

1 **The taxonomy and palaeobiogeography of small chorate dinoflagellate cysts from the Late**
2 **Cretaceous to Quaternary of Antarctica**

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15 Small chorate dinoflagellate cysts are common in Upper Cretaceous to Quaternary sedimentary
16 successions from around the Antarctic margin. Taxonomic confusion surrounding dinoflagellate
17 cysts and acritarchs of similar morphology throughout the southern high palaeolatitudes has hitherto
18 limited investigation of their palaeoecological significance. This study aims to solve the taxonomic
19 problems, and to allow a new assessment of dinoflagellate cyst acmes. A detailed morphological
20 study of new material from the López de Bertodano Formation of Seymour Island, Antarctic
21 Peninsula is presented. These dinoflagellate cysts are identified as *Impletosphaeridium clavus*
22 Wrenn & Hart 1988 emend. nov. Their gross morphology and their vast abundances in the James
23 Ross Basin are strongly suggestive of dinoflagellate blooms. This scenario implies similarities to
24 modern dinoflagellate cysts from the polar regions.

25

26 **Keywords:** dinoflagellate cysts; acritarchs; taxonomy; palaeobiogeography; Cretaceous-
27 Quaternary; Antarctica

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29

30 **1. Introduction**

31 Small chorate (spine-bearing) algal cysts have been recorded, but rarely illustrated, from Upper
32 Cretaceous to Quaternary shallow marine sediments around the Antarctic margin, (Figure 1, Table
33 1). They have rounded to ellipsoidal cyst bodies, which are ~20 μm in diameter, and bear around
34 100 thin, solid, flexible non-tabular processes. The palaeoecology of these forms is poorly
35 understood, but is likely to be significant in the southern high palaeolatitudes where they have been
36 recorded in extremely high proportions (Askin 1988; Smith 1992; Bowman et al. 2012). Vast
37 abundances of dinoflagellate cysts in the fossil record may represent the aftermath of dinoflagellate
38 blooms (Noe-Nygaard et al. 1987). It has also been suggested that these acmes may represent
39 phytoplankton blooms associated with the presence of seasonal sea ice (Wrenn et al. 1998; Warny
40 et al. 2007; Warny and Askin 2011a). We consider that taxonomic confusion is hindering the
41 interpretation of these abundant cysts in the geological record of the southern high palaeolatitudes.

42 Elucidating the detailed morphology of these small chorate cysts is difficult without scanning
43 electron microscopy (Sarjeant and Stancliffe 1994; Schrank 2003). As most palynologists routinely
44 work with transmitted light microscopy, the consistent differentiation of these morphotypes may be
45 difficult. Small chorate cysts from the Late Cretaceous to Quaternary of the Antarctic margin have
46 been attributed to the acanthomorph acritarch genus *Micrhystridium* Deflandre 1937 and the
47 dinoflagellate cyst genus *Impletosphaeridium* Morgenroth 1966 (Table 1). Eaton et al. (2001)
48 considered *Impletosphaeridium* to be a convenient genus to attribute problematical morphotypes
49 (i.e. a “grab-bag”).

50 This paper assesses the taxonomy of these small chorate cysts using highly productive material
51 from the Maastrichtian to Danian López de Bertodano Formation exposed on Seymour Island at the

52 northeastern tip of the Antarctic Peninsula (Figures 1, 2). We consider that these cysts are
53 *Impletosphaeridium clavus*, which is emended herein, extending its range back to the Late
54 Campanian. The palaeogeographical distribution of small chorate cysts in Upper Cretaceous to
55 Quaternary sediments around the Antarctic margin is reconsidered in the context of this study,
56 which shows that many of these published records can be re-classified as *Impletosphaeridium*
57 *clavus* Wrenn & Hart 1988 emend. nov.

58

59 **2. Geological background**

60 Seymour Island is located in the James Ross Basin at the northeastern tip of the Antarctic
61 Peninsula; in its southern part, shallow marine to deltaic sediments of the Coniacian to Danian
62 Marambio Group are exposed (Figure 1; Pirrie et al. 1997a; Crame et al. 2004; Montes et al. 2007;
63 Olivero et al. 2007; Olivero 2012). Here, the uppermost Snow Hill Island Formation (the Haslum
64 Crag Member), the López de Bertodano Formation and the Sobral Formation crop out with the
65 Cretaceous-Paleogene (K-Pg) boundary within the upper López de Bertodano Formation (Figure 2;
66 Macellari 1988; Crame et al. 2004). The oldest beds exposed on Seymour Island are probably
67 Maastrichtian in age (Bowman et al. 2012; Tobin et al. 2012). In the northern part of the island, the
68 stratigraphical relationships within the Paleogene Seymour Island Group remain uncertain, but this
69 succession is divided into the Cross Valley Formation (early Late Paleocene) and the La Meseta
70 Formation (Eocene) (Figure 2; Sadler 1988; Marensi et al. 2012).

71 A stratigraphical section (named D5.251), approximately 1100 m thick, was measured and
72 sampled every 1-2 m throughout the highly fossiliferous Maastrichtian to Danian López de
73 Bertodano Formation (Figure 1; Thorn et al. 2009; Bowman et al. 2012). The sedimentology is
74 relatively monotonous, consisting of hundreds of metres of silty-clays and clayey-silts. The López
75 de Bertodano Formation has yielded well-preserved palynofloras (Askin 1988; Thorn et al. 2009;
76 Bowman et al. 2012) and is an exceptional locality for studying palaeobiology across the K-Pg
77 transition.

78 The López de Bertodano Formation of southern Seymour Island was deposited at ca. 65°S
79 palaeolatitude, at a similar latitude to the location today (Lawver et al. 1992). This unit represents a
80 siliciclastic deltaic setting, with the sediment sourced from the rapidly rising volcanic arc to the
81 west and deposited in a back-arc basin open to the current Weddell Sea region in the east (Hathway
82 2000; Crame et al. 2004; Olivero 2012). Dating of the López de Bertodano Formation has been
83 established using strontium isotope analysis (McArthur et al. 1998), dinoflagellate cyst
84 biostratigraphy (Bowman et al. 2012), magnetostratigraphy (Tobin et al., 2012) and the presence of
85 an iridium anomaly at the K-Pg boundary horizon (Elliott et al. 1994).

