

# 1 A synthesis of the *Sentusidinium* complex of 2 dinoflagellate cysts

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4 Stephanie E.L. Wood <sup>a\*</sup>, James B. Riding <sup>b</sup>, Robert A. Fensome <sup>c</sup>, Graham L. Williams <sup>c</sup>

5 <sup>a</sup> *Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building,*  
6 *Western Bank, Sheffield S10 2TN, UK*

7 <sup>b</sup> *British Geological Survey, Environmental Science Centre, Keyworth, Nottingham NG12 5GG,*  
8 *UK*

9 <sup>c</sup> *Natural Resources Canada, Geological Survey of Canada (Atlantic), Bedford Institute of*  
10 *Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2*

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12 \*Corresponding author. Tel.: +44(0)114 2220123

13 *E-mail address:* selw89@gmail.com (S.E.L. Wood).

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## 15 **ABSTRACT**

16 The Jurassic to Neogene (Miocene) dinoflagellate cyst genus *Sentusidinium* has a relatively  
17 simple overall morphology. This genus, together with *Batiacasphaera*, *Kallosphaeridium* and  
18 *Pentafidia*, comprises the *Sentusidinium* complex. This is distinct from the superficially similar  
19 laterally asymmetrical and subspheroidal/lenticular *Cyclonephelium* complex. The genus  
20 *Sentusidinium* is an acavate, subcircular, proximate to proximochorate sexiform gonyaulacacean  
21 genus, typically with low relief ornamentation and an apical archaeopyle. Since the erection of  
22 *Sentusidinium* in 1978, three other similar genera have been established, which are considered to  
23 be taxonomic junior synonyms of that genus: these are *Barbatacysta*, *Escharisphaeridia* and  
24 *Pilosidinium*. However, the Early Cretaceous to Miocene genera *Batiacasphaera*,  
25 *Kallosphaeridium* and *Pentafidia* are deemed to be valid, and differ significantly from  
26 *Sentusidinium*. The Early Cretaceous to Miocene genus *Batiacasphaera* has a reticulate to  
27 rugulate autophragm and an apical archaeopyle with a free operculum and no or shallow  
28 accessory archaeopyle sutures between the precingular plates. By contrast, *Kallosphaeridium*  
29 has a ventrally attached apical archaeopyle with five plates that can be interpreted as type

30 (4A1I)<sub>@</sub> or type (5A)<sub>@</sub>; it also has a small operculum relative to the overall cyst diameter. The six  
31 accepted *Kallosphaeridium* species are confined to the Palaeogene. The Australian genus  
32 *Pentafidia* is unusual in appearing to only have five precingular plates; this comprises two  
33 species from the Jurassic–Cretaceous transition of Western Australia. Therefore, we emend  
34 *Sentusidinium* to restrict it to acavate, proximate or proximochorate dinoflagellate cysts. The  
35 autophragm is either devoid of, or covered with, highly variable ornamentation which can be  
36 evenly distributed or concentrated locally. Occasionally the elements of ornamentation may be  
37 connected, but rarely is a cingulum indicated, and the tabulation is never clearly evident. A  
38 kalyptra may be occasionally present. The archaeopyle is apical, type (tA), with a free  
39 operculum. Following a comprehensive literature review, we consider that there are 17 valid  
40 species of *Batiacasphaera*. In the genus *Kallosphaeridium*, we recognise six accepted and six  
41 problematical species. There are 38 (34 accepted and four problematical) species assignable to  
42 the most diverse genus, *Sentusidinium*. *Kallosphaeridium? helbyi* is here transferred to  
43 *Cyclonephelium* without question. The species *Batiacasphaera angularis* is occasionally  
44 tabulate hence we transfer, with question, this species to *Meiourgonyaulax*. The *Sentusidinium*  
45 complex is clearly polyphyletic, and all three genera are in the order Gonyaulacales. However,  
46 *Batiacasphaera* and *Pentafidia* can not be confidently assigned to a family, whereas  
47 *Kallosphaeridium* and *Sentusidinium* are both in the family Gonyaulacaceae. The number of  
48 species within the complex has been reduced to xxx to yyy; furthermore, all infraspecific taxa  
49 have been eliminated.

50

51 **Keywords:** dinoflagellate cysts; Mesozoic-Cenozoic; morphology; *Sentusidinium* complex;  
52 taxonomic review

53

## 54 **1. Introduction**

55 Many species of acavate, subspheroidal to lenticular, sexiform gonyaulacalean dinoflagellate  
56 cysts (Fensome et al. 1993) with broadly apical archaeopyles, low-relief ornamentation and  
57 generally no or very weak development of parasutures have been described from the Mesozoic  
58 and Cenozoic. These can be divided into two groups, the *Cyclonephelium* complex and the  
59 *Sentusidinium* complex. The *Sentusidinium* complex is characterised by laterally symmetrical  
60 cysts that belong to the family Gonyaulacaceae; this complex, which is the focus of the present  
61 study, comprises the genera *Barbatacysta*, *Batiacasphaera*, *Escharisphaeridia*,

