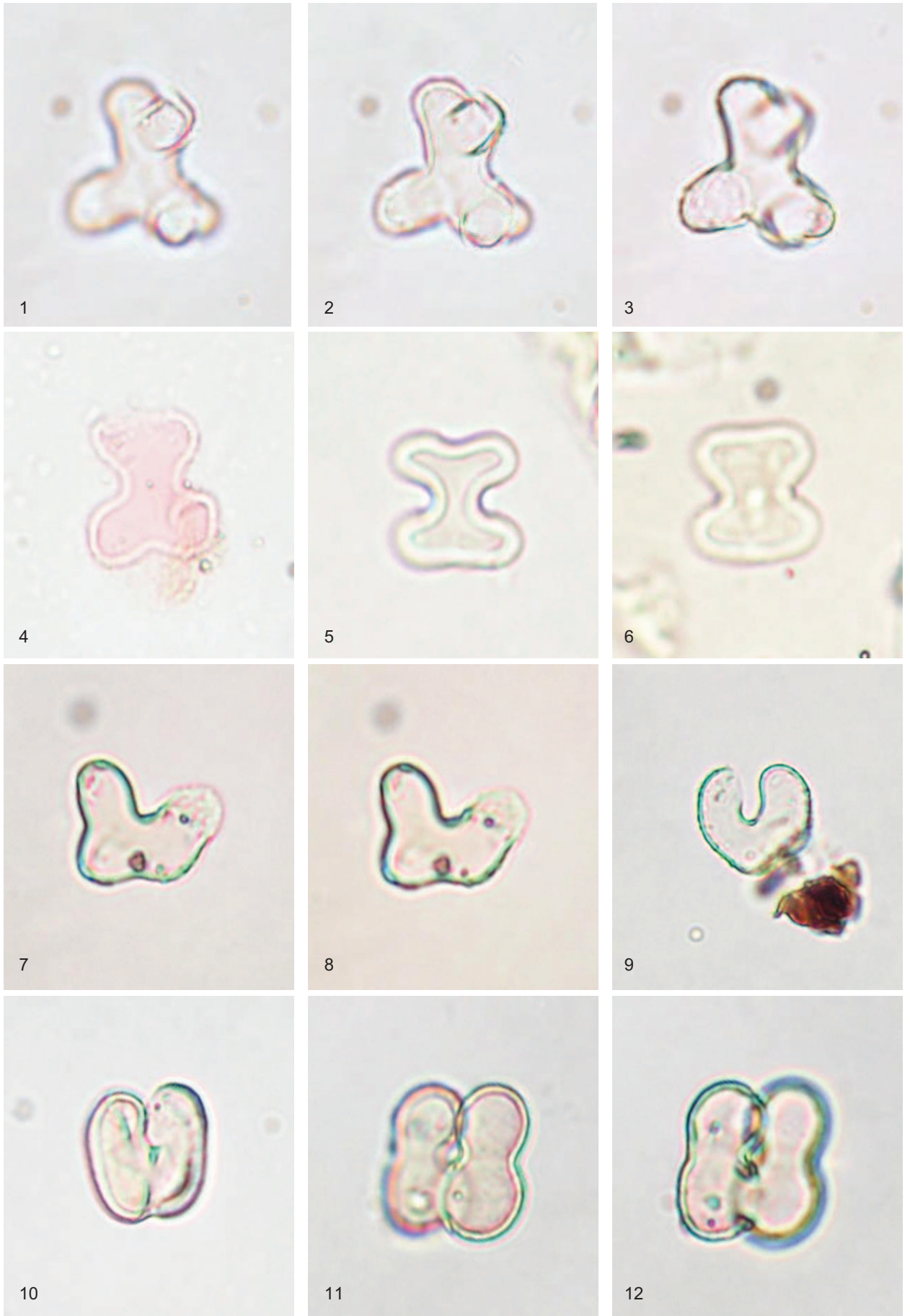


Plate 4

Paucilobimorpha spinigera

Figure 1-3 Sample J42/f303, slide L23133/SM001; Hampden Formation, Hampden Beach Section (Bortonian); specimen measures 23 x 15 μm

Paucilobimorpha spinosa

Figure 4-5 Sample J42/f096, slide L10951/SM103; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 30 x 29 μm

Figure 6 Sample J42/f096, slide L10951/SM102; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 29 x 33 μm

Paucilobimorpha tricornus

Figure 7-9 Sample J42/f301, slide L23131/SM005; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); specimen measures 18 x 20 μm

Figure 10-11 Sample U24/f419, slide L23127/SM096; Wanstead, Te Uri Stream (Porangan); specimen measures 20 x 20 μm

Figure 12 Sample U24/f419, slide L23127/SM002; Wanstead, Te Uri Stream (Porangan); specimen measures 23 x 23 μm

Plate 4

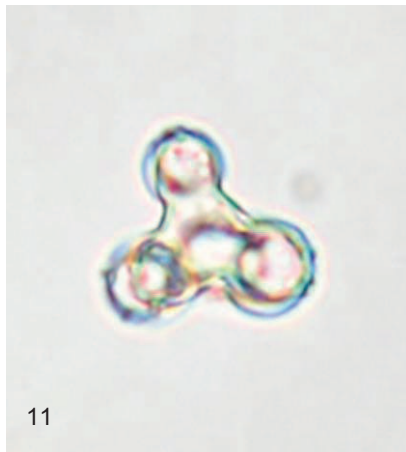


Plate 5

Paucilobomorpha tripa

Figure 1-3 Sample J42/f301, slide L23131/SM006A; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); specimen measures 25 x 25 μm

Figure 4-5 Sample J42/f041, slide L09198/1-1314-127; Hampden Formation, Hampden Beach Section (Bortonian); specimen measures 31 x 37 μm

Figure 6 Sample J42/f489, slide L23124/SM003; Hampden Formation, Hampden Beach Section (Bortonian); specimen measures 19 x 17 μm

Fenestridium clathrodermum

Figure 7-9 Sample J42/f097, slide L10952/SM2965; Totara Limestone, Kakanui River (?early Whaingaroan); x 875; specimen measures 53 x 48 μm

Figure 10-12 Sample J42/f097, slide L10952/SM013; Totara Limestone, Kakanui River (?early Whaingaroan); x 850; specimen measures 50 x 50 μm

Plate 5

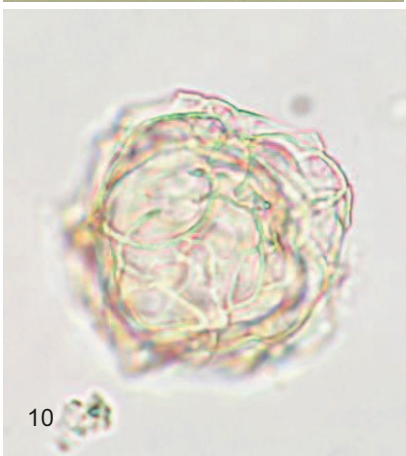


Plate 6

Fenestridium clathrodermum

Figure 1-3 Sample J42/f097, slide L10952/SM012; Totara Limestone, Kakanui River (?early Whaingaroan); x 1000; specimen measures 47 x 42 μm

Figure 4-6 Sample J42/f097, slide L10952/SM011; Totara Limestone, Kakanui River (?early Whaingaroan); x 975; specimen measures 45 x 43 μm

Deflandrea phosphoritica

Figure 7-9 Sample K29/f115, slide L11051/SM001; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 325; specimen measures 142 x 108 μm

Figure 10-12 Sample K29/f097, slide L10914/SM016; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 325; specimen measures 150 x 105 μm

Plate 6

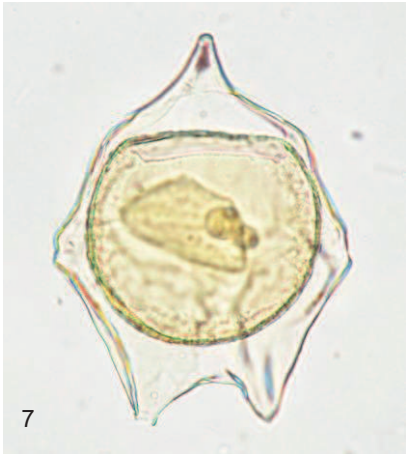
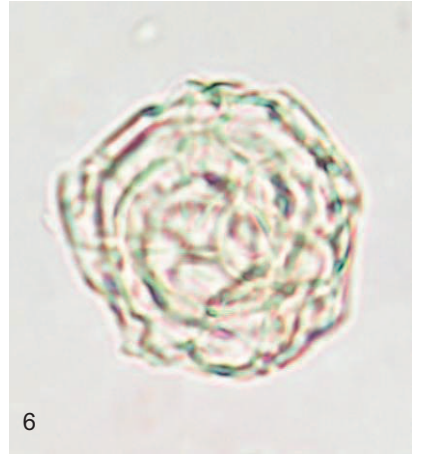
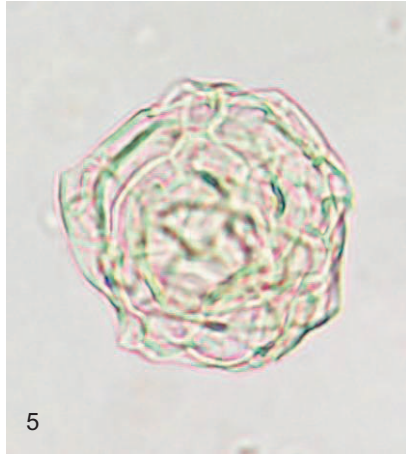
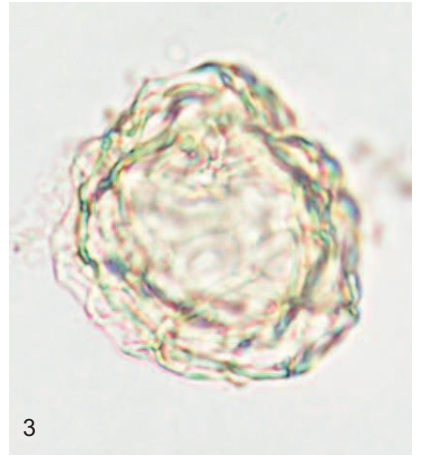
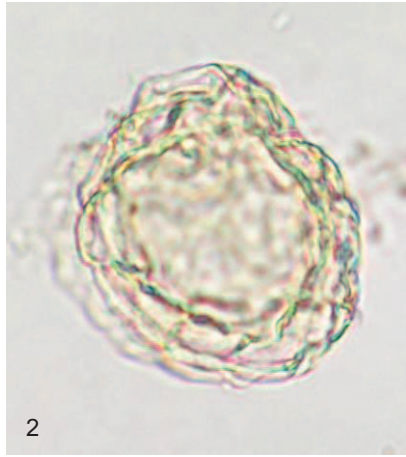


Plate 7

Deflandrea phosphoritica

Figure 1-3 Sample K29/f114, slide L11050/SM016; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 325; specimen measures 148 x 117 μm

Figure 4-6 Sample K29/f115, slide L11051/SM002; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 350; specimen measures 137 x 103 μm

Figure 7-9 Sample K29/f102, slide L11038/SM004; Kaiata Mudstone, Cape Foulwind Section (Runangan); x 350; specimen measures 130 x 100 μm

Deflandrea aff. phosphoritica

Figure 10-12 Sample J42/f097, slide L10952/SM006; Totara Limestone, Kakanui River (?early Whaingaroan); x 325; specimen measures 142 x 110 μm

Plate 7

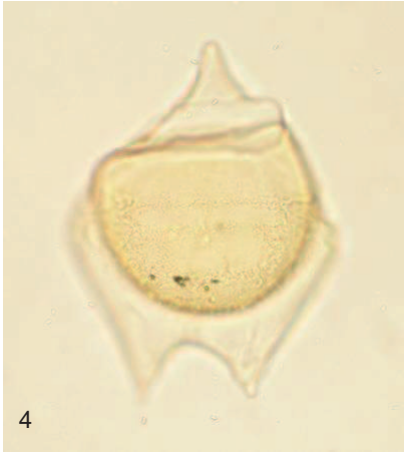


Plate 8

Deflandrea aff. phosphoritica

- Figure 1-3 Sample J42/f097, slide L10952/SM2964; Totara Limestone, Kakanui River (?early Whaingaroan); x 325; specimen measures 149 x 114 μm
- Figure 4 Sample J42/f097, slide L10952/SM002; Totara Limestone, Kakanui River (?early Whaingaroan); x 375; specimen measures 125 x 105 μm
- Figure 5 Sample K29/f114, slide L11050/SM024; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 350; specimen measures 137 x 117 μm
- Figure 6 Sample J42/f097, slide L10952/SM007; Totara Limestone, Kakanui River (?early Whaingaroan); x 350; specimen measures 130 x 108 μm

Deflandrea ?heterophlycta

- Figure 7-12 Sample I43/f089, slide L16337/SM114; Burnside Formation, Puketeraki Core (Bortonian); x 350; specimen measures 130 x 100 μm

Plate 8

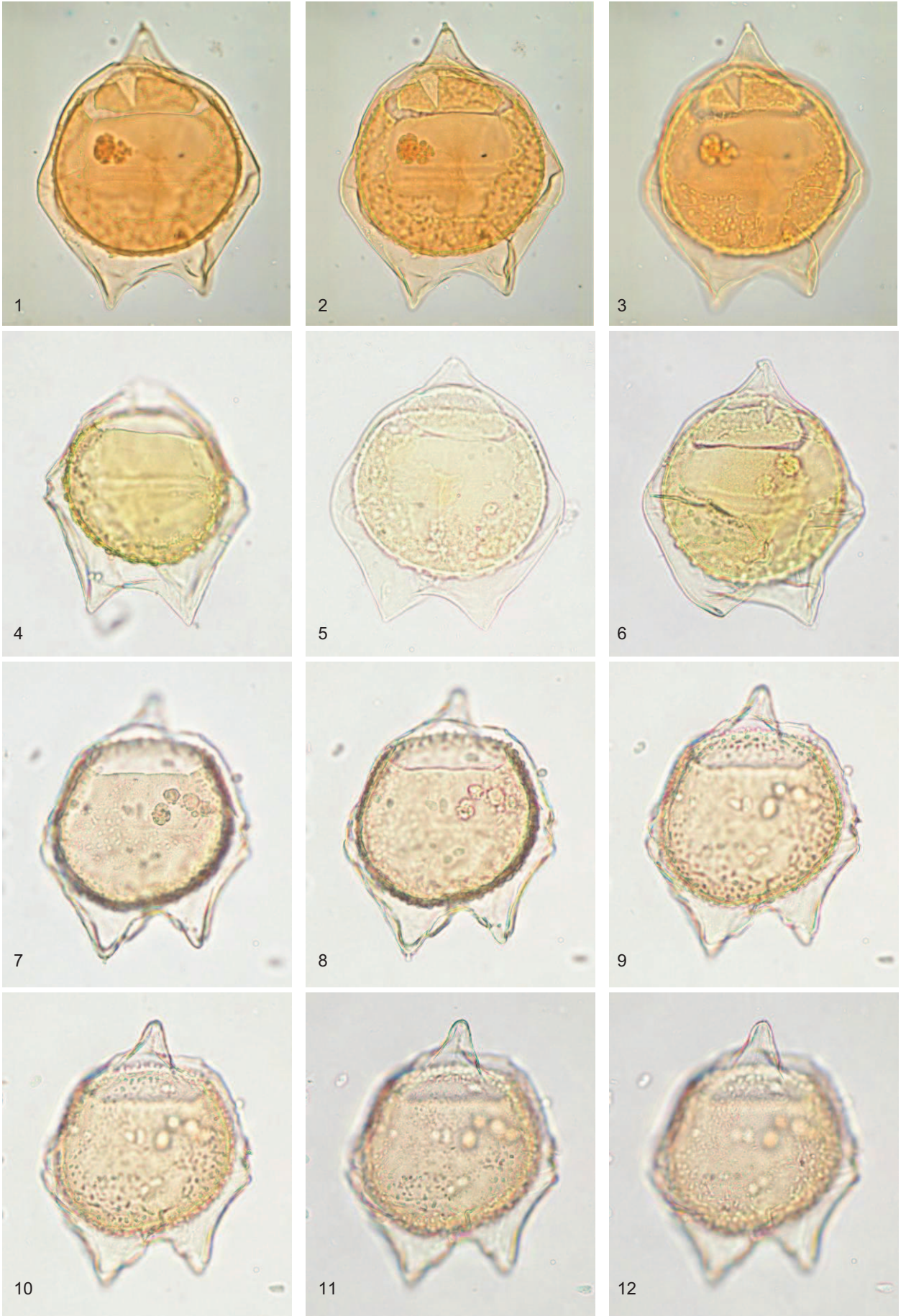


Plate 9

Deflandrea ?heterophlycta

Figure 1-6 Sample I43/f090, slide L16338/SM012; Burnside Formation, Puketeraki Core (Bortonian);
x 400; specimen measures 115 x 82 μm

Figure 7-9 Sample I43/f089, slide L16337/SM033; Burnside Formation, Puketeraki Core (Bortonian);
x 375; specimen measures 127 x 98 μm

Deflandrea sp. 3

Figure 10-12 Sample I43/f089, slide L16337/SM081; Burnside Formation, Puketeraki Core (Bortonian);
x 375; specimen measures 127 x 88 μm

Plate 9

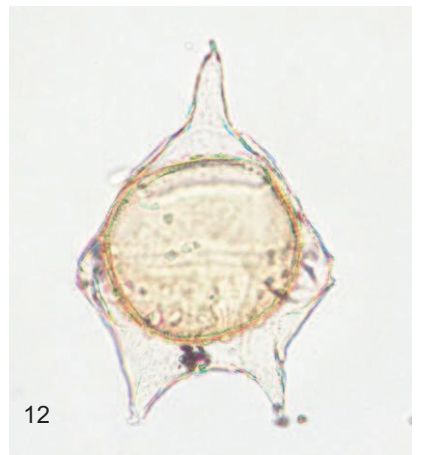


Plate 10

***Deflandrea* sp. 3**

Figure 1-3 Sample I43/f089, slide L16337/SM081; Burnside Formation, Puketeraki Core (Bortonian); x 375; specimen measures 127 x 88 μm

Figure 4-9 Sample I43/f089, slide L16337/SM031; Burnside Formation, Puketeraki Core (Bortonian); x 375; specimen measures 127 x 82 μm

Deflandrea cygniformis

Figure 10-12 Sample J42/f488, slide L23123/SM006; Hampden Formation, Hampden Beach Section (Bortonian); x 400; specimen measures 120 x 72 μm

Plate 10

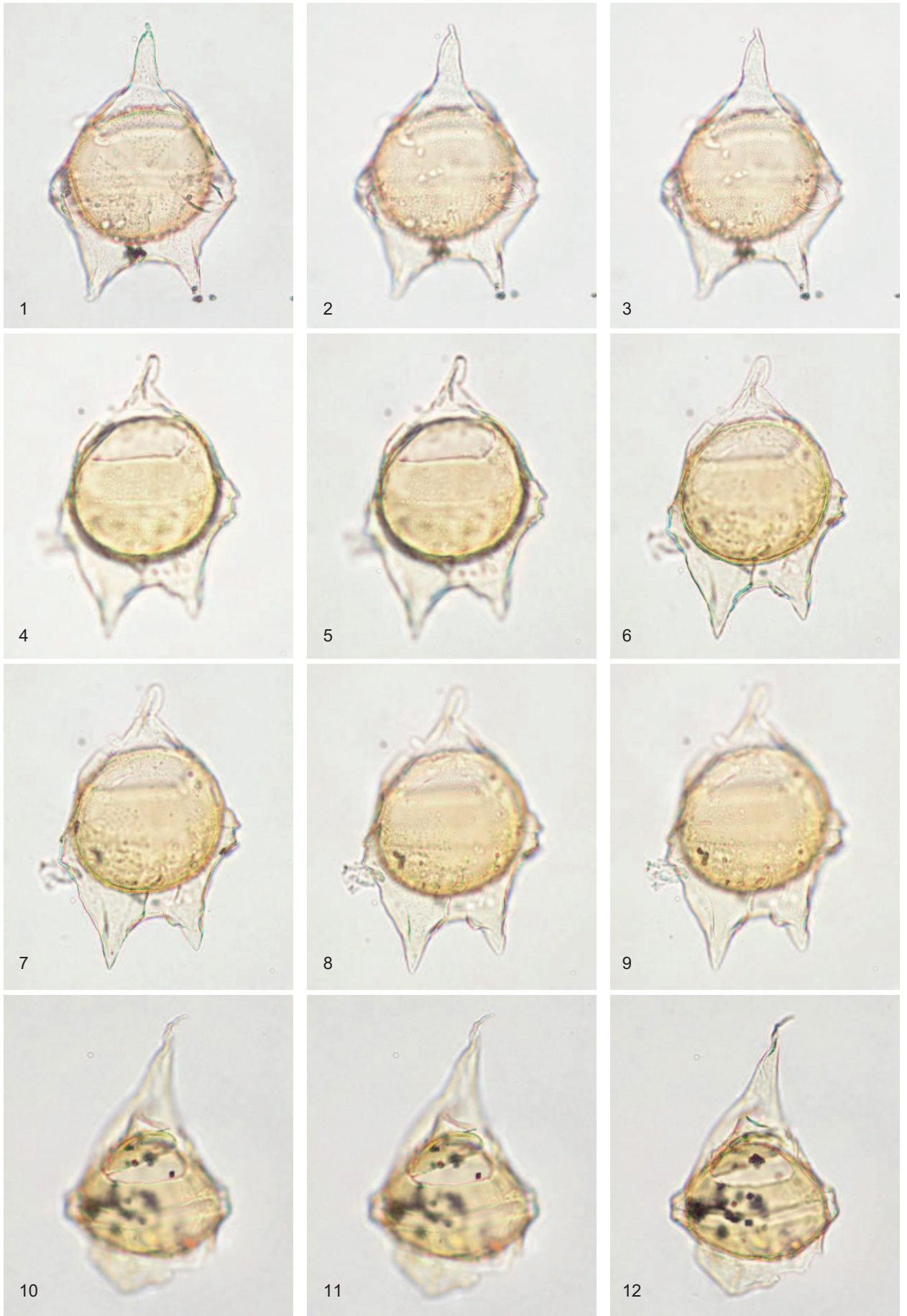


Plate 11

Deflandrea cygniformis

Figure 1-3 Sample J42/f488, slide L23123/SM006; Hampden Formation, Hampden Beach Section (Bortonian); x 400; specimen measures 120 x 72 μm

***Deflandrea* sp. 4**

Figure 4-6 Sample K29/f114, slide L11050/SM025; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 400; specimen measures 117 x 92 μm

Deflandrea antarctica

Figure 7-12 Sample J42/f488, slide L23123/SM004; Hampden Formation, Hampden Beach Section (Bortonian); x 425; specimen measures 108 x 65 μm

Plate 11

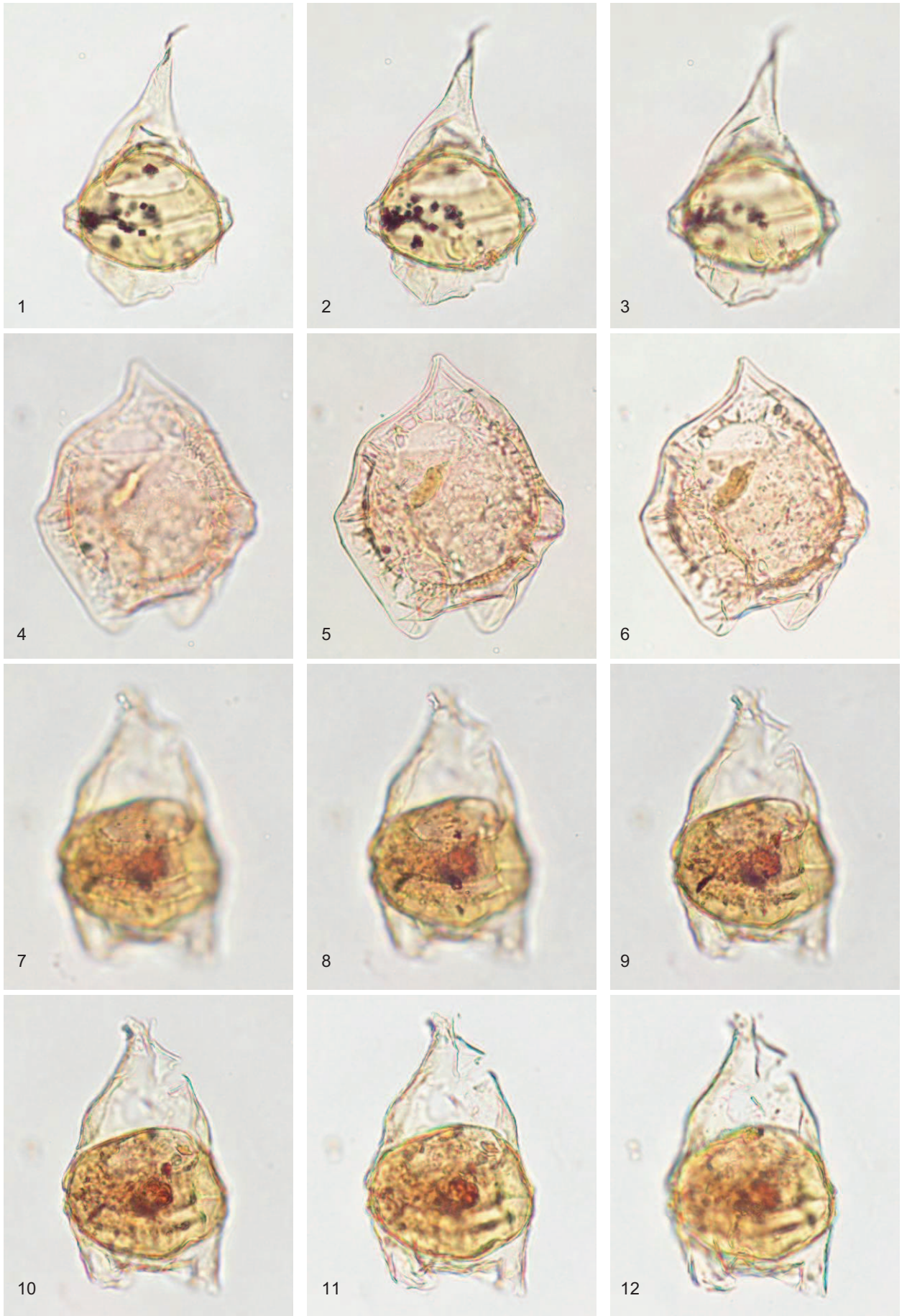


Plate 12

Deflandrea aff. antarctica

Figure 1-3 Sample U24/f419, slide L23127/SM005B; Wanstead, Te Uri Stream (Porangan); x 375; specimen measures 123 x 68 μm

Deflandrea convexa

Figure 4-6 Sample U24/f418, slide L23126/SM006; Wanstead, Te Uri Stream (Porangan); x 550; specimen measures 80 x 75 μm

Figure 7-9 Sample U24/f418, slide L23126/SM007; Wanstead, Te Uri Stream (Porangan); x 475; specimen measures 97 x 80 μm

Figure 10-12 Sample I43/f090, slide L16338/SM014; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 103 x 85 μm

Plate 12

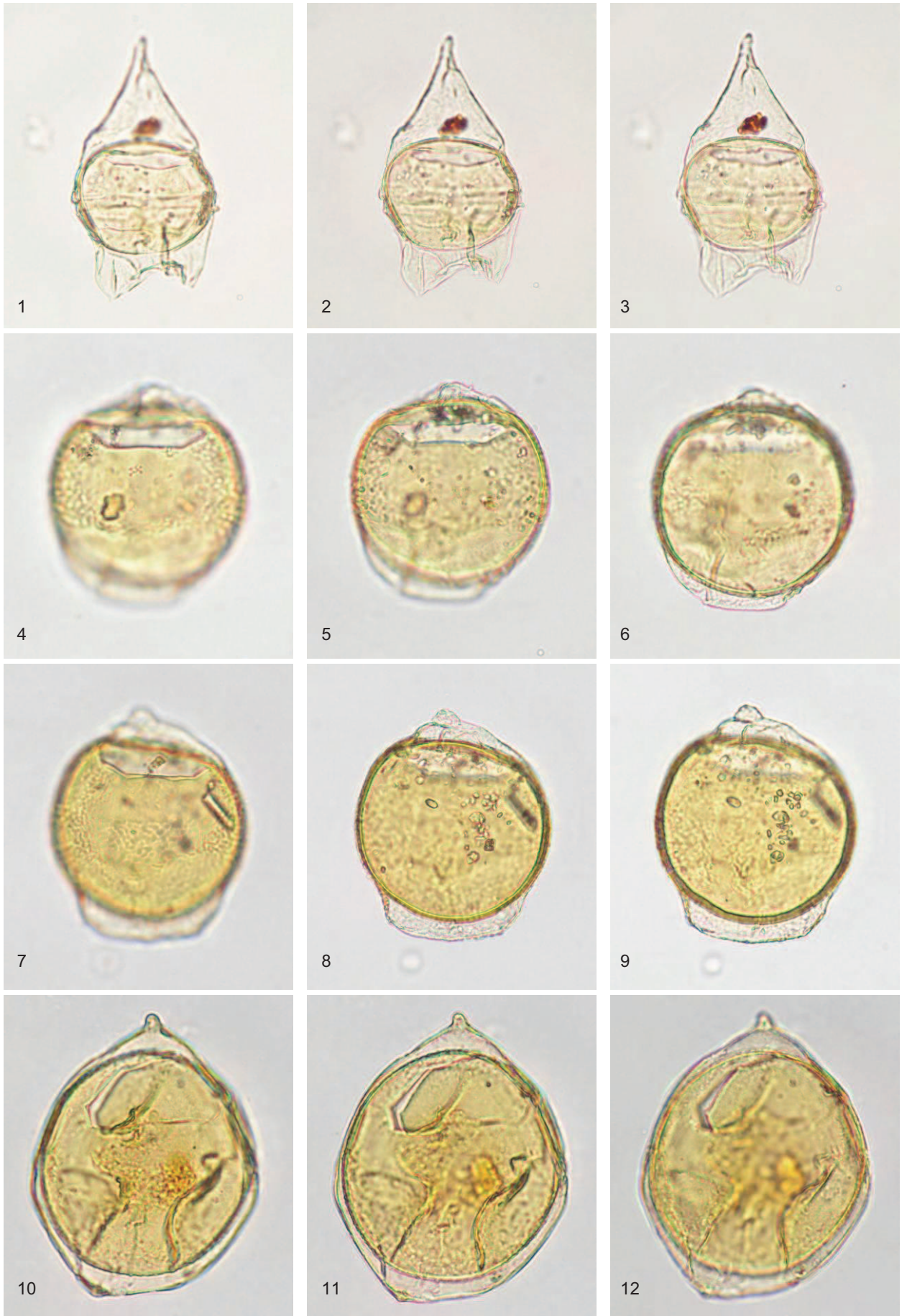


Plate 13

Deflandrea ?leptodermata

Figure 1-2 Sample J42/f098, slide L10953/SM004; Totara Limestone, Kakanui River (Runangan); x 400; specimen measures 115 x 98 μm

Figure 3 Sample J42/f098, slide L10953/SM2967; Totara Limestone, Kakanui River (Runangan); x 350; specimen measures 138 x 101 μm

Deflandrea micropoda

Figure 4-6 Sample I43/f093, slide L16341/SM127; Burnside Formation, Puketeraki Core (Bortonian); x 475; specimen measures 100 x 80 μm

Deflandrea sp. 1

Figure 7-9 Sample K29/f106, slide L11042/SM001; Kaiata Mudstone, Cape Foulwind Section (Runangan-early Whaingaroan)

Deflandrea totara

Figure 10-11 Sample J42/f096, slide L10951/SM091; Totara Limestone, Kakanui River (early Whaingaroan); x 375; specimen measures 126 x 92 μm

Figure 12 Sample J42/f096, slide L10951/SM086; Totara Limestone, Kakanui River (early Whaingaroan); x 350; specimen measures 135 x 95 μm

Plate 13

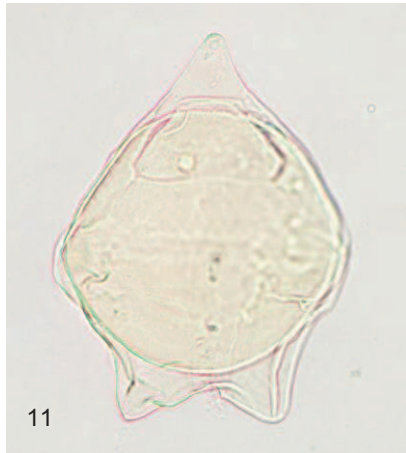
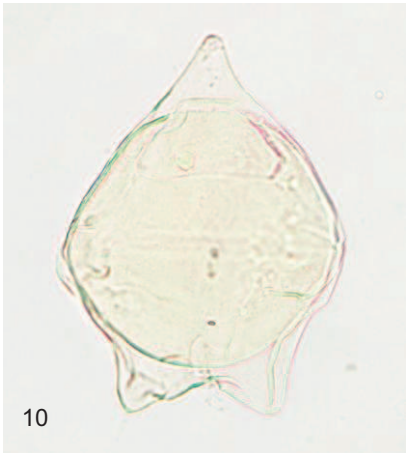
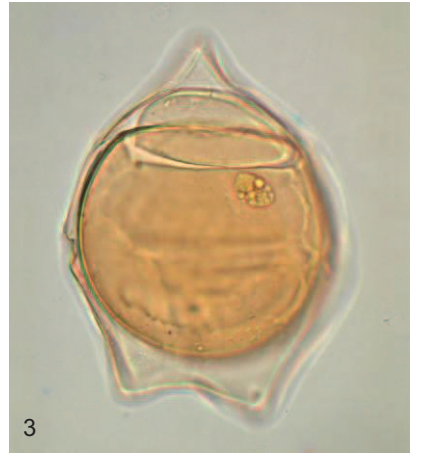


