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A review of *Scriniodinium*
Klement 1957 and *Endoscrinium*
(Klement 1960) Vozzhennikova
1967 and related dinoflagellate
cyst taxa

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INTERNAL REPORT IR/02/52

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Foreword

This report is the result of a collaborative study on aspects of the Mesozoic palynology of Australia by the British Geological Survey (BGS) and Geoscience Australia (GA) under the auspices of the Virtual Centre of Economic Micropalaeontology and Palynology (VCEMP).

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FIGURES

Figure 1. Line drawings of a Southern Hemisphere representative of *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960, based on the specimen illustrated in Plate 1 herein (CPC 37000) from the latest Oxfordian-earliest Kimmeridgian of the Peak-1 well. a - ventral view; b - dorsal view. The endocyst is lightly shaded and the paraplates are indicated using Kofoidian notation. The parasutural ridges on specimen CPC 37000 are not fully developed, and some of the paratabulation pattern illustrated is inferred; based on Gocht (1979, fig. 7). The parasulcus in a and the archeopyle in b are shaded in a darker tone for emphasis. Note that the paracingular and parasulcal paraplates are not differentiated. There is a single equatorial claustrum on the right lateral side. The specimen shows clear dextral torsion because the 4'''/5''' boundary lies within the 3'' precingular paraplate and the 2''' and 5''' paraplates are small and large respectively.

Figure 2. The stratigraphical ranges of Jurassic and earliest Cretaceous representatives of *Endoscrinium* and *Scriniodinium* in Europe and Australasia. In the European Age column, both the *sensu anglico* and the Boreal stage nomenclatures are depicted; these are indicated * and ** respectively. The European dinoflagellate cyst subzones are those of Woollam and Riding (1983) and Riding and Thomas (1992). The *Spiniferites ramosus* (Sr) Zone (indicated ⁺) is that of Davey (1979). The Australasian palynomorph zones are those of Helby et al. (1987) and Foster (2001); these are all dinoflagellate cyst zones except the *Callialasporites turbatus* Oppel Zone (Ctu), which is a spore-pollen zone. The taxa in bold typeface are considered to be key biostratigraphical markers. All four subspecies of *Scriniodinium dictyotum* are illustrated for Europe. The columns marked '*S. dictyotum* ⁺⁺' refer to the entire species, inclusive of all subspecies. The Australasian range data are taken from Cookson and Eisenack (1958, 1960), Helby et al. (1987), Backhouse (1988) and Helby (personal communication, 2000). The European range data are drawn from a wide literature base, but largely from Riding and Thomas (1992) and Costa and Davey (1992).

Figure 3. A line drawing of an idealised specimen of a Northern Hemisphere representative of *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960. The drawing is based on the specimen illustrated by Klement (1960, pl. 1, fig. 1) from the Late Jurassic of south-west Germany. The archeopyle is labelled using traditional Kofoidian notation and is shaded darker than the endocyst. Note the single apical and paired equatorial claustra, the irregularly perforate periphragm and the fold in the periphragm near the antapex which is suggestive of dextral torsion. The operculum has been dislodged into the endocyst.

Figure 4. Line drawings of *Endoscrinium luridum* (Deflandre 1939) Gocht 1970 and *E. attadalense* (Cookson & Eisenack 1958) comb. nov. The paraplates are indicated using Kofoidian notation and the endocysts and archeopyles are shaded light and dark respectively. Note the neutral torsion. a - the cosmopolitan species *Endoscrinium luridum* in dorsal view, based on the paratype (Deflandre, 1939, pl. 5, fig. 6), from the Middle Oxfordian of Villers-sur-Mer, Normandy, northern France (sample AM 59). b - the Southern Hemisphere species *Endoscrinium attadalense* in dorsal view, based on the holotype (Cookson & Eisenack 1958, pl. 1, fig. 7), from the South Perth Formation (Lower Cretaceous, ?Aptian) of the Attadale Borehole, Western Australia at 246.58m.

PLATES

PLATE 1

A single specimen of *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960 from ditch cuttings between 1463.04m and 1466.09m in the Peak-1 well, offshore Western Australia

(Foster, 2001, fig. 1). This interval lies within the the Dingo Claystone Formation and is referable to the latest Oxfordian-earliest Kimmeridgian *Wanaea clathrata* (6bi) Acme Zone of Helby et al. (1987). Note the small apical horn developed by the periphragm only, the single paraplate precingular archeopyle, the equatorial claustrum on the right lateral side and the circumcavate cyst organisation. The specimen exhibits clear gonyaulacalean paratabulation via low, smooth ridges on the periphragm; dextral torsion, characteristic of the Subfamily Cribroperidinioideae, is clearly visible in fig. 4. Magnification: all figures x500; all photomicrographs taken using plain transmitted light. The figured specimen number is CPC 37000 and it is housed in the Commonwealth Palaeontological Collection (CPC) of Geoscience Australia, Canberra, ACT 2601, Australia (see Appendix). The specimen is in ventral view and figures 1 to 4 are a high to low focus sequence.

- 1 High focus.
- 2 High/median focus.
- 3 Median/low focus.
- 4 Low focus.

PLATE 2

Magnification: all figures x500; all photomicrographs taken using plain transmitted light.

1-7 *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960 emend. nov. All specimens are typical of the Northern Hemisphere in that they lack indications of paratabulation except for the archeopyle and paracingulum. Note the possible presence of small apical and antapical horns/protuberances formed from periphragm, the single paraplate precingular archeopyle, the apical and equatorial claustra and the circumcavate cyst organisation.

- 1 Specimen MPK 12602, Ampthill Clay Formation, Middle Oxfordian, *C. tenuiserratum* Standard (ammonite) Zone of the Nettleton Bottom Borehole. A large specimen in dorsal view, high/median focus. Note the apical claustrum.
- 2 Specimen MPK 4547, Ampthill Clay Formation, Upper Oxfordian, *A. glosense* Standard (ammonite) Zone of the Nettleton Bottom Borehole. Specimen in dorsal view, median focus. Note the operculum inside the endocyst.
- 3 Specimen MPK 12603, Weymouth Member, Oxford Clay Formation, Lower Oxfordian, *Q. mariae* Standard (ammonite) Zone/*C. scarburgense* Standard (ammonite) Subzone of the Warboys Borehole. A relatively small, squat specimen in ventral view, median focus. Note the apical claustrum.
- 4 Specimen MPK 12604, details as fig. 1. A relatively large specimen in dorsal view, high focus. Note the clearly defined paracingulum and the lack of polar horns.
- 5 Specimen MPK 12605, Weymouth Member, Oxford Clay Formation, Lower Oxfordian, *C. cordatum* Standard (ammonite) Zone of the Nettleton Bottom Borehole. Specimen in dorsal view, high/median focus. Note that the operculum is displaced and is in the endocyst.
- 6 Specimen MPK 3557, Weymouth Member, Oxford Clay Formation, Lower Oxfordian, *Q. mariae* Standard (ammonite) Zone/*C. scarburgense* Standard (ammonite) Subzone of the Warboys Borehole. A relatively small specimen in ventral view, median/low focus. Note the displaced operculum, the apical and equatorial claustra and the polar horns/protuberances formed from periphragm only.
- 7 Specimen MPK 12606, Ampthill Clay Formation, Upper Oxfordian, *A. regulare* Standard (ammonite) Zone of the Nettleton Bottom Borehole. An elongate specimen in ventral view, median/low focus. Note the prominent equatorial claustra and the apical horn/protuberance.

8, 9 *Endoscrinium luridum* (Deflandre 1939) Gocht 1970. Note the rounded, subpentangular outline, the subcircular endocyst, the tapered, blunt-ended antapex, the circumcavate cyst organisation, the single paraplate precingular archeopyle and the gonyaulacalean paratabulation with neutral torsion.

8 Specimen MPK 12607, details as fig. 1. Specimen in dorsal view, high focus. This is an exceptionally well-preserved specimen, note the small apical protuberance formed by periphragm.

9 Specimen MPK 12608, details as fig. 2. Specimen in ventral view, low focus. Note the folded antapical region and the almost perfectly circular endocyst.

PLATE 3

Magnification: all figures x500, except figure 4, which is x750. All photomicrographs taken using plain transmitted light. Figure 5 is a composite photomicrograph.

1 *Scrinioidinium dictyotum* Cookson & Eisenack 1960 subsp. *pyra* Gitmez 1970. Specimen MPK 4684, Kimmeridge Clay Formation, Lower Kimmeridgian, *R. cymodoce* Standard (ammonite) Zone of the Nettleton Bottom Borehole. Specimen in oblique dorsal/right lateral view, median focus. Note the apical horn, the holocavate cyst organisation and the clear dextral torsion exhibited by the middorsal 4"/5" parasutural ridge.

2 *Scrinioidinium inritibile* Riley in Fisher & Riley 1980. Specimen MPK 4065, Kimmeridge Clay Formation, Lower Kimmeridgian, *A. mutabilis* Standard (ammonite) Zone of the Nettleton Bottom Borehole. Specimen in dorsal view, high/median focus. Note the narrow pericoel, the single paraplate precingular archeopyle and the few, discontinuous parasutural ridges, which appear to indicate dextral torsion.

3 *Endoscrinium luridum* (Deflandre 1939) Gocht 1970. Specimen MPK 6716, Digg Siltstone Member, Staffin Shale Formation, Middle Oxfordian, *C. tenuiserratum* Standard (ammonite) Zone of the foreshore outcrop at Digg, Isle of Syke. Specimen in dorsal view, high focus. Note the angular outline, the single paraplate precingular archeopyle and the clear neutral torsion.

4, 7 *Scrinioidinium crystallinum* (Deflandre 1939) Klement 1960 emend. nov. 4 - Specimen MPK 12609, Amptill Clay Formation, Middle Oxfordian, ?*C. tenuiserratum* Standard (ammonite) Zone of Warboys Brick Pit. An isolated operculum, median focus; note the presence of both endophragm and periphragm. 7 - Specimen MPK 12610, Weymouth Member, Oxford Clay Formation, Lower Oxfordian, *Q. mariae* Standard (ammonite) Zone of Castle Hill, Scarborough. Specimen in dorsal view, median focus. A specimen with strong body colour, note the equatorial claustra.

5, 6 *Endoscrinium galeritum* (Deflandre 1939) Vozzhennikova 1967 emend. nov. 5 - Specimen MPK 4656, Amptill Clay Formation, Middle Oxfordian, *C. tenuiserratum* Standard (ammonite) Zone of the Nettleton Bottom Borehole. Specimen in oblique ventral view. Note the biconical outline, the bicavate cyst organisation and the gonyaulacacean paratabulation. 6 - Specimen MPK 6719, details as fig. 3. Specimen in ventral view, high focus. Note the distinct paracingulum and the partially reticulate periphragm.

8-9 *Scrinioidinium pharo* (Duxbury 1977) Davey 1982. Specimen MPK 1281, Bed 6, the basal Cretaceous nodule bed, of the Sandringham Sands Formation (Casey, 1973), Lower Ryazanian, *R. runctoni* Standard (ammonite) Zone of Manor Farm, Norfolk. Specimen in ventral view, high to low focus sequence. Note the elongate outline, the prominent apical horn formed from periphragm, the circumcavate cyst organisation and the full gonyaulacacean paratabulation indicated by parasutural and penitabular ridges. Figure 10 (low focus) clearly illustrates dextral torsion, with the 4"/5" paraplate boundary located middorsally at the centre of the 3" paraplate.