62 *Kallosphaeridium*, *Pentafidia*, *Pilosidinium* and *Sentusidinium*. The *Cyclonephelium* complex  
63 consists typically of laterally asymmetrical, subspheroidal to lenticular cysts that belong to the  
64 family Areoligeraceae; this complex is the focus of a separate ongoing study and includes the  
65 genera *Aptea*, *Canningia*, *Canninginopsis*, *Cerbia*, *Circulodinium*, *Cyclonephelium*,  
66 *Senoniasphaera* and *Tenua*. The genera *Prolixosphaeridium*, *Bourkidinium* and  
67 *Tanyosphaeridium* are similar to *Sentusidinium* in having process-bearing cysts with apical  
68 archaeopyles. However, all three genera have markedly elongate cyst bodies and generally  
69 longer, nontabular processes. Consequently, we do not consider them in this paper.

70 Due to the relatively simple morphology of cysts in the *Sentusidinium* complex and the large  
71 number of species, individual taxa are difficult to consistently recognise. The principal criterion  
72 for identification is the nature of the ornamentation. We aim to simplify the *Sentusidinium*  
73 complex at the generic and specific levels and to determine the most stratigraphically useful  
74 species.

75

76

## 77 **2. A brief history of the *Sentusidinium* complex**

78 The first genus to be described in the *Sentusidinium* complex was *Kallosphaeridium*, which was  
79 established by de Coninck (1969) and emended by Jan du Chêne et al. (1985a).

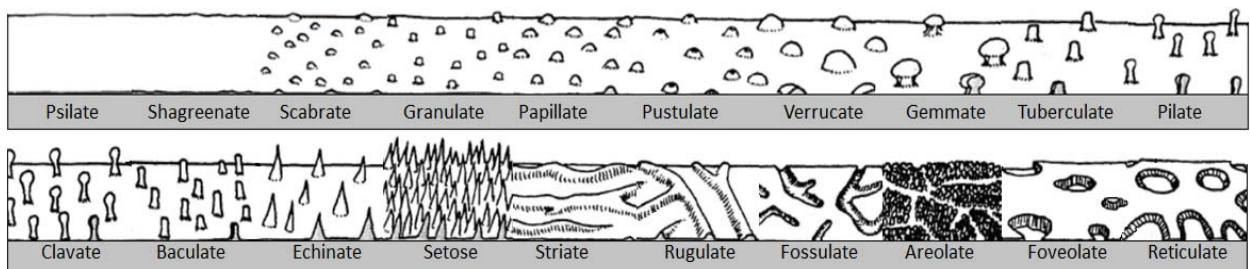
80 *Kallosphaeridium* comprises proximate cysts with a five-plate archaeopyle that can be  
81 interpreted as apical (5A) or combination (4A1I); the operculum is attached ventrally. Drugg  
82 (1970, p. 813) proposed *Batiacasphaera* for proximate cysts with “rod-shaped elements, either  
83 separate or arranged to form a reticulum”, and with an apical archaeopyle. This genus was later  
84 emended by Morgan (1975) and Dörhöfer and Davies (1980) (see section 3). *Sentusidinium* was  
85 erected by Sarjeant and Stover (1978) to contain proximate to proximochorate cysts with an  
86 apical archaeopyle and bearing low-relief ornamentation. Psilate forms with apical archaeopyles,  
87 including some previously referred to as *Sentusidinium*, were separated by Erkmen and Sarjeant  
88 (1980) to establish the genus *Escharisphaeridia*. *Pentafidia*, described by Backhouse (1988),  
89 consists of proximate cysts with an apical archaeopyle, but is characterised by having only five  
90 (in contrast to the more normal “gonyaulacoid” six) precingular plates. Courtinat (1989)  
91 established *Barbatacysta* and *Pilosidinium*, and also emended *Sentusidinium* to simplify its  
92 description (see section 3). *Barbatacysta* and *Pilosidinium* were defined on minor details of  
93 ornamentation, and are clearly very similar to *Sentusidinium*. More recently, Sangiorgi et al.

94 (2009) noted the similarities between their new genus *Arcticacysta* and genera of the  
95 *Sentusidinium* complex. However, these similarities are superficial, as *Arcticacysta* belongs to  
96 the Peridiniales, and is thus excluded from this study.

97 Given the relatively simple morphology of cysts in the *Sentusidinium* complex, we consider it  
98 contains too many genera and species, and so propose to simplify the taxonomy. We retain only  
99 the following genera: *Batiacasphaera*, *Kallosphaeridium*, *Pentafidia* and *Sentusidinium*.

100 *Sentusidinium*, the main focus of this taxonomic review, has a type (4A) apical archaeopyle and  
101 a free operculum, typically deep accessory archaeopyle sutures between precingular plates, and  
102 an autophragm that is either psilate or ornamented (Figure 1) with generally isolated elements  
103 (for example granula, spines or short processes). *Batiacasphaera* has ornamentation that is  
104 rugulate to reticulate, or consists of isolated elements that are aligned to form a rugulate to  
105 reticulate pattern; it also typically has no or only weakly developed accessory archaeopyle  
106 sutures. *Kallosphaeridium* has an apical (5A) or combination (4A1I) archaeopyle and a ventrally  
107 attached operculum. *Pentafidia* has apparently only five precingular plates.