86

87 **3. Material and methods**

88 Samples from section D5.251 were processed for palynomorphs using quantitative techniques
89 (Wood et al. 1996). Twenty-five grammes of dry sediment from each sample were sieved at 180 µm
90 and the smaller fraction treated with hydrochloric and hydrofluoric acids. The acidified residue was
91 oxidized using nitric acid for one or two minutes, then the organic matter was gravity-separated
92 from any resistant minerals using zinc chloride centrifugation and physical swirling. The organic
93 fraction was then sieved at 10 µm and made up to 50 ml with distilled water. A standard aliquot of 1
94 ml (0.5 g of the initial 25 g dry weight) was then permanently mounted onto a microscope slide. All
95 samples and slides are curated at the British Antarctic Survey, Cambridge, United Kingdom.

96 At least 300 marine and terrestrial palynomorph specimens were counted from each slide along
97 regularly spaced transects allowing the calculation of palynomorphs per gramme of dry sediment.
98 In many samples below 830 m in the measured stratigraphical section, small chorate cysts dominate
99 the palynofloras. These were counted to 100 specimens thereby allowing their overall proportion in
100 the assemblage to be calculated. One hundred well-preserved specimens of the small chorate cysts
101 were measured from sample D5.930.1 (slide D5.930.1A) where they were most abundant (407 m
102 from the base of section D5.251 and 340 m from the base of the López de Bertodano Formation;
103 Bowman et al. 2012, Fig. 2). Despite extensive folding of the cyst bodies, the good preservation, the

104 apparent homogeneity of sedimentology and sedimentation rate and their abundance in the samples
105 compared to other obviously reworked palynomorphs led to the assumption that the small chorate
106 cysts are autochthonous.

107 To illustrate the description of these cysts, transmitted light photomicrographs and scanning
108 electron microscope images of selected well-preserved specimens are presented in Plates 1 to 3.
109 Transmitted light images, and palynological analysis was undertaken on a Leica DM750P
110 transmitted light microscope at the University of Leeds, United Kingdom. The scanning electron
111 microscope images were taken on a FEI Nova 200 NanoLab high resolution Field Emission Gun
112 Scanning Electron Microscope with precise Focused Ion Beam housed in the Faculty of
113 Engineering of the same institution. The organic residue was evaporated directly onto aluminium
114 stubs with no pre-treatment and was coated with platinum to 10 Nm. Fluorescence microscopy on
115 slide D5.930.1A was undertaken at the British Geological Survey, Keyworth, United Kingdom,
116 using a Zeiss Universal microscope fitted with a Zeiss ultraviolet epifluorescence attachment, which
117 is powered by an Osram HBO[®] mercury short-wave arc lamp.

118

119 **4. Results**

120 Eighty-one samples from the López de Bertodano Formation of Seymour Island were analysed by
121 Bowman et al. (2012) and all contain well-preserved marine and terrestrial palynomorphs. The
122 marine component comprises acritarchs (e.g. *Nummus* Morgan 1975 spp.), dinoflagellate cysts
123 (notably *Manumiella* Bujak & Davies 1983 spp. below the K-Pg transition) and other marine algae
124 (such as *Palamblages* Wetzel 1961 spp. and *Tasmanites* Newton 1875 spp.). However, the most
125 consistently abundant are small chorate cysts, identified herein as dinoflagellate cysts. The
126 sedimentological homogeneity of this succession strongly suggests that palynomorph abundance
127 reflects palaeoecological phenomena rather than facies changes. These small chorate dinoflagellate
128 cysts vary dramatically between 2% and 99% of the marine palynomorph assemblage throughout
129 the López de Bertodano Formation on Seymour Island.

130

131 **5. Systematic palaeontology**

132

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

134 Subdivision DINOKARYOTA Fensome et al. 1993

135 Class DINOPHYCEAE Pascher 1914

136 Subclass PERIDINIPHYCIDAE Fensome et al. 1993

137 Order GONYAULACALES Taylor 1980

138 Family Uncertain

139

140 **Genus:** *Impletosphaeridium* Morgenroth 1966 emended Islam 1993141 **Type:** *Impletosphaeridium transfodum* Morgenroth 1966

142

143 **Remarks:** *Impletosphaeridium* was established by Morgenroth (1966, p. 32) to encompass
144 spherical to occasionally ellipsoidal chorate dinoflagellate cysts with smooth or slightly granular
145 cyst bodies bearing solid processes. The process terminations are acuminate, capitate, conical or
146 furcate, but no mention was made of the archaeopyle type or size by Morgenroth (1966). Stover and
147 Evitt (1978, p. 232) stated that the archaeopyle type is uncertain. Masure (2004, p. 337-349)
148 differentiated species assigned to “*Impletosphaeridium*” on the basis of the presence or absence of
149 an apical archaeopyle and the nature of the processes. Specimens of *Impletosphaeridium* can be
150 readily differentiated from similar genera, for example, solid processes in *Impletosphaeridium*
151 differentiate it from the acritarch *Baltisphaeridium* Eisenack 1958, which has hollow processes.
152 Similarly, the superficially similar dinoflagellate cyst *Cordosphaeridium* Eisenack 1963 is
153 characterised by striate processes. However, there are certain issues pertaining to the differentiation
154 of *Impletosphaeridium* from the chorate dinoflagellate cyst *Cleistosphaeridium* Davey et al. 1966
155 and the acanthomorph acritarch genus *Micrhystridium*.

156 A re-study of the type species of *Cleistosphaeridium*, *Cleistosphaeridium diversispinosum*
157 Davey et al. 1966, by Islam (1993) revealed process complexes on the holotype. This made the
158 genus superfluous and Islam (1993) transferred *Cleistosphaeridium diversispinosum* to
159 *Systematophora* Klement 1960. Consequently, Islam (1993) transferred many former species of
160 *Cleistosphaeridium* to *Impletosphaeridium*, emending the diagnosis of *Impletosphaeridium* to
161 include an apical archaeopyle [type tA or (tA)] as evident in the illustration of the paratype of
162 *Impletosphaeridium transfodum* Morgenroth 1966 (see Morgenroth, 1966, pl. 10, fig. 4). The
163 emendation of Islam (1993) also included a weakly granulate or psilate, single or double-walled
164 cyst body with nontabular processes with simple to complex distal terminations. Eaton et al. (2001)
165 preferred to retain *Cleistosphaeridium*, although recognising that the differentiation of
166 *Cleistosphaeridium* from *Impletosphaeridium* is highly problematical. Eaton et al. (2001)
167 considered the types of these two genera might be conspecific, with that of the former type being
168 the junior synonym. Masure (2004) agreed that the holotype of *Impletosphaeridium transfodum*, the
169 type of *Impletosphaeridium*, might be referable to *Cleistosphaeridium*. However, the type material
170 of *Impletosphaeridium transfodum* is lost and, with the images of Morgenroth (1966, pl. 10, figs. 4,
171 5) being unclear, doubt remains as to whether the holotype and paratype are conspecific. Therefore,
172 Eaton et al. (2001) suggested that the use of the name *Impletosphaeridium* should only be used for
173 material comparable to *Impletosphaeridium transfodum*, and that other species of
174 *Impletosphaeridium* are questionable.