Summary

Specimens of the well known and distinctive Jurassic (typically Oxfordian) dinoflagellate cyst species *Scriniodinium crystallinum* from Australia and New Zealand vary from being nonparatabulate to paratabulate. Where present, the paratabulation, which is manifested by low parasutural ridges on the periphragm, shows a clear dextral torsion, indicating affinity with the gonyaulacacean subfamily Cribroperidinioideae. Other species of *Scriniodinium*, such as *S. pharo* and *S. playfordii* confirm that this genus unequivocally belongs in the subfamily Cribroperidinioideae. *Scriniodinium* and *S. crystallinum* are both emended in order to note the cribroperidinioid paratabulation. The morphologically similar genus *Endoscrinium*, however, exhibits neutral torsion and thus belongs in the subfamily Leptodinioideae. *Endoscrinium* and its type, *E. galeritum*, are emended to note this paratabulation style. On the basis of this clear paratabulation difference between *Scriniodinium* and *Endoscrinium*, nine species are transferred to the most appropriate genus. *Endoscrinium anceps* is transferred to *Scriniodinium* as it has dextral torsion. *Endoscrinium acroferum*, *E. attadalense*, *E. heikeae*, *E. indicum*, *E. irregulare*, *E? novissimum*, *E. obscurum* and *E. reticulatum* are all new combinations of taxa with neutral torsion which were previously placed in *Scriniodinium*. Additionally, *Aldorfia warringtonii* is transferred to *Apteodinium* because it displays dextral torsion. *Scriniodinium* and *Endoscrinium* peaked worldwide during the late Callovian to early Kimmeridgian. There are some stratigraphical range differences of species of *Scriniodinium* and *Endoscrinium* between the Northern and Southern hemispheres. For example, in Europe, *Scriniodinium crystallinum* ranges from the late Callovian to the earliest Kimmeridgian and is a reliable marker species. However, in the Southern Hemisphere, the species has a significantly younger range. It is present consistently from the early Oxfordian to the mid Tithonian and occurs in low numbers to the late Berriasian. However, there are many strong global consistencies with these two important genera. Notably, *Endoscrinium* has the older range base and this is consistent with the phylogeny of the subfamilies Leptodinioideae and Cribroperidinioideae. Some potential evolutionary trends have been noted; these include *Endoscrinium asymmetricum* and *E. acroferum* (late Bajocian to Callovian) possibly being precursors to *E. luridum* (Oxfordian-Kimmeridgian) in Europe.

1 Introduction

This report is the fourth in a series representing the results of the BGS-GA palynology collaborative work undertaken under the auspices of the Virtual Centre of Economic Micropalaeontology and Palynology (VCEMP) during the BGS financial year 2001-2002. This is a major taxonomic review of two important cosmopolitan dinoflagellate cyst genera and related taxa. It is part of an initiative to improve Mesozoic correlations between Australasia and Europe. The intention is to formally publish the principal text of this work in order that the validation of the several taxonomic changes may proceed. This internal report is not a publication in terms of International Code of Botanical Nomenclature (ICBN) criteria and this document in itself does not formally validate the new combinations and emendations.

In the first major publication on Jurassic dinoflagellate cysts of the modern era, Deflandre (1939) described Oxfordian marine palynofloras from Villers-sur-Mer, Normandy, northern France. The magnificent cliff exposures west of the town of Villers-sur-Mer, near Auberville (Riout et al., 1991, fig. 6), locally known as Vaches Noires (Black Cows), include the most extensive and complete exposures of Lower Oxfordian rocks in France. The strata exposed at Villers-sur-Mer are the uppermost Callovian Marnes de Dives Formation to the Middle Oxfordian Coral-Rag Formation (Bignot, 1957; Riout et al., 1991). All the samples studied by Deflandre (1939) are

from the Oxfordian succession; the majority were collected from the Marnes de Villers and Oolithe Ferrugineuse de Villers formations. Many of the most important early and mid Oxfordian dinoflagellate cysts were described in this landmark publication (see also Albert and Wharton, 1987). The majority of the illustrations are line drawings, with some photomicrographs. Six of the most important species formally described in Deflandre (1939), including *Gymnodinium* (now *Scriniodinium*) *crystallinum*, were earlier illustrated, but not formally described, by Deflandre (1938).

In this report, a re-evaluation of *Scriniodinium crystallinum*, one of the largest, most widespread and distinctive of all Jurassic dinoflagellate cyst species, is presented as well as a discussion of some closely related taxonomic matters. Sarjeant (1978, p. 29) gave a brief review of the principal Jurassic cavate dinoflagellate cyst genera and stated that a restudy of *Scriniodinium* and *Endoscrinium* would be 'of great value to biostratigraphy'. The restudy is based on observations of material from Australia and New Zealand, which unequivocally show that *Scriniodinium crystallinum* has attributes with the gonyaulacacean subfamily Cribroperidinioideae (Figure 1; Plate 1). This is in contrast with the treatment of Fensome et al. (1993), who listed *Scriniodinium* (of which *Scriniodinium crystallinum* is the type) within subfamily uncertain of the family Gonyaulacaceae. *Scriniodinium crystallinum* is a species of subconical/ovoidal, circumcavate cysts with a single-paraplate precingular archeopyle, variable development of claustra, and a periphragm that is often extended into polar protuberances. A pair of equatorial claustra is especially characteristic. In Europe, the species is a reliable marker for the late Callovian to the earliest Kimmeridgian interval (Woollam and Riding, 1983; Riding, 1987; Riding and Thomas, 1992; Riding et al., 1993). It is rare in the earliest Kimmeridgian (Partington et al., 1993) and, in higher northerly latitudes, it is entirely absent in the late Callovian (Riding and Thomas, 1997). Therefore it is most characteristic of the Oxfordian Stage in Europe (Figure 2). In Australasia the species has been recorded by Cookson and Eisenack (1958, pl. 1, figs 1, 2, 5), Wilson (1984, fig. 5.1), Davey (1987, pl. 7, fig. 9; 1999, fig. 9), Dettmann and Thomson (1987, fig 8c), Helby et al. (1987, fig. 18I), Wilson and Helby (1987, pl. 1, fig. 12) and Helby et al. (1988, figs 7F, 9Q). The composite range of these records is Oxfordian to Berriasian, but the post Kimmeridgian occurrences are sparse and inconsistent, as summarized in Helby et al. (1987, fig. 21). Many of the Tithonian to Berriasian occurrences may be reworked. The species is prominent in the early to mid Oxfordian *Wanaea spectabilis* Interval Zone of Helby et al. (1987, fig. 15). Elsewhere in the Southern Hemisphere, there have been several reports of *Scriniodinium crystallinum*, for example by Davey (1987, fig. 14; 1999). The specimen from the Antarctic Peninsula illustrated by Dettmann and Thomson (1987, fig 8c) was reworked into Upper Cretaceous (Campanian) strata. In summary, *Scriniodinium crystallinum* is widely distributed and most characteristic of the Oxfordian in Europe and the Southern Hemisphere, but appears to range significantly higher, possibly into the Tithonian, in the Southern Hemisphere (Figure 2).

The genera, species and subspecies of dinoflagellate cysts mentioned in this contribution are listed in Appendix 1 with full author citations. Appendix 2 lists all the taxa which have ever been assigned to *Scriniodinium* and *Endoscrinium* in three categories, currently accepted, questionably assigned and reassigned species and subspecies. The figured specimen from Australia is housed in the Commonwealth Palaeontological Collection (CPC) of Geoscience Australia, Canberra, ACT 2601, Australia. The British specimens are curated in the palaeontological collections of the British Geological Survey, Nottingham NG12 5GG, UK. All the figured specimens are listed in Appendix 3.

2 The paratabulation of *Scrinodinium crystallinum* and its taxonomic implications

In specimens of *Scrinodinium crystallinum* found in the Northern Hemisphere, including the type, paratabulation is indicated by only the monoplacoid precingular endoarcheopyle and the low parasutural ridges on the periphragm that delineate the paracingulum (Klement, 1960; Jan du Chêne et al., 1986; 1999; Riding, 1987; Riding et al., 1999). However, some European specimens appear to exhibit faint, discontinuous parasutural ridges. For example, such lineations are present on a specimen from the Upper Jurassic of the Dutch sector of the North Sea (Herngreen et al., 2000, pl. 10, fig. 5); however, it is not clear whether they are all parasutures. By contrast, specimens of *Scrinodinium crystallinum* from the Southern Hemisphere illustrated by Wilson and Helby (1987, pl. 1, fig. 12), Helby et al. (1988, fig. 7F), and herein (Plate 1) are at least partially paratabulate. These paratabulate specimens clearly show that, in the postcingular paraplate series, the 4"/5" boundary is closely aligned with the centre of the 3" precingular paraplate (Figure 1; Plate 1). This configuration is referred to as dextral torsion (Fensome et al., 1993). Other paratabulation features that generally accompany dextral torsion, such as a small 2", a large 5" and a markedly asymmetrical 1" paraplate also occur (Gocht, 1979; Helenes, 1984; Evitt, 1985, fig. 10.9I, J; Lucas-Clark, 1987). The presence of dextral torsion indicates that *Scrinodinium crystallinum* has a *Cribroperidinium*-like paratabulation pattern and thus belongs in the subfamily Cribroperidinioideae (see below). Further evidence for the cribroperidinioid paratabulation style of *S. crystallinum* is the occasional presence of a median antapical protuberance developed in the periphragm (Plate 2, fig. 6). This is a feature often associated with the 4"/5" paraplate boundary in cribroperidinioids. Not all specimens of *Scrinodinium crystallinum* from the Southern Hemisphere are paratabulate, however. The figured specimens of Cookson and Eisenack (1958, pl. 1, figs 1, 2, 5), Davey (1987, pl. 7, fig. 9), Dettmann and Thomson (1987, fig. 8c), Helby et al. (1987, fig. 18I) and Helby et al. (1988, figs 9Q), have parasutural ridges that indicate only the paracingulum. Wilson (1984, fig. 5.1) illustrated a specimen from the Heterian (Kimmeridgian) of New Zealand in ventral view and focus. It appears to be paratabulate except dorsally, and hence no evidence of dextral torsion is apparent.