108



109

110 *Figure 1* Surface ornamentation terminology applied to dinoflagellate cysts (Modified from Williams et al. 1978)

111

112 In the following systematic section, these four genera are discussed in detail and emendations  
113 and synonymys proposed.

114 Throughout the systematics we use the three categories of size outlined by Stover and Evitt  
115 (1978, p. 5): small (<50  $\mu\text{m}$ ), intermediate (50–100  $\mu\text{m}$ ), and large (>100  $\mu\text{m}$ ); the use of an  
116 asterisk denotes the type species for each genus. We also use the concepts of “accepted”,  
117 “provisionally accepted” and “problematical” species as used by Stover and Evitt (1978, p. 5).  
118 The accepted species are listed along with the age and geographical location from which they  
119 were first described. Provisionally accepted species do not belong to the respective genus with  
120 certainty and have a question mark following the generic name. Problematical species are even

121 more doubtfully assigned to the genus. Stover and Evitt denoted problematical species with  
122 quotation marks around the generic abbreviation and did not use a question mark. We add a  
123 question mark after the generic name, as leaving it out might be seen to imply that such species  
124 are less questionable than provisionally accepted species, which is clearly not the case; and we  
125 omit quotation marks as their use might lead to problems with nomenclatural validity (see  
126 McNeill et al. 2012, Article 36.1) and confusion with their different usage in the DINOFLAJ  
127 database (Fensome et al. 2008).

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129

### 130 **3. Systematic Palaeontology**

131

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

133 Subdivision DINOKARYOTA Fensome et al. 1993

134 Class DINOPHYCEAE Pascher 1914

135 Subclass PERIDINIPHYCIDAE Fensome et al. 1993

136 Order GONYAULACALES Taylor 1980

137 Suborder UNCERTAIN

138 Family UNCERTAIN

139 Subfamily UNCERTAIN

140

141 ***Genus Batiacasphaera* Drugg 1970 emend. nov.**

142

143 **Type:** *Batiacasphaera compta* Drugg 1970

144

145 1970 *Batiacasphaera* Drugg, p. 813.

146 1975 *Batiacasphaera* Drugg 1970 emend. Morgan, p. 161.

147 1980 *Batiacasphaera* Drugg 1970 emend. Dörhöfer & Davies, p. 40.

148

149 **Original diagnosis:** Tract spherical to subspherical with an angular apical archaeopyle. The  
150 ornamentation consists of rod-shaped elements, either separate or arranged to form a reticulum.  
151 In the latter case, they may be fused (Drugg 1970, p. 813).

152

153 **Emended diagnosis:** Proximate, acavate gonyaulacalean dinoflagellate cysts with a  
154 subspheroidal to ovoidal central body. The autophragm bears nontabulate ornament that is  
155 rugulate to reticulate, or isolated elements that align. The archaeopyle is apical, typically with a  
156 free operculum. Accessory archaeopyle sutures between precingular plates are not, or are only  
157 weakly, developed.

158

159 **Emended description:** Small to intermediate, acavate, proximate dinoflagellate cysts that are  
160 subspherical to ovoidal in shape, occasionally elongate. The autophragm is generally thick and  
161 bears a rugulate to reticulate ornament, or bears typically rod-shaped elements that are arranged,  
162 or may fuse, to form a reticulum or polygonal, semi-polygonal or rugulate pattern. The  
163 presumed gonyaulacacean tabulation is only indicated by the apical archaeopyle, which  
164 normally has a free operculum. Accessory archaeopyle sutures are not, or only weakly,  
165 developed. The cingulum and sulcus are not indicated.

166

167 **Comments:** We restrict *Batiacasphaera* to species with a generally reticulate to rugulate  
168 ornamentation and a consistent lack, or weak development, of accessory archaeopyle sutures.  
169 We consider both these features to be diagnostic, so species similar to the type in terms of  
170 archaeopyle development, such as *Batiacasphaera baculata*, but with isolated sculptural  
171 elements, are reassigned to *Sentusidinium*. The lack of well-developed accessory archaeopyle  
172 sutures can give the superficial impression of a precingular archaeopyle, especially in poorly  
173 preserved or obliquely oriented specimens; however, closer examination of better specimens  
174 reveals the shape of an apical archaeopyle. The holotype of *Batiacasphaera compta*, the type of  
175 *Batiacasphaera*, shows an unconventional outline to its archaeopyle and is thus difficult to  
176 interpret precisely in terms of tabulation. However, other species of the genus show a  
177 conventional type (tA) archaeopyle.

178 Fensome and Williams (2004, p. 73–78) listed 49 species of *Batiacasphaera*. However, only 17  
179 of these species have a rugulate to reticulate autophragm, and these are all Early Cretaceous to  
180 Late Miocene in age. They are listed below in both the accepted species list and in summary in  
181 Table 1. Morgan (1975, p. 161) gave an emended description, which noted the lenticular shape  
182 and that the ornamental elements may fuse to form rugulae. Dörhöfer and Davies (1980, p.  
183 40) emended the genus to include some species that were formerly in the genus *Tenua*.