175 The findings of Eaton et al. (2001), and the lack of clarity regarding the archaeopyle type of
176 *Impletosphaeridium*, does not allow the distinction of these cysts from the acritarch *Micrhystridium*.
177 The original diagnosis of *Micrhystridium* is rather broad and includes all globular/spherical
178 palynomorphs below 20 µm in diameter with various ornamentation and processes (Deflandre
179 1937). Subsequent emendations refined this generic concept, culminating in Sarjeant and Stancliffe
180 (1994), to comprise approximately spherical, typically single-walled chorate cysts generally below
181 20 µm in diameter with a psilate to granulate wall and a slit or cryptosuture. Nine to 35 hollow or

182 solid spines are present, which may be proximally flared and normally have simple distal
183 terminations. Rarely the processes may be distally clavate or bifurcate (Sarjeant and Stancliffe
184 1994).

185 A comparison of the most recent generic diagnoses of *Impletosphaeridium* and *Micrhystridium*
186 indicates that they are distinguishable only by an apical archaeopyle in the former and a slit or
187 irregular opening (epitypche) in the latter. Cyst body size or number of spines is included in the
188 diagnosis of *Impletosphaeridium*. Wrenn and Hart (1988) noted that archaeopyles were either not
189 developed or indeterminate in their *Impletosphaeridium* spp. from the Cross Valley and La Meseta
190 formations on Seymour Island. Warny and Askin (2011a,b) also noted the inconsistent occurrence
191 of an archaeopyle in the small chorate cysts they observed in the SHALDRIL cores in the Weddell
192 Sea, east of the Antarctic Peninsula. Where an archaeopyle is not evident in these small chorate
193 cysts, identification is based on spine terminations. These are usually distally pointed and smooth in
194 *Micrhystridium* (see Sarjeant and Stancliffe 1994). Clearly, the taxonomic confusion between
195 *Impletosphaeridium* and *Micrhystridium* in the southern high latitudes is entirely understandable.

196 We suggest that cysts with a definite or probable archaeopyle (see *Impletosphaeridium clavus*
197 below) and mainly complex distal process terminations be assigned to the dinoflagellate cyst
198 *Impletosphaeridium*. Where an archaeopyle is not evident, but the cyst still possesses mainly
199 complex distal process terminations, this material should be questionably assigned to
200 *Impletosphaeridium*. If no archaeopyle is evident and the distal process terminations are mainly
201 simple, these specimens should be referred to the acritarch *Micrhystridium*. Assignment to species
202 level then relies on further morphological details, including the cyst and process surface texture, the
203 density of processes and the detailed distal and proximal morphology of the processes.

204

205 *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

206 Plate 1, figures. 1-10; Plate 2, figures 1, 4, 6; Plate 3, figures 1-6, 8

207

208 **Synonymy:**

- 209 *Impletosphaeridium clavus* Wrenn & Hart 1988. Wrenn and Hart (1988, p. 356, figs. 27.10, 27.11,
 210 27.13) (latest Early Eocene, Seymour Island, Antarctic Peninsula)
- 211 *Micrhystridium* spp. Pirrie et al. (1991, fig. 7g) (Late Campanian to Late Maastrichtian, Vega Island,
 212 Antarctic Peninsula)
- 213 *Impletosphaeridium clavus* Wrenn & Hart 1988. Coccozza and Clarke (1992, fig. 4f) (?reworked
 214 Eocene, Seymour Island, Antarctic Peninsula)
- 215 *Impletosphaeridium lorum* Wrenn & Hart 1988. Coccozza and Clarke (1992, fig. 4g) (?reworked
 216 Eocene, Seymour Island, Antarctic Peninsula)
- 217 *Micrhystridium* sp. Dolding (1992, fig. 6l) (Late Campanian, Humps Island)
- 218 *Micrhystridium* sp. A Smith (1992, fig. 11a) (Late Campanian – Late Maastrichtian, Vega Island,
 219 Antarctic Peninsula)
- 220 *Micrhystridium piliferum* Smith (1992, fig. 11b) (Late Campanian – Late Maastrichtian, Vega
 221 Island, Antarctic Peninsula)
- 222 *Impletosphaeridium clavus* Wrenn & Hart 1988. Levy and Harwood (2000, pl. 7, figs. a, b) (Mid
 223 and Late Eocene glacial erratics, McMurdo Sound, Ross Sea, Antarctica)
- 224 *Impletosphaeridium* spp. Warny et al. (2007, figs. 2a-d) (reworked Eocene – Miocene, Weddell Sea,
 225 Antarctica)
- 226 *Impletosphaeridium* sp. Salzmann et al. (2011, fig. 4d) (Neogene, James Ross Island, Antarctic
 227 Peninsula)
- 228 *Micrhystridium* spp. Warny and Askin (2011a, figs. 2.4 - 2.6) (Mid Miocene and ?reworked
 229 Cretaceous, SHALDRIL core NBP0602A-5D, Weddell Sea, Antarctica)
- 230 *Micrhystridium* sp. Warny and Askin (2011b, fig. 4.9) (Late Pleistocene to Holocene, SHALDRIL
 231 core NBP0602A-3C, Weddell Sea, Antarctica)
- 232 *Impletosphaeridium?* sp. Warny and Askin (2011b, fig. 4.10) (Late Pleistocene to Holocene,
 233 SHALDRIL core NBP0602A-3C, Weddell Sea, Antarctica)

234 *Impletosphaeridium clavus* Wrenn & Hart 1988. Bowman et al. (2012, pl. 1, fig. 5) (Maastrichtian
235 to earliest Danian) (Seymour Island, Antarctic Peninsula)

236

237 **Original diagnosis of Wrenn and Hart (1988, p. 356):** “A species of *Impletosphaeridium*
238 characterized by its thin solid, nail-like processes. The processes taper slightly to pad-like
239 terminations that may appear to be bifid, trifid, or multifurcate.”