Plate 14

Deflandrea totara

Figure 1 Sample J42/f096, slide L10951/SM086; Totara Limestone, Kakanui River (early Whaingaroan); x 350; specimen measures 135 x 95 μ m

Figure 2-3 Sample J42/f096, slide L10951/SM093; Totara Limestone, Kakanui River (early Whaingaroan); x 350; specimen measures 130 x 95 μ m

Deflandrea sp. 2

Figure 4-6 Sample K29/f102, slide L11038/SM002; Kaiata Mudstone, Cape Foulwind Section (Runangan)

Deflandrea sp. not identified

Figure 7-9 Sample U24/f417, slide L23125/SM003; Wanstead, Te Uri Stream (Porangan)

Alterbidinium cf. acutulum

Figure 10-12 Sample J42/f486, slide L23121/SM001; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 825; specimen measures 57 x 45 μ m

Plate 14

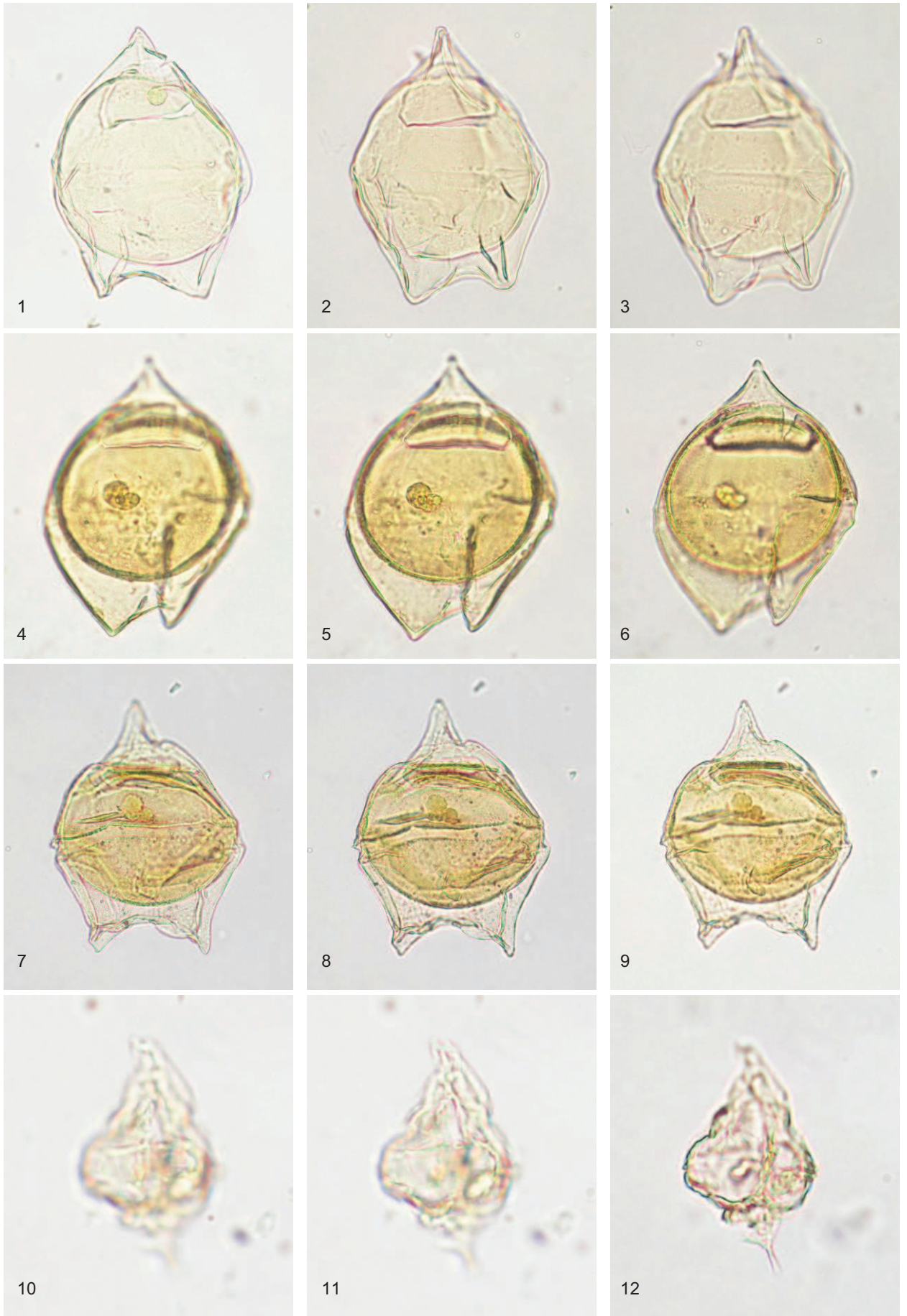


Plate 15

Cerodinium medcalfii

Figure 1-3 Sample U24/f419, slide L23127/SM061; Wanstead, Te Uri Stream (Porangan); x 300; specimen measures 155 x 72 μm

Figure 4-6 Sample U24/f419, slide L23127/SM074; Wanstead, Te Uri Stream (Porangan); x 350; specimen measures 135 x 80 μm

Isabelidinium cf. bakeri

Figure 7-9 Sample J42/f063, slide L09220/2-1422-215; Mokihi Formation, Hampden Beach Section (Kaiatan); x 275; specimen measures 165 x 96 μm

Planoperidinium gracile

Figure 10-12 Sample K29/f097, slide L10914/SM044; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 600; specimen measures 78 x 65 μm

Plate 15

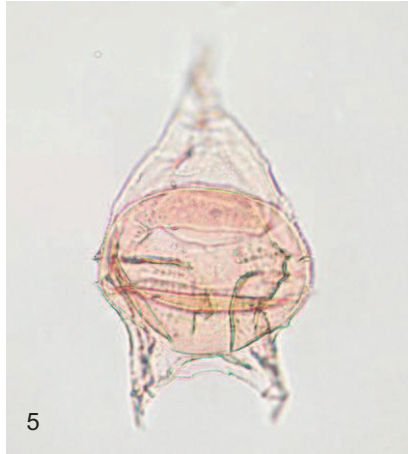
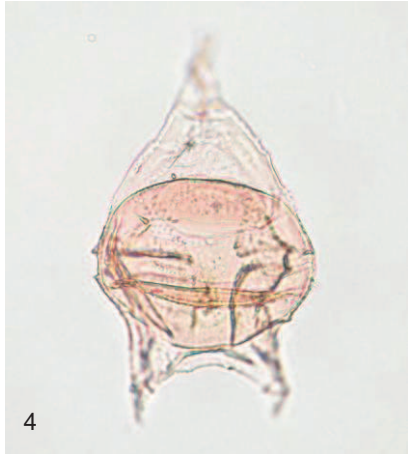


Plate 16

Planoperidinium gracile

Figure 1-3 Sample K29/f097, slide L10914/SM045; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 550; specimen measures 87 x 67 μm

?*Planoperidinium* sp. 2

Figure 4-6 Sample K29/f097, slide L10914/SM002; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 625; specimen measures 75 x 55 μm

Figure 7-9 Sample K29/f097, slide L10914/SM042B; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 650; specimen measures 72 x 50 μm

Spinidinium* cf. *styloniferum

Figure 10-12 Sample I44/f080, slide L08947/SM024; Burnside Formation, Burnside Marl Pit (Bortonian); x 850; specimen measures 56 x 47 μm

Plate 16

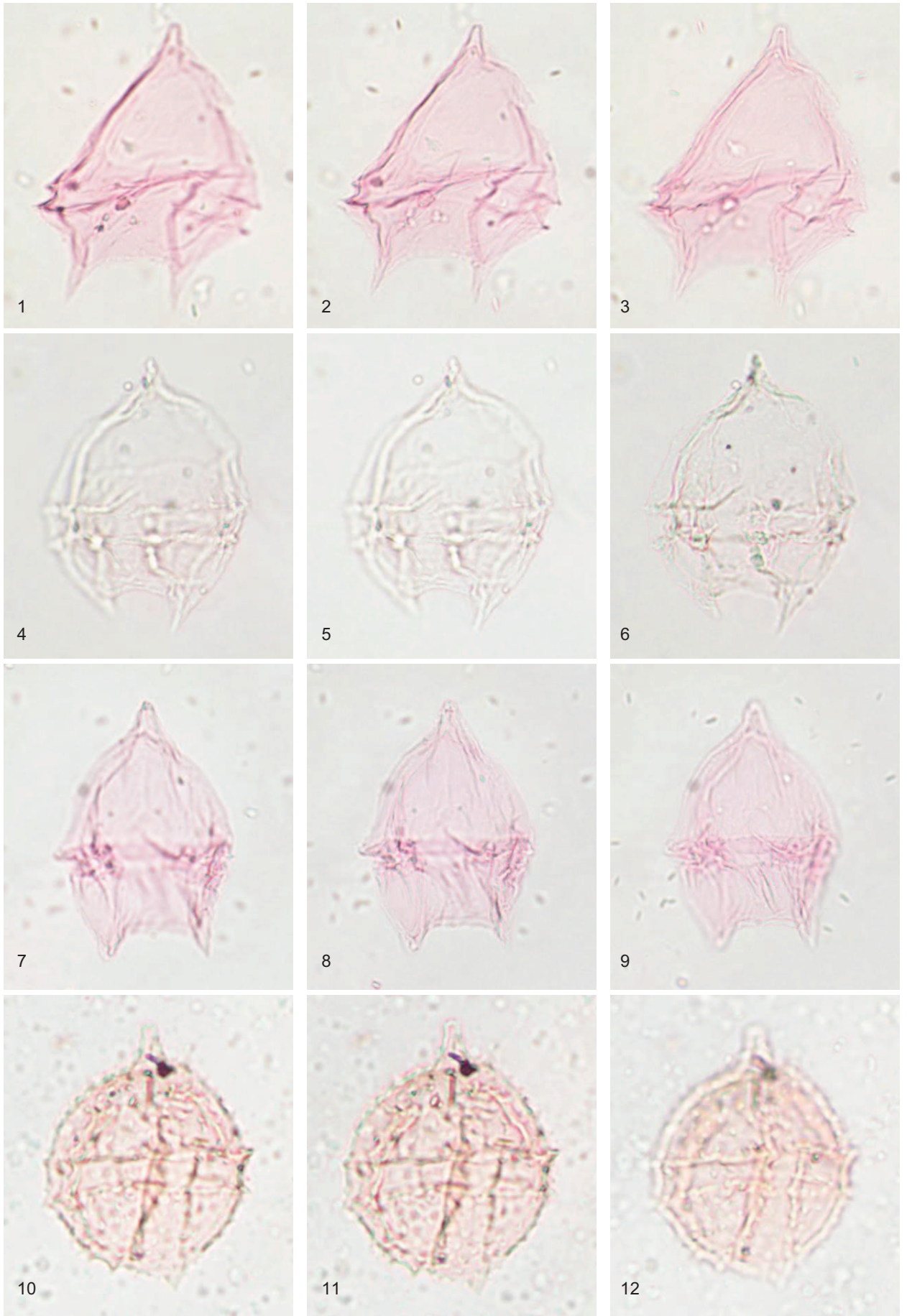


Plate 17

Spinidinium colemanii

Figure 1-3 Sample U24/f417, slide L23125/SM028; Wanstead, Te Uri Stream (Porangan); x 1000; specimen measures 47 x 42 μm

Figure 4-9 Sample J42/f488, slide L23123/SM007; Hampden Formation, Hampden Beach Section (Bortonian); x 775; specimen measures 60 x 37 μm

Spinidinium essoii

Figure 10-11 Sample U24/f419, slide L23127/SM057; Wanstead, Te Uri Stream (Porangan); x 850; specimen measures 55 x 42 μm

Spinidinium macmurdoense

Figure 12 Sample J42/f485, slide L23120/SM005; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 850; specimen measures 55 x 46 μm

Plate 17

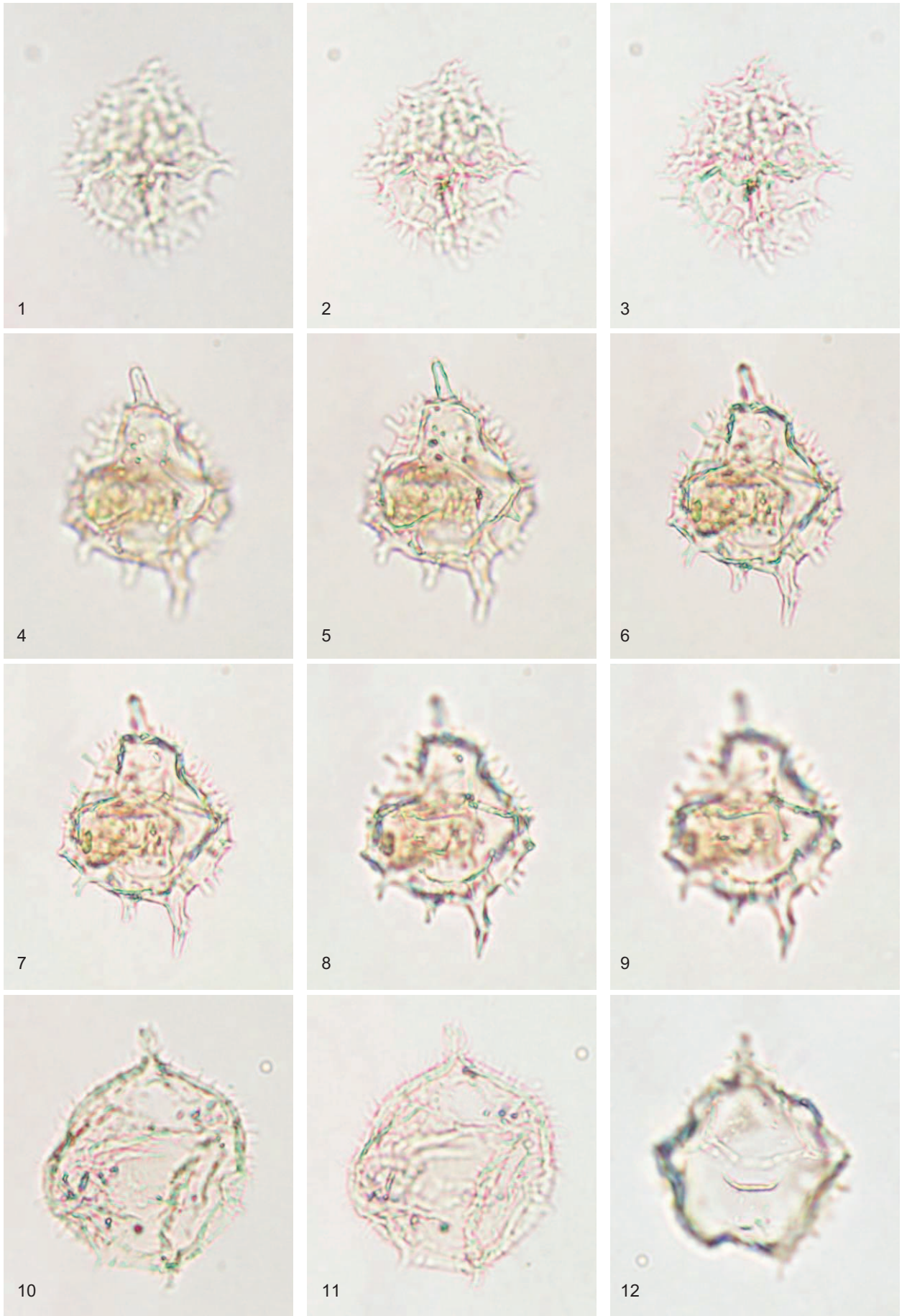


Plate 18

Spinidinium macmurdoense

Figure 1-3 Sample J42/f485, slide L23120/SM005; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 850; specimen measures 55 x 46 μm

Vozzhennikovia apertura

Figure 4-6 Sample I43/f092, slide L16340/1-1431-224; Burnside Formation, Puketeraki Core (Bortonian); x 1125; specimen measures 42 x 31 μm

Figure 7-9 Sample I43/f092, slide L16340/1-1304-197; Burnside Formation, Puketeraki Core (Bortonian); x 1050; specimen measures 45 x 33 μm

Figure 10-12 Sample J42/f301, slide L23131/SM030; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); specimen measures 38 x 35 μm

Plate 18

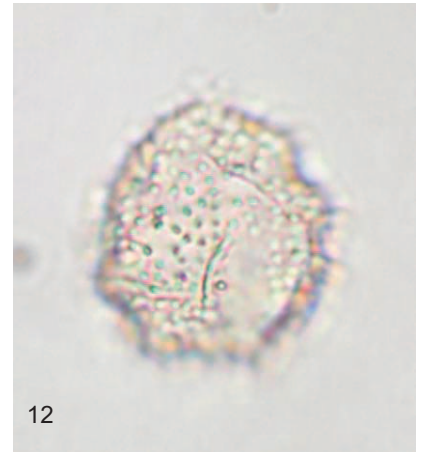
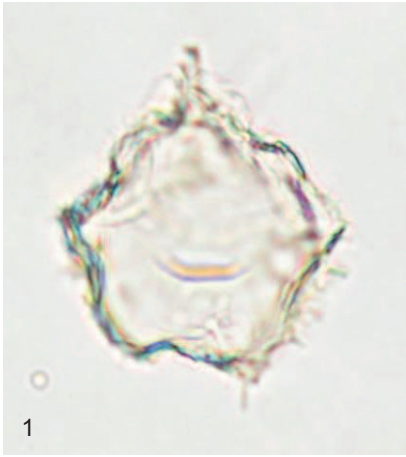


Plate 19

Phthanoperidinium ?crenulatum

Figure 1-3 Sample I43/f090, slide L16338/SM007; Burnside Formation, Puketeraki Core (Bortonian);
x 775; specimen measures 61 x 53 μm

Figure 4-6 Sample I43/f089, slide L16337/2-1418-106; Burnside Formation, Puketeraki Core (Bortonian);
x 1000; specimen measures 47 x 39 μm

Phthanoperidinium dentatum

Figure 7-12 Sample J42/f8690, slide L06958/SM0382; Hampden Formation, Hampden Beach Section
(Bortonian); x 1175; specimen measures 40 x 34 μm

Plate 19

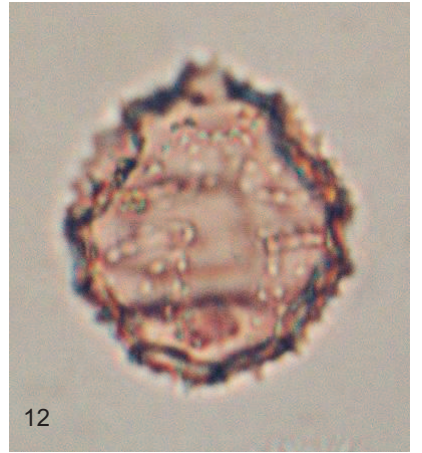
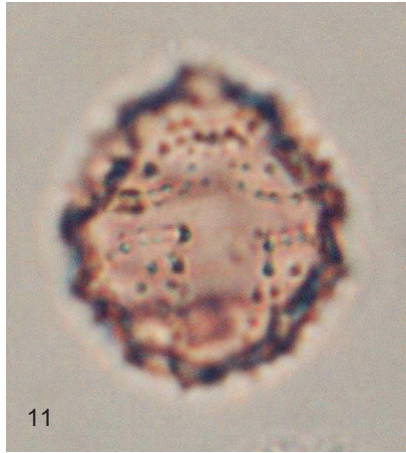
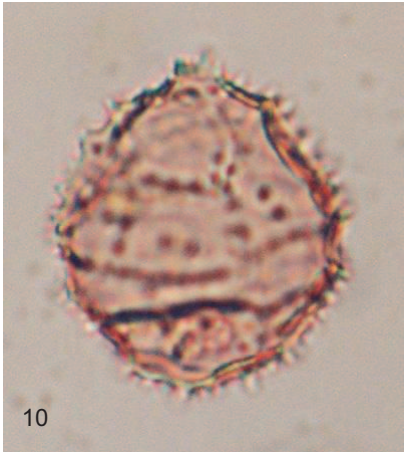


Plate 20

Phthanoperidinium dentatum

Figure 1-3 Sample J42/f8690, slide L06958/SM0392; Hampden Formation, Hampden Beach Section (Bortonian); x 1050; specimen measures 43 x 40 μm

Phthanoperidinium echinatum

Figure 4-6 Sample I43/f093, slide L16341/SM077; Burnside Formation, Puketeraki Core (Bortonian); x 950; specimen measures 49 x 39 μm

Figure 7-12 Sample I43/f093, slide L16341/SM133; Burnside Formation, Puketeraki Core (Bortonian); x 900; specimen measures 52 x 38 μm

Plate 20



Plate 21

Phthanoperidinium eocenicum

Figure 1-3 Sample I43/f093, slide L16341/SM012; Burnside Formation, Puketeraki Core (Bortonian); x 925; specimen measures 51 x 35 μm

Figure 4-6 Sample J41/f8914, slide L04979/SM1084; Waiareka Volcanics, Jacksons Paddock (Kaiatan-Runangan); x 725; specimen measures 64 x 45 μm

Phthanoperidinium geminatum

Figure 7-12 Sample I43/f093, slide L16341/SM107; Burnside Formation, Puketeraki Core (Bortonian); x 1125; specimen measures 42 x 32 μm

Plate 21

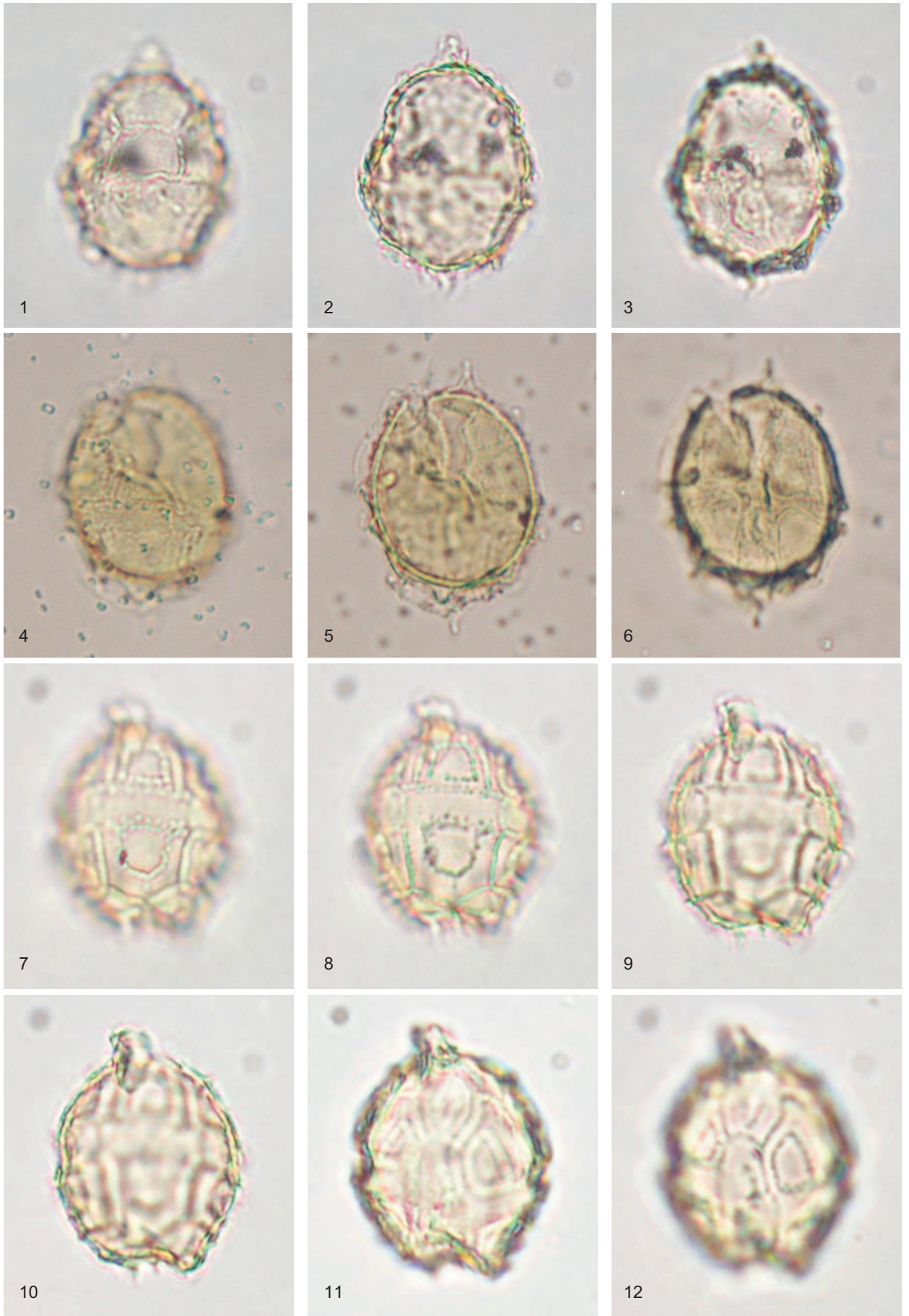


Plate 22

Phthanoperidinium granulatum

Figure 1-6 Sample I43/f108, slide L16358/SM4832; Burnside Formation, Tumai (Runangan); x 825; specimen measures 57 x 41 μm

Phthanoperidinium ?resistente

Figure 7-9 Sample I43/f093, slide L16341/SM061; Burnside Formation, Puketeraki Core (Bortonian); x 975; specimen measures 48 x 35 μm

Phthanoperidinium spumosum

Figure 10-12 Sample I43/f093, slide L16341/SM078; Burnside Formation, Puketeraki Core (Bortonian); x 1050; specimen measures 45 x 37 μm

Plate 22



Plate 23

Phthanoperidinium spumosum

Figure 1-3 Sample I43/f093, slide L16341/SM078; Burnside Formation, Puketeraki Core (Bortonian);
x 1050; specimen measures 45 x 37 μm

Phthanoperidinium aculeatum

Figure 4-9 Sample I43/f093, slide L16341/SM082A; Burnside Formation, Puketeraki Core (Bortonian);
x 900; specimen measures 52 x 42 μm

Phthanoperidinium tenuimurum

Figure 10-12 Sample S14/f8599, slide L10662/SM014; Waikato Coal Measures, Old Mountain Road
(Runangan-early Whaingaroan); x 700; specimen measures 63 x 60 μm

Plate 23

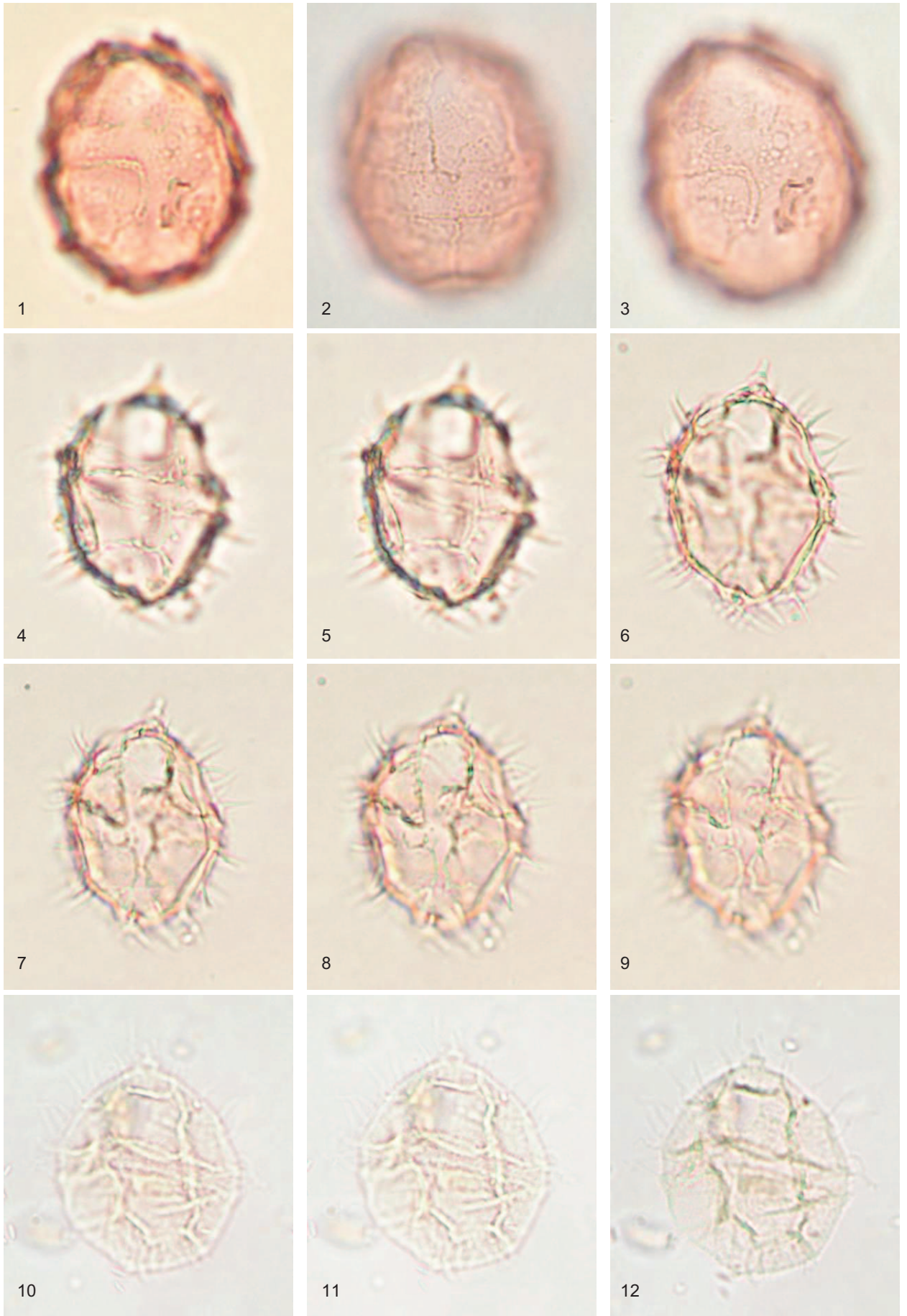


Plate 24

Phthanoperidinium tritonium

Figure 1-3 Sample I43/f093, slide L16341/SM103; Burnside Formation, Puketeraki Core (Bortonian);
x 750; specimen measures 62 x 45 μm

Phthanoperidinium sp. 4

Figure 4-6 Sample I43/f090, slide L16338/1-1273-187; Burnside Formation, Puketeraki Core (Bortonian);
x 1050; specimen measures 45 x 33 μm

Figure 7-12 Sample I43/f090, slide L16338/SM002; Burnside Formation, Puketeraki Core (Bortonian);
x 975; specimen measures 48 x 35 μm

Plate 24

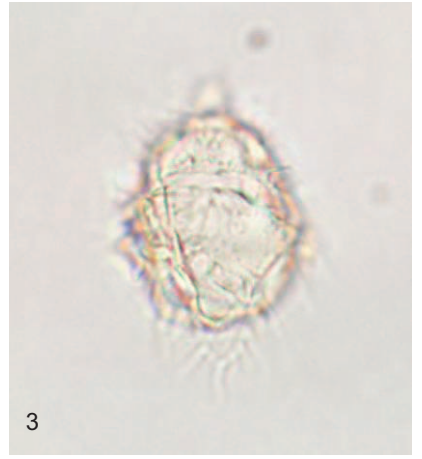
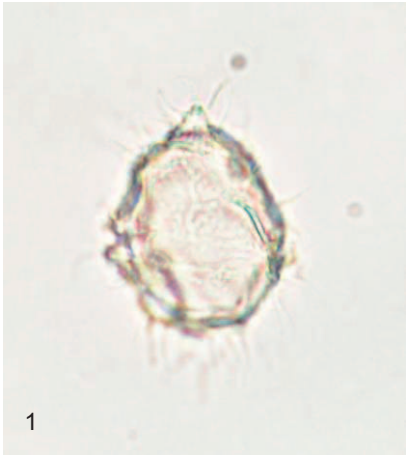


Plate 25

Wetziella hampdenensis

Figure 1-3 Sample J42/f055, slide L09212/6-1486-045; Hampden Formation, Hampden Beach Section (Bortonian); x 400; specimen measures 97 x 102 μm

Charlesdownia coleothrypta

Figure 4-6 Sample U24/f418, slide L23126/SM002; Wanstead, Te Uri Stream (Porangan); x 425; specimen measures 105 x 97 μm

Dracodinium granulatum

Figure 7-9 Sample I43/f094, slide L16342/1-1252-070; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 87 x 95 μm

Rhombodinium glabrum

Figure 10-12 Sample I43/f093, slide L16341/SM131; Burnside Formation, Puketeraki Core (Bortonian); x 400; specimen measures 115 x 108 μm

Plate 25

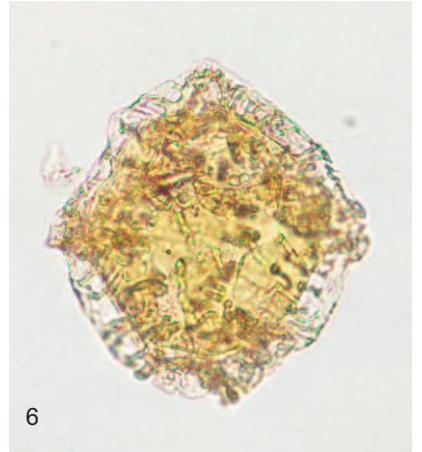
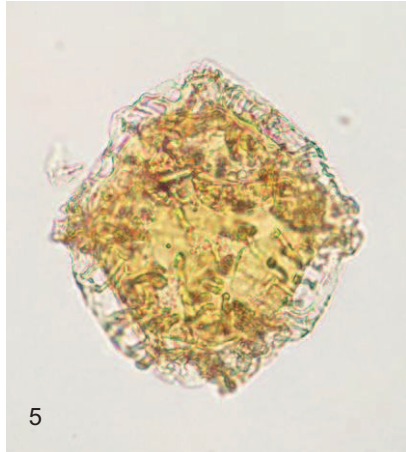
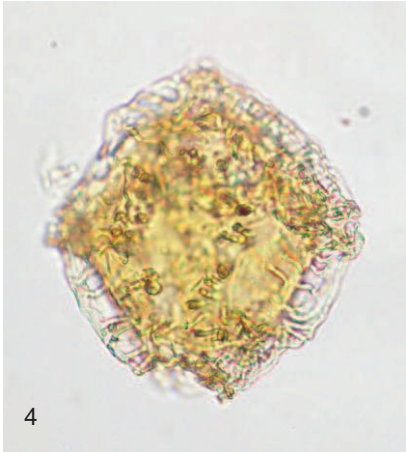