184

185 **Comparison:** *Batiacasphaera* differs from all three other genera in the *Sentusidinium* complex  
186 by its strongly developed reticulate to rugulate ornamentation.

187

188 **Accepted species:**

189 *Batiacasphaera bergenensis* Schreck & Matthiessen 2014 (Early–Middle Miocene, Iceland)

190 *Batiacasphaera cassiculus* Wilson 1988 (Middle Eocene, New Zealand)

191 \**Batiacasphaera compta* Drugg 1970 (Late Eocene, USA)

192 *Batiacasphaera cooperi* Hannah et al. 1998 (Miocene, Antarctica)

193 *Batiacasphaera dictyophora* Gao Ruiqi et al. 1992 (Late Cretaceous, China)

194 *Batiacasphaera edwardsiae* Louwye et al 2008 (Middle Miocene, Ireland)

195 *Batiacasphaera grandis* Roncaglia et al. 1999 (Late Cretaceous, New Zealand)

196 *Batiacasphaera imperfecta* Stover & Helby 1987 (Early Cretaceous, Australia)

197 *Batiacasphaera kekerengensis* Schiøler & Wilson 1998 (Late Cretaceous, New Zealand)

198 *Batiacasphaera microreticulata* Shaw Chenglong 1999 (Eocene, Taiwan)

199 *Batiacasphaera reticulata* Davey 1979 (Late Cretaceous, South Africa)

200 *Batiacasphaera retirugosa* Xu Jinli et al. 1997 ex He Chengquan et al. 2009 (Middle–Late  
201 Eocene, China)

202 *Batiacasphaera rugulata* Schiøler & Wilson 1998 (Late Cretaceous, New Zealand)

203 *Batiacasphaera saidensis* Below 1981 (Early Cretaceous, Morocco)

204 *Batiacasphaera solida* Slimani 2003 (Late Cretaceous, Belgium)

205 *Batiacasphaera spherica* Stover 1977 (Early Miocene, Atlantic Ocean)

206 *Batiacasphaera subtilis* Stover & Helby 1987c (Early Cretaceous, Australia)

207

208 **Reattributed and synonymised species:**

209 *Batiacasphaera agglutinata* McIntyre & Brideaux 1980, to *Sentusidinium* as *Sentusidinium*

210 *agglutinatum* comb. nov. herein.

211 *Batiacasphaera angularis* Stevens & Helby 1987, to *Meiourogonyaulax* as *Meiourogonyaulax*

212 *angularis* comb. nov. herein.

213 *Batiacasphaera asperata* Backhouse 1987, considered a taxonomic junior synonym of

214 *Sentusidinium euteichum*.

215 *Batiacasphaera baculata* Drugg 1970, to *Sentusidinium* as *Sentusidinium bifidum* (Jiabo 1978)

216 He Chengquan et al. 1989.

217 *Batiacasphaera? bellula* (Jiabo 1978) Jan du Chêne et al. 1985, retained as *Sentusidinium*

218 *bellulum* (Jiabo 1978) Xu Jinli et al. 1997.

219 *Batiacasphaera biornata* (Jiabo 1978) Jan du Chêne et al. 1985a, considered a taxonomic junior

220 synonym of *Sentusidinium baculatum* (Dodekova 1975) Sarjeant & Stover 1978

221 *Batiacasphaera biornata* subsp. *biornata* (autonym), considered a taxonomic junior synonym of

222 *Sentusidinium baculatum*.

223 *Batiacasphaera biornata* subsp. *conspicula* Liu Zhili & Zheng Yuefang in Liu Zhili et al. 1992,

224 considered a taxonomic junior synonym of *Sentusidinium baculatum*.

225 *Batiacasphaera biornata* subsp. *crassa* (Jiabo 1978) Lentin & Williams 1989, considered a

226 taxonomic junior synonym of *Sentusidinium bifidum* (Jiabo 1978) He Chengquan et al. 1989.

227 *Batiacasphaera consolidata* Pan Zhaoren in Xu Jinli et al 1997 ex He Chengquan et al. 2009,

228 considered a taxonomic junior synonym of *Sentusidinium bellulum*.

229 *Batiacasphaera curiosa* (Bujak 1984) Jan du Chêne et al. 1985a, considered a taxonomic junior

230 synonym of *Sentusidinium sahi* (Khanna & Singh 1981) comb. nov. herein.

231 *Batiacasphaera deheinzelinii* Louwye 1999, considered a taxonomic junior synonym of

232 *Sentusidinium hirsutum* (Stover 1977) comb. nov. herein.

233 *Batiacasphaera euteiches* (Davey 1969a) Davey 1979, to *Sentusidinium* as *Sentusidinium*

234 *euteichum* (Davey 1969a) comb. nov. herein.



235 *Batiacasphaera explanata* (Bujak in Bujak et al. 1980) Islam 1983, to *Sentusidinium* as  
236 *Sentusidinium explanatum* (Bujak in Bujak et al. 1980) herein.