Scrinodinium crystallinum is the type of the genus *Scrinodinium* which Fensome et al. (1993, p. 94) classified questionably as 'subfamily Uncertain' within the Family Gonyaulacaceae. That the this genus is characterised by dextral torsion is strongly supported by the morphology of other species of *Scrinodinium*. The most convincing support comes from a specimen of the cosmopolitan species *Scrinodinium playfordii* figured by Brenner (1988, pl. 10, fig. 3) from the Upper Jurassic of Germany. *Scrinodinium playfordii* is morphologically very similar to *S. crystallinum*, and Jan du Chêne et al. (1986, p. 316) synonymised the two species. However, Brenner (1988, p. 79) preferred to retain both species, with *S. playfordii* distinguished by its partially reticulate periphragm and prominent apical horn. The holotype of *S. playfordii* from Western Australia also appears to have a *Cribroperidinium*-style paratabulation pattern (Cookson and Eisenack, 1960, pl. 37, fig. 6). *Scrinodinium bucinatum* is also closely similar to *S. crystallinum* and exhibits dextral torsion (Brenner, 1988, pl. 12, fig. 1), as does *Scrinodinium inritibile*. The latter is a European mid Oxfordian to earliest Portlandian species. It is most prominent in the Kimmeridgian and, although similar in overall morphology to *S. crystallinum*, its pericoel is extremely narrow (Plate 3, fig. 2). It consistently exhibits a *Cribroperidinium*-like paratabulation with clear dextral torsion. The 4"/5" paraplate boundary is clearly middorsal (Ioannides et al., 1976, pl. 4, fig. 9; Fisher and Riley, 1980, pl. 2, fig. 9; Riding, 1984, pl. 4, fig. 9; Riding and Thomas, 1988, pl. 2, fig. 2; Herngreen et al., 2000, pl. 10, fig. 6). There are several other species of *Scrinodinium*, such as *S. campanula* and *S. pharo*, which also have unequivocal hypocystal dextral torsion (Habib, 1974; Davey, 1979) and hence are characteristic of the subfamily Cribroperidinioideae. Lucas-Clark (1987, table 1) listed '*Endoscrinium* (part)'

as part of the *Cribroperidinium* and *Aptiana-Ventriosum* Complex. This was presumably due to the clear cribroperidinioid paratabulation of some species of *Scriniodinium*.

3 The taxonomic implications for *Scriniodinium* and *Endoscrinium*

Because *Scriniodinium crystallinum* is shown here to have a *Cribroperidinium*-like paratabulation, with dextral torsion, by extension all other unequivocal representatives of *Scriniodinium* should have a similar paratabulation. *Endoscrinium* was erected by Klement (1960) as a subgenus of *Scriniodinium*, and was subsequently elevated to generic rank by Vozzhennikova (1967). As separate genera, *Scriniodinium* and *Endoscrinium* are broadly similar cavate gonyaulaclean genera distinguished from one another on the absence (in *Scriniodinium*) or presence (in *Endoscrinium*) of paratabulation. That the two genera have been synonymized periodically by some authors (e.g. Stover and Evitt, 1978; Dodekova, 1990) reflects the generally unsatisfactory nature of presence or absence of paratabulation in separating genera. These two genera have also been re-separated (e.g. Lentin and Williams, 1981; 1985), in recognition of their disparate detailed morphologies, despite their superficial similarities. The new evidence presented here confirms that the two genera can be separated on the basis of their paratabulation. The type of *Endoscrinium*, *E. galeritum*, clearly has a mid dorsal 4th paraplate and a symmetrical 1st paraplate (Deflandre, 1939). Other species, such as *Endoscrinium asymmetricum*, *E. attadalense*, and *E. luridum* also have neutral torsion, thus conforming to the paratabulation pattern characteristic of the subfamily Leptodinioideae (Fensome *et al.*, 1993).

Thus, in the following systematic section, species of *Scriniodinium* and *Endoscrinium* are re-assessed with regard to whether their tabulation is cribroperidinioid or leptodinioid, and re-assigned where necessary. Some taxa are either not paratabulate or their illustrations are not clear enough to assess hypocystal dextral torsion. Since neutral torsion is markedly more common than dextral torsion among gonyaulaccean dinoflagellates, these species are placed into *Endoscrinium* by default.

4 Systematic Palaeontology

The intent of this section is to provide primarily a systematic treatment, with revisions where warranted, of the genera *Scriniodinium* and *Endoscrinium* based on the observations discussed herein. However, during the course of the present work, observations were made with regard to several other taxa, for example the genus *Aldorfia* and so these are also included where appropriate. The three subfamilies of the family Gonyaulacaceae are discussed in order of importance to this work, viz. Cribroperidinioideae, Leptodinioideae and Gonyaulacoideae. Genera are listed within the subfamilies in alphabetical order except in the case of the Cribroperidinioideae, where *Scriniodinium* is treated before *Apteodinium* due to the relative importance of these genera in terms of this contribution. A single genus, *Trithyrodinium*, of the order Peridiniales is discussed in relation to a transfer.

Division DINOFLAGELLATA (Bütschli 1885) Fensome *et al.* 1993

Subdivision DINOKARYOTA Fensome *et al.* 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome *et al.* 1993

Order GONYAULACALES Taylor 1980

Suborder GONYAULACINEAE (autonym)

Family GONYAULACACEAE Lindemann 1928

Subfamily CRIBROPERIDINIOIDEAE Fensome et al. 1993

Genus *Scriniodinium* Klement 1957 emend. nov.

Type. *Scriniodinium crystallinum* (Deflandre 1939) Klement 1960 emend. nov.

Emended diagnosis. Proximate cribroperidinioidean cysts that are cavate and possess a simple precingular archeopyle. Paratabulation typically absent to weakly developed, but may be well developed.

Emended description. Subellipsoidal to lenticular, proximate, cavate dinoflagellate cysts, intermediate to large in size. Typically circumcavate, but may be bicavate and occasionally partially holocavate. Endocyst ellipsoidal to subspherical. Apical and antapical protruberances may be present. Periphragm markedly thinner than endophragm. Both cyst walls smooth, perforate or bearing low relief ornamentation, the majority of which is nontabular. Occasionally, in holocavate forms, endophragm and periphragm may be connected by nontabular slender, solid elements or by septa. A sexiform gonyaulacacean paratabulation may be partially to fully indicated by low, parasutural ridges or low crests on periphragm. Parasutural features normally distally smooth, but occasionally surmounted by low-relief elements. Paratabulation formula is ?pr, 4', 6", 6c, 6"', 1p, 1"', xs and hypocystal paratabulation, where indicated, exhibits dextral torsion. Archeopyle monoplacoid precingular, type P₃", with free operculum. Claustra may be present equatorially or in polar regions.

Remarks. The genus *Scriniodinium*, as emended here, is restricted to forms with a cribroperidinioidean paratabulation. This is a paratabulation exhibiting dextral torsion and concomitant features such as small paraplates 1" and 2"', a large 5" and a strongly asymmetrical 1"". Although traditionally this genus was regarded as lacking paratabulation, or at most possessing a weak paratabulation, paratabulate forms closely similar to the type exist and unequivocally attest to the cribroperidinioidean affinity of typical members of the genus. The original generic description of Klement (1960, p. 409) is no longer useful in a modern context. Stover and Evitt (1978, p. 187) gave a modified description but did not formally emend the genus. The emendation of Prauss (1989, p. 45) provided only a restated paratabulation formula and archeopyle type and did not represent a true differentiation of the genus. As emended here, *Scriniodinium* is consistently primarily dorsoventrally flattened; most representatives are circumcavate but occasional forms may be bicavate and exhibit lateral contact of the cyst walls; others may be partially holocavate. The outline varies from subcircular to elongate ovoidal. The parasutural ridges or low crests may be faint and discontinuous, but the paracingulum is normally present. The parasulcus is not subdivided. A periarcheopyle is present (Plate 3, fig. 4) and the operculum is often displaced within the cyst (Plate 2, figs 2, 6). The inclusion of nontabular elements between the wall layers of this genus is a departure from earlier descriptions of *Scriniodinium*. Most representatives do not exhibit these features and, where developed, they are not normally densely distributed. The species *Scriniodinium bucinatum* and *S. dictyotum* clearly possess septa between the endophragm and periphragm (Brenner, 1988, pls 10-12). These forms are not representatives of *Aldorfia* because they lack a dense, differentiated autophragm.

Comparison. *Scriniodinium* differs from *Endoscrinium*, the most similar dinoflagellate cyst genus, in having dextral torsion and not being consistently paratabulate. *Gonyaulacysta* is normally bicavate and typically has denticulate/spinose parasutural crests and an elongate epicyst and apical horn. This genus is also characterised by an S-type ventral paratabulation arrangement and neutral torsion. *Aldorfia* has neutral torsion and a dense, differentiated

('spongy') autophragm. The largely Jurassic genera *Ambonosphaera* and *Sirmiodiniopsis*, like *Scriniodinium*, are circumcavate; *Sirmiodiniopsis* also has two prominent claustra. However, both *Ambonosphaera* and *Sirmiodiniopsis* have apical archeopyles and the claustra in *Sirmiodiniopsis* are close to the antapex in the lateral regions. *Sirmiodinium* is also gonyaulacacean, circumcavate and has a claustrum. However, the archeopyle in *Sirmiodinium* is combination (apical/precingular) and the claustrum is antapical.

Scriniodinium crystallinum (Deflandre 1939) Klement 1960 emend. nov.

(Plate 1, figs 1-4; Plate 2, figs 1-7; Plate 3, figs 4, 7; Figures 1, 3).

Emended diagnosis. A species of *Scriniodinium* with a subovoidal to biconical shape, usually weakly-developed paratabulation at best, and claustra developed at least in the lateral equatorial areas.

Emended description. A subovoidal, biconical species of *Scriniodinium* which may exhibit small, distally rounded apical and antapical protrusions. Paracingulum equatorial, subdividing the cyst into an epicyst and hypocyst of equal size. Paratabulation indicated by variably developed paracingular ridges and the archeopyle. Periphragm and endophragm smooth to microscabrate, occasionally partially microperforate. A partial cribroperidinioid paratabulation pattern may be indicated by low, smooth parasutural ridges. A pair of claustra occur in the lateral equatorial areas and a claustrum may be present apically. Small, subcircular/ovoidal claustra may penetrate the periphragm in the periphery of the cyst, close to the base of the pericoel. Size, intermediate to large.

Dimensions. These are all in micrometres (μm): 25 specimens were measured.

	Minimum	Mean	Maximum
Overall length including apical protuberance(s):	71	87	102
Length of endocyst:	56	67	76
Overall width at paracingulum:	67	76	87
Width of endocyst at paracingulum:	49	59	71
Maximum width of pericoel in the lateral areas:	6	9	11

The measured specimens are from the late Callovian to Oxfordian interval from conventional core samples from the Warboys and Nettleton Bottom boreholes and outcrop samples from Warboys Brick Pit and the North Yorkshire coast (Appendix 2; Woollam and Riding, 1983). These data are presented because there appears to be a difference in size between European and Australasian specimens of this species (see Remarks below).

Remarks. The description of this species is emended herein in order to fully document the presence of claustra and the dextral torsion in the hypocystal paratabulation. The species has not been formally emended since the original description of Deflandre (1939, p. 165), although Klement (1960, p. 18-20) gave a comprehensive morphological description and detailed measurements. The equatorial claustra are unique; their presence means that the species can be recognised even if only a fragment of the equatorial lateral area is observed. Although the polar claustra are not consistently developed, they are widespread as shown in the specimens illustrated by Stancliffe (1991, pl. 2, fig. 7) and Jan du Chêne et al (1999, pl. 6, fig. 2). The Australian specimen illustrated in Plate 1 is relatively large; the pericyst is $122\ \mu\text{m} \times 102\ \mu\text{m}$ and the endocyst is $96\ \mu\text{m} \times 78\ \mu\text{m}$. Material from Europe is significantly smaller (see Dimensions above; and also Deflandre, 1939, p. 165 and Klement, 1960, p. 20). For each parameter measured, the Australian specimen is larger than the largest European specimen studied. This size disparity was also noted by Cookson and Eisenack (1958, p. 24).