Plate 26

Rhombodinium glabrum

Figure 1-2 Sample I44/f080, slide L08947/SM027; Burnside Formation, Burnside Marl Pit (Bortonian); x 250; specimen measures 181 x 146 μm

Figure 3 Sample I43/f090, slide L16338/SM018; Burnside Formation, Puketeraki Core (Bortonian); x 375; specimen measures 128 x 115 μm

Wilsonidium cf. echinosuturatum

Figure 4-6 Sample J42/f303, slide L23133/SM003; Hampden Formation, Hampden Beach Section (Bortonian); x 450; specimen measures 94 x 92 μm

Wilsonidium lineidentatum

Figure 7-9 Sample J42/f055, slide L09212/6-1471-031; Hampden Formation, Hampden Beach Section (Bortonian); x 350; specimen measures 135 x 95 μm

Lejeunecysta ?fallax

Figure 10-12 Sample K29/f114, slide L11050/SM014; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 600; specimen measures 72 x 69 μm

Plate 26

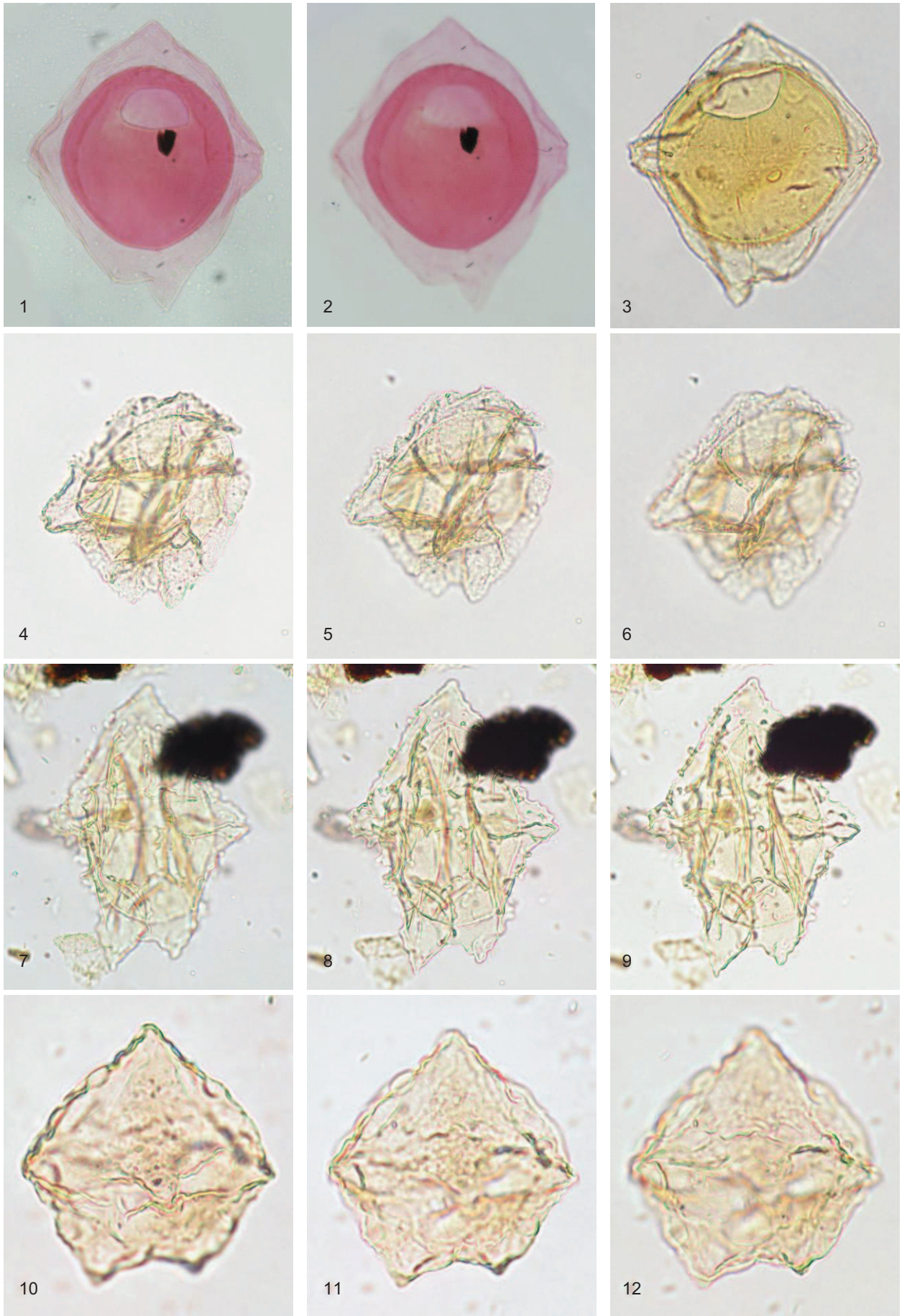


Plate 27

Spiniferites ramosus

Figure 1-3 Sample J42/f096, slide L10951/SM050; Totara Limestone, Kakanui River (early Whaingaroan); x 450; specimen measures 105 x 92 μm

Figure 4-6 Sample J42/f489, slide L23124/SM010; Hampden Formation, Hampden Beach Section (Bortonian); x 425; specimen measures 100 x 97 μm

Spiniferites ramosus* subsp. *gracilis

Figure 7-8 Sample I43/f089, slide L16337/SM066B; Burnside Formation, Puketeraki Core (Bortonian); x 700; specimen measures 60 x 60 μm

Figure 9 Sample I43/f093, slide L16341/SM006; Burnside Formation, Puketeraki Core (Bortonian); x 775; specimen measures 53 x 55 μm

Spiniferites* aff. *mirabilis

Figure 10-12 Sample I43/f093, slide L16341/1-1269-068; Burnside Formation, Puketeraki Core (Bortonian); x 525; specimen measures 91 x 79 μm

Plate 27

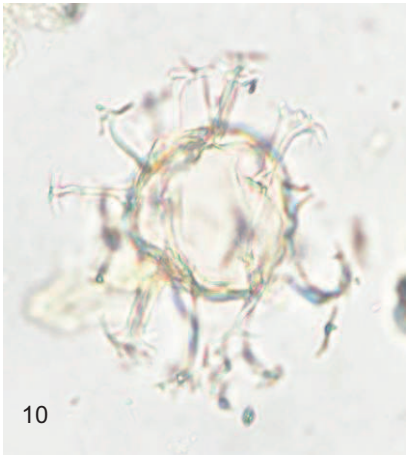
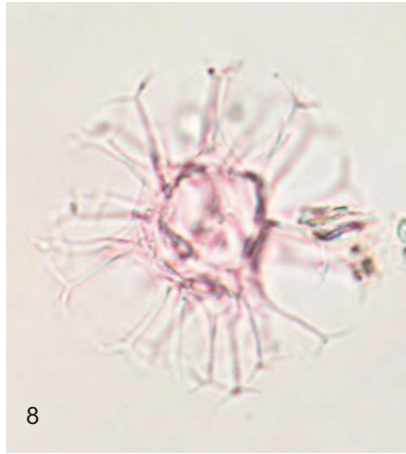
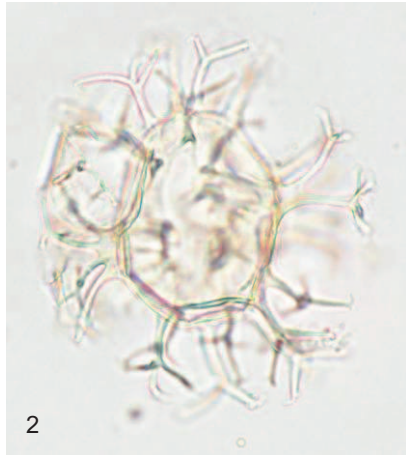


Plate 28

Achomosphaera alcornu

Figure 1-6 Sample I43/f093, slide L16341/SM147; Burnside Formation, Puketeraki Core (Bortonian);
x 500; specimen measures 95 x 75 μm

Hafniasphaera ?septata

Figure 7-9 Sample U24/f419, slide L23127/SM082; Wanstead, Te Uri Stream (Porangan); x 675;
specimen measures 70 x 62 μm

Hystrihostrogylon membraniphorum

Figure 10-12 Sample I43/f093, slide L16341/SM053; Burnside Formation, Puketeraki Core (Bortonian);
x 525; specimen measures 80 x 80 μm

Plate 28

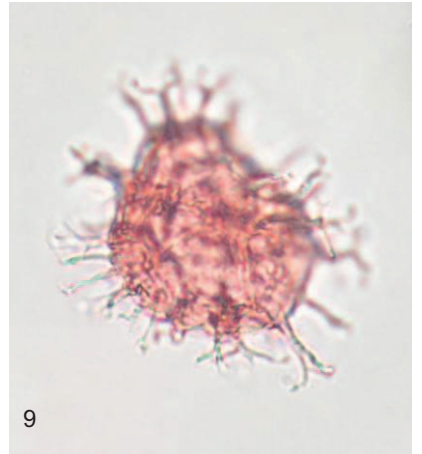
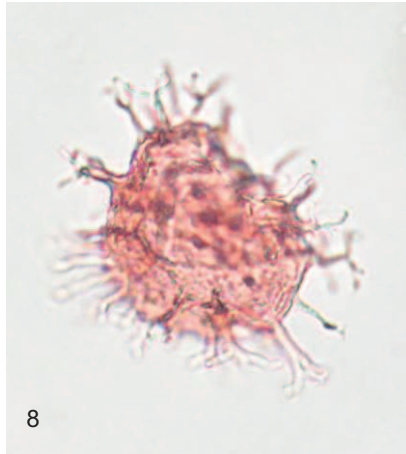
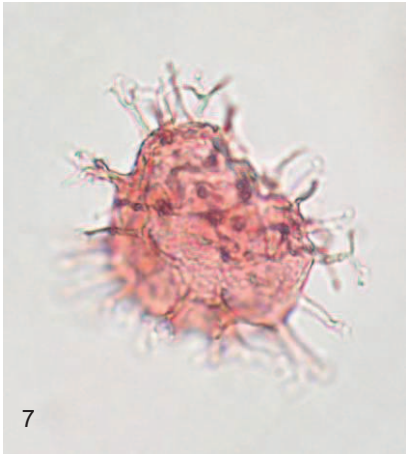
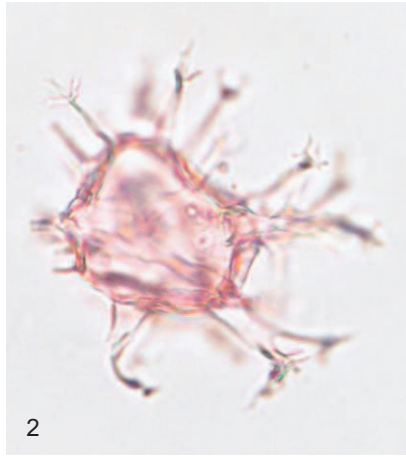
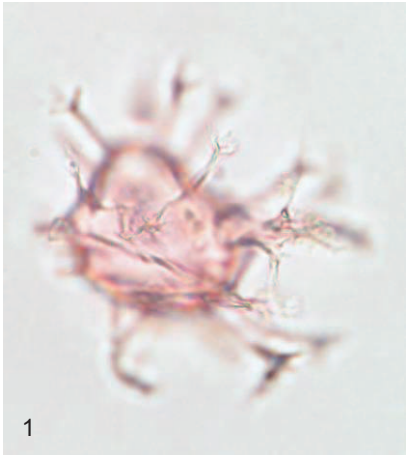


Plate 29

Nematosphaeropsis balcombiana

Figure 1-3 Sample J42/f096, slide L10951/SM044; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 39 x 40 μm

Figure 4-6 Sample J42/f096, slide L10951/SM047; Totara Limestone, Kakanui River (early Whaingaroan); x 925; specimen measures 47 x 45 μm

Rottnestia borussica

Figure 7-12 Sample I43/f093, slide L16341/SM115; Burnside Formation, Puketeraki Core (Bortonian); x 525; specimen measures 90 x 54 μm

Plate 29

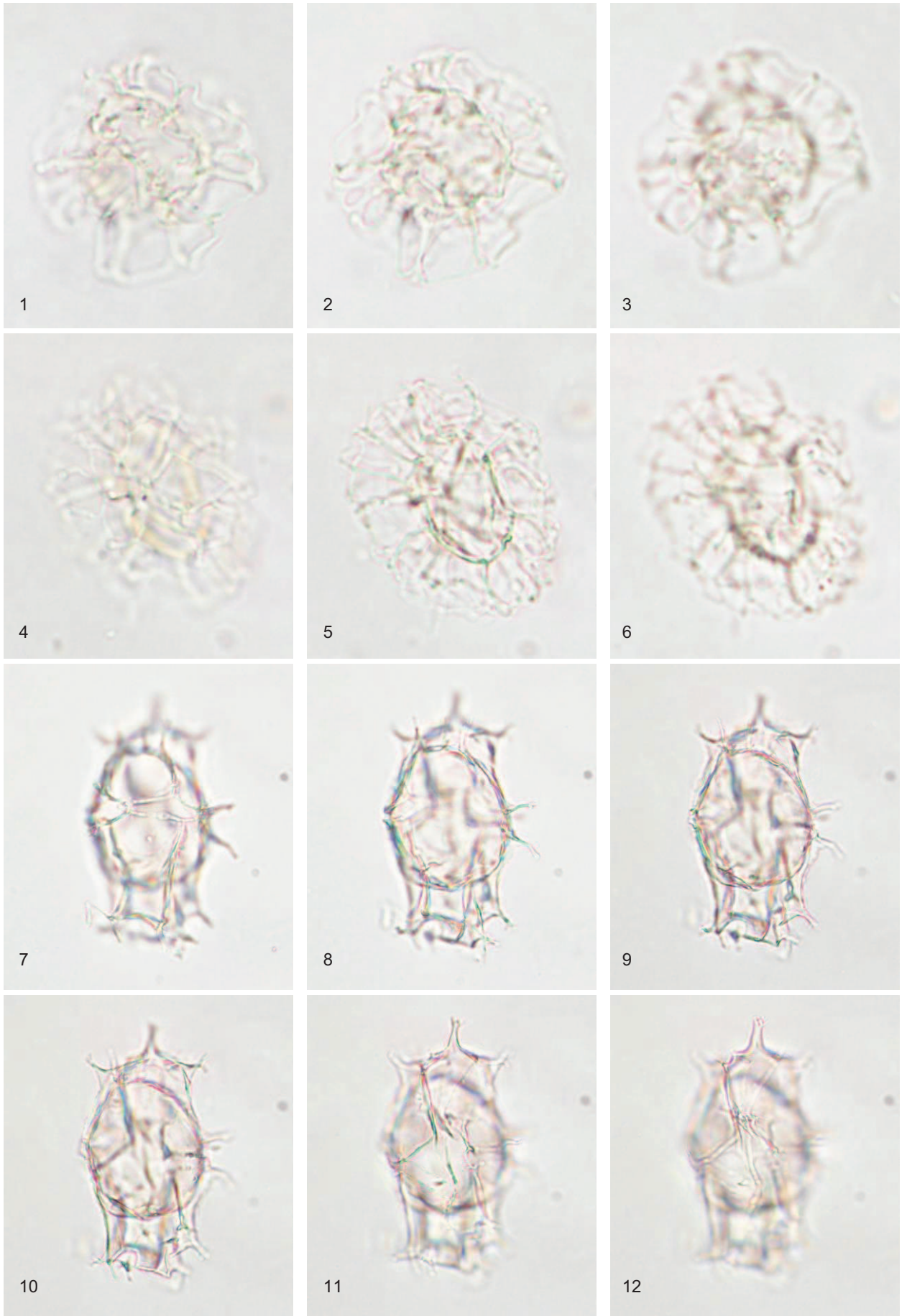


Plate 30

?*Cannosphaeropsis* sp. 1

Figure 1-3 Sample I43/f093, slide L16341/SM015; Burnside Formation, Puketeraki Core (Bortonian); x 800; specimen measures 59 x 53 μ m

Corrudinium incompositum

Figure 4-6 Sample K29/f116, slide L11052/SM4890; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 925; specimen measures 51 x 42 μ m

Corrudinium bujakii

Figure 7-9 Sample I43/f090, slide L16338/SM053; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 32 x 33 μ m

Corrudinium eyrense

Figure 10-12 Sample L34/f7538, slide L06997/SM2572; View Hill Volcanics, Upper Eyre River (Mangaorapan); x 800; specimen measures 53 x 53 μ m

Plate 30

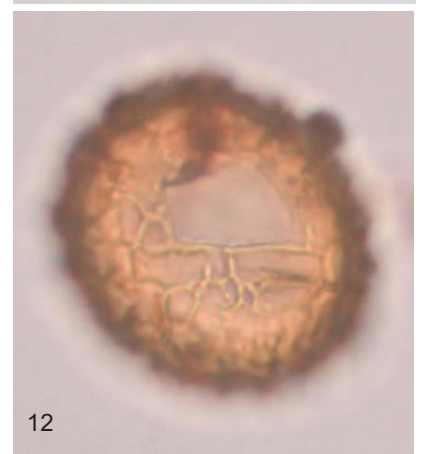
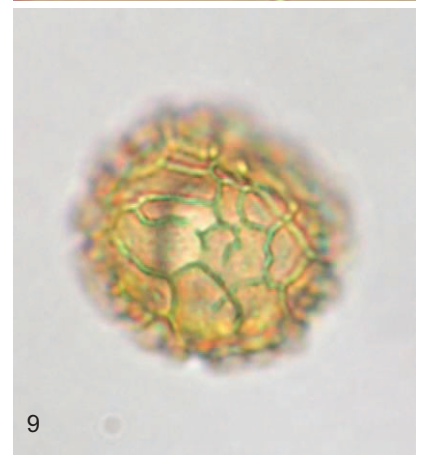


Plate 31

Corrudinium eyrense

Figure 1-3 Sample L34/f7538, slide L06997/SM2572; View Hill Volcanics, Upper Eyre River (Mangaorapan); x 800; specimen measures 53 x 53 μm

Corrudinium obscurum

Figure 5-6, Sample J42/f299, slide L23129/SM010; Hampden Formation, Hampden Beach Section
8-9 (Porangan); x 775; specimen measures 55 x 55 μm

Corrudinium otagoense

Figure 4, 7, Sample I43/f089, slide L16337/SM117; Burnside Formation, Puketeraki Core (Bortonian);
10 x 800; specimen measures 52 x 53 μm

Figure 11-12 Sample U24/f419, slide L23127/SM012; Wanstead, Te Uri Stream (Porangan); x 775;
specimen measures 56 x 55 μm

Plate 31

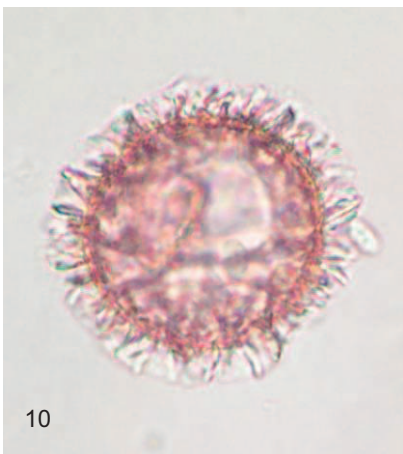
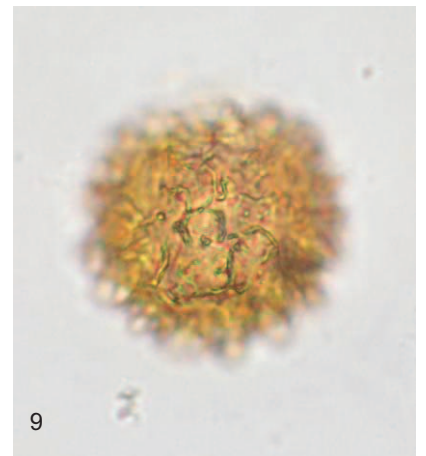
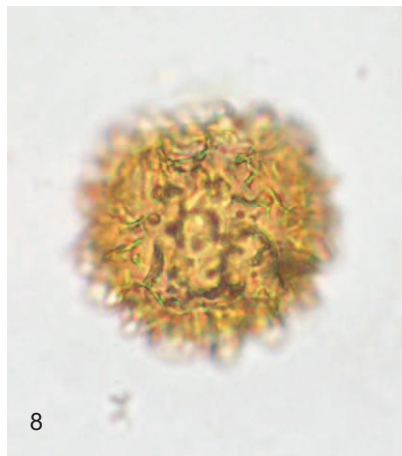
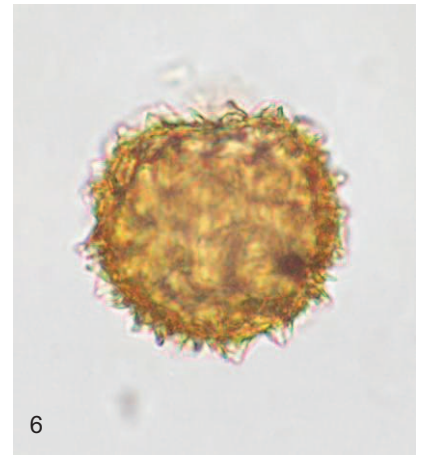
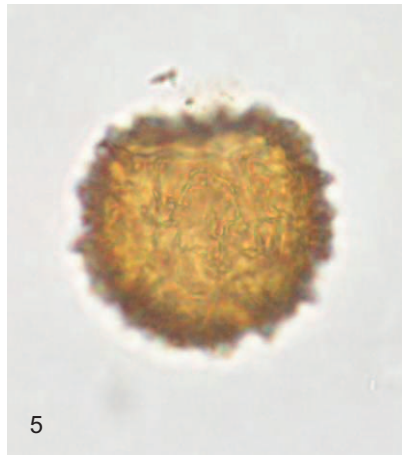


Plate 32

Corrudinium otagoense

Figure 1-3 Sample U24/f419, slide L23127/SM012; Wanstead, Te Uri Stream (Porangan); x 775; specimen measures 56 x 55 μm

Corrudinium regulare

Figure 4-6 Sample I44/f080, slide L08947/SM4886; Burnside Formation, Burnside Marl Pit (Bortonian)

Figure 7 Sample I44/f080, slide L08947/SM4885; Burnside Formation, Burnside Marl Pit (Bortonian); x 825; specimen measures 51 x 51 μm

Figure 8-9 Sample I44/f080, slide L08947/SM4887; Burnside Formation, Burnside Marl Pit (Bortonian)

Impagidium dispertitum

Figure 10-12 Sample U24/f417, slide L23125/SM022; Wanstead, Te Uri Stream (Porangan); specimen measures 38 x 36 μm

Plate 32

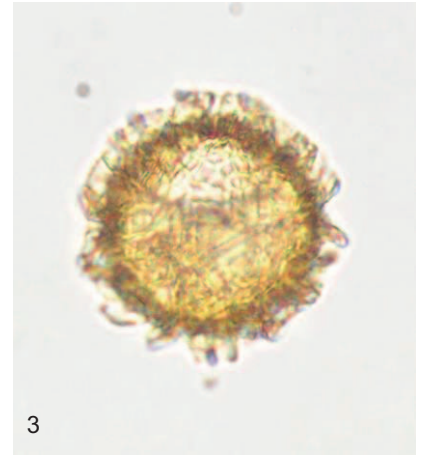
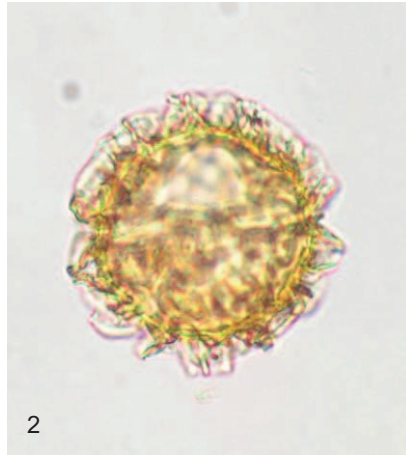


Plate 33

Impagidinium victorianum

Figure 1-3 Sample J42/f096, slide L10951/SM2955; Totara Limestone, Kakanui River (early Whaingaroan); x 550; specimen measures 82 x 78 μm

Figure 4-6 Sample J42/f096, slide L10951/SM2956; Totara Limestone, Kakanui River (early Whaingaroan); x 575; specimen measures 82 x 72 μm

Figure 7-9 Sample J42/f096, slide L10951/SM110; Totara Limestone, Kakanui River (early Whaingaroan); x 625; specimen measures 70 x 68 μm

Impagidinium aculeatum

Figure 10-12 Sample I43/f089, slide L16337/SM051; Burnside Formation, Puketeraki Core (Bortonian); x 850; specimen measures 43 x 49 μm

Plate 33

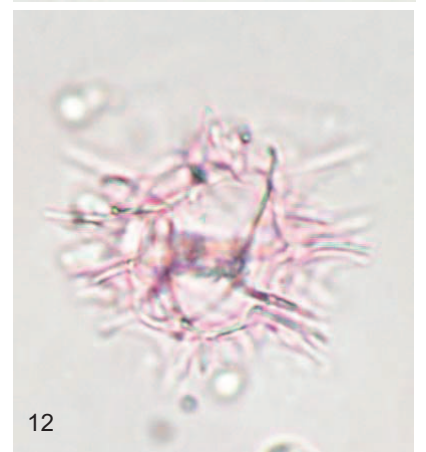
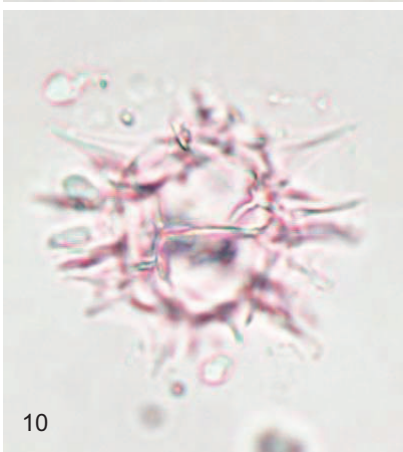
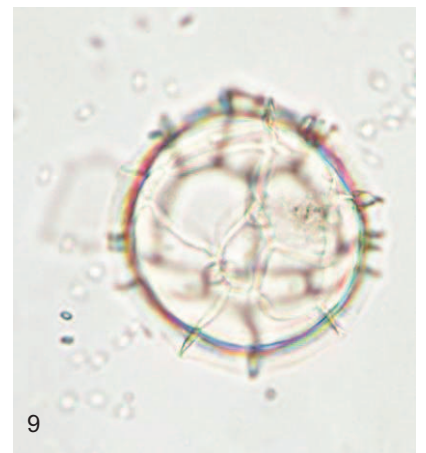
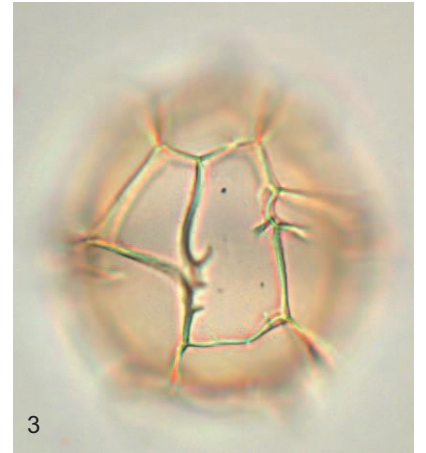
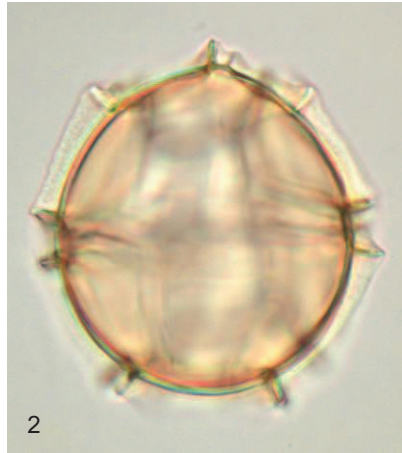


Plate 34

Impagidinium aculeatum

Figure 1-3 Sample I43/f092, slide L16340/1-1340-100; Burnside Formation, Puketeraki Core (Bortonian); x 900; specimen measures 51 x 47 μm

Impagidinium elegans

Figure 4-6 Sample J42/f125, slide L11625/SM014; Totara Limestone, Kakanui River (Runangan-early Whaingaroan); x 375; specimen measures 117 x 112 μm

Figure 7-9 Sample I43/f093, slide L16341/SM020; Burnside Formation, Puketeraki Core (Bortonian); x 425; specimen measures 101 x 100 μm

Figure 10-12 Sample I43/f093, slide L16341/SM093; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 85 x 95 μm

Plate 34

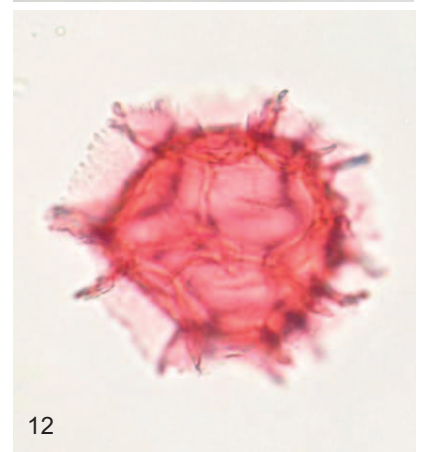
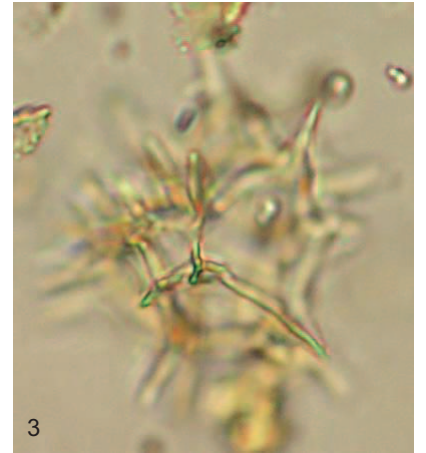
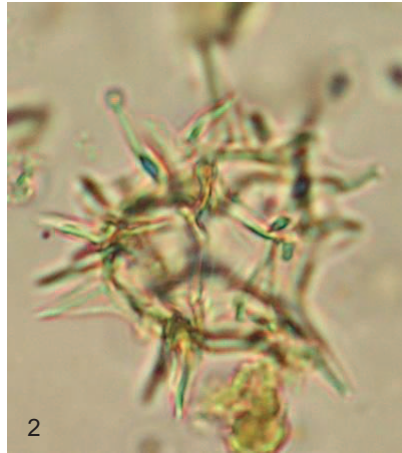


Plate 35

Impagidinium elegans

Figure 1-3 Sample I43/f096, slide L16344/SM027; Burnside Formation, Puketeraki Core (Kaiatan); x 400; specimen measures 113 x 105 μm

Impagidinium maculatum

Figure 4-9 Sample J42/f485, slide L23120/SM038; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 1000; specimen measures 45 x 42 μm

Figure 10-12 Sample U24/f419, slide L23127/SM068; Wanstead, Te Uri Stream (Porangan); x 1050; specimen measures 45 x 37 μm

Plate 35

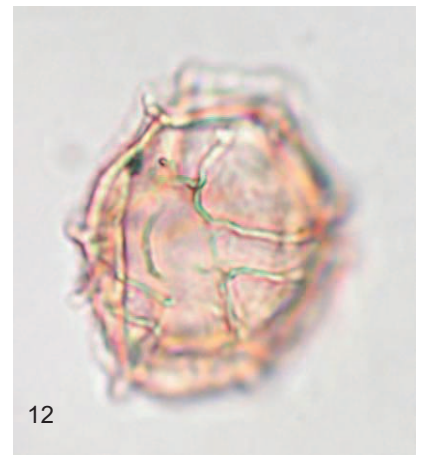
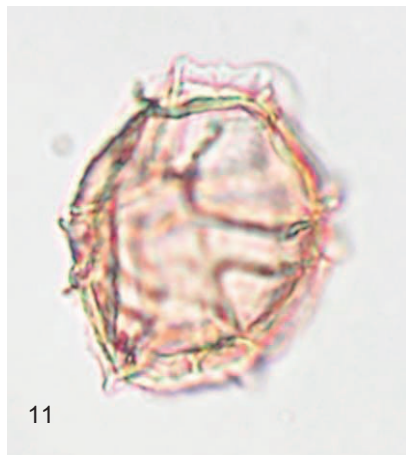
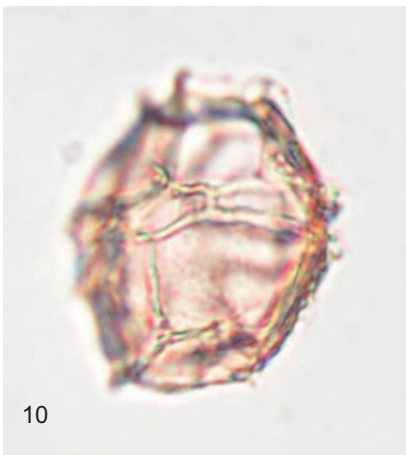
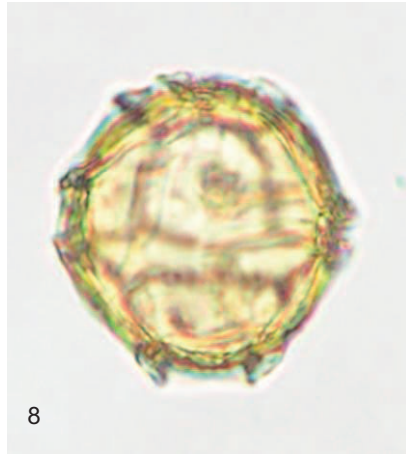
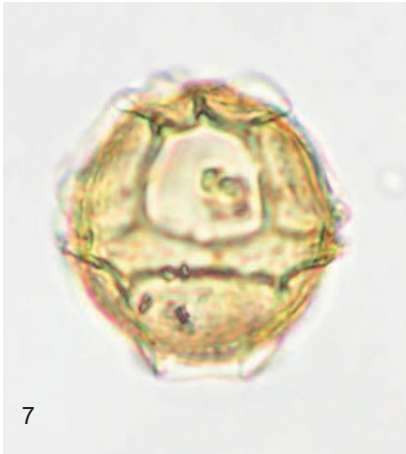