237 *Batiacasphaera extravermiculata* Shaw Chenglong 1999, to *Sentusidinium* as *Sentusidinium*  
238 *extravermiculatum* (Shaw Chenglong 1999) comb. nov. herein.

239 *Batiacasphaera gemmata* Head et al 1989, considered a taxonomic junior synonym of  
240 *Sentusidinium bellulum* (Jiabo 1978) Xu Jinli et al. 1997.

241 *Batiacasphaera granofoveolata* Pan Zhaoren in Xu Jinli et al 1997 ex He Chengquan,  
242 considered a taxonomic junior synonym of *Sentusidinium ringnesiorum* (Manum & Cookson  
243 1964) comb. nov. herein.

244 *Batiacasphaera granospina* He Chengquan 1991, considered a taxonomic junior synonym of  
245 *Sentusidinium granulosum* (Cookson & Eisenack 1974) comb. nov. herein.

246 *Batiacasphaera granulata* Shaw Chenglong 1999, considered a taxonomic junior synonym of  
247 *Sentusidinium extravermiculatum* (Shaw Chenglong 1999) comb. nov. herein.

248 *Batiacasphaera granulosa* (Cookson & Eisenack 1974) Jansonius 1989, to *Sentusidinium* as  
249 *Sentusidinium granulosum* comb. nov. herein.

250 *Batiacasphaera henanensis* He Chengquan, Zhu Shenzhao and Jin Guangxing in He Chengquan  
251 et al. 1989, considered a taxonomic junior synonym of *Sentusidinium ringnesiorum* (Manum &  
252 Cookson 1964) comb. nov. herein.

253 *Batiacasphaera hirsuta* Stover 1977, to *Sentusidinium* as *Sentusidinium hirsutum* (Stover 1977)  
254 comb. nov. herein.

255 *Batiacasphaera hystricosa* Mao Shaozhi & Norris 1988, considered a taxonomic junior  
256 synonym of *Sentusidinium baculatum* (Dodekova 1975) Sarjeant & Stover 1978.

257 *Batiacasphaera? kutharensis* (Khanna & Singh 1981) Lentin & Williams 1993, considered a  
258 taxonomic junior synonym of *Sentusidinium bifidum* (Jiabo 1978) He Chengquan et al. 1989

259 *Batiacasphaera laevigata* (Smelror 1988) Feist-Burkhardt & Monteil 1997, considered a  
260 taxonomic junior synonym of *Sentusidinium explanatum* (Bujak in Bujak et al. 1980) comb. nov  
261 herein.

262 *Batiacasphaera macrogranulata* Morgan 1975, considered a taxonomic junior synonym of  
263 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

264 *Batiacasphaera macropyla* He Chengquan et al 2009, considered a taxonomic junior synonym  
265 of *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

266 *Batiacasphaera mica* Harding 1990, considered a taxonomic junior synonym of *Sentusidinium*  
267 *ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

268 *Batiacasphaera micropapillata* Stover 1977, to *Sentusidinium* as *Sentusidinium micropapillatum*  
269 comb. nov herein.

270 *Batiacasphaera minuta* (Matsuoka 1983) Matsuoka & Head 1992, considered a taxonomic  
271 junior synonym of *Sentusidinium micropapillatum* (Stover 1977) comb. nov. herein.

272 *Batiacasphaera norvickii* (Burger 1980a) Lentin & Williams 1989, considered a taxonomic  
273 junior synonym of *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

274 *Batiacasphaera oblongata* Xu Jinli et al 1997 ex He Chengquan et al 2009, considered a  
275 taxonomic junior synonym of *Batiacasphaera retirugosa* Xu Jinli et al. 1997 ex He Chengquan  
276 et al. 2009.

277 *Batiacasphaera oligacantha* He Chengquan, Zhu Shenzhao & Jin Guangxing in He Chengquan  
278 et al. 1989, considered a taxonomic junior synonym of *Sentusidinium baculatum* (Dodekova  
279 1975) Sarjeant & Stover 1978.

280 *Batiacasphaera ovata* Backhouse 1987, considered a taxonomic junior synonym of  
281 *Batiacasphaera subtilis* Stover & Helby 1987c.

282 *Batiacasphaera? sahii* (Khanna & Singh 1981) Lentin & Williams 1993, to *Sentusidinium* as  
283 *Sentusidinium sahii* (Khanna & Singh 1981) comb. nov herein.

284 *Batiacasphaera setulosa* Shaw Chenglong 1999, to *Sentusidinium* as *Sentusidinium setulosum*  
285 Shaw Chenglong 1999 comb. nov herein.

286 *Batiacasphaera setulosa* var. *minima* Shaw Chenglong 1999, considered a taxonomic junior  
287 synonym of *Sentusidinium setulosum* Shaw Chenglong 1999 comb. nov herein.

288 *Batiacasphaera? simlaensis* (Khanna & Singh 1981) Lentin & Williams 1993, considered a  
289 taxonomic junior synonym of *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989.