Holotype and type occurrence. Deflandre (1939, pl. 5, figs 1, 2), from the lowermost Oxfordian (Upper Jurassic) Marnes de Villers Formation, Villers-sur-Mer, Normandy, northern France.

Stratigraphical distribution. In Europe and adjacent regions in the Northern Hemisphere, *Scriniodinium crystallinum* ranges from the late Callovian, *P. athleta* Standard (ammonite) Zone to the earliest Kimmeridgian, *P. baylei* Standard (ammonite) Zone (Figure 2). The earliest Kimmeridgian records are relatively sparse and in Scotland and areas to the north, the species is not present in the late Callovian so it is especially characteristic of the Oxfordian Stage. In Australasia, *S. crystallinum* is also prominent in the early-Mid Oxfordian and ranges up to the mid-late Tithonian in lower proportions (Figure 2).

Other species.

Scriniodinium? amalthei (W. Wetzel 1966) Sarjeant 1980.

Remarks. This late Pliensbachian species is apparently paratabulate, but the precise paraplate configuration is not clear. This taxon was based upon a single specimen and it has not been recorded with certainty since its original description. It is therefore not deemed to be a useful taxon. Sarjeant (1980) and Jan du Chêne et al. (1986, p. 317) both deemed this species to be a questionably accepted species of *Scriniodinium*.

Scriniodinium anceps (Raynaud 1978) comb. nov.

Basionym. *Endoscrinium anceps* Raynaud 1978, p. 392, pl. 1, fig. 17.

Remarks. This Late Jurassic-Early Cretaceous species, which is similar to *Scriniodinium pharo*, unequivocally exhibits dextral torsion of the hypocyst (Raynaud, 1978, pl. 2, fig. 17; Riding et al., 1999, pl. RP17, fig. 2), and is therefore transferred to *Scriniodinium*. Although Jan du Chêne et al. (1986, p. 315) listed this species under *Scriniodinium*, they did not make a formal transfer.

Scriniodinium bucinatum Brenner 1988.

Remarks. The holotypes of both subspecies (*Scriniodinium bucinatum* subspecies *bucinato* and *Scriniodinium bucinatum* subspecies *labyrinthus*) of this Late Jurassic species from Germany both show evidence of dextral torsion (Brenner, 1988, pl. 12, figs. 1, 2). The species is thus appropriately encompassed within the genus *Scriniodinium*.

Scriniodinium campanula Gocht 1959.

Remarks. Stover and Evitt (1978, p. 187) deemed this form to be a provisionally accepted species of *Scriniodinium*, because they were uncertain if the species is cavate. It is clear, however, that the type material is *Scriniodinium campanula* is circumcavate (Jan du Chêne et al., 1986, pl. 110, figs 1-4). It is retained in *Scriniodinium* because it clearly exhibits dextral torsion (Habib, 1974). The subspecies *S. campanula* subsp. *nichan* (Below 1981) Jan du Chêne et al. 1986 also has criboepidinioid paratabulation.

Scriniodinium? ceratophorum Cookson & Eisenack 1960.

Remarks. This Late Jurassic (Oxfordian-Tithonian) Southern Hemisphere species lacks evidence of paratabulation except for the single-paraplate precingular archeopyle. Folds in the periphragm, however, may indicate the paracingulum (Cookson and Eisenack, 1960, pl. 37, fig. 7). Its assignment to *Scriniodinium* was questioned by Stover and Evitt (1978, p. 187) due to its

relatively small pericoels. The species has a short hypocyst and a long epicyst, an unusual characteristic of *Scriniodinium*, but typical of species of *Gonyaulacysta*, such as *Gonyaulacysta dualis*, *G. jurassica* and *G. fenestrata* (see Stover and Evitt, 1978, p.275-279). *Scriniodinium? ceratophorum* is similar in morphology, cyst organisation, size and stratigraphical/geographical distribution to these species of *Gonyaulacysta*. It is possible that *Scriniodinium? ceratophorum* should be transferred to *Gonyaulacysta*, but this this would require a comprehensive restudy that is beyond the mandate of the present work.

Scriniodinium? dictyophorum (Deflandre 1939 ex Sarjeant 1967) Brenner 1988.

Remarks. The assignment of this species to *Scriniodinium* is here questioned because the hypocystal dextral torsion, if any, of the type material (Deflandre, 1939, pl. 8, figs 1-3) is not clear. The specimen figured by Brenner (1988, pl. 11, fig 4) unequivocally exhibits dextral torsion, but appears to be indistinguishable from *Scriniodinium dictyotum*.

Scriniodinium dictyotum Cookson & Eisenack 1960.

(Plate 3, fig. 1).

Remarks. Cookson and Eisenack (1960) originally placed this species, which is currently subdivided into four subspecies, into *Scriniodinium*. It was subsequently transferred to *Scrinioecassis* by Beju (1971), then moved to *Aldorfia* by Davey (1982). It is clear from the type material, and the specimens figured by Habib (1974), Riding (1987, figs 11.1, 11.3) and Brenner (1988, pl. 10, figs 5, 6, pl. 11, figs 1-3, 5), that this species exhibits hypocystal dextral torsion and hence is most appropriately accommodated in *Scriniodinium*.

Scriniodinium? echinatum Jain & Garg in Jain et al. 1984.

Remarks. The assignment of this species to *Scriniodinium* is here questioned. The paratabulation pattern of the type material is only partially resolvable, largely due to the thermally-altered nature of the material. The paratabulation of the holotype (Jain et al., 1984, pl. 2, fig. 21) is not clear. However, the paratype (Jain et al., 1984, pl. 3, fig. 45) appears to exhibit hypocystal dextral torsion, implying that this species is best accommodated in *Scriniodinium*. The type material is sparsely echinate and thus the only representative of this genus which may be proximochorate, as opposed to proximate. However, due to the uncertainty of the generic placement of this species, *Scriniodinium* is considered to be proximate (see the emended diagnosis above).

Scriniodinium? eocaenicum Olaru 1978.

Remarks. This Late Eocene taxon cannot with certainty be attributed to either *Scriniodinium* or *Endoscrinium* on the basis of the type material. Jan du Chêne et al. (1986, p. 317) deemed it to be questionably attributable to *Scriniodinium*.

Scriniodinium? heusseri Habib 1970.

Remarks. This species was described from the mid Cretaceous of the south-west North Atlantic. The paratabulation style of the holotype (Habib, 1970, pl. 8, fig. 4) is not clear. However, the specimen appears to be inverted and there are vague indications of dextral torsion. Jan du Chêne et al (1986, p. 317) stated that this species should be questionably attributed to *Scriniodinium*.

Scriniodinium inritibile Riley in Fisher & Riley 1980.

(Plate 3, fig. 2)

Remarks. *Scriniodinium inritibile* is present from the mid Oxfordian to earliest Portlandian in Europe and exhibits dextral torsion via a middorsal 4"/5" paraplate boundary (e.g. Riding and Thomas, 1988, pl. 2, fig. 2).

Scriniodinium? oxfordianum Sarjeant 1962.

Remarks. This species appears to be identical to *S. crystallinum* and hence may be a junior synonym. The type material was not figured in the exhaustive redescriptions by Jan du Chêne et al. (1986), and therefore may be lost. The specimens figured by Brenner (1988, pl. 10, figs. 2, 4) appear to be smaller than *S. crystallinum*, and to have a narrower pericoel and occasional connections between the endophragm and periphragm.

Scriniodinium parvimarginatum (Cookson & Eisenack 1958) Eisenack 1967.

Remarks. This species from the Late Jurassic of Australia has a narrow pericoel and is similar in overall morphology to *Scriniodinium inritibile*. However, it lacks an apical protuberance and the periphragm is variably reticulate. Paratabulation is lacking, but the holotype exhibits vague lineations which may indicate a middorsal paraplate boundary on the hypocyst (Jan du Chêne et al, 1986, pl. 112, figs 10-12). The species is not regarded as a key biostratigraphical marker in Australia (R. Helby, personal communication, 2001).

Scriniodinium pharo (Duxbury 1977) Davey 1982.

(Plate 3, figs 8-10).

Remarks. *Scriniodinium pharo* is an important marker species for the early Portlandian to earliest Valanginian in Europe (Figure 2). It is a distinctive form which is elongate with a prominent apical horn. The species unequivocally exhibits dextral torsion with a middorsal 4"/5" paraplate boundary (Plate 3, fig. 10).

Scriniodinium playfordii Cookson & Eisenack 1960.

Remarks. This species was deemed to be a junior synonym of *Scriniodinium crystallinum* by Jan du Chêne et al. (1986, p. 316). However, Brenner (1988, p. 79) maintained the separation of these species on the basis of its reticulate ornamentation and the the marked apical protuberance. It is also larger than *S. crystallinum*. *Scriniodinium playfordii* is not generally used in modern studies in either the Northern or Southern hemispheres and probably represents an extreme morphotype of *S. crystallinum*. For example, the specimen of *S. crystallinum* from Australia illustrated here (Plate 1) approaches the morphology of *S. playfordii* in that it is relatively large and has a small apical horn. Formal synonymisation of these two species, however, should await a restudy of the type material of *S. playfordii*. *Scriniodinium playfordii*, *S. bucinatum* and some forms of *S. dictyotum* appear to represent extreme variants of *S. crystallinum*; these variant morphotypes emerged in the Kimmeridgian worldwide. They are all relatively large, have elements inserted between the wall layers and have apical horns (Brenner, 1988, pls 10-12).

Scriniodinium prolatum Stevens 1987.

Remarks. *Scriniodinium prolatum* is a marker species for the Berriasian in Australia (Stevens, 1987; Figure 2). It is similar in morphology and stratigraphical range to *Scriniodinium pharo*.

This species is deemed to belong to *Scriniodinium* due to its middorsal 4'''/5''' paraplate boundary indicating dextral torsion (Stevens, 1987, figs 9A-9H).

Scriniodinium? scutella Eisenack 1958.

Remarks. The paratabulation of this Aptian species is not clear, and thus its assignment to *Scriniodinium* is here questioned. See discussion in Jan du Chêne et al. (1986, p. 318).

Scriniodinium? speciosum He Chengquan in Zheng Yahui & He Chengquan 1984.

Remarks. *Scriniodinium? speciosum* was described from the Late Cretaceous of China and appears to be a cavate peridiniacean cyst (Zheng Yahui and He Chengquan 1984, pl. 6, figs 21, 22, pl. 10, fig. 6). The light photomicrographs have been cropped and it is not possible to be certain as to the generic affinity of this species. It is possibly a representative of *Senegalinium*. It does not appear to be referable to *Scriniodinium*. However the species is maintained as a questionable species of this genus, pending a restudy of the type material. Williams et al. (1998, p. 550) retained *speciosum* in *Scriniodinium* without question.