Plate 36

Impagidinium cf. maculatum

Figure 1-3 Sample U24/f419, slide L23127/SM071; Wanstead, Te Uri Stream (Porangan); x 1000; specimen measures 45 x 42 μm

Figure 4-6 Sample J42/f302, slide L23132/SM007; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 675; specimen measures 65 x 63 μm

Impagidinium waipawaense

Figure 7-9 Sample U24/f418, slide L23126/SM025; Wanstead, Te Uri Stream (Porangan); x 625; specimen measures 75 x 60 μm

Pentadinium sp. 1

Figure 10-12 Sample J42/f485, slide L23120/SM037; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 600; specimen measures 62 x 70 μm

Plate 36

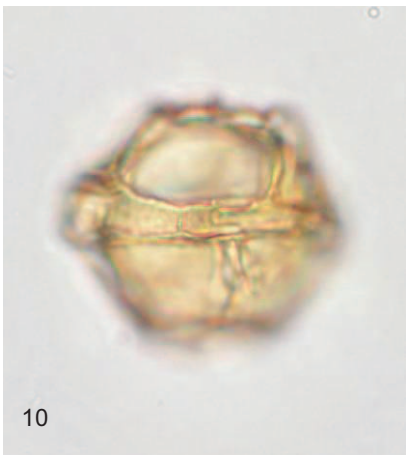
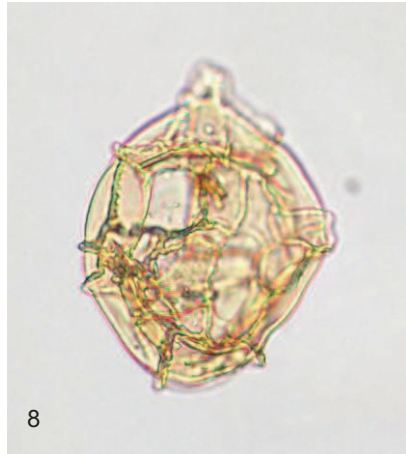
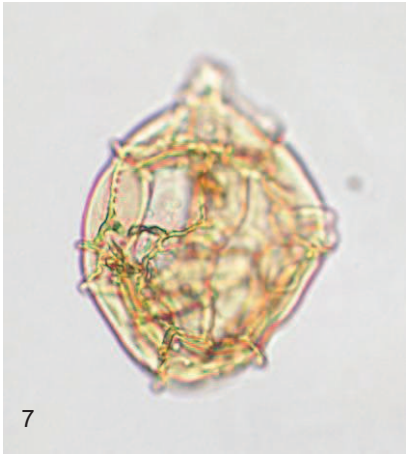


Plate 37

***Pentadinium* sp. 1**

Figure 1-3 Sample J42/f485, slide L23120/SM037; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 600; specimen measures 62 x 70 μm

Tectatodinium pellitum

Figure 4-6 Sample J42/f096, slide L10951/SM067; Totara Limestone, Kakanui River (early Whaingaroan); x 1050; specimen measures 43 x 40 μm

Figure 7-9 Sample J42/f096, slide L10951/SM065; Totara Limestone, Kakanui River (early Whaingaroan); x 800; specimen measures 48 x 52 μm

***Tectatodinium* sp. 1**

Figure 10-12 Sample J42/f098, slide L10953/SM006; Totara Limestone, Kakanui River (Runangan); x 700; specimen measures 60 x 60 μm

Plate 37

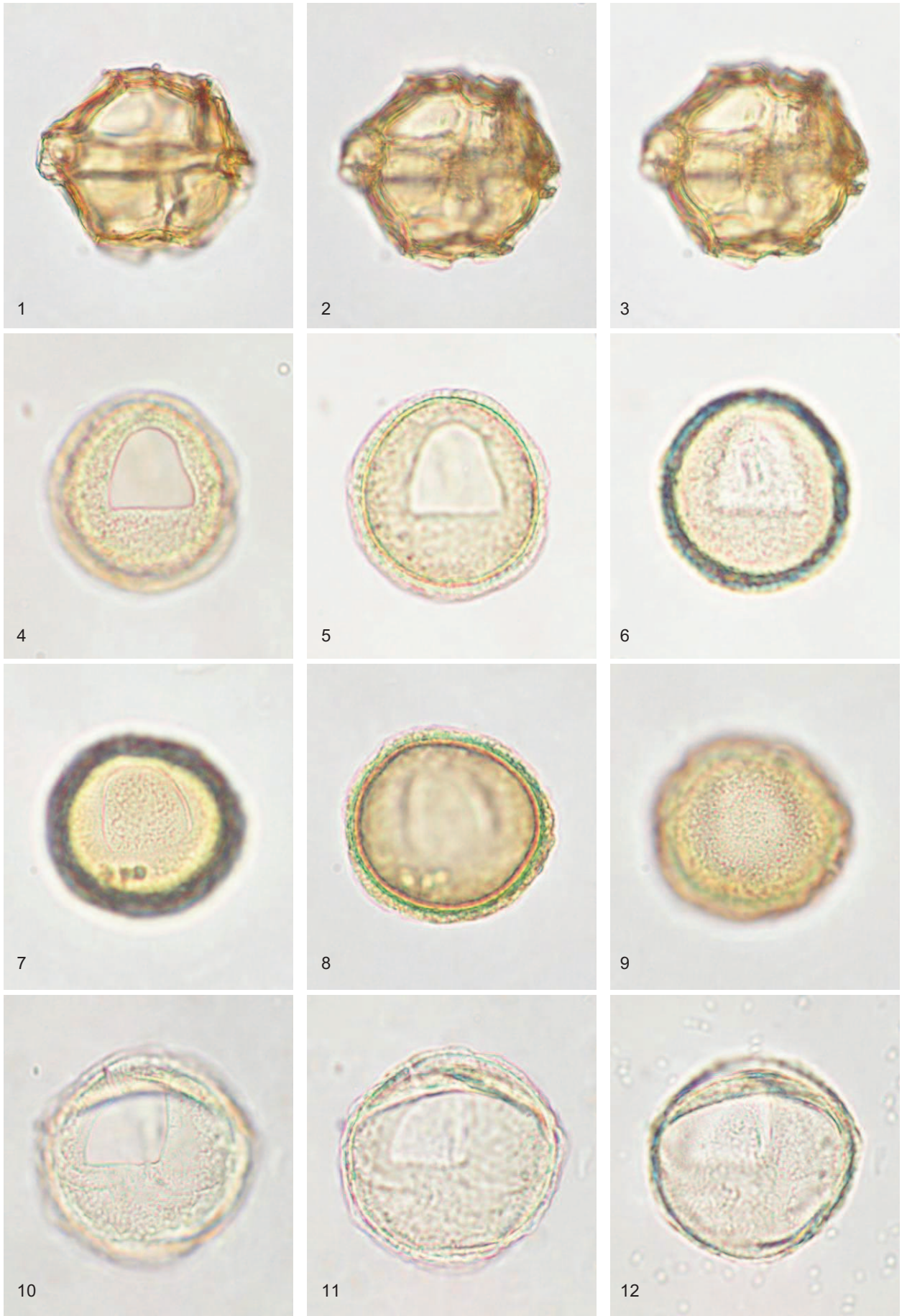


Plate 38

***Tectatodinium* sp. 2**

Figure 1-3 Sample J42/f098, slide L10953/SM010; Totara Limestone, Kakanui River (Runangan); x 1150; specimen measures 41 x 30 μm

Figure 4-6 Sample J42/f098, slide L10953/SM009; Totara Limestone, Kakanui River (Runangan); specimen measures 38 x 32 μm

***Filisphaera* sp. 3**

Figure 7-9 Sample J42/f098, slide L10953/SM011; Totara Limestone, Kakanui River (Runangan); specimen measures 38 x 36 μm

'*Apteodinium*' *australiense*

Figure 10-12 Sample J42/f096, slide L10951/SM2958; Totara Limestone, Kakanui River (early Whaingaroan); x 450; specimen measures 94 x 91 μm

Plate 38



Plate 39

'*Apteodinium*' ?*tenuitabulatum*

Figure 1-4 Sample I43/f089, slide L16337/SM087A; Burnside Formation, Puketeraki Core (Bortonian); x 575; specimen measures 73 x 73 μm

Figure 5-6 Sample I43/f090, slide L16338/SM055; Burnside Formation, Puketeraki Core (Bortonian); x 575; specimen measures 70 x 74 μm

Figure 7-9 Sample I43/f090, slide L16338/SM054; Burnside Formation, Puketeraki Core (Bortonian); x 675; specimen measures 63 x 63 μm

Achilleodinium biformoides

Figure 10-12 Sample J42/f483, slide L23118/SM026; Kurinui Formation, Hampden Beach Section (Heretaungan); x 425; specimen measures 110 x 88 μm

Plate 39

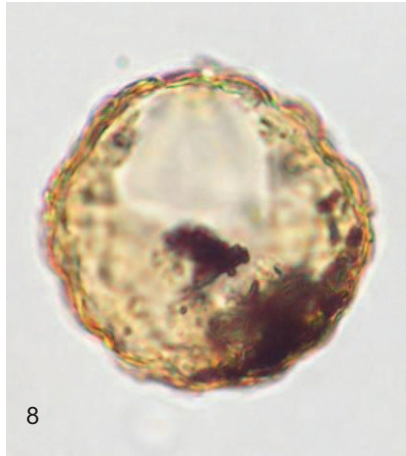


Plate 40

Achilleodinium biformoides

Figure 1-3 Sample J42/f483, slide L23118/SM026; Kurinui Formation, Hampden Beach Section (Heretaungan); x 425; specimen measures 110 x 88 μm

Figure 4-6 Sample J42/f483, slide L23118/SM025; Kurinui Formation, Hampden Beach Section (Heretaungan); x 500; specimen measures 80 x 84 μm

Achilleodinium cf. biformoides

Figure 7-9 Sample I44/f240, slide L15506/SM4820; Abbotsford Formation, M26 Core (Heretaungan-Bortonian); x 450; specimen measures 107 x 96 μm

Achilleodinium echinatum

Figure 10-12 Sample J42/f485, slide L23120/SM026; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 425; specimen measures 97 x 100 μm

Plate 40

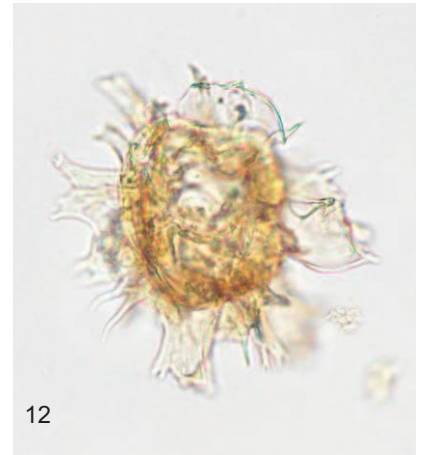
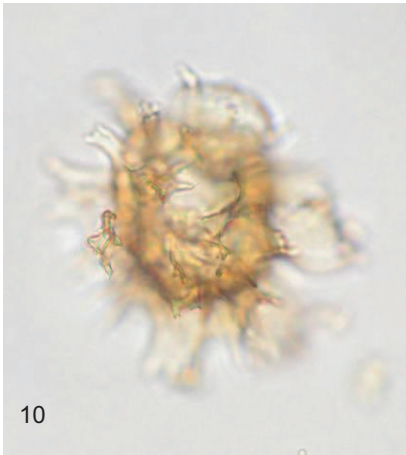


Plate 41

Achilleodinium echinatum

Figure 1-3 Sample J42/f485, slide L23120/SM026; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 425; specimen measures 97 x 100 μm

Achilleodinium improcerum

Figure 4-6 Sample J42/f484, slide L23119/SM020; Kurinui Formation, Hampden Beach Section (Heretaungan); x 650; specimen measures 72 x 55 μm

Figure 7-9 Sample I43/f090, slide L16338/SM4829; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 104 x 88 μm

Figure 10-12 Sample I43/f090, slide L16338/SM4830; Burnside Formation, Puketeraki Core (Bortonian); x 375; specimen measures 126 x 112 μm

Plate 41

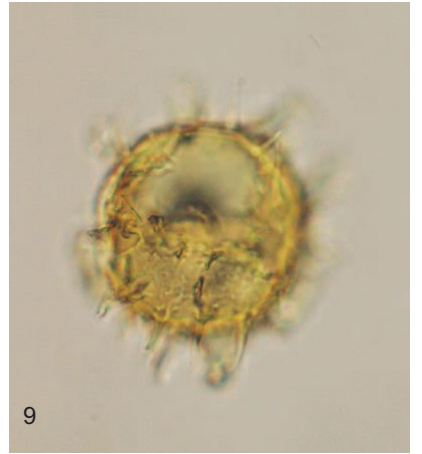
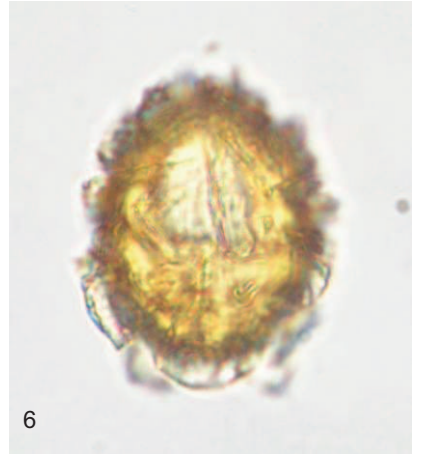
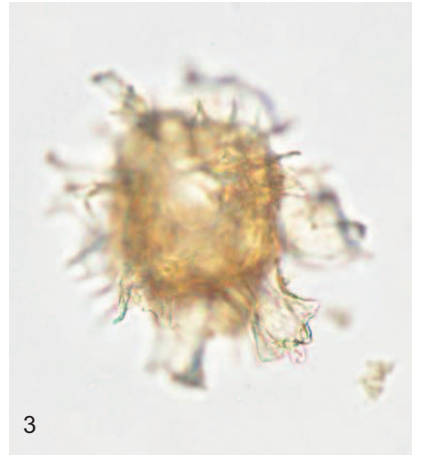


Plate 42

Achilleodinium improcerum

Figure 1-6 Sample I43/f093, slide L16341/SM085; Burnside Formation, Puketeraki Core (Bortonian);
x 450; specimen measures 105 x 96 μm

'*Araneosphaera*' *stephanophora*

Figure 7-10 Sample J42/f486, slide L23121/SM011; ?Hampden Formation, Hampden Beach Section
(Porangan-Bortonian); x 1000; specimen measures 47 x 40 μm

Figure 11-12 Sample J42/f486, slide L23121/SM012A; ?Hampden Formation, Hampden Beach Section
(Porangan-Bortonian); specimen measures 39 x 37 μm

Plate 42

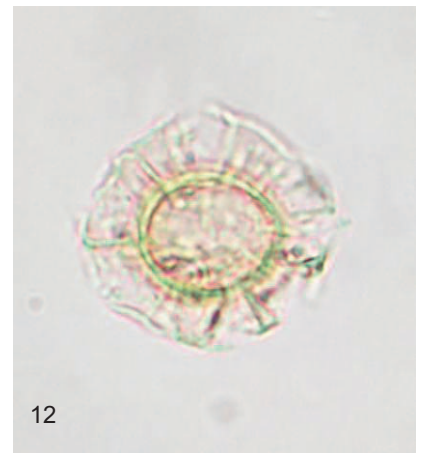
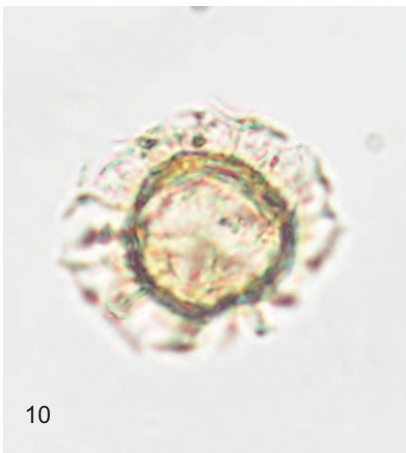


Plate 43

'Araneosphaera' stephanophora

Figure 1-3 Sample I43/f089, slide L16337/SM087B; Burnside Formation, Puketeraki Core (Bortonian);
x 1050; specimen measures 40 x 40 μm

Figure 4-6 Sample I43/f089, slide L16337/SM072B; Burnside Formation, Puketeraki Core (Bortonian);
x 1125; specimen measures 42 x 32 μm

Cordosphaeridium inodes

Figure 7-12 Sample J42/f483, slide L23118/SM022; Kurinui Formation, Hampden Beach Section
(Heretaungan); x 450; specimen measures 100 x 95 μm

Plate 43

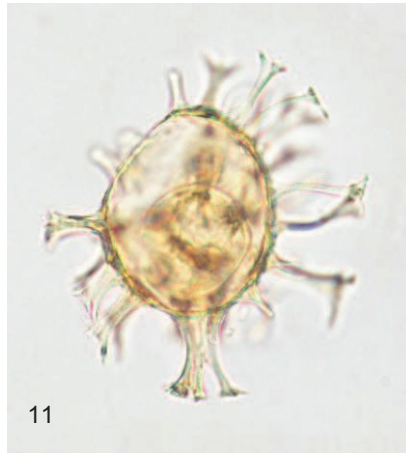
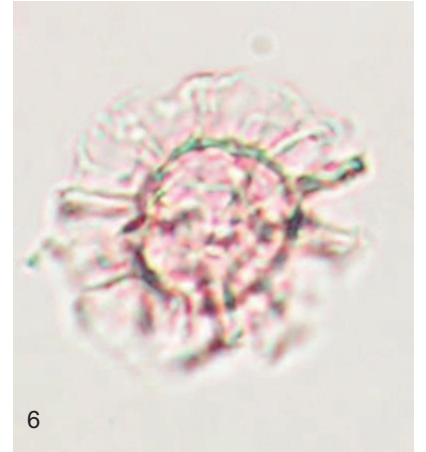
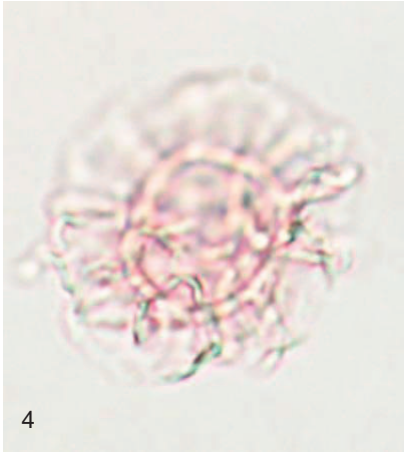


Plate 44

Cordosphaeridium inodes

Figure 1-3 Sample J42/f301, slide L23131/SM016; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 500; specimen measures 85 x 84 μm

Cordosphaeridium gracile

Figure 4-5 Sample I43/f096, slide L16344/SM016; Burnside Formation, Puketeraki Core (Kaiatan); x 250; specimen measures 143 x 160 μm

Figure 6 Sample I43/f093, slide L16341/SM037; Burnside Formation, Puketeraki Core (Bortonian); x 300; specimen measures 163 x 117 μm

Cordosphaeridium fibrospinosum

Figure 7-9 Sample I43/f090, slide L16338/SM039; Burnside Formation, Puketeraki Core (Bortonian); x 400; specimen measures 115 x 105 μm

Figure 10-12 Sample I43/f093, slide L16341/SM089; Burnside Formation, Puketeraki Core (Bortonian); x 350; specimen measures 85 x 120 μm

Plate 44

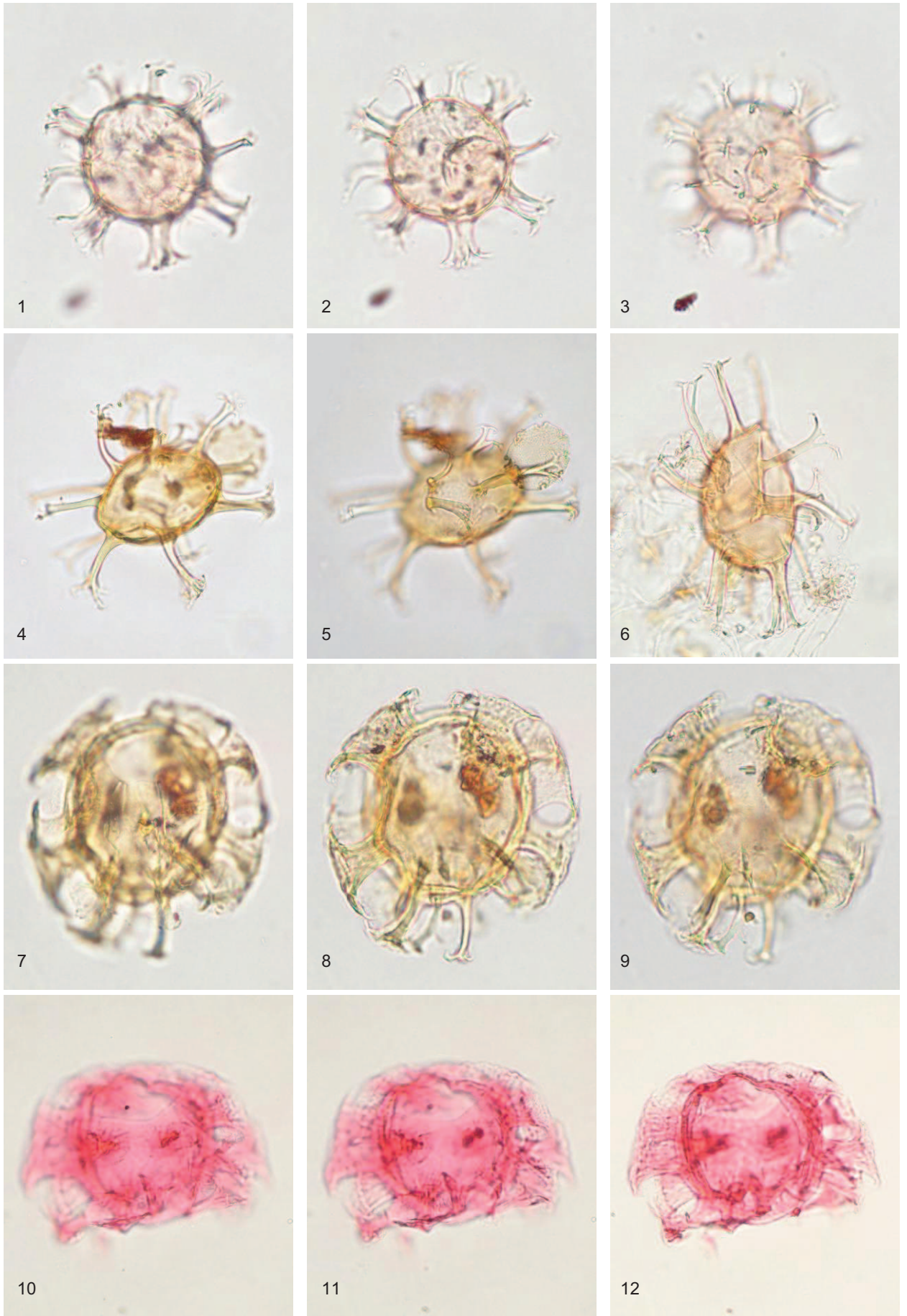


Plate 45

Cordosphaeridium aff. funiculatum

- Figure 1-6 Sample K29/f114, slide L11050/SM009; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 350; specimen measures 125 x 122 μm
- Figure 7-8 Sample K29/f114, slide L11050/SM005; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 225; specimen measures 175 x 177 μm
- Figure 9 Sample K29/f114, slide L11050/SM010; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan)
- Figure 10-12 Sample K29/f114, slide L11050/SM039; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 375; specimen measures 125 x 112 μm

Plate 45

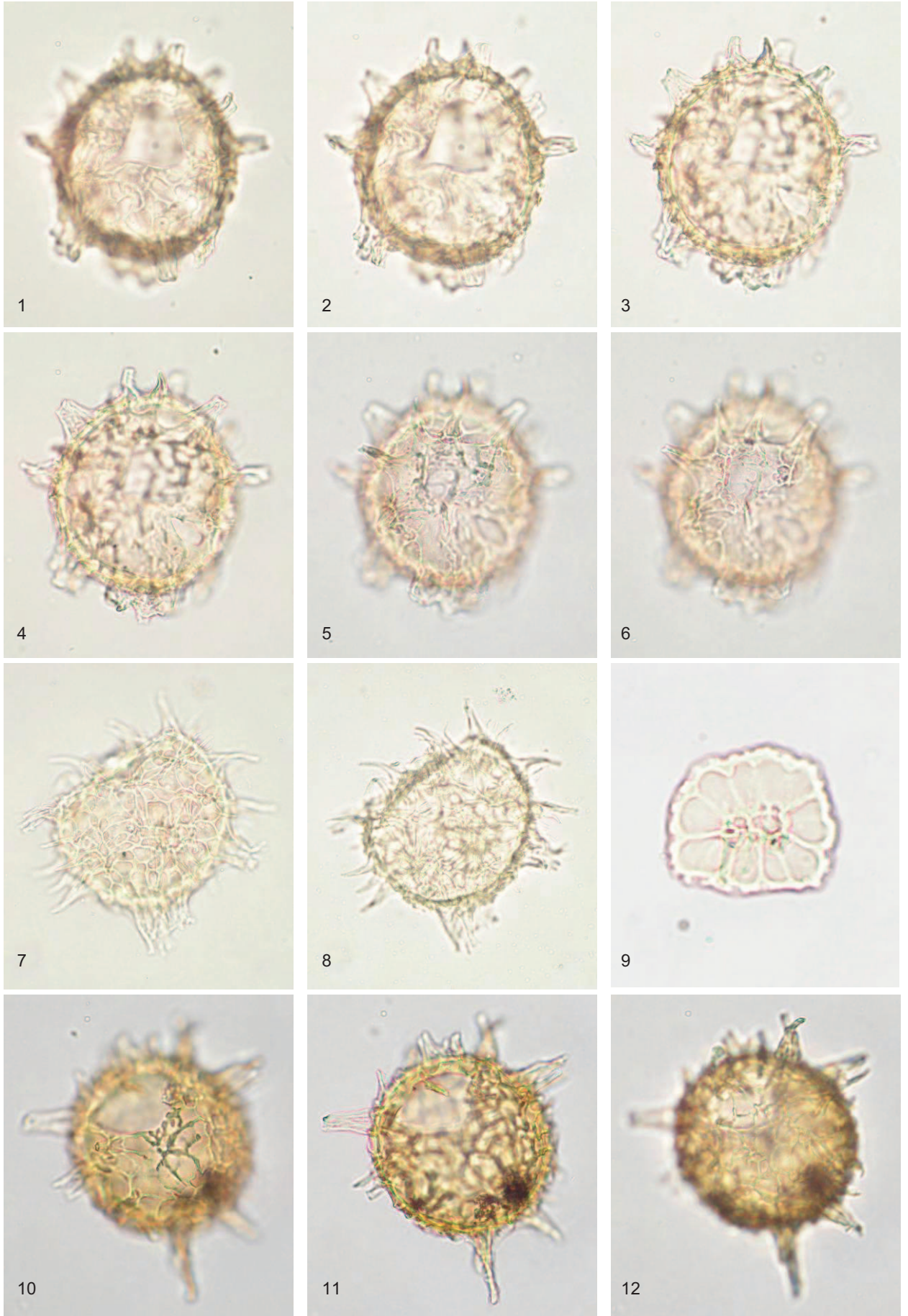


Plate 46

Cordosphaeridium minimum

Figure 1-2 Sample J42/f300, slide L23130/SM027; Hampden Formation, Hampden Beach Section (Porangan); specimen measures 34 x 33 μm

Figure 3 Sample J42/f485, slide L23120/SM029B; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 1100; specimen measures 40 x 38 μm

Figure 4-6 Sample J42/f483, slide L23118/SM024; Kurinui Formation, Hampden Beach Section (Heretaungan); specimen measures 38 x 37 μm

Figure 7-9 Sample I43/f090, slide L16338/SM040; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 37 x 40 μm

Turbiosphaera filosa

Figure 10-12 Sample U24/f418, slide L23126/SM017B; Wanstead, Te Uri Stream (Porangan); x 350; specimen measures 137 x 110 μm

Plate 46

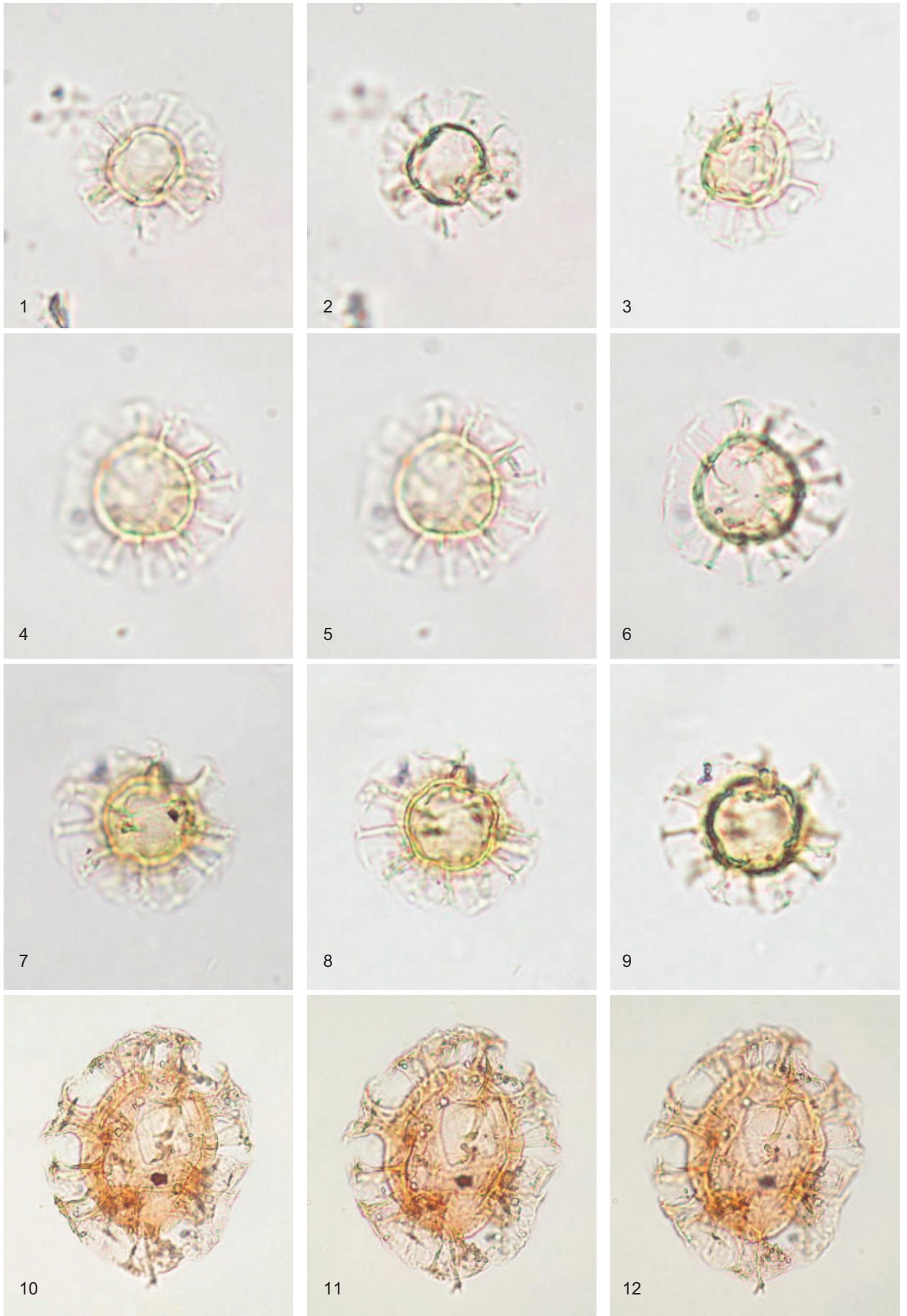


Plate 47

Turbiosphaera filosa

Figure 1 Sample U24/f418, slide L23126/SM017B; Wanstead, Te Uri Stream (Porangan); x 350; specimen measures 137 x 110 μm

Figure 2-3 Sample U24/f418, slide L23126/SM021; Wanstead, Te Uri Stream (Porangan); x 425; specimen measures 109 x 98 μm

Turbiosphaera sp. 1

Figure 4-12 Sample J42/f485, slide L23120/SM030; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 425; specimen measures 102 x 97 μm