290 *Batiacasphaera sinensis* Lentin & Williams 1989 to *Sentusidinium* as *Sentusidinium minus*  
291 (Jiabo 1978) He Chengquan et al. 1989.

292 *Batiacasphaera sparsa* He Chengquan 1991, considered a taxonomic junior synonym of  
293 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

294 *Batiacasphaera spumosa* (Brideaux 1977) Below 1981, considered a taxonomic junior synonym  
 295 of *Sentusidinium capillatum* (Davey 1975) Lentin & Williams 1981.

296 *Batiacasphaera tuberculata* He Chengquan 1991, considered a taxonomic junior synonym of  
 297 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

298 *Batiacasphaera verrucatum* Xu Jinli et al 1997 ex He Chengquan, considered a taxonomic  
 299 junior synonym of *Sentusidinium bellulum* (Jiabo 1978) Xu Jinli et al. 1997.

300 *Batiacasphaera xinjiangensis* He Chengquan 1991, considered a taxonomic junior synonym of  
 301 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

302

303

Species Name	Reference	Defining Features	Size (S, I, L)	Age	Location
<i>Batiacasphaera bergenensis</i>	Schreck and Matthiessen 2014	Subspherical, thick wall, pronounced irregular reticulum	S-I	Middle to Early Miocene	Eastern Iceland Plateau
<i>Batiacasphaera cassiculus</i>	Wilson 1988	Subspherical, thick wall, reticulum	I	Middle Eocene	Hawkes Bay, New Zealand
* <i>Batiacasphaera compta</i>	Drugg 1970b	Subspherical, thin wall and fine reticulum	I	Late Eocene	Alabama, USA
<i>Batiacasphaera cooperi</i>	Hannah et al 1998	Subspherical, dense reticulum	I	Miocene	McMurdo Sound, Antarctica
<i>Batiacasphaera dictyophora</i>	Gao Ruiqi et al 1992b	Subspherical, large coarse reticulum	S	Late Cretaceous	China
<i>Batiacasphaera edwardsiae</i>	Louwey et al 2008	Subspherical, thin wall, irregular microreticulum	I	Middle Miocene	Porcupine Basin, Southwest Ireland
<i>Batiacasphaera grandis</i>	Roncaglia et al 1999	Large size, uniform microreticulum	I-L	Late Cretaceous	Birch Hollow, New Zealand
<i>Batiacasphaera imperfecta</i>	Stover and Helby 1987d	Elongate, thick wall, imperfect reticulum	S-I	Early Cretaceous	Western Australia
<i>Batiacasphaera kekerengensis</i>	Schiøler and Wilson 1998	Elongate, thick wall and uniform reticulum	I	Late Cretaceous	Marlborough, New Zealand
<i>Batiacasphaera microreticulata</i>	Shaw Chenglong 1999b	Subspherical, thick wall, microreticulum	I	Eocene	Taiwan
<i>Batiacasphaera ovata</i>	Backhouse 1987	Elongate, dark, thick walls at the cingulum, thinning towards the apex and antapex, fine reticulum	I	Early Cretaceous	Western Australia
<i>Batiacasphaera reticulata</i>	Davey 1969b	Elongate, thick wall, microreticulum	S	Late Cretaceous	Natal, South Africa
<i>Batiacasphaera retirugosa</i>	Xu Jinli et al 1997; ex He Chengquan et al 2009	Subspherical to ovoidal, thin wall and a fine reticulum	I	Middle to Late Eocene	China
<i>Batiacasphaera rugulata</i>	Schiøler and Wilson 1998	Subspherical, coarse irregular reticulum	I	Late Cretaceous	Marlborough, New Zealand
<i>Batiacasphaera saidensis</i>	Below 1981a	Subspherical, thick wall, reticulate	S-I	Early Cretaceous	Southwest, Morocco
<i>Batiacasphaera solida</i>	Slimani 2003	Elongate, thick wall, fine reticulum	I	Late Cretaceous	Turnhout, Belgium
<i>Batiacasphaera sphaerica</i>	Stover 1977	Small subspherical, fine microreticulum	S	Early Miocene	Blake Plateau, Atlantic Ocean

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305 *Table 1 Accepted species for Batiacasphaera. \* denotes the type. Size guide S <50µm, I 50>100µm, L >100µm (Evitt*  
 306 *1978, p. 57)*

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*Batiacasphaera microreticulata* Shaw Chenglong 1999

- 1999 *Batiacasphaera microreticulata* Shaw Chenglong, p. 180–182, figs. 66–69, 82–83.  
1999 *Batiacasphaera microreticulata* var. *microreticulata* (autonym). Shaw Chenglong, p. 180–181, figs. 66–67.  
1999 *Batiacasphaera microreticulata* var. *minima* Shaw Chenglong, p. 182, figs. 82–83.

**Remarks:** Shaw Chenglong (1999) distinguished two varieties of *Batiacasphaera microreticulata*. *Batiacasphaera microreticulata* var. *minima* is slightly smaller than *Batiacasphaera microreticulata* var. *microreticulata*, and has a marginally thinner autophragm. We consider that these minor differences are insufficient to justify differentiation and hence synonymise the two varieties under the species.