240 **Emended diagnosis:** A species of *Impletosphaeridium* with a rounded to ellipsoidal outline.
241 Autophragm is externally microbaculate to microgranulate, and bears numerous solid, flexuous,
242 nontabular processes. Process distal terminations are typically bifurcate or acuminate (commonly
243 recurved); some may be capitate, trifurcate or multifurcate. Process bases are simple and contiguous
244 with the autophragm. Archaeopyle apical, type (4A), operculum free or rarely adherent.

245 **Emended description:** Small skolochorate dinoflagellate cysts with a rounded, sub-rounded to
246 ellipsoidal cyst body in outline. The autophragm is thin, with an external surface texture, which
247 appears smooth under transmitted light but is microbaculate to microgranulate using scanning
248 electron microscopy. Randomly-distributed dark granules, between less than 0.5 μm and 2 μm in
249 diameter, adhere to the cyst body of most specimens. The density of these granules is variable. Up
250 to around 100 solid, nontabular, randomly distributed processes are present on the cyst body. The
251 processes are flexuous to straight, thin (0.5 μm at the base) and taper slightly distally. The process
252 bases are simple and contiguous with the cyst body surface. The distal process terminations are
253 dominantly bifurcate or acuminate, the latter commonly recurved. Many of the recurved processes
254 have acuminate distal terminations which are angulate at close to 90°, i.e. are recurved in an angular
255 sense; others are more smoothly curved. Some apparently angulate recurved terminations bear a
256 minor accessory pinnule making them asymmetrically bifurcate. Some distal terminations may be
257 capitate (slightly bulbous), trifurcate or multifurcate. A single specimen can exhibit various distal
258 termination morphologies, all of which are resolvable using a transmitted light microscope. There is
259 no indication of tabulation other than the apical, type (4A), archaeopyle. An angular principal

260 archaeopyle suture is rarely observed; it is commonly irregular, but is consistently in an apical
261 position; the operculum is free or rarely adherent. The cingulum and sulcus are not evident.
262 Specimens of *Impletosphaeridium clavus* do not autofluoresce (i.e. emit induced light) under
263 ultraviolet epifluorescence illumination.

264 **Dimensions:** All 63 measured specimens identified as *Impletosphaeridium clavus* are on slide A
265 from sample D5.930.1, which is from the Maastrichtian of the López de Bertodano Formation
266 (Bowman et al. 2012). Length of central body: 15 (22) 32 μm [minimum (mean) maximum];
267 breadth of central body: 12 (18) 28 μm ; maximum process length: 5 (8) 14 μm . The process length
268 was measured from the base to the furcation junction, and is approximate due to their frequently
269 sinuous nature. The longest processes observed on each specimen were measured.

270 **Remarks:** Wrenn and Hart (1988) recorded four species of *Impletosphaeridium* from the Cross
271 Valley and La Meseta formations on Seymour Island; these are *Impletosphaeridium clavus*,
272 *Impletosphaeridium ligospinosum* (de Coninck 1969) Islam 1993, *Impletosphaeridium lorum*
273 Wrenn & Hart 1988 and *Impletosphaeridium* sp. B. Separation of these taxa is based primarily on
274 process morphology including the shape of the process bases, the flexibility of the process shafts
275 and the nature of the process terminations. Wrenn and Hart (1988) stated that the archaeopyle is
276 indeterminate or not developed. Despite the indeterminate nature of the archaeopyle in the original
277 description, we consider that the small chorate cysts described in this paper from the López de
278 Bertodano Formation are assignable to *Impletosphaeridium clavus*. This determination is on the
279 basis of the frequent distally furcate solid processes, the finely granular autophragm and the size.

280 We consider that *Impletosphaeridium clavus* requires emendation in order to clarify certain
281 features noted using scanning electron microscopy. These fine scale morphological features do not
282 preclude its identification using transmitted light microscopy. The process terminations are largely
283 furcate to acuminate (commonly recurved) on the same specimen (Plate 1, figures 4, 14; Plate 2,
284 figures 3, 5; Plate 3, figures 5, 10). Many of the processes exhibit acuminate distal terminations
285 which are angulate close to 90°; this means that they are recurved in an angular fashion (Plate 1,

286 figures 3, 9, 16; Plate 2, figures 1, 3; Plate 3, figures 3, 5, 10). Other distal terminations are
287 smoothly curved with acuminate terminations (Plate 3, figures 2, 3). Some bifurcate processes have
288 strongly asymmetrical pinnules, superficially appearing to be distally angulate, but possessing one
289 much smaller pinnule (Plate 3, figures 2, 3, 5). Some processes appear to be slightly capitate (“pad-
290 like” of Wrenn and Hart 1988) under transmitted light (Plate 1, figures 4, 15; Plate 3, figures 5, 7).
291 The complexity of rare multifurcate processes becomes evident when using the scanning electron
292 microscope (Plate 3, figures 11, 12), although they are resolvable using transmitted light
293 microscopy (Plate 1, figure 6). The species appears to be acavate; the microbaculate to
294 microgranulate autophragm of the cyst body extends onto the processes, although this
295 ornamentation is finer on the spines (Plate 2, figure 2; Plate 3, figures 11, 12). Moreover, a cross-
296 section of the cyst wall at the principal archaeopyle suture indicates an autophragm only (Plate 2,
297 figure 4). On the basis of these observations, it seems likely that *Impletosphaeridium clavus* may be
298 synonymous with *Impletosphaeridium ligospinosum*; this would require a restudy of the type
299 material of the latter.

300 Of the 100 specimens of *Impletosphaeridium* measured herein, 25 had definite apical
301 archaeopyles with either angular or irregular principle archaeopyle sutures (Plate 1, figures 3, 4, 9,
302 10; Plate 2, figure 4). The former (Plate 1, figure 3) indicate dehiscence between the apical and
303 precingular plates, however this is frequently difficult to comprehensively observe in a single
304 specimen due to the small size and the susceptibility of these thin-walled cysts to folding. The
305 somewhat irregular principal archaeopyle sutures (Plate 1, figures 4, 9, 10) may appear similar to
306 acritarch epityches, but this again is perhaps a result of the thin autophragm causing folding of the
307 autophragm at the cyst apex. A further 38 specimens probably have an archaeopyle, but they are
308 unclear and the margin commonly appears as a flat, truncated edge of the cyst body in dorso-ventral
309 compression (Plate 1, figures 5, 8; Plate 2, figure 1). Both these cyst types can be assigned to
310 *Impletosphaeridium clavus*. The remaining 37 specimens showed no indication of an archaeopyle,
311 but are otherwise identical to *Impletosphaeridium clavus*. We consider, due to the large number of

312 specimens observed and their otherwise identical morphology, that they are cysts of the same
313 species that had not yet excysted (Plate 1, figures 11, 14; Plate 2, figures 2, 3).