Plate 47

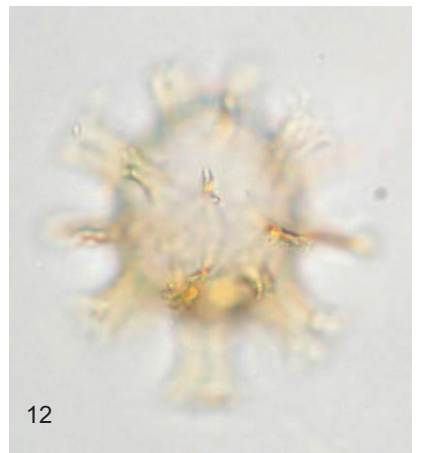
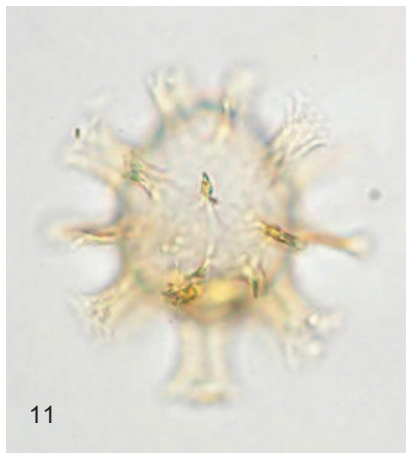
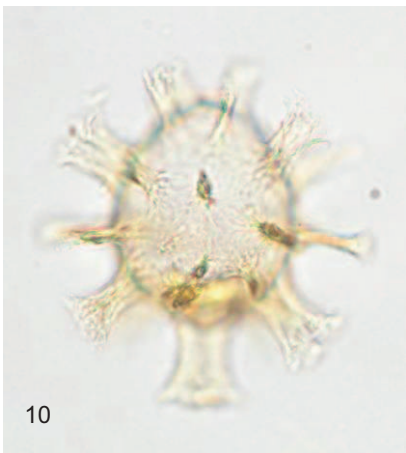
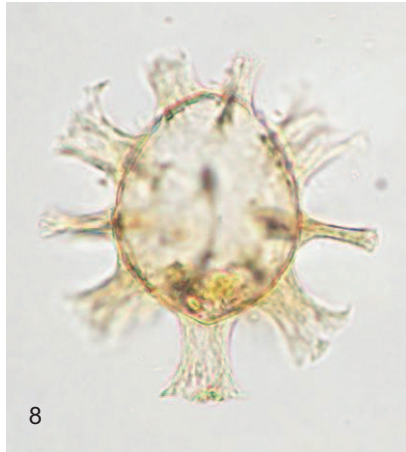
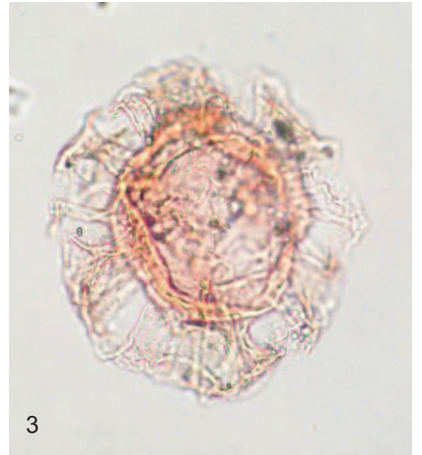
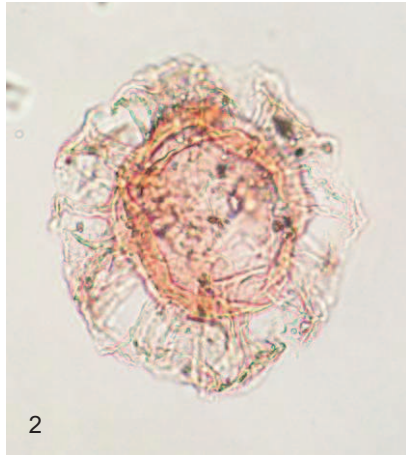


Plate 48

Disphaerogena morgansii

Figure 1-6 Sample J42/f486, slide L23121/SM015; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 425; specimen measures 103 x 99 μm

Figure 7-9 Sample J42/f300, slide L23130/SM016; Hampden Formation, Hampden Beach Section (Porangan); x 425; specimen measures 103 x 97 μm

Figure 10-12 Sample J42/f485, slide L23120/SM027; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 425; specimen measures 110 x 85 μm

Plate 48

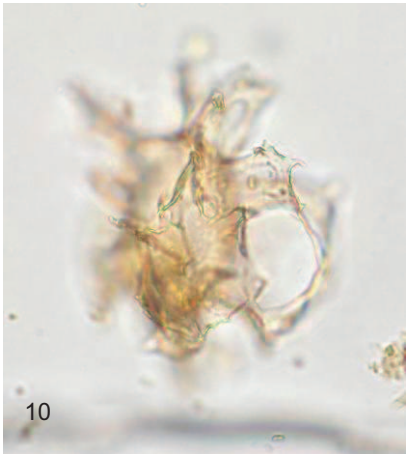
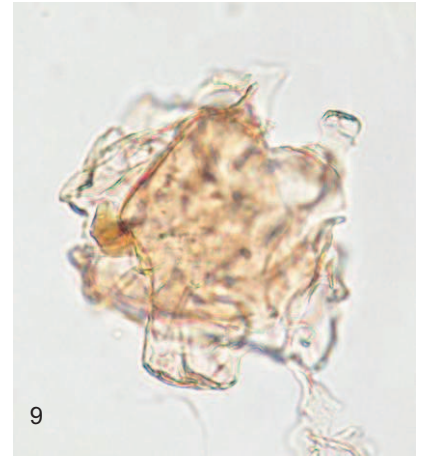
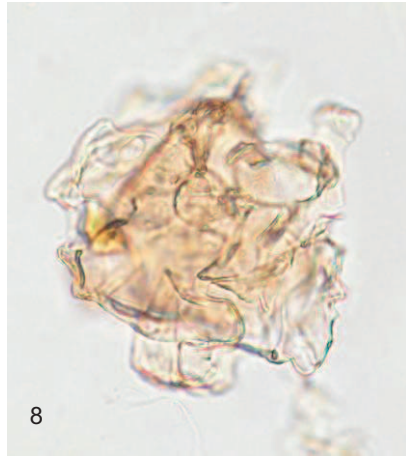
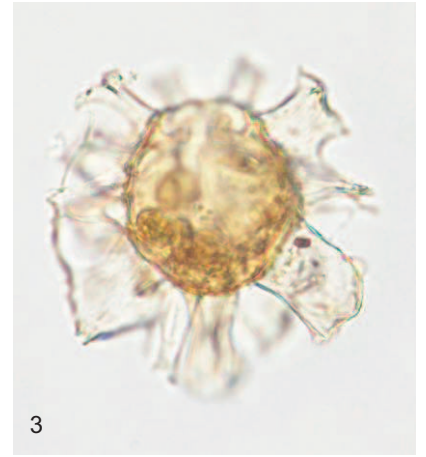


Plate 49

Hystrichokolpoma cinctum

Figure 1-3 Sample K29/f101, slide L11037/SM002; Kaiata Mudstone, Cape Foulwind Section (Runangan)

Hystrichokolpoma rigaudiae

Figure 4-6 Sample J42/f125, slide L11625/SM004; Totara Limestone, Kakanui River (Runangan-early Whaingaroan); x 525; specimen measures 85 x 79 μm

Figure 7-9 Sample K29/f114, slide L11050/SM002; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 450; specimen measures 105 x 83 μm

Hystrichokolpoma sp. 3

Figure 10-12 Sample I43/f093, slide L16341/SM092; Burnside Formation, Puketeraki Core (Bortonian); x 750; specimen measures 55 x 56 μm

Plate 49

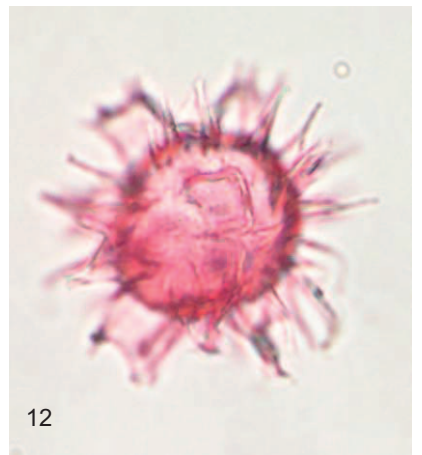


Plate 50

Hystrichokolpoma sp. 3

Figure 1-3 Sample I43/f093, slide L16341/SM158; Burnside Formation, Puketeraki Core (Bortonian);
x 450; specimen measures 58 x 94 μm

Hystrichokolpoma spinosum

Figure 4-9 Sample J42/f486, slide L23121/SM013; ?Hampden Formation, Hampden Beach Section
(Porangan-Bortonian); x 600; specimen measures 58 x 71 μm

Figure 10-12 Sample J42/f483, slide L23118/SM019; Kurinui Formation, Hampden Beach Section
(Heretaungan); x 650; specimen measures 70 x 65 μm

Plate 50

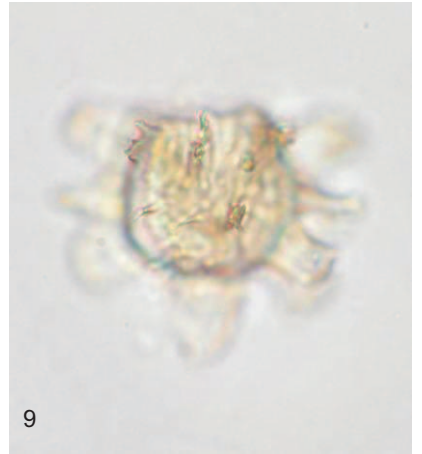
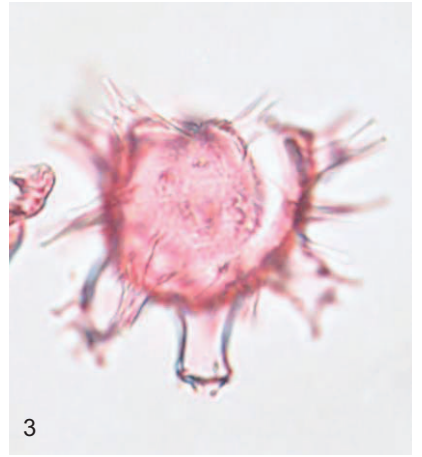


Plate 51

Hystrichokolpoma spinosum

Figure 1-3 Sample J42/f483, slide L23118/SM019; Kurinui Formation, Hampden Beach Section (Heretaungan); x 650; specimen measures 70 x 65 μm

Diphyes colligerum

Figure 4 Sample I43/f093, slide L16341/SM007; Burnside Formation, Puketeraki Core (Bortonian); x 725; specimen measures 64 x 54 μm

Figure 5 Sample I43/f093, slide L16341/SM008A; Burnside Formation, Puketeraki Core (Bortonian); x 600; specimen measures 58 x 69 μm

Figure 6 Sample J42/f483, slide L23118/SM012; Kurinui Formation, Hampden Beach Section (Heretaungan); x 650; specimen measures 58 x 65 μm

Figure 7-9 Sample J42/f302, slide L23132/SM023; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 675; specimen measures 61 x 62 μm

Diphyes aff. colligerum

Figure 10-12 Sample I43/f093, slide L16341/SM171; Burnside Formation, Puketeraki Core (Bortonian); x 600; specimen measures 52 x 69 μm

Plate 51

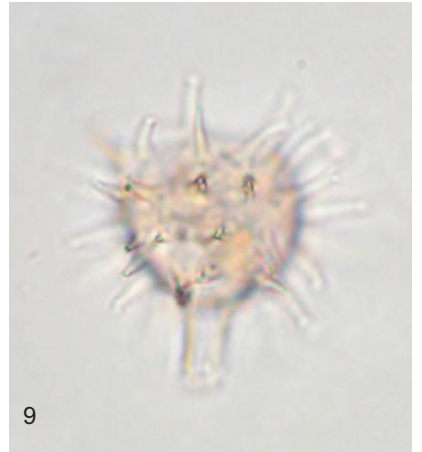
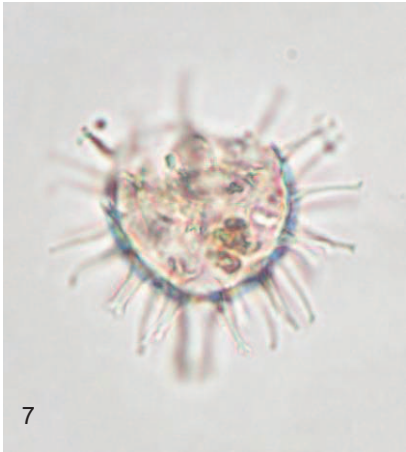
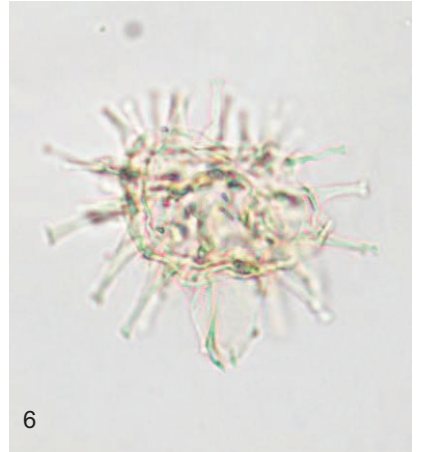
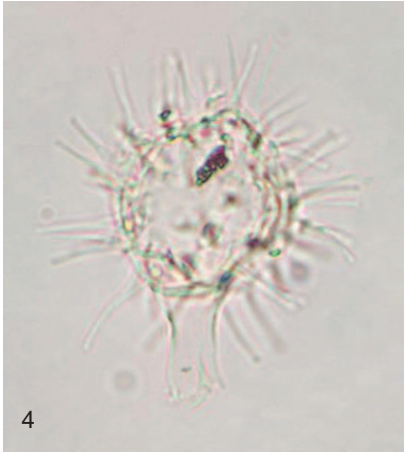
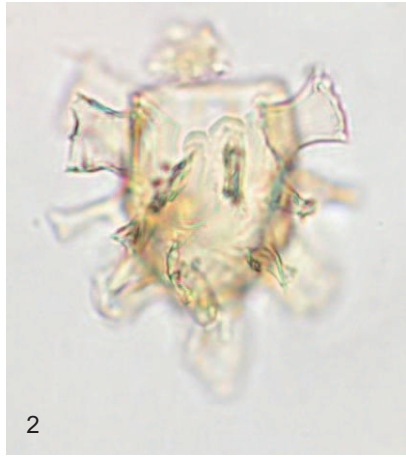


Plate 52

Diphyes aff. colligerum

Figure 1-3 Sample I43/f093, slide L16341/SM171; Burnside Formation, Puketeraki Core (Bortonian); x 600; specimen measures 52 x 69 μm

Figure 4-9 Sample I43/f093, slide L16341/1-1424-176; Burnside Formation, Puketeraki Core (Bortonian); x 725; specimen measures 62 x 58 μm

Diphyes ficusoides

Figure 10-12 Sample J41/f8914, slide L04979/SM1085; Waiareka Volcanics, Jacksons Paddock (Kaiatan-Runangan); x 550; specimen measures 69 x 75 μm

Plate 52

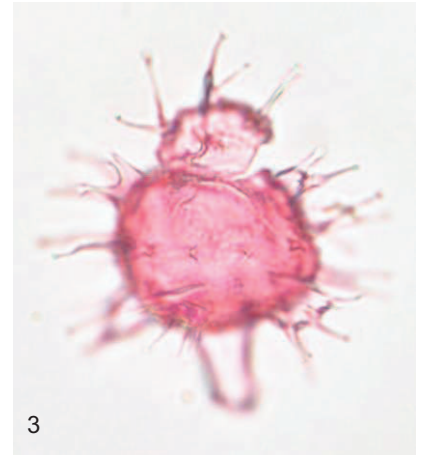


Plate 53

Diphyes brevispinum

Figure 1-3 Sample I43/f096, slide L16344/1-1329-020; Burnside Formation, Puketeraki Core (Kaiatan);
x 775; specimen measures 60 x 55 μm

Lingulodinium ?machaerophorum

Figure 4-9 Sample I43/f093, slide L16341/SM168; Burnside Formation, Puketeraki Core (Bortonian);
x 575; specimen measures 78 x 73 μm

Operculodinium ?centrocarpum

Figure 10-12 Sample J42/f096, slide L10951/SM074; Totara Limestone, Kakanui River (early
Whaingaroan); x 675; specimen measures 60 x 62 μm

Plate 53

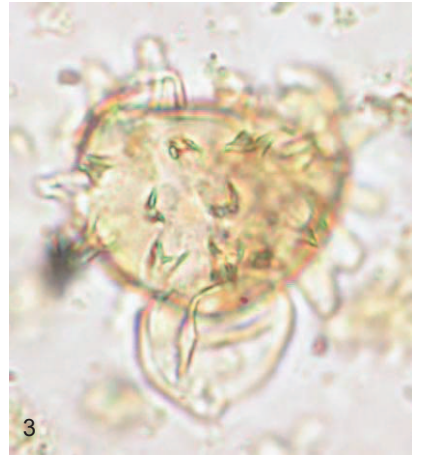
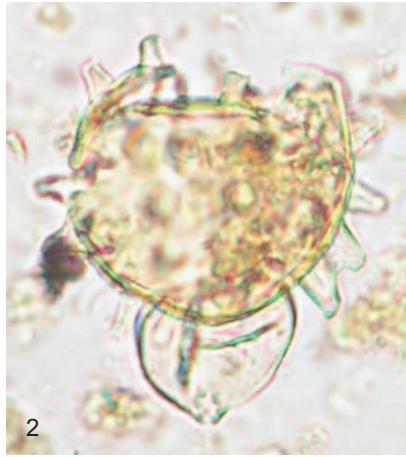
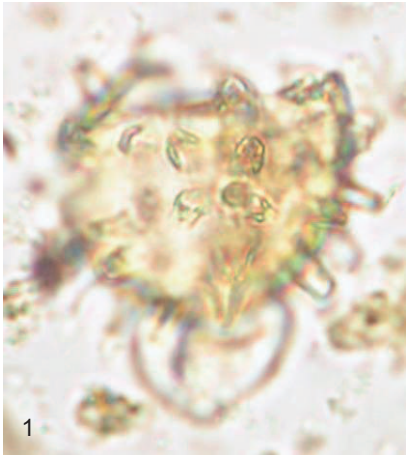


Plate 54

Operculodinium ?centrocarpum

Figure 1-3 Sample J42/f096, slide L10951/SM075; Totara Limestone, Kakanui River (early Whaingaroan); x 675; specimen measures 58 x 63 μm

Operculodinium schioleri

Figure 4-9 Sample K29/f097, slide L10914/SM031; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 325; specimen measures 133 x 127 μm

Figure 10-12 Sample K29/f097, slide L10914/SM027; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 375; specimen measures 116 x 110 μm

Plate 54

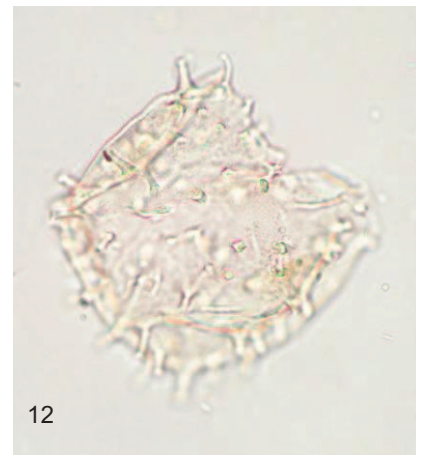
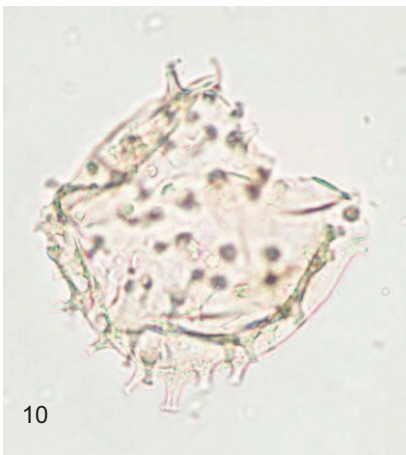
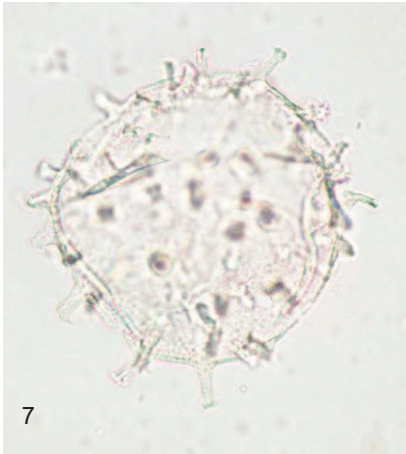
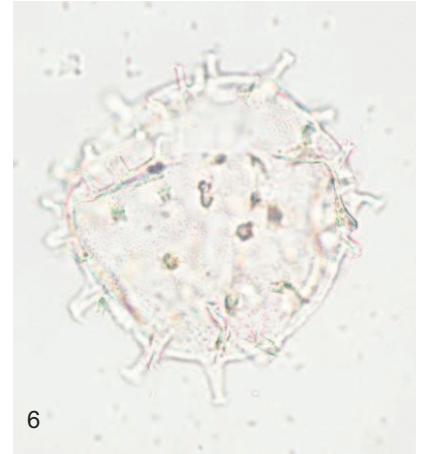
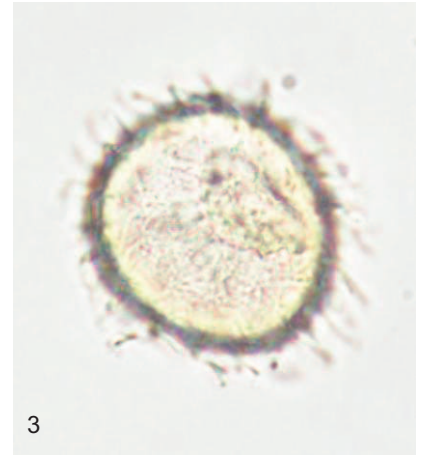
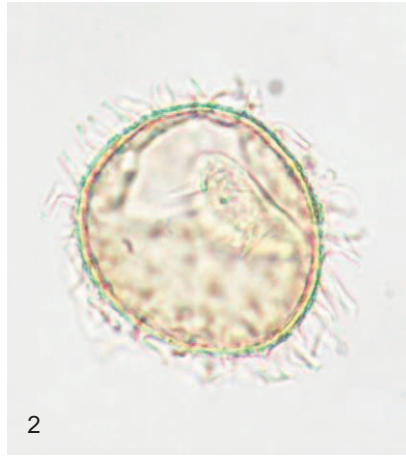


Plate 55

Operculodinium sp. 10

Figure 1-3 Sample K29/f097, slide L10914/SM033; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 350; specimen measures 125 x 122 μm

Operculodinium vulgare

Figure 4-6 Sample I43/f093, slide L16341/SM066; Burnside Formation, Puketeraki Core (Bortonian); x 500; specimen measures 81 x 82 μm

Figure 7-9 Sample K29/f097, slide L10914/SM025; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 300; specimen measures 150 x 135 μm

Operculodinium ?janduchenei

Figure 10-12 Sample J42/f302, slide L23132/SM013; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 850; specimen measures 48 x 49 μm

Plate 55

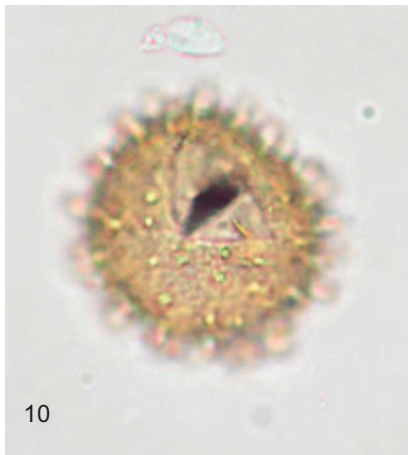
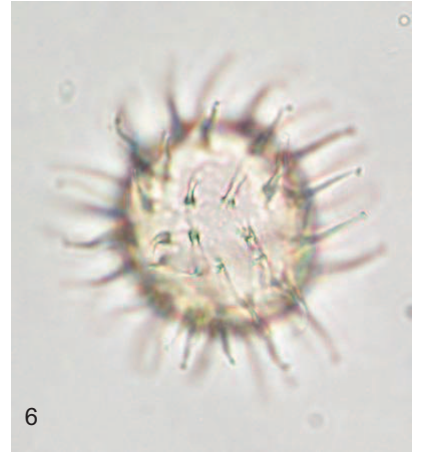


Plate 56

Operculodinium ?janduchenei

Figure 1-2 Sample J42/f302, slide L23132/SM013; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 850; specimen measures 48 x 49 μm

Operculodinium pulcher

Figure 3 Sample I43/f093, slide L16341/SM109; Burnside Formation, Puketeraki Core (Bortonian); x 725; specimen measures 53 x 57 μm

Figure 4-6 Sample I43/f093, slide L16341/SM042; Burnside Formation, Puketeraki Core (Bortonian); x 700; specimen measures 58 x 59 μm

Figure 7-9 Sample I43/f093, slide L16341/SM065; Burnside Formation, Puketeraki Core (Bortonian); x 775; specimen measures 55 x 55 μm

Figure 10-12 Sample I43/f093, slide L16341/SM048; Burnside Formation, Puketeraki Core (Bortonian); x 775; specimen measures 53 x 55 μm

Plate 56

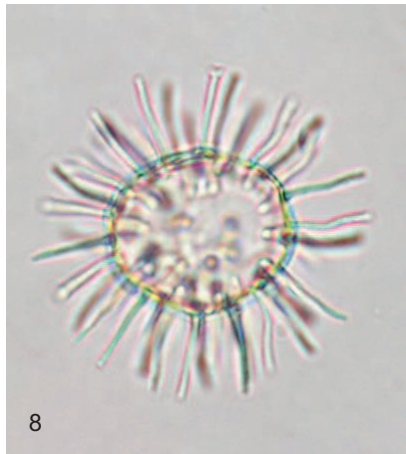
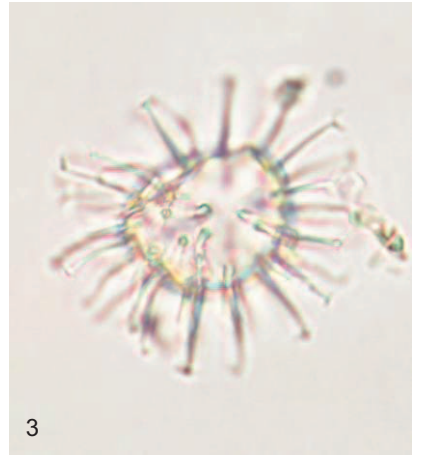
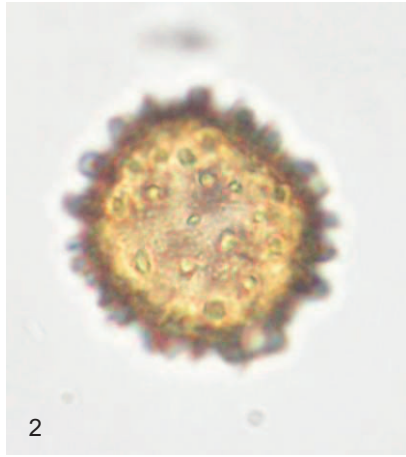


Plate 57

***Operculodinium* sp. 5**

Figure 1-3 Sample U24/f419, slide L23127/SM042; Wanstead, Te Uri Stream (Porangan); x 850;
specimen measures 55 x 45 μm

Figure 4-6 Sample U24/f419, slide L23127/SM043; Wanstead, Te Uri Stream (Porangan); x 800;
specimen measures 51 x 52 μm

***Operculodinium* sp. 7**

Figure 7-12 Sample I43/f092, slide L16340/1-1332-041; Burnside Formation, Puketeraki Core (Bortonian);
x 875; specimen measures 44 x 48 μm

Plate 57

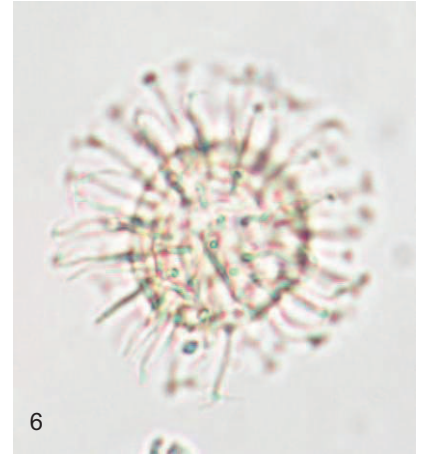
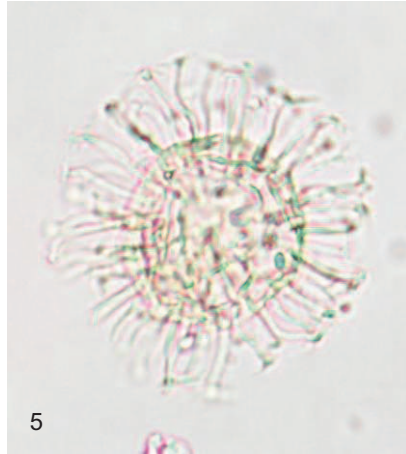


Plate 58

Operculodinium ?xanthium

Figure 1-3 Sample I43/f089, slide L16337/2-1349-101; Burnside Formation, Puketeraki Core (Bortonian); x 775; specimen measures 54 x 54 μm

Operculodinium sp. 3

Figure 4-6 Sample J42/f096, slide L10951/SM076; Totara Limestone, Kakanui River (early Whaingaroan); x 650; specimen measures 70 x 65 μm

Operculodinium sp. 6

Figure 7-9 Sample J42/f483, slide L23118/SM017; Kurinui Formation, Hampden Beach Section (Heretaungan); x 625; specimen measures 63 x 67 μm

Operculodinium crouchii

Figure 10-12 Sample J42/f302, slide L23132/SM019; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 625; specimen measures 75 x 60 μm

Plate 58

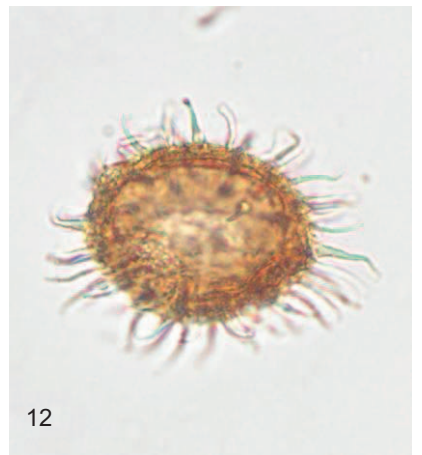
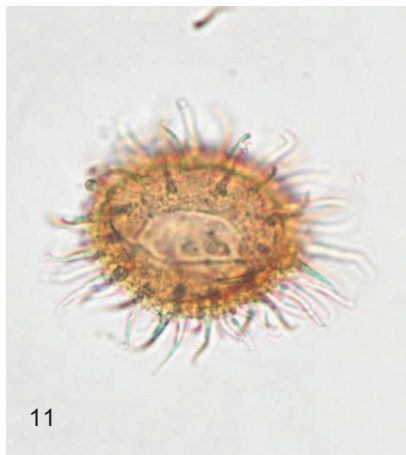
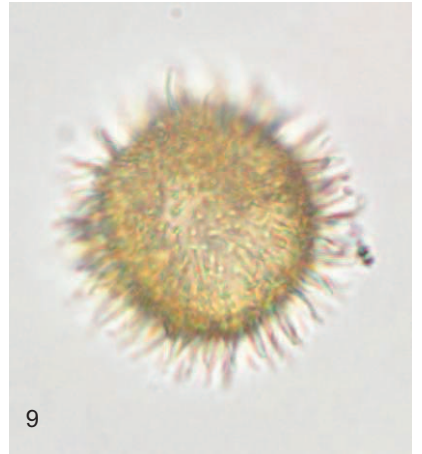
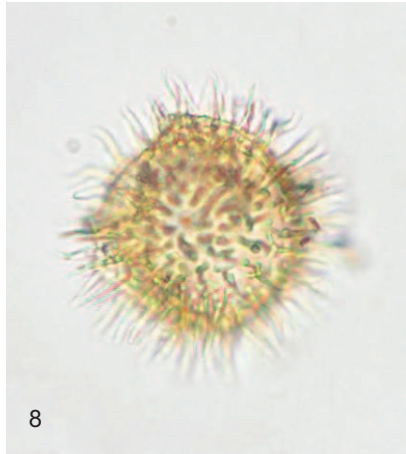
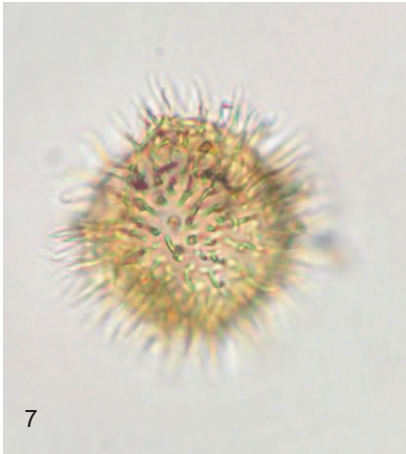


Plate 59

Operculodinium crouchii

Figure 1-3 Sample J42/f302, slide L23132/SM018; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 500; specimen measures 82 x 85 μm

Figure 4-6 Sample J42/f302, slide L23132/SM017; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 600; specimen measures 78 x 65 μm

Figure 7-9 Sample J42/f303, slide L23133/SM006; Hampden Formation, Hampden Beach Section (Bortonian); x 675; specimen measures 57 x 62 μm

Figure 10-12 Sample J42/f301, slide L23131/SM011; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 575; specimen measures 70 x 72 μm