Scriniodinium? torulosum (Deflandre 1943) Lentin & Williams 1973.

Remarks. Stover and Evitt (1978, p. 188) suggested that this species is probably an acritarch. However, the specimen illustrated by Jan du Chêne et al. (1986, pl. 104, figs 7-9) has an unequivocal paracingulum therefore is of dinoflagellate affinity. The paratabulation is unclear and any hypocystal dextral torsion is not discernible. Consequently, *torulosum* is questionably attributed to *Scriniodinium*, as was first suggested by Lentin and Williams (1973, p. 124).

Genus *Apteodinium* Eisenack 1958 emend. Lucas-Clarke 1987.

Type. *Apteodinium granulatum* Eisenack 1958

Remarks. This important gonyaulacacean genus was also emended by Sarjeant (1985), prior to a comprehensive emendation by Lucas-Clarke (1987). It unequivocally exhibits dextral torsion (Lucas-Clarke, 1987, fig. 5).

Apteodinium warringtonii (Poulsen 1996) comb. nov.

Basionym. *Aldorfia warringtonii* Poulsen 1996, p. 69-70, pl. 11, figs 1-4, pl. 12, figs 1-4.

Remarks. This species was originally attributed to *Aldorfia* by Poulsen (1996). The species is covered by a low-relief, complex ectophragm and clearly exhibits dextral torsion (Poulsen, 1996, pl. 12). The ectophragm is not complete, and is variably reticulate. Given the paratabulation style and morphology, *Apteodinium* is the most appropriate genus for this species. *Aldorfia aldorfiensis* has an entire ectophragm, dense differentiated autophragm and lacks dextral torsion (Gocht, 1970, fig. 9, pl. 32, fig. 2).

Subfamily LEPTODINIOIDEAE Fensome et al. 1993

Genus *Aldorfia* Stover & Evitt 1978

Type. *Aldorfia aldorfiensis* (Gocht 1970) Stover & Evitt 1978

Remarks. *Aldorfia* is distinguished from other genera by having dense, differentiated autophragm and neutral dextral torsion. With the transfer of *Aldorfia warringtonii* to

Apteodinium and the retention of *Aldorfia dictyota* in *Scriniodinium* (see above), *Aldorfia* becomes a monospecific genus.

Genus *Endoscrinium* (Klement 1960) Vozzhennikova 1967 emend. nov.

Type. *Endoscrinium galeritum* (Deflandre 1939) Vozzhennikova 1967 emend. nov.

Emended diagnosis. Proximate, cavate, typically paratabulate leptodinioid cysts with a simple precingular archeopyle.

Emended description. Subellipsoidal to rounded subangular, lenticular, proximate, typically circumcavate dinoflagellate cysts. Representatives may also be bicavate and, occasionally, holocavate. Intermediate to large in size. Endocyst ellipsoidal to subspherical. Apical horn generally lacking, but an antapical protruberance made of periphragm may occur. Periphragm significantly thinner than endophragm. The periphragm and endophragm may be psilate, perforate or have nontabular ornamentation of low relief. A sexiform gonyaulacacean paratabulation is largely fully indicated by low parasutural ridges or crests on the periphragm. Parasutural ridges/crests typically distally smooth, but occasionally they may be denticulate/echinate. The paratabulation formula is ?pr, 4', 6'', 6c, 6''', 1p, 1''', 6s and the hypocystal paratabulation exhibits neutral torsion. Archeopyle monoplacoid precingular, type P₃'', with a free operculum.

Remarks. *Endoscrinium* was originally described by Klement (1960) as a subgenus of *Scriniodinium*, being raised to generic rank by Vozzhennikova (1967). It was emended by Vozzhennikova (1965) and Gocht (1970). The genus is emended here in order to describe the variety of morphological variation and to formally document the sexiform gonyaulacacean paratabulation with neutral torsion and the paratabulation formula. The shape of *Endoscrinium* is somewhat variable; it is typically subellipsoidal, but may be subcircular, rounded subangular, elongate (e.g. *Endoscrinium galeritum*) or kite-shaped (e.g. *Endoscrinium asymmetricum*). All species, however are lenticular. Most species are circumcavate but bicavate and holocavate forms are known. Most representatives have a full paratabulation pattern indicated by low, distally smooth parasutural ridges or crests. Occasionally, however, the parasutural ornament, especially in the polar areas, may be faint and discontinuous or denticulate/echinate, e.g. *Endoscrinium irregulare*. The parasulcus may rarely be subdivided into paraplatelets (Gocht, 1970, fig. 12a). The operculum is frequently displaced within the cyst.

Comparison. *Endoscrinium* is most similar to *Scriniodinium*, but the latter genus exhibits dextral torsion and is not consistently paratabulate. *Gonyaulacysta* is also similar to *Endoscrinium*. *Gonyaulacysta*, however, has an S-type ventral configuration, typically has denticulate or spinose parasutural crests and is consistently bicavate and elongate.

Endoscrinium galeritum (Deflandre 1939) Vozzhennikova 1967 emend. nov.

(Plate 3, figs 5, 6).

Emended diagnosis. A bicavate to circumcavate species of *Endoscrinium* with a subovoidal shape, a thick endophragm and well developed parasutural ridges on the thin periphragm.

Emended description. A biconical, elongate subovoidal or rounded subpentangular species of *Endoscrinium*. There may be a small apical boss or protuberance formed from endophragm. Cyst bicavate to circumcavate, the maximum separation of the wall layers is at the antapex, which is truncate. Hypocyst generally markedly longer than the epicyst. Paratabulation indicated by distally smooth parasutural ridges or low crests. Endophragm thick, varying from smooth to having nontabular low relief ornamentation (e.g. scabration). Periphragm significantly thinner and variably ornamented, being either smooth, granulate or reticulate.

Small subcircular/ovoidal claustra may penetrate the periphragm in the peripheral regions. Intermediate to large in size.

Remarks. The description of this species is emended herein in order to fully document the overall morphology and variability of this species. The possible occurrence of small claustra at the periphery is noted for the first time. Although the emendation of Klement (1960, p. 22-27) is somewhat dated, his comprehensive measurements of German material remains useful. Klement (1960) subdivided the species into three subspecies, *galeritum*, *fornicatum* and *reticulatum*, based on whether the periphragm is smooth, granulate or reticulate respectively. According to Klement (1960, p. 23), the subspecies *galeritum* is by far the most common form. Klement (1960, p. 22) stated that he only attributed his material to the species *Endoscrinium galeritum* 'with the greatest hesitation' (translation). He reasoned that Deflandre (1939) only illustrated three reference specimens and did not present a detailed original description. No unequivocal evidence of discrete elements connecting the two wall layers was observed in *Endoscrinium galeritum*. Occasionally, the positioning of rims of claustra at the periphery make it appear that the endophragm and periphragm are connected by solid processes (e.g. Klement, 1960, pl. 1, figs 10-12).

Holotype and type occurrence. Deflandre (1939, pl. 5, figs 7, 8), from the lowermost Oxfordian (Upper Jurassic) Marnes de Villers Formation, Villers-sur-Mer, Normandy, northern France.

Stratigraphical distribution. In Europe and elsewhere in the Northern Hemisphere, *Endoscrinium galeritum* ranges from the early Callovian, *M. herveyi* Standard (ammonite) Zone to the early Kimmeridgian, *R. cymodoce* Standard (ammonite) Zone (Figure 2). The early-mid Callovian and early Kimmeridgian records are inconsistent and this species especially characteristic of the late Callovian to Oxfordian interval and *Endoscrinium galeritum* is most common in the early to earliest late Oxfordian (Riding et al., 1999, figs 16, 25). In Australasia, *E. galeritum* has a similar range and is confined to the Oxfordian (R. Helby, personal communication, 2000; Figure 2).

Other species.

Endoscrinium acroferum (Prauss 1989) comb. nov.

Basionym. *Scriniodinium acroferum* Prauss 1989, p. 45-46, pl. 9, figs 1, 2; pl. 14, figs 17-22; fig. 21.

Remarks. This echinate, circumcavate species clearly lacks dextral torsion (Beju, 1971, pl. 8, figs 4, 5; Riding et al., 1985, pl. 4, fig. 5; Prauss, 1989, fig. 21, pl. 14, figs 17, 18), and is therefore transferred to *Endoscrinium*.

Endoscrinium asymmetricum Riding 1987.

Remarks. This late Bajocian to Callovian species from Europe has a distinctive asymmetrical outline in dorsoventral view (Riding, 1987) and may be an evolutionary precursor to *Endoscrinium luridum*.

Endoscrinium attadalense (Cookson & Eisenack 1958) comb. nov.

(Figure 4B).

Basionym. *Scriniodinium attadalense* (Cookson & Eisenack 1958, p. 25, pl. 1, fig. 7.) Eisenack 1967, p. 193.

Remarks. The holotype of this Australasian species has a hypocyst with neutral torsion (Cookson & Eisenack 1958, pl. 1, fig. 7; Jan du Chêne et al., 1986, pl. 112, figs 8, 9; Figure 4B), and hence it is most appropriately placed in *Endoscrinium*.

Endoscrinium bessebae Below 1981.

Remarks. This species was first described from the Barremian of southwest Morocco and has neutral torsion (Below, 1981, figs 48b, 49b).

Endoscrinium granulatum (Raynaud 1978) Lentin & Williams 1981.

Remarks. This species was described from the early-mid Volgian of the Norwegian sector of the North Sea by Raynaud (1978). It belongs in *Endoscrinium* due to its neutral torsion (Raynaud, 1978, pl. 2, figs 6, 12).

Endoscrinium heikeae (Prössl 1990 ex Prössl 1992) comb. nov.

Basionym. *Scriniodinium heikeae* Prössl 1990, p. 106, pl. 12, figs 1, 2, 4, 5, 9 ex Prössl 1992, p. 112, 113.

Remarks. This Albian species from northwest Germany has a relatively small endocyst (Prössl, 1992, pl. 12, figs 1-2, 4-5, 9). Furthermore it clearly has no dextral torsion, and is thus here transferred to *Endoscrinium*.

Endoscrinium indicum (Jain & Garg in Jain et al. 1984) comb. nov.

Basionym. *Scriniodinium indicum* Jain & Garg in Jain et al. 1984, p. 72, 73, pl. 2, figs 22, 23.

Remarks. The detailed paratabulation of the type material of Jain et al. (1984, pl. 2, figs. 22, 23) is unclear. However, the specimen illustrated by Cookson and Eisenack (1960, pl. 37, fig. 10) clearly exhibits neutral hypocystal torsion, and so this species is here transferred to *Endoscrinium*.

Endoscrinium irregulare (Cookson & Eisenack 1958) comb nov.

Basionym. *Scriniodinium?* *irregulare* (Cookson & Eisenack 1958, p. 28, 29, pl. 10, figs 1, 2) Stover & Evitt 1978, p.188.

Remarks. This unusual and distinctive species with a spinose periphragm clearly exhibits neutral torsion (Jan du Chêne et al., 1986, pl. 109, figs 1-5; Helby et al., 1987, figs 22I, 22J), and is hence transferred here to *Endoscrinium*. See discussion of this species in Williams et al. (1998, p. 549).