314 *Impletosphaeridium clavus* is abundant in the López de Bertodano Formation and was recorded
315 as common by Wrenn and Hart (1988) throughout the overlying Cross Valley and La Meseta
316 formations of the Seymour Island Group. On the basis of the generic emendation above, concluding
317 that only specimens with definite or probable apical archaeopyles should be unequivocally assigned
318 to *Impletosphaeridium*, we suggest that the material of Wrenn and Hart (1988) should be
319 questionably referred to this genus until further study of the type material can be made. The
320 material of Thorn et al. (2009, as *Micrhystridium* spp.) and Bowman et al. (2012, pl. 1, fig. 5) from
321 the López de Bertodano Formation of Seymour Island is now confidently assigned to
322 *Impletosphaeridium clavus*. Similarly, Askin (1988, fig. 8.5; 1999, fig. 3.2) referred to “swarms of
323 acanthomorph acritarchs” and “abundant *Micrhystridium* spp.” respectively from the López de
324 Bertodano Formation. Pirrie et al. (1997a) also recorded “extremely abundant” *Micrhystridium* spp.
325 from the lower part of the López de Bertodano Formation on Seymour Island. Study of the material
326 of Askin (1988; 1999) and Pirrie et al. (1997a) was beyond the scope of this study, however, we
327 confidently assume that the acritarchs referred to by these authors are *Impletosphaeridium clavus*
328 because they are from the López de Bertodano Formation of Seymour Island.

329 A feature of *Impletosphaeridium clavus* from the López de Bertodano Formation of Seymour
330 Island is the colour. In transmitted light, the cyst bodies of well-preserved specimens vary from
331 almost transparent to having a dark golden brown colour; an indication of the range can be seen in
332 greyscale throughout Plate 1. This variation in colour may reflect differential absorption of
333 amorphous organic matter (the “humic staining” of Sarjeant and Stancliffe 1994), sporadic
334 pigmentation possibly related to heterotrophy (Rochon et al. 1999; Brenner and Biebow, 2001) or
335 different levels of thermal maturity suggestive of reworking. Due to the predominance and well-
336 preserved nature of the small chorate cysts in many López de Bertodano Formation samples, we
337 consider this colour variation is most likely attributable to humic staining implying the assemblage

338 is autochthonous. In addition, during their study of the Cross Valley Formation and La Meseta
339 Formation palynofloras on Seymour Island, Wrenn and Hart (1988) reported finding no evidence of
340 reworking into the Upper Cretaceous and Paleocene in this basin. Higher in the regional
341 stratigraphical succession, dinoflagellate cyst colour may still help to differentiate reworked
342 Maastrichtian from much younger Neogene and Quaternary material (Warny and Askin 2011a, fig.
343 2.6; 2011b).

344 **Comparison with other species:** The earliest illustrated record of cysts assignable to
345 *Impletosphaeridium clavus* in Antarctic sediments is that of Dolding (1992, Fig. 6l, as
346 *Micrhystridium* spp.) from the Late Campanian Herbert Sound Member (Santa Marta Formation) of
347 Humps Island. On Seymour Island, the similarity of *Impletosphaeridium lorum* to *Micrhystridium*
348 sp. A of Wrenn and Hart (1988) from the Eocene La Meseta Formation was acknowledged by
349 Wrenn and Hart (1988) who differentiated these forms by the more numerous, denser and shorter
350 processes in the latter. *Impletosphaeridium clavus* differs primarily from *Impletosphaeridium lorum*
351 in having furcate process terminations, in contrast to the entirely acuminate terminations of the
352 latter. Furthermore, *Impletosphaeridium lorum* has 50-100 processes, whereas the diagnosis of
353 *Micrhystridium* restricts this genus to forms with 9-35 processes (Sarjeant and Stancliffe 1994),
354 suggesting that *Micrhystridium* sp. A of Wrenn and Hart (1988) requires further analysis.
355 *Impletosphaeridium clavus* differs from *Impletosphaeridium* sp. B of Wrenn and Hart (1988) in
356 being single-layered, having a microbaculate or microgranulate cyst body and simple, solid process
357 bases.

358 Coccozza and Clarke (1992) recorded low abundances (0-5% of the marine assemblage) of both
359 *Impletosphaeridium clavus* and *Impletosphaeridium lorum* from the Eocene La Meseta Formation
360 of Seymour Island. Two similar specimens were illustrated, neither of which has a definite
361 archaeopyle. They appear to be assignable to *Impletosphaeridium clavus* emend. nov. (see Coccozza
362 and Clarke 1992, figs. 4f, g).

363 Warny et al. (2007, figs. 2a-d) illustrated reworked specimens of *Impletosphaeridium* spp. that
364 occur unusually abundantly in piston cores from offshore Seymour Island, which are of Eocene to
365 Miocene age. The images are mostly out of focus, but one specimen shows a probable archaeopyle
366 (Warny et al. 2007, fig. 2a). These specimens are all comparable with the material described herein
367 from the López de Bertodano Formation but without clearer illustration they can only be assigned to
368 *Impletosphaeridium* sp. or ?*Impletosphaeridium* sp. However, Warny et al. (2007) suggested that
369 the most common species observed was *Impletosphaeridium lorum* despite conceding that species
370 of *Impletosphaeridium* are difficult to differentiate consistently. It is likely that *Impletosphaeridium*
371 *lorum* represents an uncertain assignment by Warny et al. (2007). These authors noted the presence
372 of closely related, undescribed species of very similar overall morphology and size, differing only
373 in process thickness.

374 **Stratigraphical range:** Late Campanian to Holocene.

375

376 **6. Discussion**

377

378 Small chorate cysts comparable to *Impletosphaeridium clavus*, assigned either to
379 *Impletosphaeridium* or *Micrhystridium*, are not restricted to Seymour Island but have been recorded
380 from many localities around Antarctica (Figure 1, Table 1). *Micrhystridium* spp. was recorded in
381 low abundances in the ?Valanginian and Hauterivian of ODP cores from offshore Dronning Maud
382 Land (Mohr 1990) and from the Cenomanian to Coniacian (?to Early Santonian) of the Kerguelen
383 Plateau (Mohr and Gee 1992). These were not illustrated so the taxonomic assignment of these
384 records needs to be verified.