Plate 59

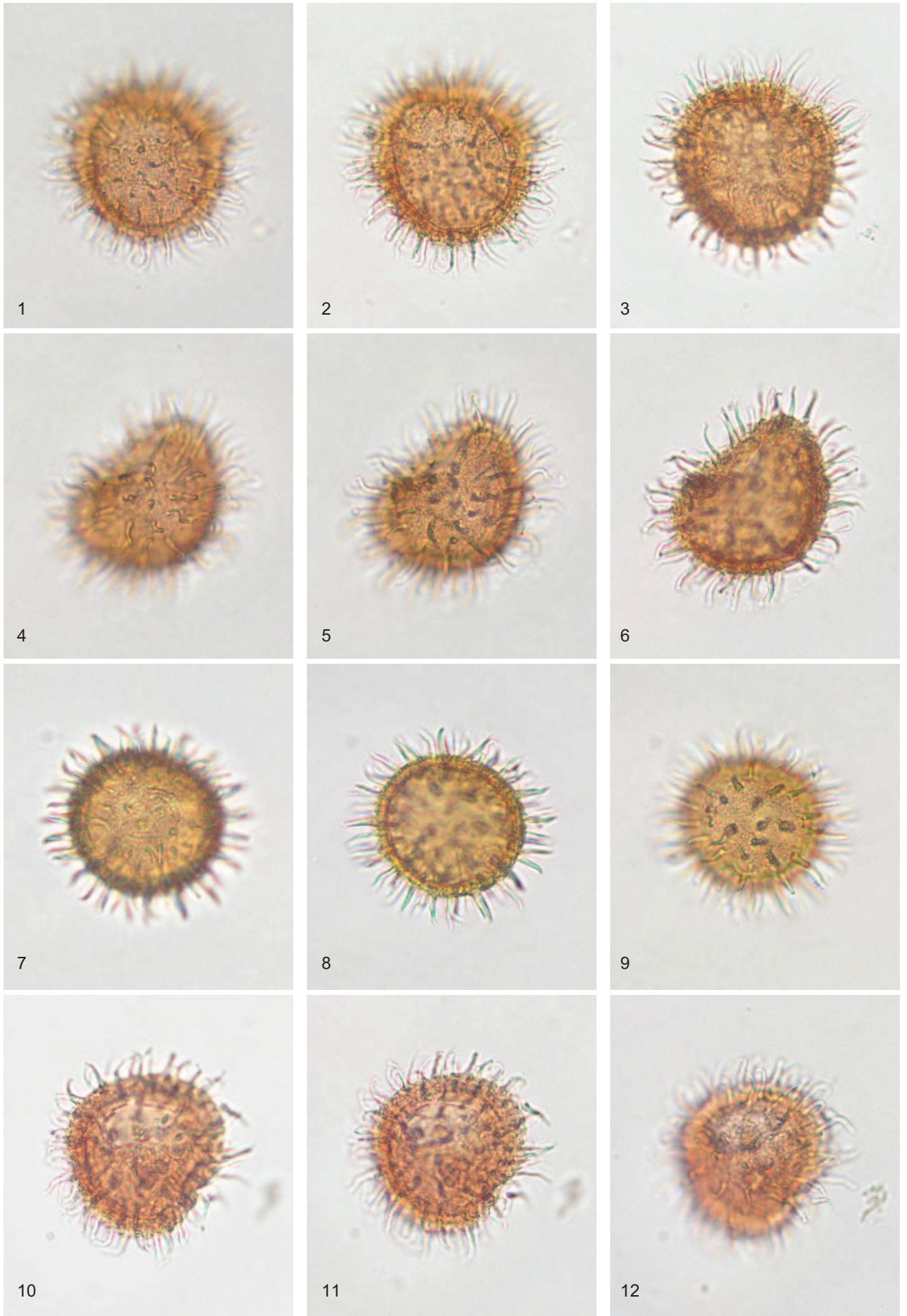


Plate 60

***Operculodinium* sp. 11**

Figure 1-6 Sample I43/f090, slide L16338/SM035; Burnside Formation, Puketeraki Core (Bortonian); x 525; specimen measures 82 x 80 μm

***Operculodinium* sp. 12**

Figure 7-9 Sample J42/f488, slide L23123/SM011; Hampden Formation, Hampden Beach Section (Bortonian); x 725; specimen measures 65 x 50 μm

Figure 10-12 Sample U24/f417, slide L23125/SM007; Wanstead, Te Uri Stream (Porangan); x 625; specimen measures 70 x 68 μm

Plate 60

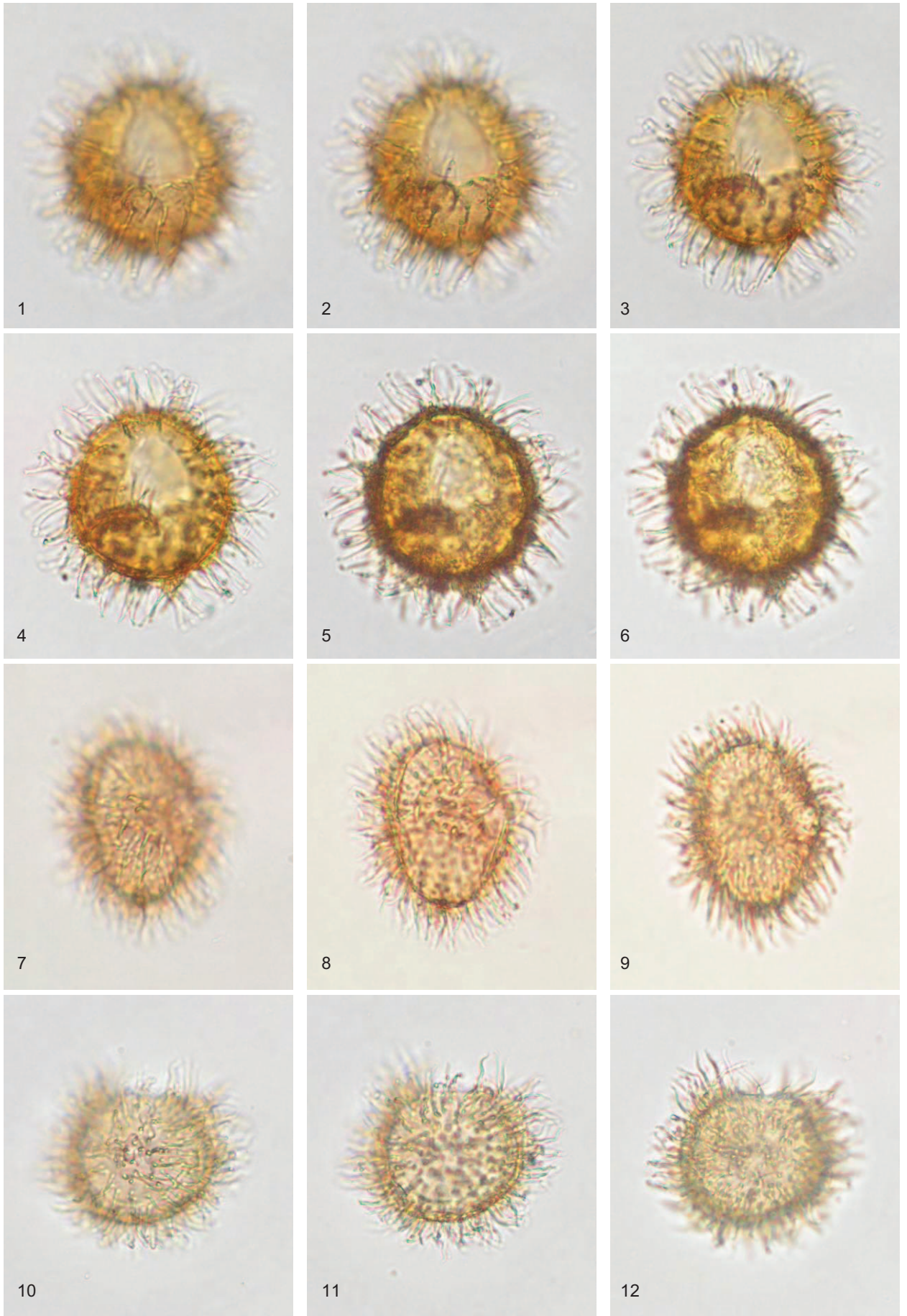


Plate 61

Samlandia reticulifera

Figure 1-3 Sample I43/f093, slide L16341/SM003; Burnside Formation, Puketeraki Core (Bortonian);
x 450; specimen measures 106 x 77 μm

Figure 4-6 Sample J42/f097, slide L10952/SM2963; Totara Limestone, Kakanui River (?early
Whaingaroan); x 450; specimen measures 102 x 78 μm

Samlandia tenuis

Figure 7-12 Sample K29/f097, slide L10914/SM019; Port Elizabeth Member, Cape Foulwind Section (early
Whaingaroan); x 375; specimen measures 122 x 100 μm

Plate 61

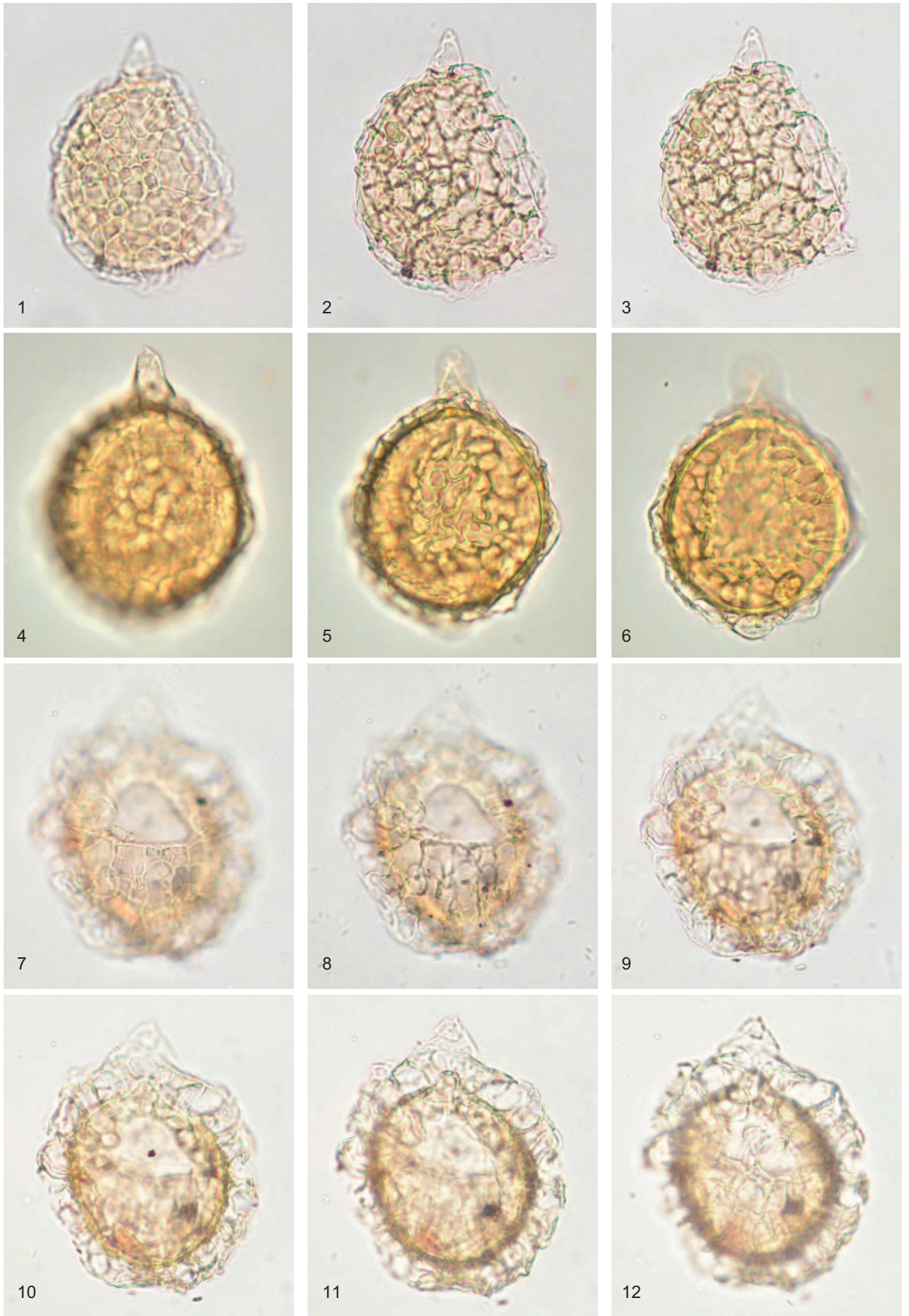


Plate 62

Samlandia tenuis

Figure 1-3 Sample I43/f093, slide L16341/SM166; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 107 x 90 µm

Stoveracysta kakanuiensis

Figure 4-6 Sample J42/f096, slide L10951/SM014; Totara Limestone, Kakanui River (early Whaingaroan); x 700; specimen measures 65 x 60 µm

Stoveracysta ?ornata

Figure 7-9 Sample K29/f104, slide L11040/SM001; Kaiata Mudstone, Cape Foulwind Section (Runangan); x 700; specimen measures 49 x 60 µm

Thalassiphora pelagica

Figure 10-12 Sample K29/f097, slide L10914/SM022; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 225; specimen measures 200 x 150 µm

Plate 62

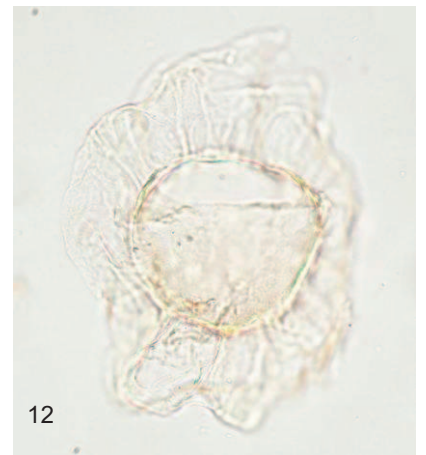
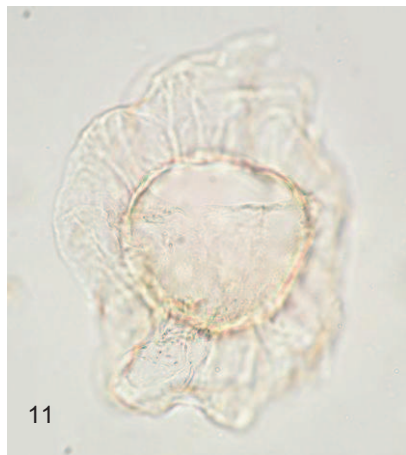
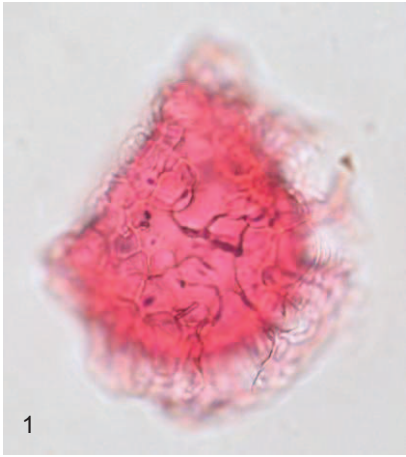


Plate 63

Thalassiphora pelagica

- Figure 1-2 Sample K29/f097, slide L10914/SM022; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 225; specimen measures 200 x 150 μm
- Figure 3-6 Sample I43/f093, slide L16341/SM095; Burnside Formation, Puketeraki Core (Bortonian); x 175; specimen measures 177 x 225 μm
- Figure 7-9 Sample J42/f484, slide L23119/SM024; Kurinui Formation, Hampden Beach Section (Heretaungan); x 250; specimen measures 122 x 165 μm
- Figure 10-12 Sample J42/f485, slide L23120/SM032; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 375; specimen measures 122 x 115 μm

Plate 63

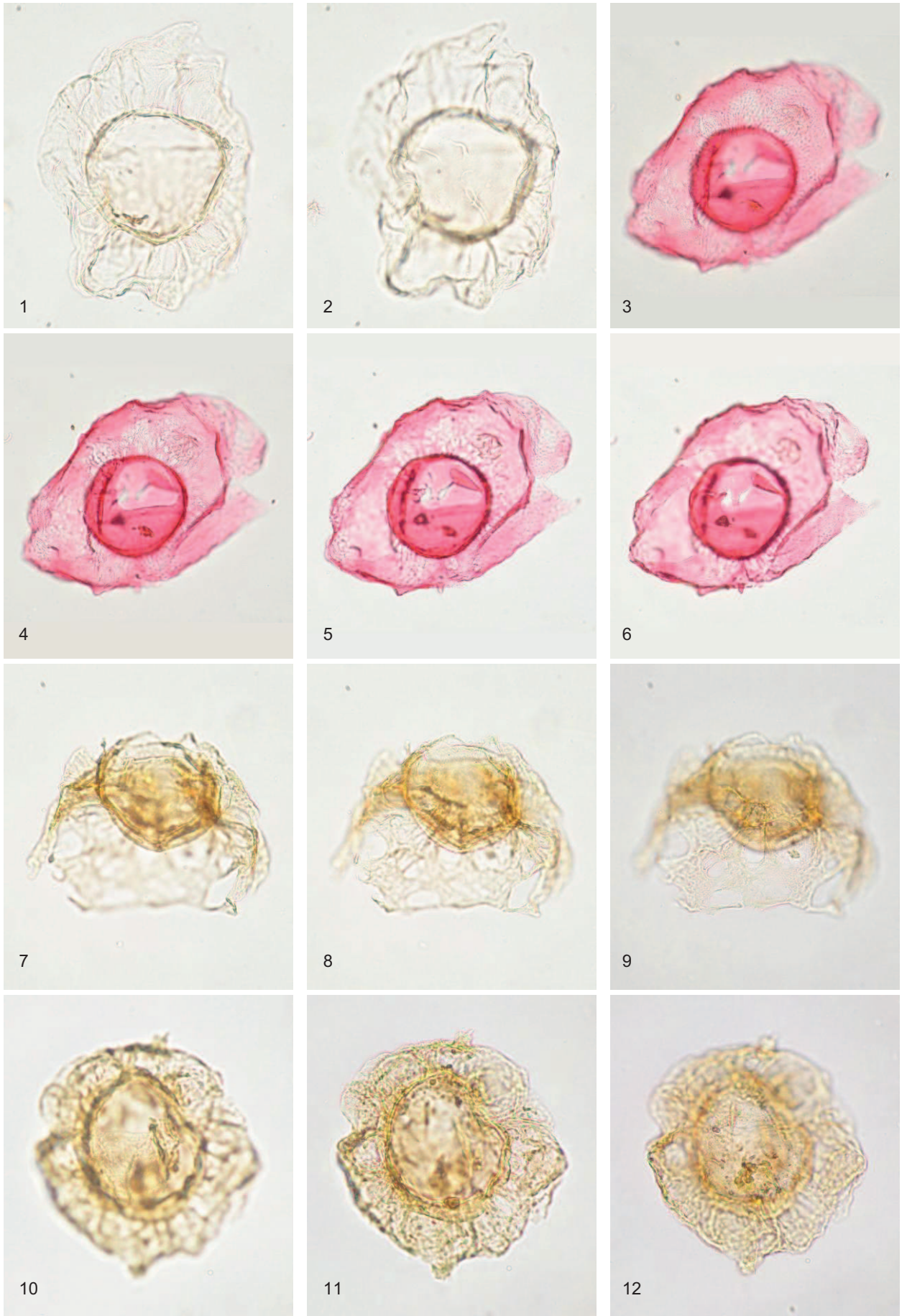


Plate 64

?*Tityrosphaeridium cantharellus*

- Figure 1-3 Sample J42/f096, slide L10951/SM034; Totara Limestone, Kakanui River (early Whaingaroan); x 725; specimen measures 60 x 58 μm
- Figure 4-6 Sample J42/f125, slide L11625/SM012; Totara Limestone, Kakanui River (Runangan-early Whaingaroan); x 600; specimen measures 70 x 70 μm
- Figure 7-10 Sample J42/f096, slide L10951/SM036; Totara Limestone, Kakanui River (early Whaingaroan); x 800; specimen measures 55 x 53 μm
- Figure 11-12 Sample J42/f096, slide L10951/SM037; Totara Limestone, Kakanui River (early Whaingaroan); x 700; specimen measures 68 x 55 μm

Plate 64

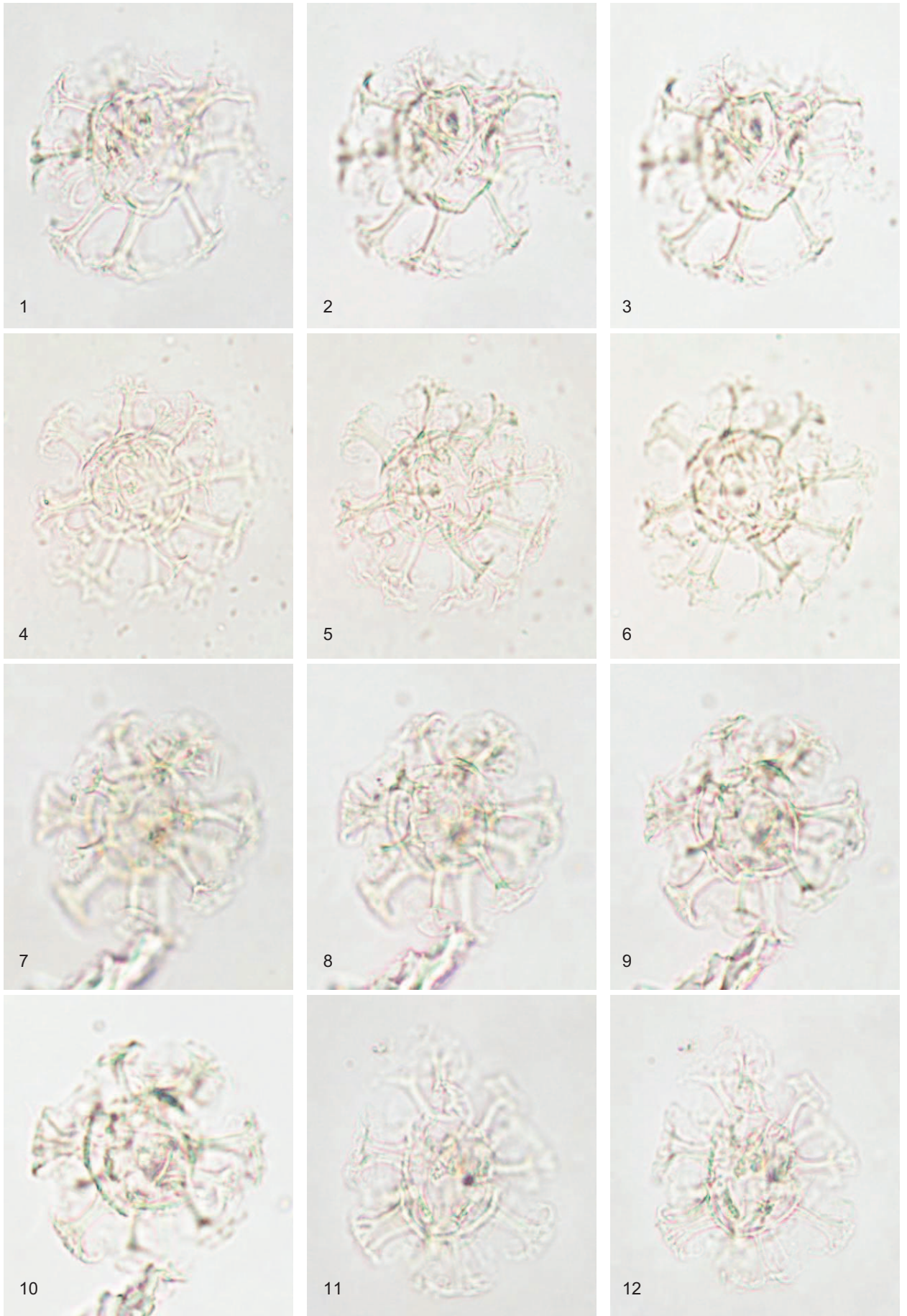


Plate 65

?*Tityrosphaeridium cantharellus*

Figure 1 Sample J42/f096, slide L10951/SM037; Totara Limestone, Kakanui River (early Whaingaroan); x 700; specimen measures 68 x 55 μm

Figure 2-3 Sample U24/f419, slide L23127/SM073C; Wanstead, Te Uri Stream (Porangan); x 1025; specimen measures 46 x 40 μm

Areosphaeridium dictyostilum

Figure 4-9 Sample I43/f096, slide L16344/SM005; Burnside Formation, Puketeraki Core (Kaiatan); x 500; specimen measures 77 x 85 μm

Figure 10-12 Sample I43/f096, slide L16344/SM008; Burnside Formation, Puketeraki Core (Kaiatan); x 525; specimen measures 90 x 80 μm

Plate 65



Plate 66

Areosphaeridium dictyostilum

Figure 1-3 Sample I43/f089, slide L16337/SM107; Burnside Formation, Puketeraki Core (Bortonian);
x 400; specimen measures 105 x 102 μm

Areosphaeridium ebdonii

Figure 4-9 Sample J42/f303, slide L23133/SM009; Hampden Formation, Hampden Beach Section
(Bortonian); x 575; specimen measures 67 x 72 μm

Areosphaeridium multicornutum

Figure 10-12 Sample I43/f090, slide L16338/SM029; Burnside Formation, Puketeraki Core (Bortonian);
x 525; specimen measures 65 x 80 μm

Plate 66

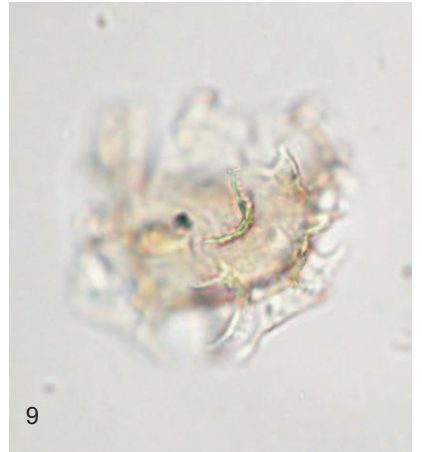
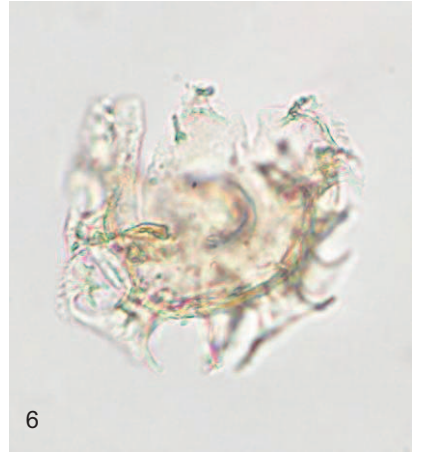
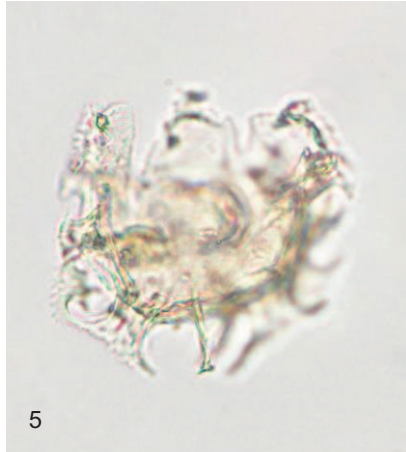


Plate 67

Areosphaeridium multicornutum

Figure 1-3 Sample I43/f090, slide L16338/SM029; Burnside Formation, Puketeraki Core (Bortonian); x 525; specimen measures 65 x 80 μm

Areosphaeridium pectiniforme

Figure 4-6 Sample I43/f089, slide L16337/SM092; Burnside Formation, Puketeraki Core (Bortonian); x 475; specimen measures 100 x 83 μm

Figure 7-9 Sample I43/f089, slide L16337/SM093; Burnside Formation, Puketeraki Core (Bortonian); x 425; specimen measures 102 x 97 μm

Figure 10-12 Sample I43/f093, slide L16341/SM167; Burnside Formation, Puketeraki Core (Bortonian); x 375; specimen measures 110 x 112 μm

Plate 67

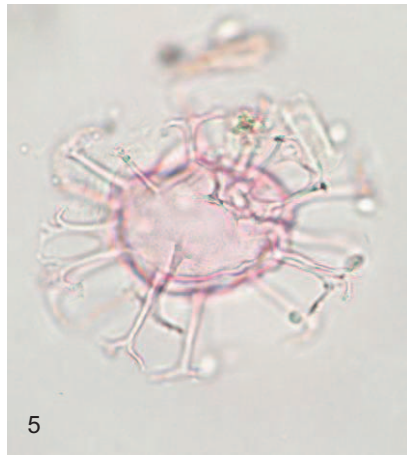


Plate 68

Cooksonidium capricornum

Figure 1-3 Sample I43/f096, slide L16344/SM004; Burnside Formation, Puketeraki Core (Kaiatan);
x 725; specimen measures 52 x 57 μm

Graptodinium inconditum

Figure 4-9 Sample I43/f090, slide L16338/SM060; Burnside Formation, Puketeraki Core (Bortonian);
specimen measures 28 x 32 μm

Figure 10-12 Sample J42/f097, slide L10952/SM014; Totara Limestone, Kakanui River (?early
Whaingaroan); x 1175; specimen measures 40 x 35 μm

Plate 68

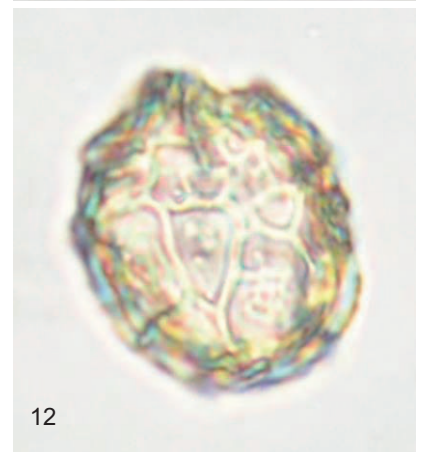
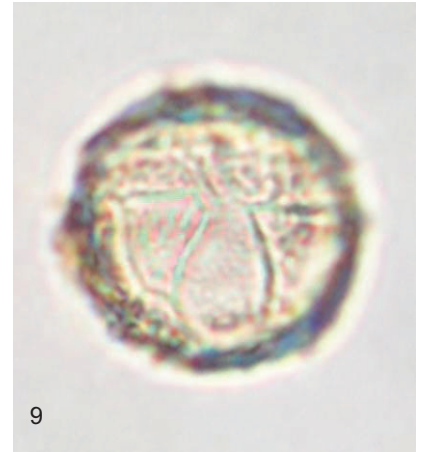
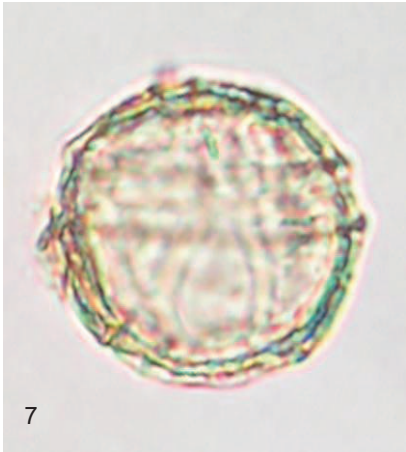
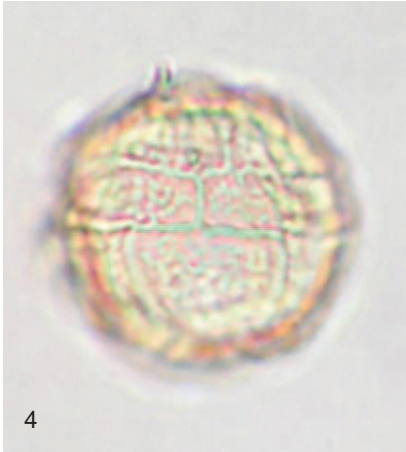


Plate 69

Graptodinium inconditum

Figure 1-6 Sample I43/f093, slide L16341/SM075; Burnside Formation, Puketeraki Core (Bortonian);
specimen measures 35 x 34 μm

Graptodinium reticulatum

Figure 7-12 Sample I43/f093, slide L16341/SM071; Burnside Formation, Puketeraki Core (Bortonian);
specimen measures 36 x 37 μm

Plate 69

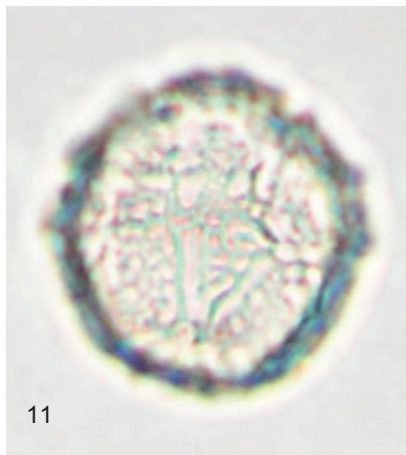
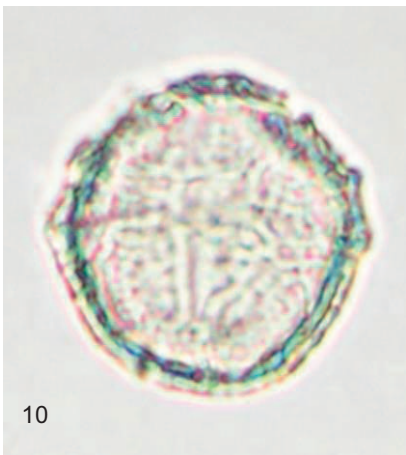


Plate 70

Graptodinium reticulatum

Figure 1-3 Sample I43/f090, slide L16338/SM059; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 34 x 26 μm

cf. *Kleithriasphaeridium* sp. 1

Figure 4-6 Sample S14/f8599, slide L10662/SM018; Waikato Coal Measures, Old Mountain Road (Runangan-early Whaingaroan); x 375; specimen measures 125 x 98 μm

Figure 7-9 Sample S14/f8599, slide L10662/SM019; Waikato Coal Measures, Old Mountain Road (Runangan-early Whaingaroan); x 400; specimen measures 103 x 107 μm

Lophocysta ?sulcolimbata

Figure 10-12 Sample I43/f089, slide L16337/SM094; Burnside Formation, Puketeraki Core (Bortonian); x 775; specimen measures 60 x 42 μm