Endoscrinium kempiae (Stover & Helby 1987) Lentin & Williams 1989.

Remarks. This distinctive taxon from the late Bathonian to early Oxfordian of Australia is similar in morphology to *E. luridum*, but has a scabrate, fibroid to irregularly fenestrate/reticulate periphragm (Stover and Helby, 1987). It exhibits neutral torsion (Stover and Helby, 1987, figs 14-16).

Endoscrinium klementii (Pocock 1972) Sarjeant 1978

Remarks. The line drawings of this species by Jansonius (1986, fig. 15) indicate neutral torsion, which is why it should be assigned to *Endoscrinium*. Pocock (1972 originally placed *klementii* in *Scriniodinium*, but the species was transferred to *Endoscrinium* by Sarjeant (1978, p. 29). Jan du Chêne et al. (1986, p. 317) interpreted this form as questionably belonging to *Scriniodinium*. Jansonius (1986) transferred the species to *Scrinocassis*. This genus is inappropriate due to its characteristic biconcave parasulcus and combination apical/precingular archeopyle (Below, 1990, fig. 8).

Endoscrinium luridum (Deflandre 1939) Gocht 1970.

(Plate 2, figs 8, 9; Plate 3, fig. 3; Figure 4A).

Remarks. *Endoscrinium luridum* normally has a non-perforate periphragm and a smooth outline in dorsoventral view (Pl. 2, figs. 8, 9). However, some specimens have variable numbers of small spherical/ovoidal perforations in the periphragm, especially in the peripheral areas. If these perforations are present at the extreme periphery of the cyst, a scalloped outline is developed. The holotype of the species is a strongly perforate morphotype (Deflandre, 1939, pl. 5, figs 4, 5). The presence of periphragmal perforations is deemed to be part of the natural variation of this species. The retention of this species in *Endoscrinium* by Lentin and Williams (1989, p. 128) following its transfer to *Tubotuberella* by Davies (1983) is fully supported. This, and all other species of *Endoscrinium*, lack the prominent claustrum in the antapical (1'') paraplate which distinguishes *Tubotuberella*.

Endoscrinium? novissimum (Morgenroth 1968) comb. nov.

Basionym. *Scriniodinium? novissimum* Morgenroth 1968, p. 540, 541, pl. 43, figs 3, 4.

Remarks. This Danian species from Denmark lacks paratabulation (Morgenroth, 1968, pl. 43, figs 3, 4). However, what appear to be folds in the periphragm of both the holotype and paratype are consistent with neutral torsion, therefore the species is here questionably assigned to *Endoscrinium*. Stover and Evitt (1978, p. 188) and Jan du Chêne et al. (1986, p. 317) questionably included this species in *Scriniodinium*.

Endoscrinium obscurum (Manum & Cookson 1964) comb. nov.

Basionym. *Scriniodinium? obscurum* Manum & Cookson 1964, p. 21, 22, pl. 4, figs 5, 6.

Remarks. This Late Cretaceous species from arctic Canada appears to be a junior synonym of *E. galeritum*. A restudy of the type material would be required to confirm this. In the interim, this species is transferred to *Endoscrinium* as there is no evidence of dextral torsion (Manum and Cookson 1964, pl. 4, figs, 5, 6). If the type material is conspecific with *E. galeritum*, the specimens were reworked from Upper Jurassic sediments. Jan du Chêne et al. (1986, p. 317) questionably included this species in *Scriniodinium*.

Endoscrinium reticulatum (Pocock 1972) comb. nov.

Basionym. *Scriniodinium reticulatum* Pocock 1972, p. 91, 92, pl. 23, fig. 3.

Remarks. The hypocystal paratabulation of this Middle Jurassic species from Canada appears to have neutral torsion (Jan du Chêne et al., 1986, pl. 108, figs 1-4; Jansonius, 1986, pl. 2, figs 4, 5). Therefore it is here transferred to *Endoscrinium*. The holotype (Pocock, 1972, pl. 23, fig. 3) appears to be holocavate; this type of cyst organisation is highly unusual for *Endoscrinium*.

Endoscrinium rostratum (Brideaux & McIntyre 1975) Below 1981.

Remarks. This species from the mid Albian of northern Canada has neutral torsion (Brideaux and McIntyre, 1975, pl. 11, figs 1-3), therefore is retained in *Endoscrinium*.

Endoscrinium subvallare (Sarjeant 1962) Lentin & Williams 1973.

Remarks. This species appears to be a junior synonym of *E. galeritum* subsp. *reticulatum* (Jan du Chêne et al., 1986, p. 316-317). The type material therefore requires restudying.

Endoscrinium? tabulatum Miles 1990.

Remarks. *Endoscrinium tabulatum* was described from the late Albian of offshore Namibia by Miles (1990). It has neutral torsion (Miles, 1990, fig. 3B). However, it is placed questionably in *Endoscrinium* here because it appears to have a sigmoidal (S-type) ventral organisation (Evitt, 1985). Furthermore, its paratabulation pattern is similar to that of *Impagidinium* from the subfamily Gonyaulacoideae (see Stover and Evitt, 1978, fig. 1). This would mean that the species probably belongs in *Impagidinium*. This transfer should be considered following a restudy of the type material.

Endoscrinium? variabile (Pocock 1972) Jansonius 1986.

Remarks. As implied by Jansonius (1986, p. 207), this is clearly a problematic species. We follow Jansonius in retaining it questionably in *Endoscrinium* for want of a better option, but recommend that its use be restricted to the holotype.

Subfamily GONYAULACOIDEAE (autonym)

Athigmatocysta Duxbury 1977

Type. *Athigmatocysta glabra* Duxbury 1977.

Remarks. Duxbury (1977, p. 24) described *Athigmatocysta glabra*, a gonyaulacacean circumcavate species which has neutral torsion, from the Ryazanian to Barremian of eastern England. Duxbury (1977) stated that this species could not be accommodated in *Endoscrinium* as the latter genus has five, not six, postcingular paraplates and lacks antapical paraplates. This is not the case: *Endoscrinium* has a standard gonyaulacacean paratabulation pattern with six postcingular paraplates and a single antapical paraplate (Gocht, 1970, fig. 12). On this basis, Below (1981) transferred *Athigmatocysta glabra* to *Endoscrinium*. However, *Athigmatocysta glabra* has an S-type ventral organisation (Harding, 1990, pl. 10, fig. 2). Therefore the contention of Harding (1990) that *Athigmatocysta* should be retained is endorsed and this monotypic genus is here placed into the family Gonyaulacoideae. Fensome et al. (1993, p. 87) placed *Athigmatocysta* in the family Leptodiniaceae as a junior synonym of *Endoscrinium*.

Order PERIDINIALES Haeckel 1894

Suborder PERIDINIINEAE (autonym)

Family PERIDINIACEAE Ehrenberg 1831

Subfamily DEFLANDREOIDEAE Bujak & Davies 1983

Genus *Trithyrodinium* Drugg 1967 emend. Marheinecke 1992

Type. *Trithyrodinium evittii* Drugg 1967.

Trithyrodinium? *velatum* (Conrad 1941 ex Sarjeant 1967) comb. nov.

Basionym. *Scriniodinium?* *velatum* Conrad 1941, p. 8, 9, pl. 1 fig. A ex Sarjeant 1967, p. 256.

Remarks. From the illustrations of Conrad (1941, fig. 2A, pl. 1A), this Maastrichtian species from Belgium appears to be a cavate peridiniacean form, attributable to *Trithyrodinium* and similar to *Trithyrodinium suspectum*. The single specimen illustrated by Conrad (1941) is probably in oblique lateral view and appears to have two antapical horns. The periphragm is intact, some indications of a peridinialean paratabulation are present and the nature of the archeopyle is not clear. Because the intercalary type 3I/3I archeopyle is not convincingly present, this species is here questionably assigned to *Trithyrodinium*.

5 Observations on the stratigraphical distributions of *Endoscrinium* and *Scriniodinium*

The stratigraphical distribution of species of *Endoscrinium* and *Scriniodinium* in the Jurassic and earliest Cretaceous of Europe and Australasia are depicted in Figure 2. These genera appear to be more diverse in the Northern Hemisphere, but this may reflect the fact that more taxonomic work has been done in Europe than in Australasia. Both genera were most common and diverse during the late Callovian to early Kimmeridgian interval in both hemispheres (Figure 2). This prominence around the Oxfordian Stage and its lower and upper boundaries generally supports the correlation of the Australian dinoflagellate cyst zonation with the European succession (Helby et al., 1987; Riding and Helby, 2001, fig. 12). Stevens (1987, p. 195) commented upon the morphological similarities between *Scriniodinium prolatum* from offshore Western Australia and the European species *Scriniodinium pharo*. These species both occur around the Jurassic-Cretaceous transition and are elongate, relatively large forms with well developed apical horns. These stratigraphical and morphological similarities appear to be age related. *Endoscrinium* and *Scriniodinium* both occur in the Cretaceous, but are far less diverse or prominent (Figure 2). The late Ryazanian/Valanginian global range base of *S. campanula* also appears to be of correlative value (Figure 2). This distinctive species is the youngest unequivocal representative of *Scriniodinium* and is long ranging; it has a Late Cretaceous (early Santonian) range top in the Northern Hemisphere (Costa and Davey, 1992). *Endoscrinium* has an older range base than that of *Scriniodinium* in both hemispheres, and this is entirely consistent with the phylogeny of their respective subfamilies. The subfamily Leptodinioideae, which includes *Endoscrinium*, is dominated by Jurassic and Early Cretaceous genera and includes many relatively old, Mid Jurassic genera such as *Aldorfia*, *Dissiliodinium*, *Durotrigia*, *Lithodinia* and *Meiourogonyaux*. By contrast, the subfamily Cribroperidinioideae is dominated by Cretaceous and Palaeogene genera; the few Jurassic representatives are all typically Late Jurassic (Fensome et al., 1993, p. 89, 90). The occurrences of *Scriniodinium crystallinum*, *S. dictyotum*, *S. parvimarginatum* and *S. playfordi* in the late Callovian and early Oxfordian of Europe and Australasia represent the earliest unequivocal representatives of the subfamily Cribroperidinioideae. Fensome et al. (1993) placed the Mid Jurassic genus *Korystocysta* in the subfamily Cribroperidinioideae; however, this genus clearly displays neutral torsion (Woollam, 1983, pl. 1, fig. 9) and thus should be placed in the subfamily Leptodinioideae, with its close relative *Ctenidodinium*. The oldest European species of *Endoscrinium*, *E. asymmetricum* and *E. acroferum*, range from the latest Bajocian to late Callovian and are morphologically similar. They are considered to be closely related, forming a species plexus that appears to be an evolutionary precursor to *E. luridum*. In turn, it is possible that *E. luridum* may have been ancestral to *E. granulatum* (Figure 2). A similar situation occurred in Australasia, where the *E. kempiae/E. luridum* complex may have given rise to *E. irregulare* and *E. attadalense*. *Endoscrinium luridum* and *E. attadalense*

are especially similar in both morphology and size (Figure 4) and can be difficult to distinguish. Therefore, the differentiation of these species, especially in Valanginian material from Australasia, may be problematical. The transition from *Endoscrinium luridum* to *E. attadalense* in the Valanginian of the Southern Hemisphere is not as clear cut as illustrated in Figure 2 because transitional morphotypes are present close to the Jurassic-Cretaceous boundary (R. Helby, personal communication, 2001). Both species are subpentagonal and circumcavate (Figure 4). However, *E. attadalense* has a consistently smooth outline, a wide pericoel, a variably perforate pericoel in the peripheral areas, and may show poorly developed paratabulation (Jan du Chêne et al., 1986, pl. 112, figs 4-8, pl. 152, fig. 8). Ironically, the type of the genus, *Endoscrinium galeritum* is morphologically distinct from the other species of the genus, suggesting that it may be slightly phylogenetically offset.