385 In the Antarctic Peninsula region, *Micrhystridium* spp. have been recorded from the Middle
386 Albian to Campanian of James Ross Island (Keating 1992; Keating et al. 1992). Small chorate cysts
387 identified as acanthomorph acritarchs from Cockburn Island (Askin et al. 1991) and common
388 *Micrhystridium* spp. from Humps Island (Wood and Askin 1992) have been recorded from strata

389 considered to be Late Campanian to Early Maastrichtian in age based on the presence of the
390 ammonite genus *Gunnarites* (J.A. Crame, unpublished data). Dolding (1992) quantified the first
391 common occurrence of these morphotypes as an acme of *Micrhystridium* spp., comprising up to
392 26% of the total palynomorphs in one sample, from the Upper Campanian Herbert Sound Member
393 (Santa Marta Formation) of Humps Island. Records from the James Ross Basin indicate that these
394 small chorate cysts increased dramatically in abundance during the Maastrichtian, reaching up to
395 99% of the marine palynomorph assemblage (Askin 1988; Pirrie et al. 1991, 1997a; Dolding 1992;
396 Smith 1992; Thorn et al. 2009; Bowman et al. 2012; this study). For example, Pirrie et al. (1991,
397 1997a) recorded abundant forms tentatively referred to *Micrhystridium* throughout the Upper
398 Campanian to Maastrichtian succession of Cape Lamb, Vega Island and the Spath Peninsula, Snow
399 Hill Island. Smith (1992) recorded extremely abundant *Micrhystridium piliferum* (up to 91.2% of
400 the assemblage) from the Cape Lamb Member (Snow Hill Island Formation) of Vega Island. We
401 consider that all of these small chorate cysts from the Antarctic Peninsula are assignable to
402 *Impletosphaeridium clavus*. Verification is required for those records that were not illustrated (e.g.
403 Askin et al., 1991; Keating, 1992; Wood and Askin, 1992)

404 There are few data on the occurrence of these cysts around the Antarctic margin during the
405 Paleocene, however they are recorded as rare in the Cross Valley Formation of Seymour Island
406 (Wrenn and Hart 1988). Wrenn and Hart (1988) recorded *Impletosphaeridium clavus* in the
407 overlying Eocene La Meseta Formation of Seymour Island, however, they discuss evidence for
408 significant reworking of marine and terrestrial palynomorphs into Eocene sediments on Seymour
409 Island. It is likely that the low abundances of *Impletosphaeridium clavus* and *Impletosphaeridium*
410 *lorum* recorded by Cocozza and Clarke (1992) from the La Meseta Formation are also reworked.
411 *Impletosphaeridium* spp. has also been noted from the Lower Eocene sediments of Cockburn Island
412 (Askin et al. 1991). In the Ross Sea region, Levy and Harwood (2000) recorded rare specimens
413 comparable to *Impletosphaeridium clavus* from modern glacial erratics composed of Eocene
414 sediments. These authors noted a rare undescribed *Impletosphaeridium* with short, solid, bifurcate

415 or trifurcate process terminations, a type that is apparently absent from Seymour Island. The rarity
416 of all these forms suggests that they may be reworked.

417 Palynomorph assemblages in Upper Eocene to Holocene sediment cores to the east of the James
418 Ross Basin in the Weddell Sea (the NBP0602A-3C SHALDRIL core) have also revealed abundant
419 small chorate cysts. The majority occurring in the youngest sediments (as *Micrhystridium* spp.) are
420 dark in colour, are associated with reworked Cretaceous dinoflagellate cysts (for example,
421 *Isabelidinium cretaceum* and *Manumiella* spp.) and hence are interpreted as being reworked from
422 Cretaceous sediments themselves (Warny and Askin 2011b). These authors distinguished dark
423 coloured specimens of *Micrhystridium* from rare ‘presumed in-place’ translucent forms with
424 capitate processes and occasional apical archaeopyles assigned to *Impletosphaeridium*. They also
425 noted variation in process base and shaft morphology in *Micrhystridium*, and compared this
426 material to the abundant *Micrhystridium* spp. of Askin (1988, 1999) in association with
427 *Isabelidinium cretaceum* (Cookson 1956) Lentin & Williams 1977 and *Manumiella seymourensis*
428 Askin 1999 on Seymour Island. We consider that all these abundant small chorate cysts from this
429 core are referable to *Impletosphaeridium clavus* (probably including *Impletosphaeridium*
430 *ligospinosum*). This suggests the youngest occurrence of cysts assignable to *Impletosphaeridium*
431 *clavus* is from Upper Pleistocene to Holocene sediments recovered in the NBP0602A-3C
432 SHALDRIL core from the Weddell Sea. The illustrations of *Micrhystridium* sp. and
433 *Impletosphaeridium?* sp. by Warny and Askin (2011b, figs. 4.9, 4.10 respectively) appear
434 indistinguishable using transmitted light microscopy, and are comparable to *Impletosphaeridium*
435 *clavus* described herein. Similarly, small chorate cysts are dominant in the lower SHALDRIL cores
436 NBP06602A-12A and NBP0602A-5D (Warny and Askin 2011a) and are also deemed referable to
437 *Impletosphaeridium clavus*. Salzmänn et al. (2011) also noted abundant *Impletosphaeridium* spp. in
438 Neogene diamictites from James Ross Island, which could be a mixture of autochthonous cysts and
439 marine palynomorphs reworked from the underlying Cretaceous. Further, from the Ross Sea region,
440 Hannah et al. (2001) recorded *Impletosphaeridium clavus* and *Impletosphaeridium* sp. B of Wrenn

441 and Hart (1988) from the Lower Oligocene in the CRP-3 core, but did not illustrate these
442 morphotypes.

443 We have demonstrated that *Impletosphaeridium clavus* is ubiquitous, and frequently extremely
444 abundant, in the Upper Cretaceous to Quaternary of the James Ross Basin and the Weddell Sea. Bijl
445 et al. (2011) also recognised its extensive distribution by including it within the endemic
446 “Transantarctic Flora”, a suite of dinoflagellate cysts considered to be characteristic of Eocene
447 Antarctic palynofloras. However, we consider that all Eocene records of small, chorate cysts
448 comparable to *Impletosphaeridium clavus* from around the Antarctic region are likely to have been
449 reworked, probably from the Campanian to Maastrichtian acmes, and should not therefore be
450 included within the Transantarctic Flora.