Plate 70

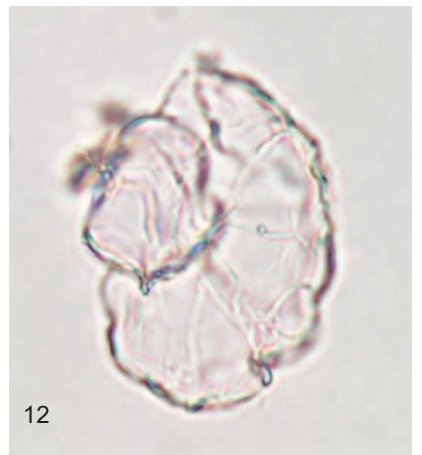
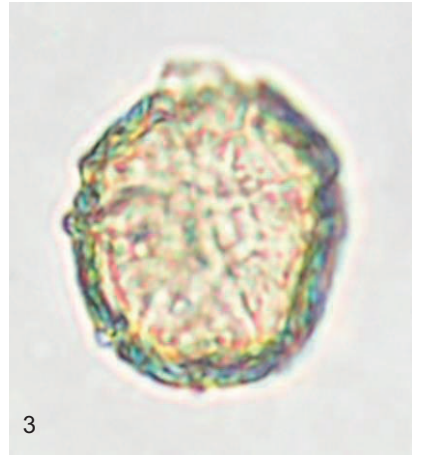
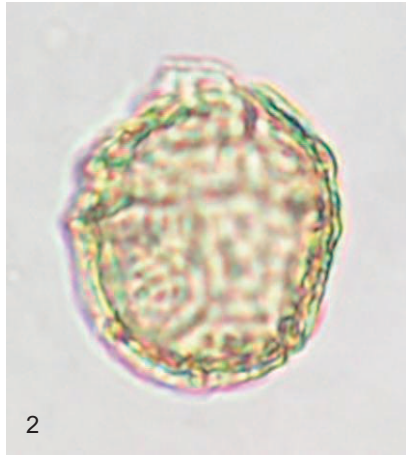
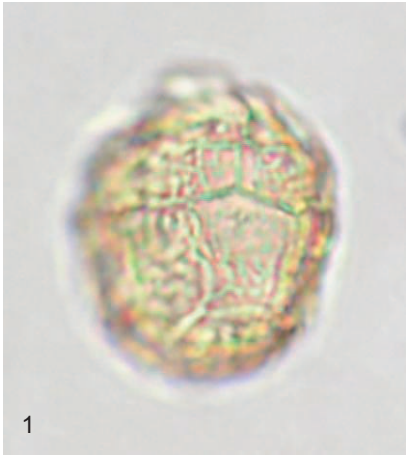


Plate 71

Lophocysta ?sulcolimbata

Figure 1-3 Sample I43/f089, slide L16337/SM115; Burnside Formation, Puketeraki Core (Bortonian);
x 850; specimen measures 56 x 40 µm

Aireiana salicta

Figure 4-6 Sample I43/f090, slide L16338/SM045; Burnside Formation, Puketeraki Core (Bortonian);
x 375; specimen measures 122 x 102 µm

Figure 7-9 Sample I43/f090, slide L16338/1-1318-117; Burnside Formation, Puketeraki Core
(Bortonian); x 325; specimen measures 95 x 128 µm

Fibrocysta bipolaris

Figure 10-12 Sample I43/f090, slide L16338/SM041; Burnside Formation, Puketeraki Core (Bortonian);
x 350; specimen measures 137 x 97 µm

Plate 71

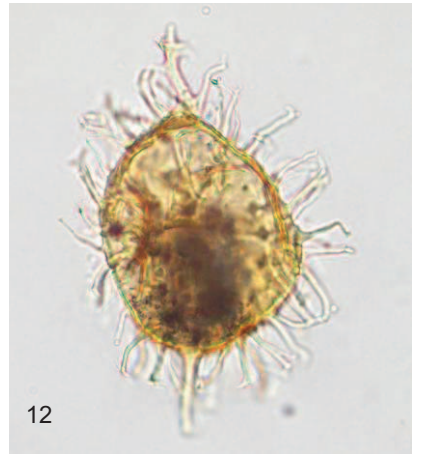


Plate 72

Fibrocysta bipolaris

Figure 1-3 Sample I43/f090, slide L16338/SM042; Burnside Formation, Puketeraki Core (Bortonian); x 425; specimen measures 108 x 95 μm

Pyxidinopsis crassimurata

Figure 4-6 Sample U24/f418, slide L23126/SM040; Wanstead, Te Uri Stream (Porangan); x 725; specimen measures 58 x 58 μm

Pyxidinopsis teuriensis

Figure 7-9 Sample J42/f484, slide L23119/SM031; Kurinui Formation, Hampden Beach Section (Heretaungan); x 575; specimen measures 80 x 72 μm

Figure 10-12 Sample J42/f484, slide L23119/SM029; Kurinui Formation, Hampden Beach Section (Heretaungan); x 550; specimen measures 75 x 77 μm

Plate 72

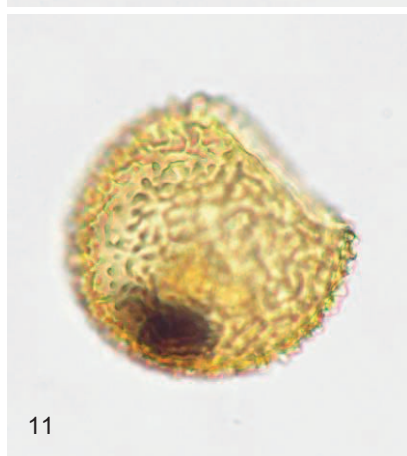
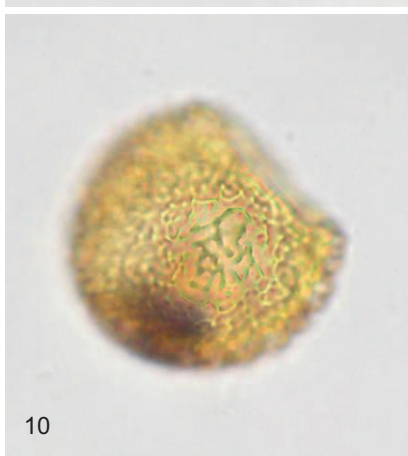
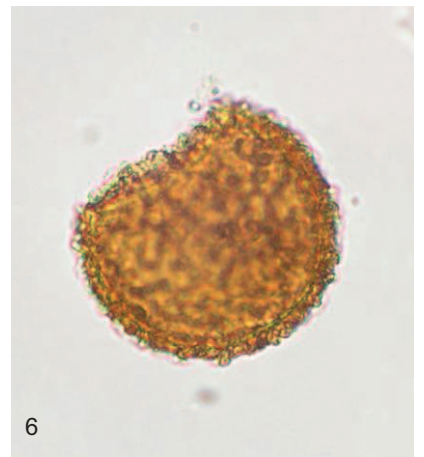
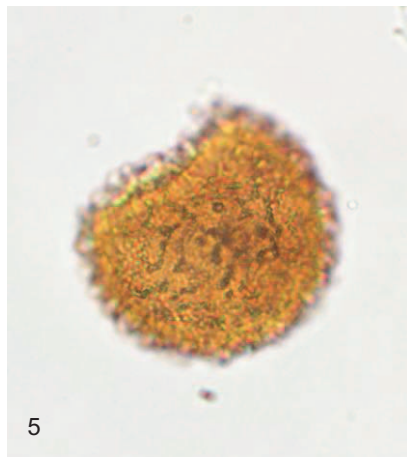


Plate 73

Pyxidinopsis teuriensis

Figure 1-3 Sample J42/f299, slide L23129/SM017; Hampden Formation, Hampden Beach Section (Porangan); x 675; specimen measures 61 x 62 μm

Figure 4-6 Sample U24/f419, slide L23127/SM088; Wanstead, Te Uri Stream (Porangan); x 600; specimen measures 70 x 70 μm

Pyxidinopsis cf. delicata

Figure 7-12 Sample I43/f090, slide L16338/SM062; Burnside Formation, Puketeraki Core (Bortonian); x 800; specimen measures 47 x 52 μm

Plate 73

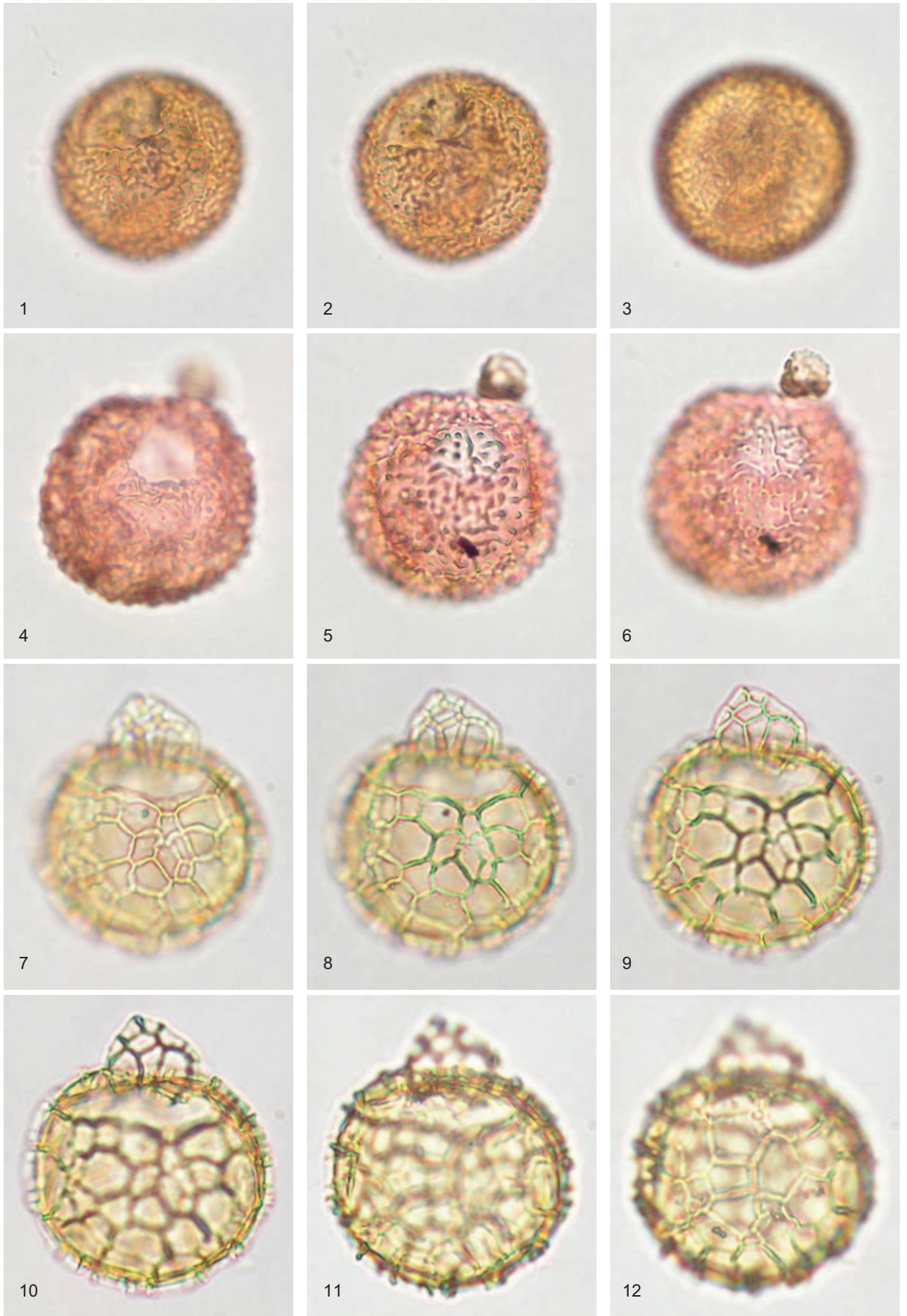


Plate 74

***Pyxidinopsis* sp. 3**

Figure 1-3 Sample U24/f419, slide L23127/SM087B; Wanstead, Te Uri Stream (Porangan); x 775; specimen measures 57 x 55 μm

Pyxidinopsis mundus

Figure 4-6 Sample U24/f419, slide L23127/SM020; Wanstead, Te Uri Stream (Porangan); x 850; specimen measures 52 x 50 μm

Figure 7-9 Sample J42/f483, slide L23118/SM031; Kurinui Formation, Hampden Beach Section (Heretaungan); x 775; specimen measures 55 x 54 μm

Figure 10-12 Sample U24/f419, slide L23127/SM032; Wanstead, Te Uri Stream (Porangan); x 950; specimen measures 50 x 43 μm

Plate 74

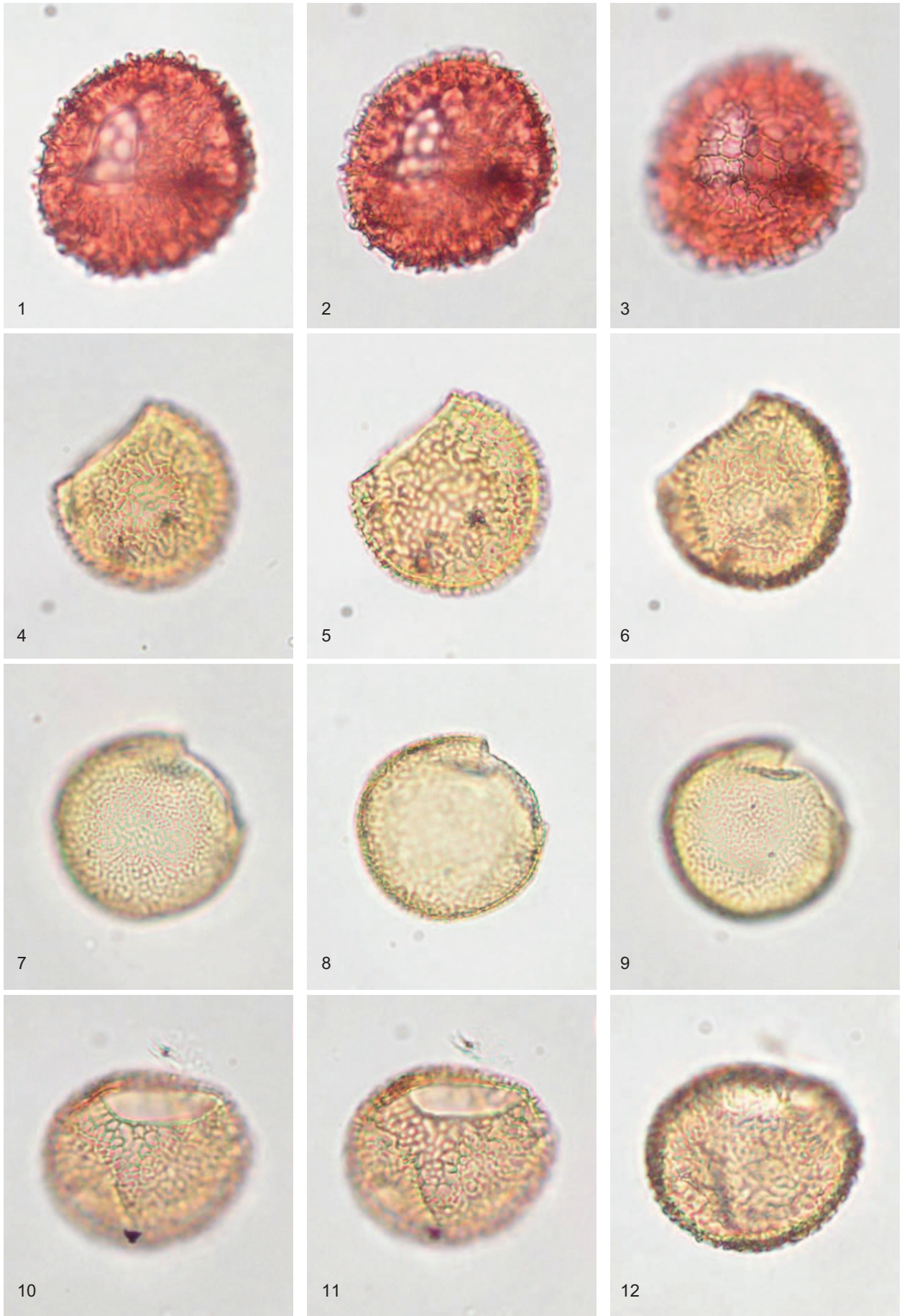


Plate 75

Pyxidinopsis waipawaensis

Figure 1-3 Sample V22/f8994, slide L12118/SM3329; Waipawa Section (Heretaungan); x 750; specimen measures 58 x 56 μm

Figure 4-5 Sample I44/f080, slide L08947/SM4888; Burnside Formation, Burnside Marl Pit (Bortonian)

Figure 6 Sample I44/f080, slide L08947/SM4926; Burnside Formation, Burnside Marl Pit (Bortonian); x 500; specimen measures 80 x 82 μm

?*Areoligera hampdenensis*

Figure 7-12 Sample J42/f483, slide L23118/SM005; Kurinui Formation, Hampden Beach Section (Heretaungan); x 525; specimen measures 75 x 80 μm

Plate 75

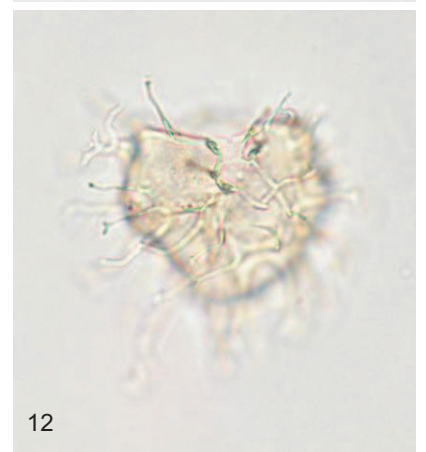
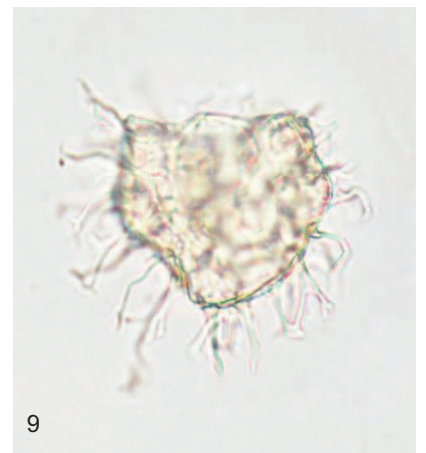
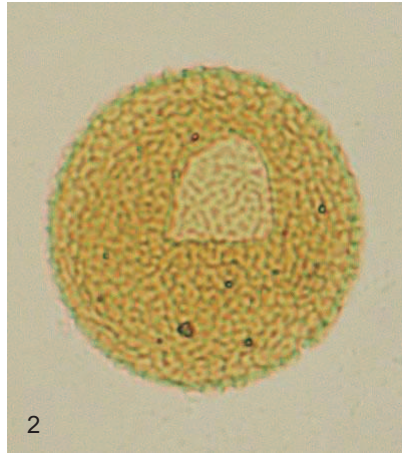


Plate 76

?Areoligera hampdenensis

- Figure 1-5 Sample J42/f483, slide L23118/SM006; Kurinui Formation, Hampden Beach Section (Heretaungan); x 425; specimen measures 110 x 97 μm
- Figure 6 Sample J42/f484, slide L23119/SM033B; Kurinui Formation, Hampden Beach Section (Heretaungan)
- Figure 7-9 Sample J42/f300, slide L23130/SM034; Hampden Formation, Hampden Beach Section (Porangan); x 375; specimen measures 125 x 84 μm
- Figure 10-12 Sample J42/f484, slide L23119/SM005; Kurinui Formation, Hampden Beach Section (Heretaungan); x 475; specimen measures 98 x 88 μm

Plate 76

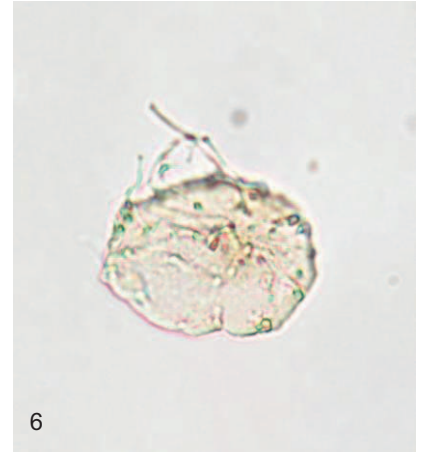
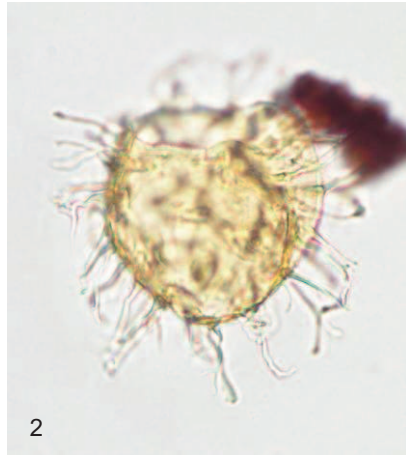
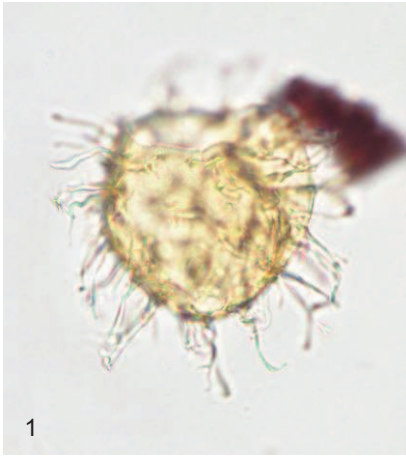


Plate 77

?*Areoligera* sp. 2

Figure 1-6 Sample J42/f300, slide L23130/SM010; Hampden Formation, Hampden Beach Section (Porangan); x 550; specimen measures 79 x 77 μ m

Figure 7-9 Sample J42/f299, slide L23129/SM022; Hampden Formation, Hampden Beach Section (Porangan); x 450; specimen measures 87 x 91 μ m

Cleistosphaeridium diversispinosum

Figure 10-12 Sample I43/f093, slide L16341/SM004; Burnside Formation, Puketeraki Core (Bortonian); x 575; specimen measures 72 x 74 μ m

Plate 77

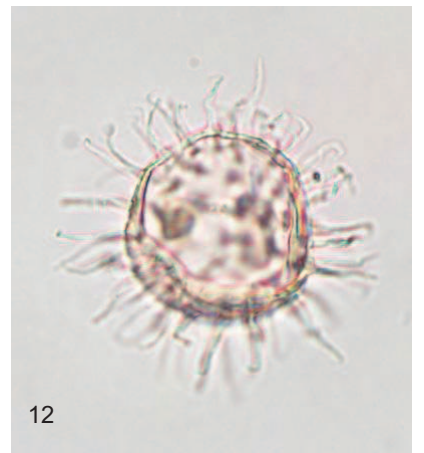
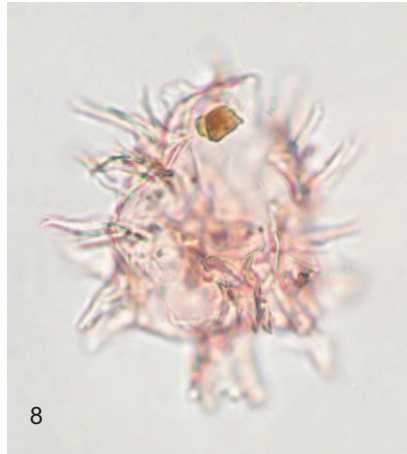
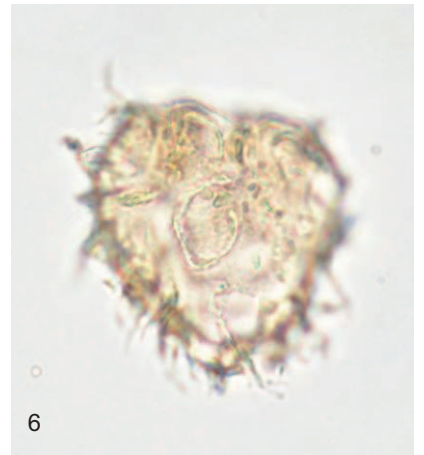
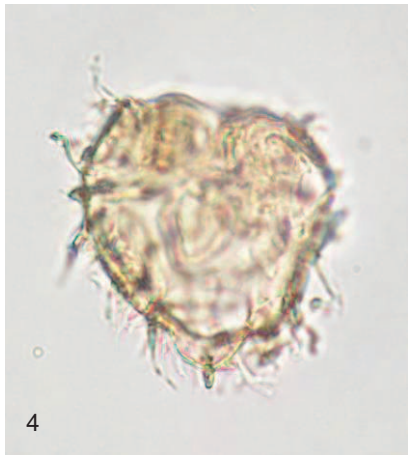


Plate 78

Cleistosphaeridium ancyreum

Figure 1-6 Sample J42/f483, slide L23118/SM009; Kurinui Formation, Hampden Beach Section (Heretaungan); x 725; specimen measures 65 x 43 μm

Cleistosphaeridium placacanthum

Figure 7-9 Sample K29/f106, slide L11042/SM003; Kaiata Mudstone, Cape Foulwind Section (Runangan-early Whaingaroan); x 450; specimen measures 84 x 93 μm

Cleistosphaeridium sp. 1

Figure 10-12 Sample I43/f089, slide L16337/SM100; Burnside Formation, Puketeraki Core (Bortonian); x 700; specimen measures 67 x 60 μm

Plate 78

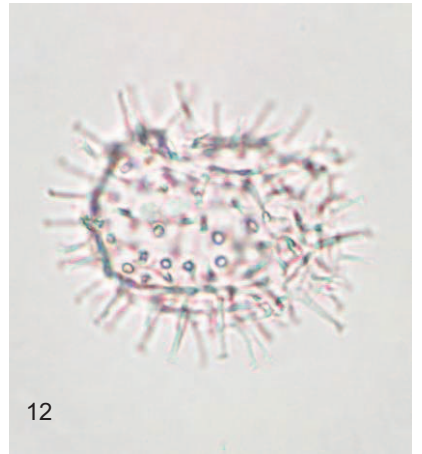
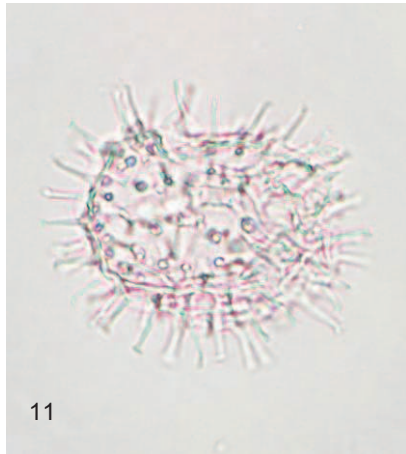
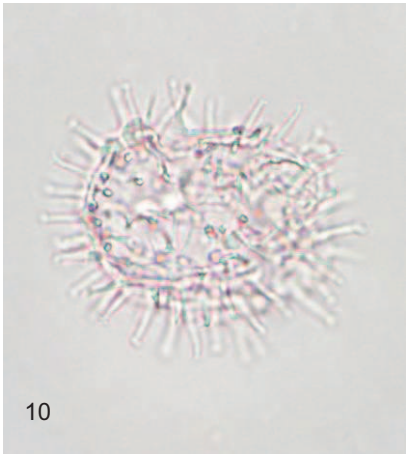
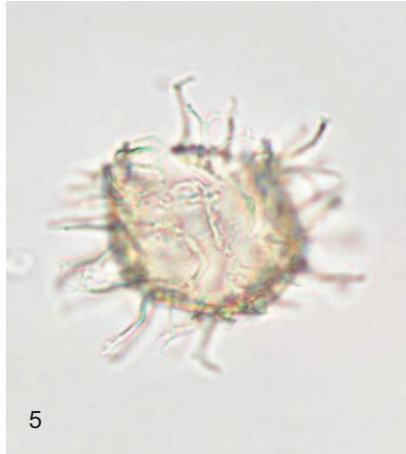
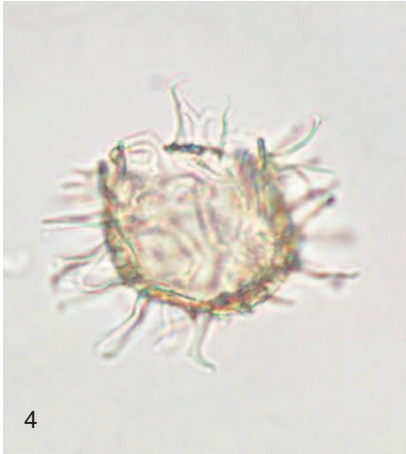
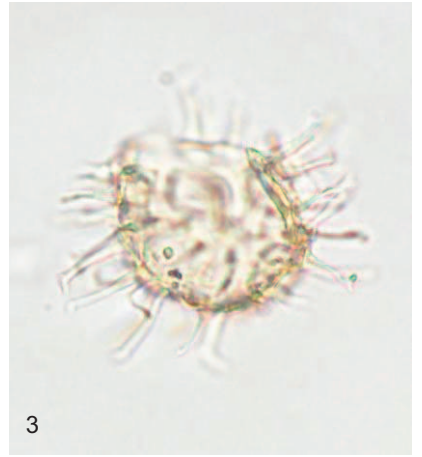
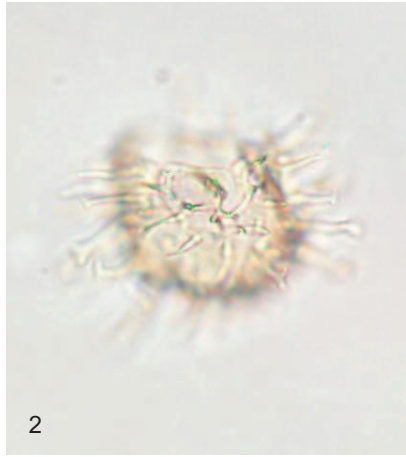


Plate 79

***Cleistosphaeridium* sp. 3**

Figure 1-6 Sample I43/f092, slide L16340/1-1438-072; Burnside Formation, Puketeraki Core (Bortonian); x 650; specimen measures 58 x 65 μm

Cyclonephelium membranophorum

Figure 7-9 Sample I43/f090, slide L16338/1-1268-107; Burnside Formation, Puketeraki Core (Bortonian); x 450; specimen measures 87 x 95 μm

Glaphyrocysta* cf. *retiintexta

Figure 10-12 Sample J42/f486, slide L23121/SM005; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian)

Plate 79

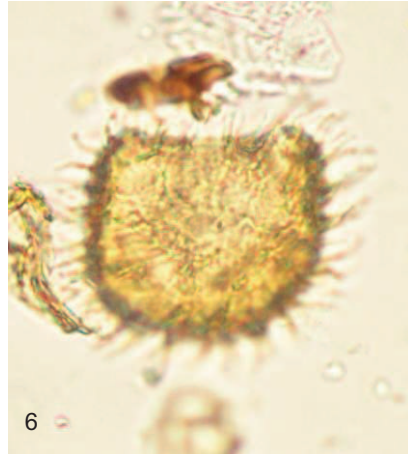


Plate 80

Glaphyrocysta cf. retiintexta

- Figure 1-2 Sample J42/f486, slide L23121/SM005; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian)
- Figure 3 Sample J42/f485, slide L23120/SM017; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian)
- Figure 4-9 Sample J42/f300, slide L23130/SM012; Hampden Formation, Hampden Beach Section (Porangan); x 375; specimen measures 90 x 115 μm
- Figure 10-12 Sample J42/f485, slide L23120/SM019; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 450; specimen measures 102 x 95 μm

Plate 80

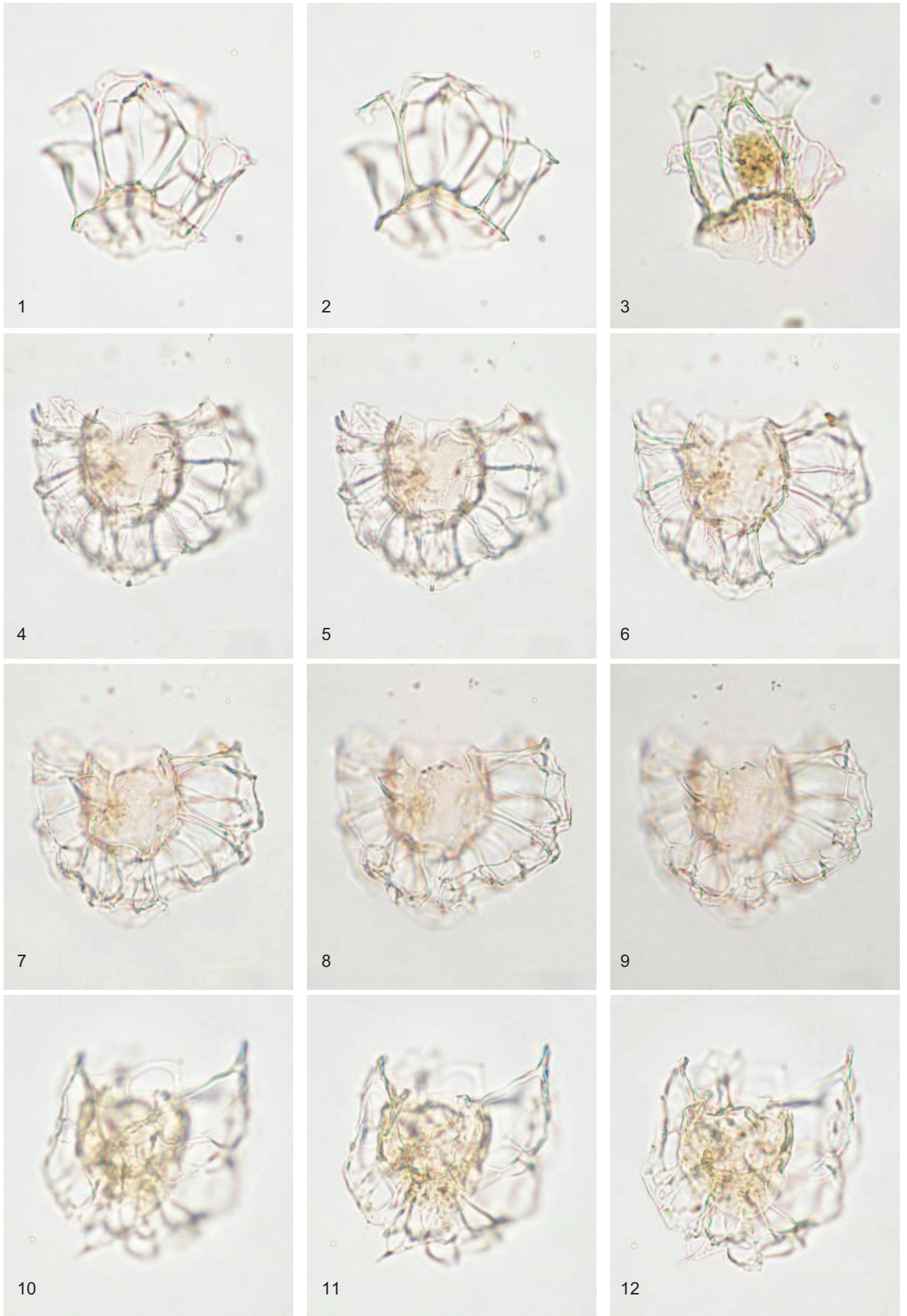


Plate 81

Glaphyrocysta cf. retiintexta

Figure 1-3 Sample J42/f485, slide L23120/SM019; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 450; specimen measures 102 x 95 μm