*Batiacasphaera reticulata* Davey 1969b

- 1969b *Chytroeisphaeridia reticulate* Davey, p. 14, pl. 4, figs. 3–4, 6.  
1978 *Fromea reticulata* (Davey 1969b) Stover & Evitt, p. 48.  
1979d *Batiacasphaera reticulata* (Davey 1969b) Davey, p. 217.  
1997 *Batiacasphaera?* *reticulata* (Davey 1969b) Mohr & Mao Shaozhi, p. 58.

**Remarks:** We retain this species in *Batiacasphaera* without question. Mohr and Mao Shaozhi (1997, p. 58–60) questioned the generic assignment because they interpreted the type material as having two wall layers. However, it seems clear that this species merely has a thick autophragm, which was the original interpretation of Davey (1969b, p. 14).

336 *Batiacasphaera retirugosa* Xu Jinli et al. 1997 ex He Chengquan et al. 2009

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338 1997 *Batiacasphaera retirugosa* Xu Jinli et al., p. 48–49, pl, 42, fig. 3; name not validly  
339 published, as there was no English or Latin description.

340 1997 *Batiacasphaera oblongata* Xu Jinli et al., p. 49, pl, 42, fig. 6; name not validly  
341 published, as there was no English or Latin description.

342 2009 *Batiacasphaera retirugosa* Xu Jinli et al. 1997, ex He Chengquan et al., p. 649.

343 2009 *Batiacasphaera oblongata* Xu Jinli et al. 1997, ex He Chengquan et al., p. 649.

344

345 **Remarks:** *Batiacasphaera retirugosa* and *Batiacasphaera oblongata* are both subspherical to  
346 elongated ovoidal cysts with a thin wall and a fine reticulum. They are both intermediate in size,  
347 and from the Middle to Late Eocene of China. We thus consider *Batiacasphaera oblongata* to  
348 be conspecific with *Batiacasphaera retirugosa*.

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351 *Batiacasphaera subtilis* Stover & Helby 1987

352

353 1987 *Batiacasphaera subtilis* Stover & Helby, p. 228–230, figs. 2A–F, 3A–L.

354 1987 *Batiacasphaera ovata* Backhouse 1987, p. 215, figs. D–F.

355

356 **Remarks:** *Batiacasphaera ovata* and *Batiacasphaera subtilis* were both described from the  
357 Early Cretaceous (Hauterivian to Barremian) of Western Australia in the same volume (Jell,  
358 1987), by Stover and Helby (1987) and Backhouse (1987) respectively. Both taxa circumscribe  
359 cysts that are elongate-ovoidal with dark, thick walls, the autophragm being thickest in the  
360 equatorial region; and they are similar in size and stratigraphical range. Accordingly, we  
361 consider them to be conspecific. Although *Batiacasphaera ovata* precedes *Batiacasphaera*  
362 *subtilis* in print order in Jell (1987), nomenclatural priority does not apply as both were  
363 published simultaneously. We consider *Batiacasphaera subtilis* to have been more fully  
364 described and illustrated and so give it precedence.

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Suborder GONYAULACINEAE Autonym

Family AREOLIGERACEAE Evitt 1963

Subfamily UNCERTAIN

**Genus *Cyclonephelium* Deflandre & Cookson 1955**

**Type** *Cyclonephelium compactum* Deflandre & Cookson 1955

*Cyclonephelium helbyi* (Cookson & Hughes 1964) comb. nov.

**Basionym:** *Kallosphaeridium? helbyi* Lentin & Williams 1989, p. 206 subsp. *helbyi* autonym.

1964 *Canningia minor* Cookson & Hughes, p. 43, pl. 8, figs. 1–3, 5.

1978 *Canningia? minor* subsp. *minor* Cookson & Hughes 1964. Stover & Evitt, p. 25.

1980 *Chytroeisphaeridia minor* subsp. *minor* (Cookson & Hughes 1964) Morgan, p. 19.

1989 *Kallosphaeridium? helbyi* Lentin & Williams, p. 206 subsp. *helbyi* autonym.

**Remarks:** This species clearly belongs in the *Cyclonephelium* complex. It is asymmetrical and lenticular, with an apical protuberance (Cookson & Hughes 1964, pl. 8, figs. 1–3, 5.). Therefore we formally transfer this species to the genus *Cyclonephelium*.

Suborder GONYAULACINEAE Autonym

Family GONYAULACACEAE Lindemann 1928

Subfamily UNCERTAIN

392 *Genus Kallosphaeridium* de Coninck 1969 emend. nov.

393

394 **Type:** *Kallosphaeridium brevibarbatum* de Coninck 1969 emend. Jan du Chêne et al. 1985

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396 1969 *Kallosphaeridium* de Coninck, p. 44.

397 1985 *Kallosphaeridium* de Coninck 1969 emend. Jan du Chêne et al., p. 8–9.