6 Conclusions

Representatives of the Jurassic dinoflagellate cyst *Scriniodinium crystallinum*, especially evidenced by specimens from the Southern Hemisphere, exhibit a gonyaulacalean paratabulation pattern with dextral torsion. They therefore belong to the subfamily Cribroperidinioideae. The Callovian forms of *Scriniodinium* are the oldest known unequivocal representatives of this subfamily. Other, younger, species of *Scriniodinium*, such as *S. campanula*, *S. pharo* and *S. playfordii* also exhibit clear dextral torsion. By contrast, the genus *Endoscrinium*, which was previously thought to be closely related to (and by some researchers even synonymous with) *Scriniodinium*, exhibits neutral torsion and is thus placed within the subfamily Leptodinioideae. *Endoscrinium* appears generally to have a significantly older range base than that of *Scriniodinium* and this difference is consistent with the apparent phylogeny of the subfamilies Leptodinioideae and Cribroperidinioideae. This study is further proof of the conservative nature of dinoflagellate cyst paratabulation patterns and that the paraplate configuration should, wherever possible, be used as a strong taxonomic discriminator in a generic and suprageneric sense. It also demonstrates how more robust taxonomy based upon paratabulation can yield enhanced phylogenetic interpretations.

Appendix 1 Listing of the dinoflagellate cyst taxa mentioned in the text

All dinoflagellate cyst genera, species, subspecies and varieties mentioned in the text are listed here, alphabetically by genera and species within genera. References for the majority of the author citations of the dinoflagellate cyst taxa mentioned in this appendix, but not in the main text, of this paper can be found in the reference list of Williams et al. (1998, p. 747-817). Note that *Paralecaniella* is an acritarch or schizosporous alga and not a dinoflagellate cyst.

Aldorfia Stover & Evitt 1978

Aldorfia alderensis (Gocht 1970) Stover & Evitt 1978

Ambonosphaera Fensome 1979

Apteodinium Eisenack 1958 emend. Lucas-Clarke 1987

Apteodinium warringtonii (Poulsen 1996) comb. nov.

Athigmatocysta Duxbury 1977

Athigmatocysta glabra Duxbury 1977

Cerodinium Vozzhennikova 1963 emend. Lentin & Williams 1987

Cornudinium Pocock 1972

Ctenidodinium Deflandre 1939
Dissiliodinium Drugg 1978
Durotrigia Bailey 1987
Endoscrinium (Klement 1960) Vozzhennikova 1967 emend. nov.
Endoscrinium acroferum (Prauss 1989) comb. nov.
Endoscrinium asymmetricum Riding 1987
Endoscrinium attadalense (Cookson & Eisenack 1958) comb. nov.
Endoscrinium bessebae Below 1981
Endoscrinium galeritum (Deflandre 1939) Vozzhennikova 1967 emend. nov.
Endoscrinium galeritum subsp. *fornicatum* (Klement 1960) Lentin & Williams 1973
Endoscrinium galeritum subsp. *galeritum* (autonym)
Endoscrinium galeritum subsp. *reticulatum* (Klement 1960) Górka 1970
Endoscrinium granulatum (Raynaud 1978) Lentin & Williams 1981
Endoscrinium heikeae (Prössl 1990 ex Prössl 1992) comb. nov.
Endoscrinium indicum (Jain & Garg in Jain et al. 1984) comb. nov.
Endoscrinium irregulare (Cookson & Eisenack 1958) comb. nov.
Endoscrinium kempiae (Stover & Helby 1987) Lentin & Williams 1989
Endoscrinium klementii (Pocock 1972) Sarjeant 1978
Endoscrinium luridum (Deflandre 1939) Gocht 1970
Endoscrinium? *novissimum* (Morgenroth 1968) comb. nov.
Endoscrinium obscurum (Manum & Cookson 1964) comb. nov.
Endoscrinium reticulatum (Pocock 1972) comb. nov.
Endoscrinium rostratum (Brideaux & McIntyre 1975) Below 1981
Endoscrinium subvallare (Sarjeant 1962) Lentin & Williams 1973
Endoscrinium tabulatum Miles 1990
Endoscrinium? *variabile* (Pocock 1972) Jansonius 1986
Gardodinium Alberti 1961 emend. Harding 1996
Gonyaulacysta Deflandre 1964 emend. Helenes & Lucas-Clark 1997
Gonyaulacysta dualis (Brideaux & Fisher 1976) Stover & Evitt 1978
Gonyaulacysta fenestrata Riding & Helby 2001
Gonyaulacysta jurassica (Deflandre 1939) Norris & Sarjeant 1965
Gonyaulacysta jurassica subsp. *adecta* Sarjeant 1982 var. *longicornis* (Deflandre 1938) Downie & Sarjeant 1965
Hystrichosphaeropsis Deflandre 1935 emend. Sarjeant 1982
Impagidinium Stover & Evitt 1978
Korystocysta Woollam 1983 emend. Benson 1985
Leptodinium Klement 1960 emend. Stover & Evitt 1978
Lithodinia Eisenack 1935 emend. Gocht 1975
Meiourogonyaulax Sarjeant 1966
Paralecaniella Cookson & Eisenack 1970 emend. Elsik 1977
Paralecaniella indentata (Deflandre & Cookson 1955) Cookson & Eisenack 1970 emend. Elsik 1977
Rhynchodiniopsis Deflandre 1935 emend. Jan du Chêne et al. 1985
Saeptodinium Harris 1974

Scriniocassis Gocht 1964 emend. Below 1990
Scriniodinium Klement 1957 emend. nov.
Scriniodinium? *amalthaei* (W. Wetzel 1966) Sarjeant 1980 emend. Sarjeant 1980
Scriniodinium anceps (Raynaud 1978) comb. nov.
Scriniodinium bucinatum Brenner 1988
Scriniodinium bucinatum subsp. *bucinatum* (autonym)
Scriniodinium bucinatum subsp. *labyrinthus* Brenner 1988
Scriniodinium campanula Gocht 1959
Scriniodinium campanula subsp. *campanula* (autonym)
Scriniodinium campanula subsp. *nichan* (Below 1981) Jan du Chêne et al. 1986
Scriniodinium? *ceratophorum* Cookson & Eisenack 1960
Scriniodinium crystallinum (Deflandre 1939) Klement 1960 emend. nov.
Scriniodinium? *dictyophorum* (Deflandre 1939 ex Sarjeant 1967) Brenner 1988
Scriniodinium dictyotum Cookson & Eisenack 1960
Scriniodinium dictyotum subsp. *dictyotum* (autonym)
Scriniodinium dictyotum subsp. *osmingtonense* Gitmez 1970
Scriniodinium dictyotum subsp. *papillatum* Gitmez 1970
Scriniodinium dictyotum subsp. *pyrum* Gitmez 1970
Scriniodinium? *echinatum* Jain & Garg in Jain et al. 1984
Scriniodinium? *eocaenicum* Olaru 1978
Scriniodinium? *heusseri* Habib 1970
Scriniodinium irritabile Riley in Fisher & Riley 1980
Scriniodinium? *oxfordianum* Sarjeant 1962
Scriniodinium parvimarginatum (Cookson & Eisenack 1958) Eisenack 1967
Scriniodinium pharo (Duxbury 1977) Davey 1982
Scriniodinium playfordii Cookson & Eisenack 1960
Scriniodinium prolatum Stevens 1987
Scriniodinium? *scutella* Eisenack 1958
Scriniodinium? *speciosum* He Chengquan in Zheng Yahui & He Chengquan 1984
Scriniodinium? *torulosum* (Deflandre 1943) Lentin & Williams 1973
Senegalinium Jain & Millepeid 1973 emend. Stover & Evitt 1978
Sirmiodiniopsis Drugg 1978
Sirmiodinium Alberti 1961 emend. Warren 1973
Sirmiodinium grossii Alberti 1961 emend. Warren 1973
Subtilisphaera Jain & Millepied 1973 emend. Lentin & Williams 1976
Subtilisphaera? *pirnaensis* (Alberti 1961) Jain & Millepied 1973
Trithyrodinium Drugg 1967 emend. Marheinecke 1992
Trithyrodinium suspectum (Manum & Cookson 1964) Davey 1969
Trithyrodinium? *velatum* (Conrad 1941 ex Sarjeant 1967) comb. nov.
Tubotuberella Vozzhennikova 1967 emend. Dodekova 1990

Appendix 2 The current status of species of *Scriniodinium* and *Endoscrinium*

This Appendix lists alphabetically all species and subspecies which have ever been assigned to *Scriniodinium* and *Endoscrinium* with full author citations (see also Williams et al., 1998).

1 *Scriniodinium* Klement 1960 emend. nov.

i) Currently accepted species and subspecies

Scriniodinium anceps (Raynaud 1978) comb. nov.

Scriniodinium bucinatum Brenner 1988

Scriniodinium bucinatum subsp. *bucinato* (autonym)

Scriniodinium bucinatum subsp. *labyrinthus* Brenner 1988

Scriniodinium campanula Gocht 1959 (retained in *Scriniodinium*)

Scriniodinium campanula subsp. *campanula* (autonym)

Scriniodinium campanula subsp. *nichan* (Below 1981) Jan du Chene et al. 1986

Scriniodinium crystallinum (Deflandre 1939) Klement 1960 emend. nov.