451 Warny et al. (2007) selected several modern dinoflagellate cyst taxa as analogues for
452 *Impletosphaeridium* spp. that are found in polar regions, although the affinity of these cysts is
453 currently unknown. These are *Echinidinium karaense* Head et al. 2001, *Islandinium? cezare* (de
454 Vernal et al. 1989) Head et al. 2001 and *Islandinium minutum* (Harland & Reid in Harland et al.
455 1980) Head et al. 2001. These species are produced by heterotrophic dinoflagellates within cold,
456 polar/subpolar waters (Harland and Pudsey 1999; De Vernal et al. 2001; Head et al. 2001; Marret
457 and Zonneveld 2003; De Vernal and Rochon 2011). They all have spherical, thin-walled cyst bodies
458 (the largest ranges up to 45 µm in diameter) and are covered in processes with a variety of
459 terminations. De Vernal and Rochon (2011) noted that only minute morphological differences
460 separate these species, however, details of process and archeopyle structure in these taxa differ from
461 *Impletosphaeridium* spp. (Kenneth N. Mertens, personal communication 2012). Warny et al. (2007)
462 also suggested the cyst of *Pentapharsodinium dalei* Indelicato & Loeblich III as an analogue for
463 *Impletosphaeridium* spp. This is a small, spherical, spiny cyst found in cold regions (e.g. Dale,
464 1983; Indelicato and Loeblich III 1986; Harland et al. 1998; Ribeiro et al. 2011; Candel et al. 2012).
465 It belongs to the family Thoracosphaeraceae and is autotrophic (Gottschling et al. 2005; 2012). The
466 specimen of *Pentapharsodinium dalei* figured by Harland et al. (1998, pl. 2, fig. 5) from the

467 Weddell Sea compares closely with *Impletosphaeridium clavus* in terms of size, number of
468 processes (with both recurved acuminate and bifurcate process terminations) and exhibiting
469 adherent organic granules on the cyst body. However Harland et al. (1998) expressed doubt about
470 the taxonomic assignment. Other illustrations of cysts now assigned to *Pentapharsodinium dalei* in
471 the literature have a similar gross morphology to *Impletosphaeridium clavus*, but differ especially in
472 the details of process terminations and wall thickness (e.g. Rochon et al. 1999; Price and Pospelova
473 2011; Ribeiro et al. 2011). Furthermore, cyst pigmentation and the lack of autofluorescence in
474 *Impletosphaeridium clavus* (compared with dull red/brown autofluorescence colours exhibited by
475 the other dinoflagellates in the same slide) may imply that the parent dinoflagellate was
476 heterotrophic (Brenner and Biebow, 2001). Therefore, there is no known direct analogue for
477 *Impletosphaeridium clavus* currently, but clearly cysts of a similar gross morphology and size are
478 found in cold, high latitude oceans today.

479 Several undescribed species of *Micrhystridium* spp., superficially similar in morphology to
480 *Impletosphaeridium clavus*, have been recorded from Lower Oligocene to Pliocene sediments from
481 the Ross Sea region (Hannah et al. 1998, 2000, 2001; Wrenn et al. 1998; M.J. Hannah, unpublished
482 data). These cysts have relatively few solid and hollow processes, with mostly simple process
483 terminations and flared bases, and have not yet been recorded from the lower palaeolatitude James
484 Ross Basin. These morphotypes, correctly identified as *Micrhystridium* spp., may reflect an
485 adaptation to colder conditions, perhaps along the margins of floating ice shelves.

486 Dolding (1992) and Smith (1992) interpreted acmes of *Micrhystridium* (now referred to
487 *Impletosphaeridium clavus*) in Upper Campanian to Maastrichtian sediments of the James Ross
488 Basin as representing shallow water, nearshore deposition in comparison with the work of Wall
489 (1965) who studied Early Jurassic microplankton from England and Wales. Acmes of
490 *Micrhystridium* in the low to mid palaeolatitudes apparently imply shallow water conditions (e.g.
491 Downie et al. 1971; Firth 1987; Oloto 1992; Prauss 2006; Götz and Feist-Burkhardt 2012). Further
492 work is required to clarify whether it is reasonable to apply this interpretation to the highly variable

493 temperature and light regime of the southern high latitudes. This inner neritic interpretation is likely
494 to be overly simplistic on a global scale, and there was probably a latitudinal pattern in
495 palaeoecological preference for chorate cysts of this type.

496

497 **7. Conclusions**

498 Small chorate algal cysts have been recorded, but rarely illustrated, in Upper Cretaceous to
499 Quaternary sediments from the southern polar palaeolatitudes. However, taxonomic confusion has
500 hitherto limited investigation of their palaeoecological significance. A detailed taxonomic analysis
501 of *Impletosphaeridium clavus* from Seymour Island, Antarctic Peninsula, has helped resolve these
502 issues for this species. We now recognise that this cyst, previously termed *Impletosphaeridium* spp.
503 or *Micrhystridium* spp., is present, often in high numbers, throughout the James Ross Basin and
504 rarely in other localities around the Antarctic margin.

505 In the light of this taxonomic clarification, a reassessment has been made of the published
506 occurrences of what is now recognised as *Impletosphaeridium clavus* in the south polar region. We
507 have found that many authors have recorded this species in extremely high numbers (up to 99% of
508 marine palynomorphs) during the Late Campanian to Maastrichtian interval. However, during the
509 Eocene, their numbers were significantly reduced. The available evidence, including rare
510 occurrences from glacial erratics from McMurdo Sound, suggests that all *Impletosphaeridium* spp.
511 recorded from Eocene sediments around the Antarctic margin are probably reworked. We therefore
512 suggest the removal of *Impletosphaeridium clavus* from the “Transantarctic Flora” of Bijl et al.
513 (2011). Additional later acmes are present in the mid Miocene of the Joinville Plateau (Warny and
514 Askin 2011a).

515 Building on the work of Warny et al. (2007), detailed comparison of *Impletosphaeridium clavus*
516 with modern cysts produced no unequivocal direct analogue. However, it is clear that diverse cysts
517 of similar gross morphology are known from cold high latitude oceans today.

518

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531

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762 Cainozoic marine palynomorphs from the CRP-1 core, Ross Sea, Antarctica. *Terra Antarctica* 5,
763 553-570.
- 764
- 765
- 766 **Captions for the display materials:**
- 767
- 768 Figure 1. The locations around the Antarctic margin where small chorate cysts (*Impletosphaeridium*
769 and *Micrhystridium*) have been recorded. Further details for each numbered location are listed in
770 Table 1. Note that there may be several publications per locality. The outcrop of Aptian-Coniacian
771 to Eocene sediments in the James Ross Basin is illustrated (refer to Fig. 2 for a lithostratigraphical

772 summary). D5.251 = the stratigraphical section throughout the oldest sediments cropping out on
773 Seymour Island from which sample D5.930.1 was collected. Boxes indicate geographical regions
774 enlarged elsewhere in the figure.