Figure 4-9 Sample J42/f485, slide L23120/SM020; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 450; specimen measures 75 x 96 μm

Membranophoridium perforatum

Figure 10-12 Sample J42/f301, slide L23131/SM027; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 400; specimen measures 83 x 102 μm

Plate 81

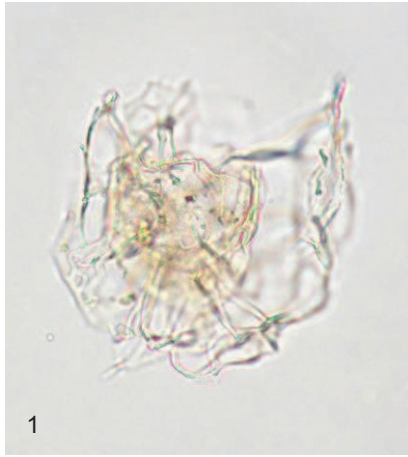


Plate 82

?*Riculacysta* sp. 1

Figure 1-3 Sample J42/f488, slide L23123/SM009; Hampden Formation, Hampden Beach Section (Bortonian)

Figure 4-6 Sample U24/f417, slide L23125/SM021; Wanstead, Te Uri Stream (Porangan); x 500; specimen measures 94 x 82 μm

Figure 7-9 Sample U24/f417, slide L23125/SM017; Wanstead, Te Uri Stream (Porangan); x 400; specimen measures 95 x 102 μm

Figure 10-12 Sample U24/f417, slide L23125/SM019; Wanstead, Te Uri Stream (Porangan); x 500; specimen measures 79 x 86 μm

Plate 82

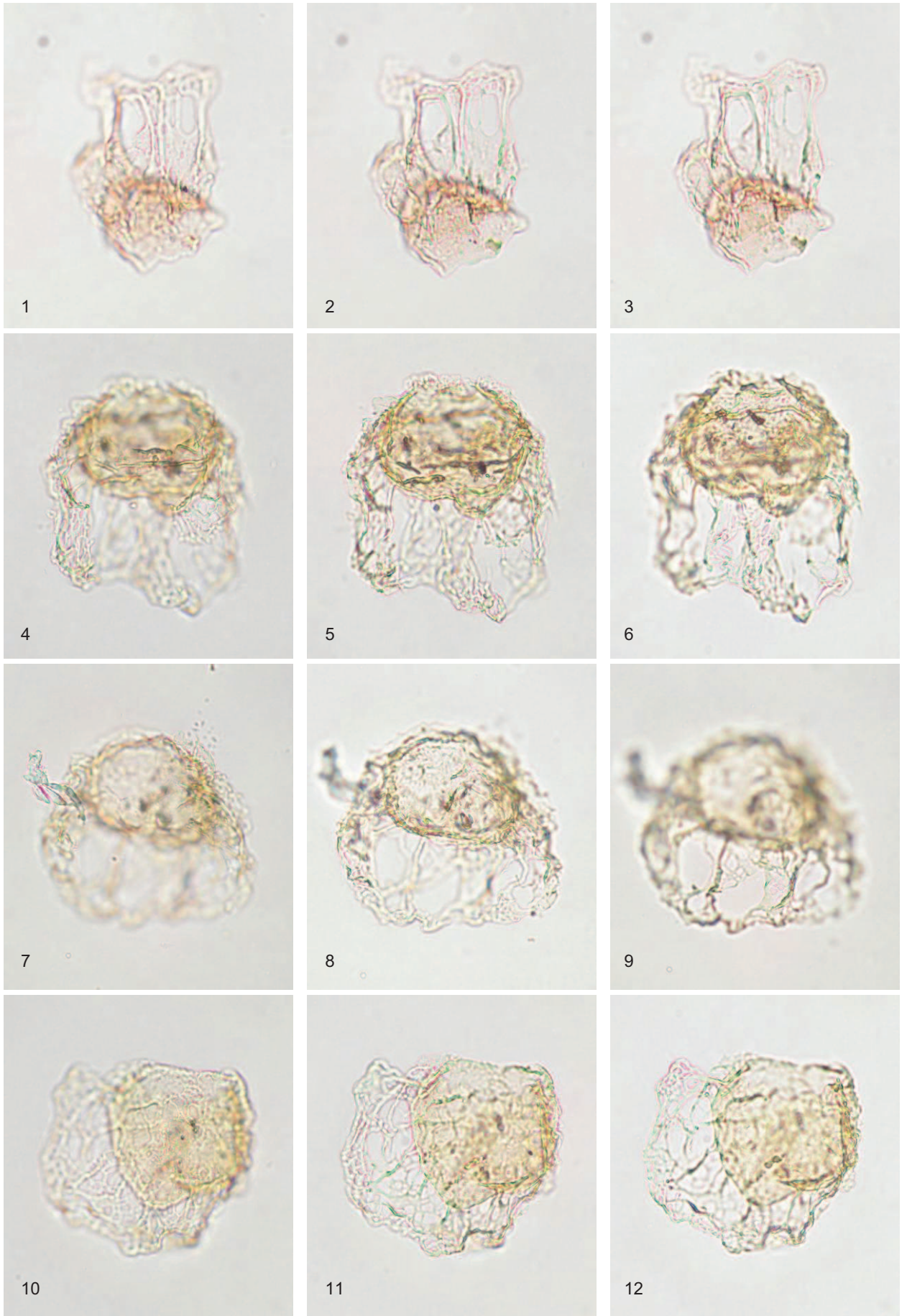


Plate 83

Eisenackia* aff. *circumtabulata

Figure 1-3 Sample I43/f092, slide L16340/1-1434-128; Burnside Formation, Puketeraki Core (Bortonian);
x 775; specimen measures 60 x 48 μm

Figure 4-6 Sample I43/f092, slide L16340/1-1307-137; Burnside Formation, Puketeraki Core (Bortonian);
x 775; specimen measures 60 x 53 μm

Figure 7-11 Sample I43/f093, slide L16341/SM121; Burnside Formation, Puketeraki Core (Bortonian);
x 750; specimen measures 62 x 56 μm

?*Eisenackia* cf. *circumtabulata*

Figure 12 Sample I43/f089, slide L16337/SM037; Burnside Formation, Puketeraki Core (Bortonian);
x 675; specimen measures 70 x 61 μm

Plate 83

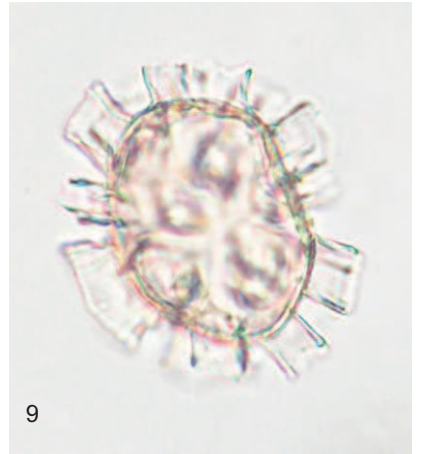


Plate 84

?*Eisenackia* cf. *circumtabulata*

Figure 1-3 Sample I43/f089, slide L16337/SM037; Burnside Formation, Puketeraki Core (Bortonian); x 675; specimen measures 70 x 61 μm

?*Eisenackia* cf. *H. wilsonii*

Figure 4-9 Sample J42/f489, slide L23124/SM014; Hampden Formation, Hampden Beach Section (Bortonian); x 825; specimen measures 57 x 51 μm

Figure 10-12 Sample U24/f419, slide L23127/SM024; Wanstead, Te Uri Stream (Porangan); x 850; specimen measures 50 x 50 μm

Plate 84

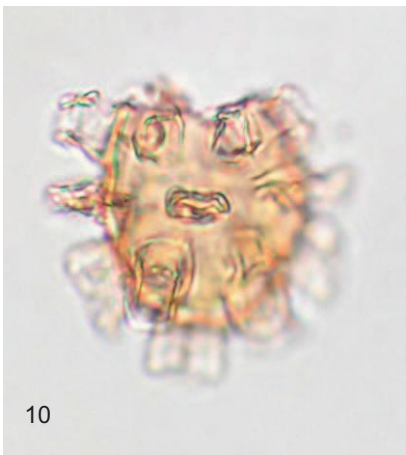


Plate 85

?*Eisenackia* cf. *H. wilsonii*

Figure 1-3 Sample U24/f419, slide L23127/SM065A; Wanstead, Te Uri Stream (Porangan); x 925; specimen measures 45 x 45 µm

***Homotryblium* sp. 2**

Figure 4 Sample I43/f089, slide L16337/SM066A; Burnside Formation, Puketeraki Core (Bortonian)

Figure 5-6 Sample I43/f092, slide L16340/1-1402-180; Burnside Formation, Puketeraki Core (Bortonian); x 925; specimen measures 50 x 45 µm

Hystrichosphaeridium tubiferum

Figure 7-12 Sample J42/f485, slide L23120/SM006B; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 500; specimen measures 79 x 85 µm

Plate 85

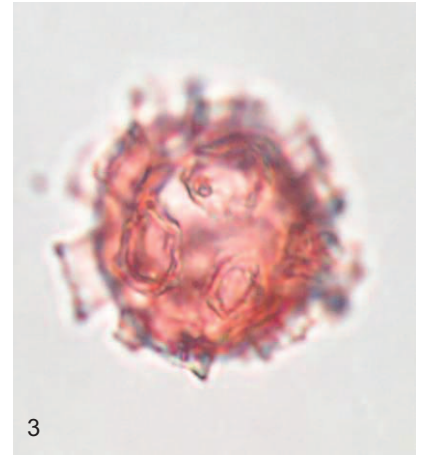
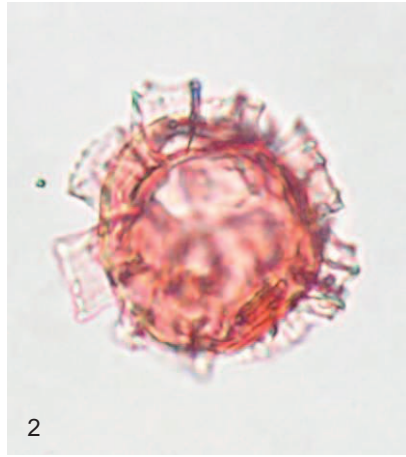


Plate 86

Hystrichosphaeridium salpingophorum

Figure 1-3 Sample J42/f302, slide L23132/SM020; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 525; specimen measures 87 x 81 μm

Figure 4-6 Sample J42/f302, slide L23132/SM004B; Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 600; specimen measures 73 x 70 μm

Hystrichosphaeridium brevispinum

Figure 7-12 Sample I43/f093, slide L16341/SM056; Burnside Formation, Puketeraki Core (Bortonian); x 550; specimen measures 67 x 77 μm

Plate 86

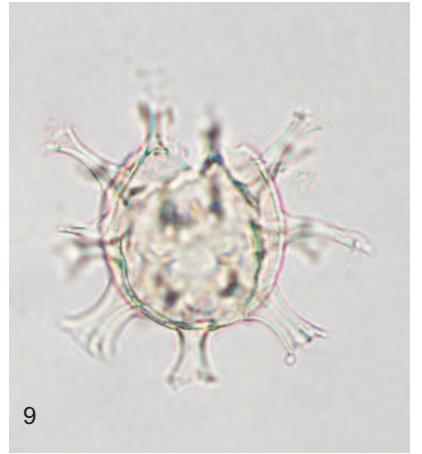


Plate 87

Hystichosphaeridium brevispinum

Figure 1-3 Sample I43/f090, slide L16338/1-1247-116; Burnside Formation, Puketeraki Core (Bortonian); x 550; specimen measures 70 x 78 μm

Batiacasphaera perforata

Figure 4-9 Sample I43/f089, slide L16337/SM102; Burnside Formation, Puketeraki Core (Bortonian); x 725; specimen measures 55 x 57 μm

Figure 10-12 Sample J41/f8914, slide L04979/SM1086; Waiareka Volcanics, Jacksons Paddock (Kaiatan-Runangan)

Plate 87

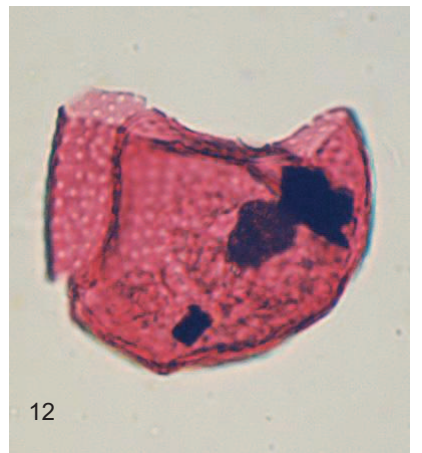
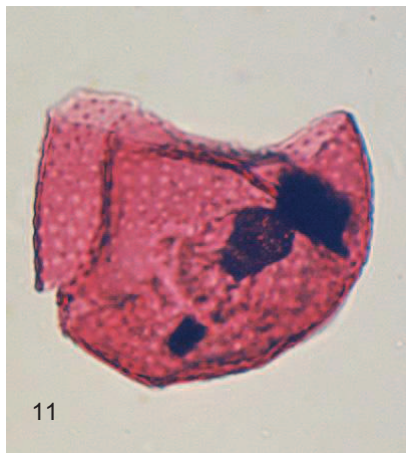
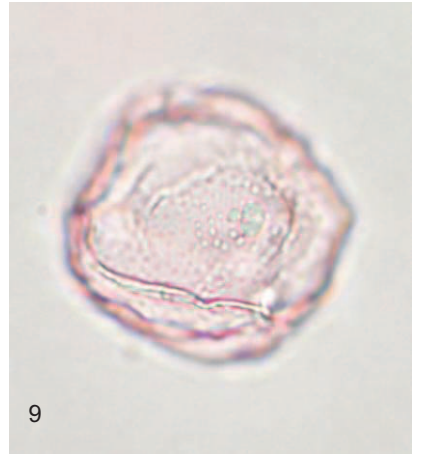
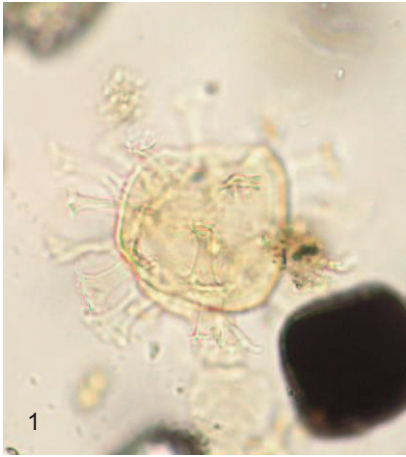


Plate 88

Batiacasphaera perforata

Figure 1-2 Sample J41/f8914, slide L04979/10-1179-070; Waiareka Volcanics, Jacksons Paddock (Kaiatan-Runangan)

Figure 3 Sample J41/f8914, slide L04979/SM1105; Waiareka Volcanics, Jacksons Paddock (Kaiatan-Runangan); x 625; specimen measures 53 x 67 μm

***Cerebrocysta* sp. 1**

Figure 4-6 Sample I43/f093, slide L16341/SM174; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 29 x 29 μm

Figure 7-9 Sample I43/f089, slide L16337/SM049; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 27 x 22 μm

***Cerebrocysta* ?sp. 2**

Figure 10-12 Sample I44/f080, slide L08947/SM003; Burnside Formation, Burnside Marl Pit (Bortonian); x 775; specimen measures 60 x 55 μm

Plate 88



Plate 89

Chlamydophorella neopilata

Figure 1-4 Sample J42/f096, slide L10951/SM2952; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 35 x 34 μm

Figure 5-6 Sample J42/f096, slide L10951/SM041; Totara Limestone, Kakanui River (early Whaingaroan); specimen measures 32 x 28 μm

Figure 7-12 Sample J42/f097, slide L10952/SM020; Totara Limestone, Kakanui River (?early Whaingaroan); specimen measures 32 x 28 μm

Plate 89

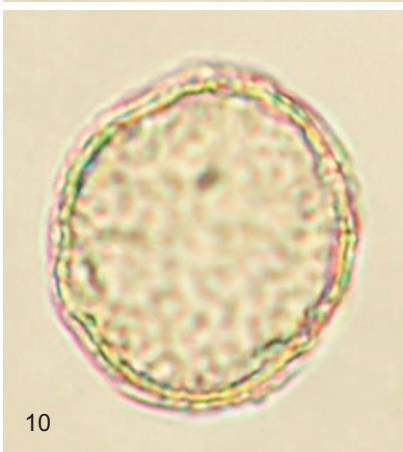


Plate 90

Chlamydophorella pilata

Figure 1-6 Sample J42/f485, slide L23120/SM046; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 850; specimen measures 56 x 33 μm

Figure 7-12 Sample J42/f485, slide L23120/SM044; ?Hampden Formation, Hampden Beach Section (Porangan-Bortonian); x 1075; specimen measures 44 x 35 μm

Plate 90



Plate 91

Dapsilidinium pseudocolligerum

Figure 1-5 Sample I43/f093, slide L16341/SM086; Burnside Formation, Puketeraki Core (Bortonian); x 550; specimen measures 72 x 75 μm

Figure 6 Sample I43/f093, slide L16341/SM116; Burnside Formation, Puketeraki Core (Bortonian); x 625; specimen measures 58 x 67 μm

Distatodinium apenninicum

Figure 7-9 Sample I43/f091, slide L16339/1-1420-223; Burnside Formation, Puketeraki Core (Bortonian); x 425; specimen measures 110 x 77 μm

?*Labyrinthodinium* sp. 1

Figure 10-12 Sample I43/f089, slide L16337/SM070; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 35 x 37 μm

Plate 91

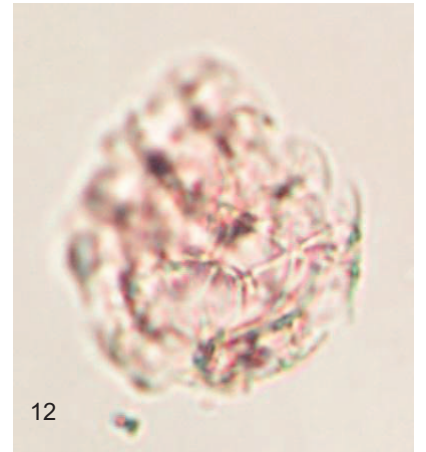
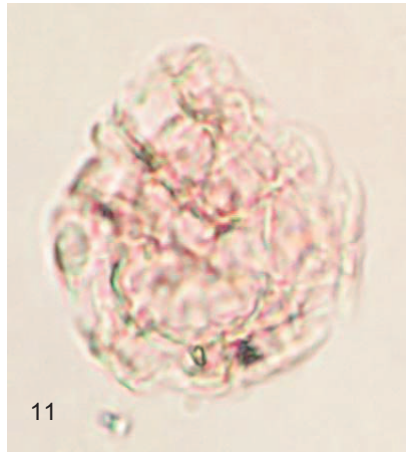
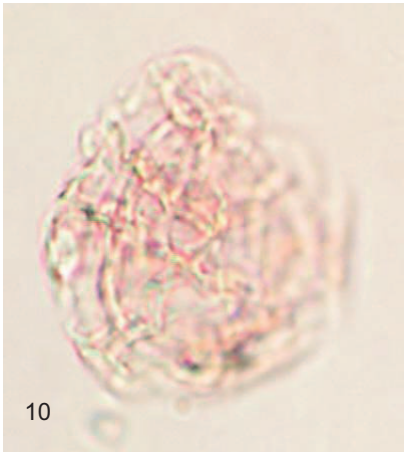
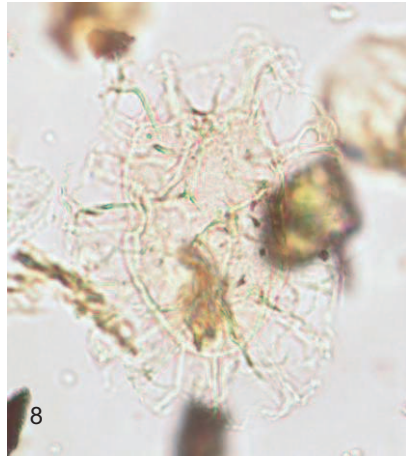
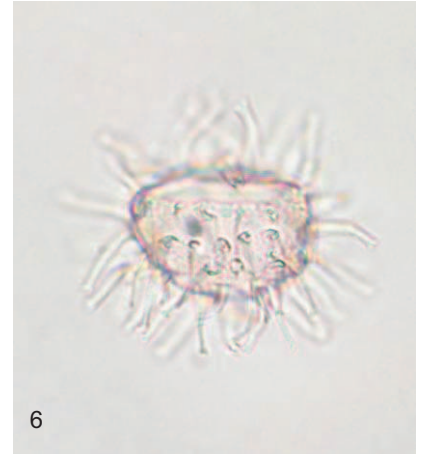


Plate 92

?*Labyrinthodinium* sp. 1

Figure 1-3 Sample I43/f089, slide L16337/2-1401-126; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 38 x 31 μm

?*Paucisphaeridium inversibuccinum*

Figure 4-6 Sample I43/f093, slide L16341/1-1445-145; Burnside Formation, Puketeraki Core (Bortonian); x 800; specimen measures 58 x 53 μm

***Indet 3* sp. 1**

Figure 7-10 Sample J42/f484, slide L23119/SM011; Kurinui Formation, Hampden Beach Section (Heretaungan); x 600; specimen measures 76 x 70 μm

Figure 11-12 Sample J42/f484, slide L23119/SM012; Kurinui Formation, Hampden Beach Section (Heretaungan); x 650; specimen measures 68 x 64 μm

Plate 92

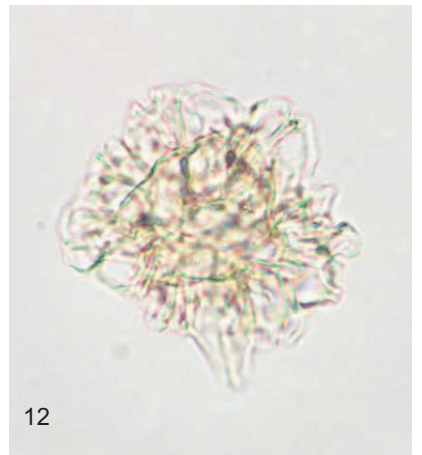
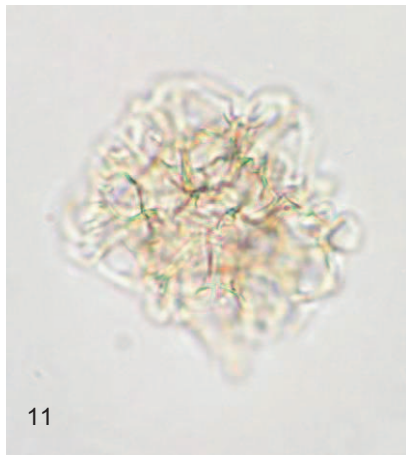
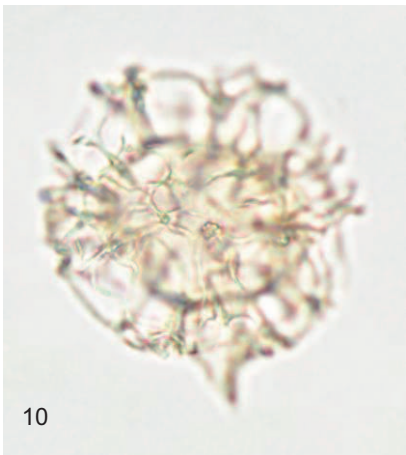
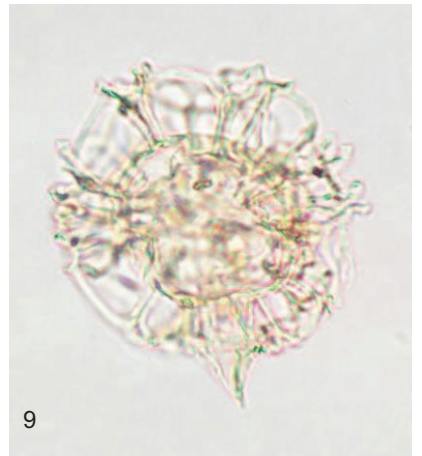
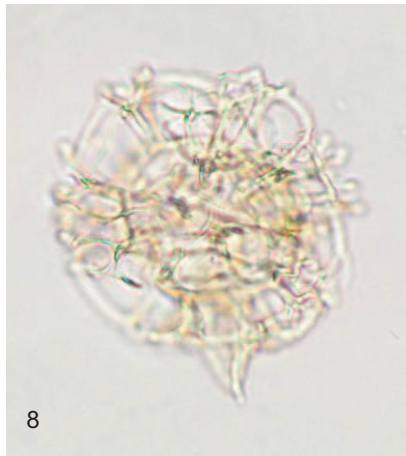
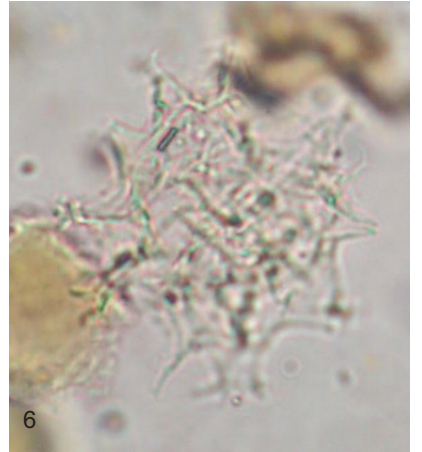
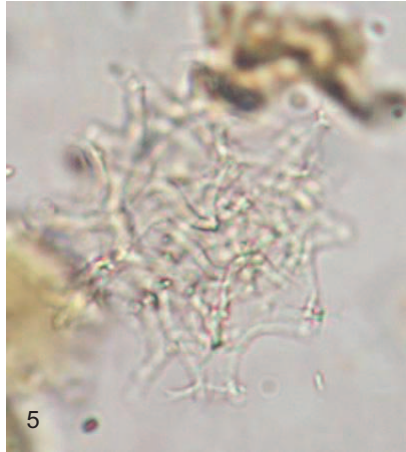
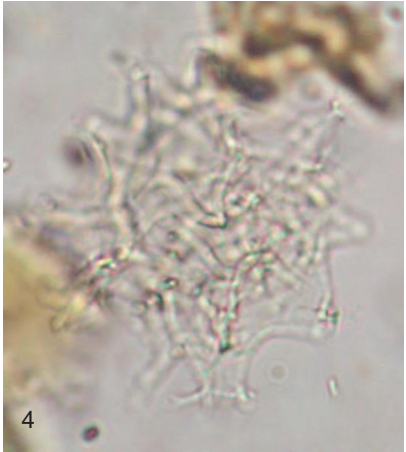
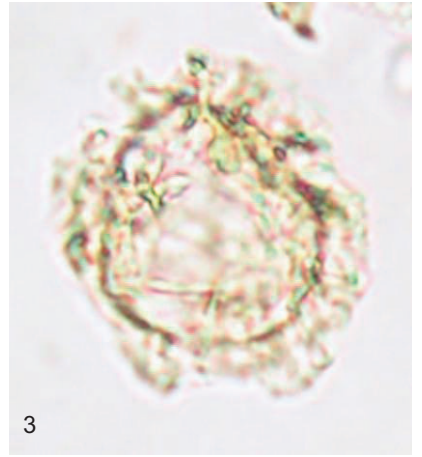
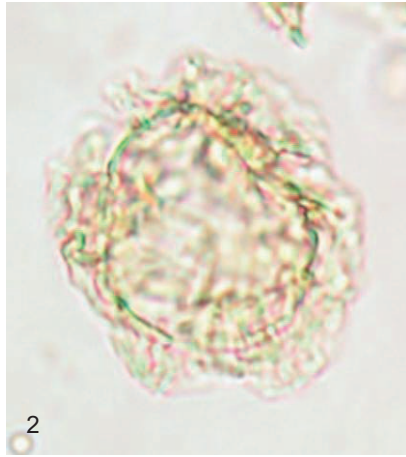


Plate 93

Indet 4 sp. 1

Figure 1-8 Sample I43/f089, slide L16337/SM103; Burnside Formation, Puketeraki Core (Bortonian);
x 625; specimen measures 75 x 55 μm

Figure 9 Sample I43/f096, slide L16344/SM041; Burnside Formation, Puketeraki Core (Kaiatan);
x 850; specimen measures 55 x 50 μm

Figure 10-12 Sample I43/f089, slide L16337/SM050; Burnside Formation, Puketeraki Core (Bortonian);
x 700; specimen measures 66 x 60 μm

Plate 93

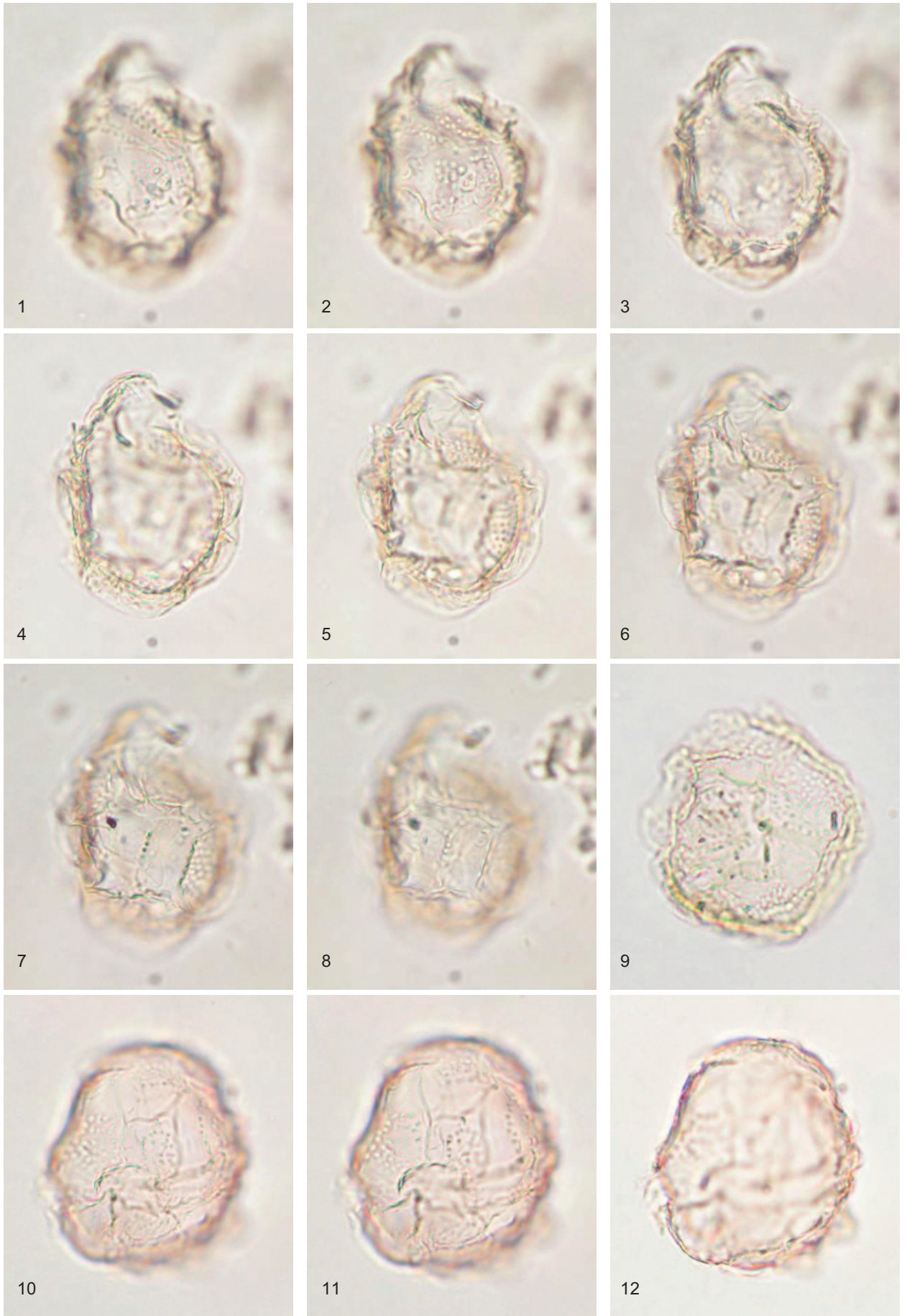


Plate 94

Indet 4 sp. 1

Figure 1-3 Sample I43/f089, slide L16337/SM050; Burnside Formation, Puketeraki Core (Bortonian); x 700; specimen measures 66 x 60 μm

?*Cymatiosphaera sp. 1*

Figure 4-6 Sample I43/f089, slide L16337/2-1453-133; Burnside Formation, Puketeraki Core (Bortonian); specimen measures 30 x 29 μm

?*Cymatiosphaera sp. 2*

Figure 7-9 Sample K29/f097, slide L10914/SM040; Port Elizabeth Member, Cape Foulwind Section (early Whaingaroan); x 675; specimen measures 58 x 62 μm

Pterospermella sp. 1

Figure 10-12 Sample U24/f419, slide L23127/SM098; Wanstead, Te Uri Stream (Porangan); x 425; specimen measures 110 x 87 μm

Plate 94