Scriniodinium dictyotum Cookson & Eisenack 1960

Scriniodinium dictyotum subsp. *dictyotum* (autonym)

Scriniodinium dictyotum subsp. *osmingtonense* Gitmez 1970

Scriniodinium dictyotum subsp. *papillatum* Gitmez 1970

Scriniodinium dictyotum subsp. *pyrum* Gitmez 1970

Scriniodinium irritabile Riley in Fisher & Riley 1980

Scriniodinium parvimarginatum (Cookson & Eisenack 1958) Eisenack 1967

Scriniodinium pharo (Duxbury 1977) Davey 1982

Scriniodinium playfordii Cookson & Eisenack 1960

Scriniodinium prolatum Stevens 1987

ii) Questionably assigned species

Scriniodinium? *amalthai* (W. Wetzel 1966) Sarjeant 1980 emend. Sarjeant 1980

Scriniodinium? *ceratophorum* Cookson and Eisenack 1960

Scriniodinium? *dictyophorum* (Deflandre 1939 ex Sarjeant 1967) Brenner 1988

Scriniodinium? *echinatum* Jain & Garg in Jain et al. 1984)

Scriniodinium? *eocaenicum* Olaru 1978

Scriniodinium? *heusseri* Habib 1970

Scriniodinium? *oxfordianum* Sarjeant 1962

Scriniodinium? *scutella* Eisenack 1958

Scriniodinium? *speciosum* He Chengquan in Zheng Yahui & He Chengquan 1984

Scriniodinium? *torulosum* (Deflandre 1943) Lentin & Williams 1973

iii) Reassigned species and subspecies (see Williams et al., 1998, p. 546-550 for further details)

Scriniodinium acroferum Prauss 1989 (now *Endoscrinium*)

Scriniodinium apatelum Cookson & Eisenack 1960 (now *Tubotuberella*)

Scriniodinium asymmetricum (Riding 1987) Dodekova 1990 (now *Endoscrinium*)

Scriniodinium attadalense (Cookson & Eisenack 1958) Eisenack 1967 (now *Endoscrinium*)

Scriniodinium australiense (Deflandre & Cookson 1955) Cookson & Eisenack 1965 (now *Apteodinium*)

- Scriniodinium bessebae* (Below 1981) Jan du Chêne et al. 1986 (now *Endoscrinium*)
- Scriniodinium bicuneatum* Deflandre 1939 ex Sarjeant 1967 (now *Cornudinium*)
- Scriniodinium cooksoniae* Anderson 1960 (taxonomic junior synonym of *Subtilisphaera? pirnaensis*)
- Scriniodinium eurypylum* Manum & Cookson 1964 (now *Saeptodinium*)
- Scriniodinium galeatum* Cookson & Eisenack 1960 (now *Hystrichosphaeropsis*)
- Scriniodinium galeritum* (Deflandre 1939) Klement 1960 (now *Endoscrinium*; includes three subspecies)
- Scriniodinium glabrum* (Duxbury 1977) Jan du Chêne et al. 1986 (now *Athigmatocysta*)
- Scriniodinium? globosum* (Olaru 1978) Lentin & Williams 1985 (now *Leptodinium?*)
- Scriniodinium? gochtii* Pocock 1972 (now *Rhynchodiniopsis*)
- Scriniodinium granulatum* (Raynaud 1978) Jan du Chêne et al. 1986 (now *Endoscrinium*)
- Scriniodinium heikeae* Prössl 1992 (now *Endoscrinium*)
- Scriniodinium indicum* Jain & Garg in Jain et al. 1984 (now *Endoscrinium*)
- Scriniodinium? irisiae* Kjellström 1973 (now *Hystrichosphaeropsis*)
- Scriniodinium? irregulare* Cookson & Eisenack 1958) Stover & Evitt 1978 (now *Endoscrinium*)
- Scriniodinium kempiae* Stover & Helby 1987 (now *Endoscrinium*)
- Scriniodinium klementii* Pocock 1972 (now *Endoscrinium*)
- Scriniodinium luridum* (Deflandre 1939) Klement 1960 (now *Endoscrinium*)
- Scriniodinium? nilsii* Kjellström 1973 (taxonomic junior synonym of *Paralecaniella indentata*)
- Scriniodinium? novissimum* Morgenroth 1968 (now *Endoscrinium?*)
- Scriniodinium? obscurum* Manum & Cookson 1964 (now *Endoscrinium*)
- Scriniodinium pontianum* Balteş 1969 ex Lentin & Williams 1973 (now *Hystrichosphaeropsis*)
- Scriniodinium pseudocrystallinum* Beju 1971 (taxonomic junior synonym of *Sirmiodinium grossii*)
- Scriniodinium reticulatum* Pocock 1972 (now *Endoscrinium*)
- Scriniodinium rostratum* Brideaux & McIntyre 1975 (now *Endoscrinium*)
- Scriniodinium subvallare* Sarjeant 1962 (now *Endoscrinium*)
- Scriniodinium trabeculosum* Gocht 1959 (now *Gardodinium*)
- Scriniodinium? verrucosum* Heisecke 1970 (now *Cerodinium*)
- 2 *Endoscrinium* (Klement 1960) Vozzhennikova 1967 emend. nov.
- i) Currently accepted species and subspecies
- Endoscrinium acroferum* (Prauss 1989) comb. nov.
- Endoscrinium asymmetricum* Riding 1987
- Endoscrinium attadalense* (Cookson & Eisenack 1958) comb. nov.
- Endoscrinium bessebae* Below 1981
- Endoscrinium galeritum* (Deflandre 1939) Vozzhennikova 1967 emend. nov.
- Endoscrinium galeritum* subsp. *fornicatum* (Klement 1960) Lentin & Williams 1973
- Endoscrinium galeritum* subsp. *galeritum* (autonym)
- Endoscrinium galeritum* subsp. *reticulatum* (Klement 1960) Górka 1970
- Endoscrinium granulatum* (Raynaud 1978) Lentin & Williams 1981
- Endoscrinium heikeae* (Prössl 1990 ex Prössl 1992) comb. nov.
- Endoscrinium indicum* (Jain & Garg in Jain et al. 1984) comb. nov.
- Endoscrinium irregulare* (Cookson & Eisenack 1958) comb. nov.
- Endoscrinium kempiae* (Stover & Helby 1987) Lentin & Williams 1989

Endoscrinium klementii (Pocock 1972) Sarjeant 1978

Endoscrinium luridum (Deflandre 1939) Gocht 1970

Endoscrinium obscurum (Manum & Cookson 1964) comb. nov.

Endoscrinium reticulatum (Pocock 1972) comb. nov.

Endoscrinium rostratum (Brideaux & McIntyre 1975) Below 1981

Endoscrinium subvallare (Sarjeant 1962) Lentin & Williams 1973

Endoscrinium tabulatum Miles 1990

ii) Questionably assigned species

Endoscrinium? novissimum (Morgenroth 1968) comb. nov.

Endoscrinium? variabile (Pocock 1972) Jansonius 1986

iii) Reassigned species and subspecies (see Williams et al., 1998, p. 212-214 for further details)

Endoscrinium amalthei (W. Wetzel 1966) Lentin & Williams 1981 (now *Scriniodinium?*)

Endoscrinium anceps Raynaud 1978 (now *Scriniodinium*)

Endoscrinium campanula (Gocht 1959) Vozzhennikova 1967 (now *Scriniodinium*; includes two subspecies)

Endoscrinium eisenackii (Deflandre 1939) Gocht 1970 (now *Gonyaulacysta*; includes two subspecies)

Endoscrinium glabrum (Duxbury 1977) Below 1981 (now *Athigmatocysta*)

Endoscrinium gochtii (Pocock 1972) Muir & Sarjeant 1978 (now *Rhynchodiniopsis*)

Endoscrinium oxfordianum (Sarjeant 1962) Vozzhennikova 1967 (now *Scriniodinium?*)

Endoscrinium pharo Duxbury 1977 (now *Scriniodinium*)

Endoscrinium prolatum (Stevens 1987) Lentin & Williams 1989 (now *Scriniodinium*)

Appendix 3 Register of figured specimens

All figured specimens are listed here, together with essential details. The specimens are curated in either the Commonwealth Palaeontological Collection, Geoscience Australia, Canberra, ACT 2601, Australia (Plate 1, figs 1-4) and the collections of the British Geological Survey, Keyworth, Nottingham NG12 5GG, UK (the remainder). The location of the specimens on the microscope slides are all 'England-Finder' co-ordinates. These were taken with the slide label to the right of the observer; the microscope stage opening away from the microscope user. SGM = single grain mount. The single grain mounts do not have unique numbers; they are numbered sequentially for each species within a particular sample.

PL./FG. NO.	SLIDE NO.	CO-ORD.	LOCALITY	DEPTH (M)	SPEC. NO.
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Scriniodinium crystallinum Deflandre 1939) Klement 1960 emend. nov.:

Pl. 1/1-4	SGM 1	K50	Peak-1	1463.04-1466.09	CPC 37000
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The Peak-1 well was drilled by WAPET in the offshore Carnarvon Basin, Western Australia at: 21° 36' 16.99"S, 114° 30' 21.99"E (Foster, 2001).

Pl. 2/1	MPA 10054/1	S42/4	N. Bottom B/H	250.20	MPK 12602
Pl. 2/2	MPA 10051/2	U30	N. Bottom B/H	235.20	MPK 4547
Pl. 2/3	MPA 12051/2	O52/2	Warboys B/H	9.14-10.67	MPK 12603
Pl. 2/4	MPA 10054/1	S46	N. Bottom B/H	250.20	MPK 12604
Pl. 2/5	MPA 10060/1	U40	N. Bottom B/H	280.20	MPK 12605
Pl. 2/6	MPA 12053/2	C54	Warboys B/H	15.24-16.76	MPK 3557
Pl. 2/7	MPA 10047/2	P43	N. Bottom B/H	215.20	MPK 12606

The Nettleton Bottom Borehole, near Caistor, Lincolnshire, England was drilled in 1979 at TF 1252 9820) (Riding, 1987).

The Warboys Borehole, Broughton, Cambridgeshire, England was drilled in 1965 at TL 2903 7839 (Riding, 1982).

Pl. 3/4	MPA 15468/1	U29/3	Warboys Brick Pit	MPK 12609
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Outcrop sample from Warboys Brick Pit Quarry, Cambridgeshire, England at TL 310 820 (Woollam, 1980).

Pl. 3/7	MPA 15491/1	R33/3	Scarborough, Yorkshire	MPK 12610
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Outcrop sample from Castle Hill, Scarborough, North Yorkshire, England (TA 049 889).

Endoscrinium luridum (Deflandre 1939) Gocht 1970.

Pl. 2/8	MPA 10054/1	L32/2	N. Bottom B/H	250.20	MPK 12607
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Pl. 2/9	MPA 10051/2	S60	N. Bottom B/H	235.20	MPK 12608
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Pl. 3/3	MPA 14089/1	F31/4	Digg, Isle of Skye, Scotland	MPK 6716
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Outcrop sample at NG 474 694 (Riding and Thomas, 1997).

Scriniodinium dictyotum Cookson & Eisenack 1960 subsp. *pyra* Gitmez 1970.

Pl. 3/1	MPA 10037/2	P57	N. Bottom B/H	145.20	MPK 4684
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Scriniodinium irritabile Riley in Fisher & Riley 1980

Pl. 3/2	MPA 10033/1	Q40/3	N. Bottom B/H	125.20	MPK 4065
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Endoscrinium galeritum (Deflandre 1939) Vozzhennikova 1967 emend. nov.

Pl. 3/5	MPA 10056/1	O34	N. Bottom B/H	260.20	MPK 4656
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Pl. 3/6	MPA 14089/1	S32/3	Digg, Isle of Skye, Scotland	MPK 6719
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Scriniodinium pharo (Duxbury 1977) Davey 1982

Pl. 3/8-10	SAL 5009/2	Q27/4	Manor Farm, Norfolk	MPK 1281
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Gas trench sample at Manor Farm, North Rington, Kings Lynn, Norfolk, England (TF 6515 1555) (Davey, 1979).

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