775

776 Figure 2. Upper Cretaceous to Neogene lithostratigraphy for the James Ross Basin, Antarctic
777 Peninsula (not to scale). Based on biostratigraphical and lithostratigraphical information (Ineson et
778 al. 1986; Pirrie et al. 1991, 1997a, 1997b; Keating 1992; Keating et al. 1992; Riding et al. 1992;
779 Barnes and Riding 1994; Jonkers and Kelley, 1998; Riding and Crame 2002; Crame et al. 2004;
780 Nývlt et al. 2011; Pirrie et al. 2011; and references therein). LDBF, López de Bertodano
781 Formation.

782

783 Table 1. The occurrences of small chorate cysts (*Impletosphaeridium* and *Micrhystridium*) in the
784 Late Cretaceous to Quaternary of the Antarctic margin. ODP = Ocean Drilling Program. The
785 superscript location numbers refer to the starred localities in Figure 1.

786

787 Plate 1. Transmitted light images of specimens of *Impletosphaeridium clavus* from sample
788 D5.930.1 (slide A). The images were taken using Differential Interference Contrast using an oil
789 immersion objective. LF, MF and HF – low, mid and high focus respectively. England Finder
790 coordinates are quoted for each specimen. All images are at the same scale; the scale bar in Figure 1
791 represents 10 µm. Note the distal terminations of the relatively densely-inserted slender, nontabular
792 processes which may be acuminate, recurved, capitate, bifurcate, trifurcate or multifurcate. Many of
793 these are recurved in an angular sense (close to 90°), and a single specimen can exhibit various
794 distal termination morphologies. Several process terminations are enlarged in Plate 3.

795 Figures 1-10 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

796 Figures 1, 2. Note that the operculum of the apical archaeopyle is attached to the cyst body; M64-3.

797 1 - LF; 2 - HF.

798 Figure 3. A specimen with an apical archaeopyle having a clear angular principal archaeopyle
799 suture (A); N62-2, MF.

800 Figure 4. Note the apical archaeopyle with an irregular suture (A); X61-1, LF.

801 Figures 5-7. A specimen with many furcate process terminations. The truncated edge in 5 (A?)
802 strongly suggests an apical archaeopyle. Note the trifurcate process termination (arrowed) in 6;
803 X62-0. 5 - MF; 6 - LF; 7 - HF.

804 Figure 8. The truncated edge (A?) suggests an apical archaeopyle; X62-2, HF.

805 Figure 9. Note the apical archaeopyle with an irregular suture (A); X66-0, HF.

806 Figure 10. Note the apical archaeopyle with an irregular suture (A); U63-3, MF.

807 Figures 11-16 - *Impletosphaeridium? clavus* Wrenn & Hart 1988 emend. nov.

808 Figures 11, 12. W65-1. 11 - MF; 12 - HF.

809 Figure 13. W60-1/2, LF.

810 Figure 14. R63-2, MF.

811 Figure 15. P64-4, HF.

812 Figure 16. N64-0, HF.

813

814 Plate 2. Scanning electron microscope images of specimens of *Impletosphaeridium clavus* from
815 sample D5.930.1. These specimens illustrate further examples of process terminations recurved in
816 an angular sense (close to 90°). The scale bars all represent 5 µm.

817 Figures 1, 4, 6 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

818 Figure 1. The flat truncated edge (A?) at the top of the cyst body suggests an apical archaeopyle
819 suture.

820 Figure 4. The principal archaeopyle suture of the apical archaeopyle (A) indicates a single wall
821 layer (autophragm).

822 Figure 6. A possible apical archaeopyle (A?).

823 Figures 2, 3, 5 - *Impletosphaeridium? clavus* Wrenn & Hart 1988 emend. nov.

824 Figure 2. The microbaculate surface ornamentation on the central body extends as finer granules
825 onto the surfaces of the processes.

826 Figure 3. A specimen with a mixture of acuminate recurved and furcate process terminations.

827 Figure 5. A specimen with a multifurcate process termination which is highlighted within a square;
828 enlarged in Plate 3, figure 12.

829

830 Plate 3. High-magnification images of process terminations observed on specimens of
831 *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov and *Impletosphaeridium? clavus*
832 Wrenn & Hart 1988 emend. nov. Figures 1-10 - transmitted light images comprising enlargements
833 of specimens illustrated in Plate 1 (slide D5.930.1A). The scale bars all represent 5 μm . Figures 11,
834 12 - Scanning electron microscope images of specimens observed in sample D5.930.1. The scale
835 bars represent 0.5 μm .

836 Figures 1-6, 8 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

837 Figure 1. Bifurcate process terminations on a free and adherent apical archaeopyle; M64-3, LF
838 (entire specimen illustrated in Plate 1, Figure 1).

839 Figures 2, 3. 2 - recurved process terminations (close to 90°), one bifurcate with minor accessory
840 pinnule (arrowed). 3 - acuminate, recurved and bifurcate process terminations. Examples of both
841 smooth and angular recurved terminations can be seen, one bifurcate with minor accessory pinnule
842 (arrowed). N62-2, MF (entire specimen illustrated in Plate 1, figure 3).

843 Figures 4, 5. 4 - acuminate and smoothly recurved process terminations. 5 - capitate (slightly
844 bulbous termination), angular recurved and bifurcate (with minor accessory pinnule; arrowed)
845 process terminations. X61-1, LF (entire specimen illustrated in Plate 1, figure 4).

846 Figures 6, 8. 6 - bifurcate process terminations. 8 - angular recurved and a trifurcate process
847 termination (arrowed). X62-0, (entire specimen illustrated in Plate 1, figures 5-7).

848 Figures 7, 9-12 – *Impletosphaeridium? clavus* Wrenn & Hart 1988 emend. nov.

849 Figure 7. Note the capitate and angular recurved process terminations; P64-4, HF (entire specimen
850 illustrated in Plate 1, figure 15).

851 Figure 9. Note the bifurcate process terminations; W60-1,2, LF (entire specimen illustrated in Plate
852 1, figure 13).

853 Figure 10. Bifurcate and angular recurved process terminations; R63-2, MF (entire specimen
854 illustrated in Plate 1, figure 14).

855 Figures 11, 12. Process shafts show detail of microgranular surface texture. 11 - multifurcate
856 process termination with minor accessory pinnule. 12 - complex multifurcate process termination
857 (entire specimen illustrated in Plate 2, figure 5).