398

399 **Original diagnosis:** Kyste de dinoflagellé à peu près globuleux, présentant un archaeopyle  
400 apical avec l'opercule attaché. Les sutures accessoires éventuelles indiquent six plaques  
401 précingulaires dont l'opercule s'est détaché. Il n'y a pas d'autres traces d'une tabulation. Des  
402 poil orment éventuellement la coque (de Coninck 1969, p. 44).

403

404 **Translation of original diagnosis:** Globular dinoflagellate cyst with an apical archaeopyle and  
405 an attached operculum. Accessory sutures may indicate six precingular plates, from which the  
406 operculum is detached. There are no other indications of tabulation. Hair-like processes may  
407 ornament the shell (translation by SELW and JBR).

408

409 **Emended diagnosis:** Acavate, nontabulate, proximate–proximochorate cysts, bearing low-relief  
410 ornamentation and subspherical in outline. The archaeopyle is apical or combination, type  
411 (5A)@ or type (4A1I)@, with an attached operculum. Accessory archaeopyle sutures are  
412 developed and the operculum is relatively narrow.

413

414 **Emended description:** Proximate to proximochorate acavate dinoflagellate cysts with a  
415 subspheroidal to ovoidal central body. The autophragm may be psilate or bear nontabular  
416 elements of low to moderate relief. The archaeopyle involves the four standard gonyaulacalean  
417 apical plates plus an additional single dorsal plate that may or may not reach the apex; thus the  
418 archaeopyle can be interpreted as type (5A)@ or type (4A1I)@; the operculum is attached  
419 ventrally; deep accessory archaeopyle sutures between the six precingular plates are typically  
420 present. The archaeopyle and operculum are relatively narrow; the overall width/cyst diameter  
421 (OW/CD) is less than 0.5 and normally between 0.4 and 0.3.

422

423 **Comments:** The principal characteristics of *Kallosphaeridium* are the small, ventrally attached  
424 operculum and the five-plate archaeopyle which exhibits accessory archaeopyle sutures. If the  
425 material is well preserved, the middorsal 1a/3' plate should be readily observable in the  
426 operculum, which tends to be small relative to the overall cyst diameter. *Kallosphaeridium* is  
427 largely speciated on the nature of its ornamentation, the most variable feature within the genus.  
428 In terms of the standard gonyaulacalean tabulation, the five plates involved in the archaeopyle  
429 include the four standard apicals, homologues 1' to 4', plus a smaller dorsal plate, inserted  
430 partially or perhaps sometimes wholly between the second and third apical homologues. The  
431 additional plate may be a homologue of one of the small dorsal anterior intercalary plates (so-  
432 called K plates of Evitt 1985; see also Fensome et al. 1993, figs. 84–85).

433 The emendation by Jan du Chêne et al. (1985, p. 8–9) provided more details than were given by  
434 de Coninck (1969), especially with regard to the archaeopyle and tabulation. Jan du Chêne et al.  
435 (1985, fig. 2.) discussed the overall width/cyst diameter (OW/CD) in *Kallosphaeridium*. This  
436 genus consistently has a relatively small archaeopyle and operculum; Jan du Chêne et al. (1985)  
437 is less than 0.5, typically between 0.4 and 0.3.

438 Twenty-one species of *Kallosphaeridium* were listed by Fensome and Williams (2004, p. 375–  
439 377). Of these, we consider six to be accepted species of *Kallosphaeridium* and six to be  
440 questionable; these are included below in the species lists as well as in Table 2. All six  
441 unequivocal species of *Kallosphaeridium* are of Palaeogene age and from the North Atlantic  
442 region. Of the six questionable species, the type material of *Kallosphaeridium? orchiesense* is  
443 also Palaeogene (Eocene), while the other five questionable species were described from the  
444 Mesozoic of Australia and Europe (Table 2).

445 We consider that there is no evidence to indicate dextral torsion in *Kallosphaeridium*. Therefore  
446 the placement of this genus in Subfamily Cribroperidinioideae by Fensome et al. (1993) is  
447 inappropriate, as such it is now considered uncertain.

448

449 **Comparison:** *Kallosphaeridium* is characterised by its relatively small operculum, attached  
450 ventrally, and the five-plate archaeopyle consistently with accessory archaeopyle sutures. The  
451 archaeopyle was interpreted to be apical (5A)<sub>@</sub>, or a combination apical (4A1I)<sub>@</sub> by Jan du  
452 Chêne et al. (1985). The evidence for the five plate archaeopyle is the marked angulation in the  
453 middorsal area (Jan du Chêne et al. 1985, fig. 1A–B). The additional dorsal plate was interpreted



454 as either the 1a or the 3' plate by these authors. No other genus in the *Sentusidinium* complex  
455 has a five plate archaeopyle.

456

457 **Accepted species:**

458 *Kallosphaeridium biornatum* Stover 1977 (Early Oligocene, Atlantic Ocean)

459 \**Kallosphaeridium brevibarbatum* de Coninck 1969 (Early Eocene, Belgium)

460 *Kallosphaeridium capulatum* Stover 1977 (Middle–Late Oligocene, Atlantic Ocean)

461 *Kallosphaeridium nigeriense* Jan du Chêne et al. 1985 (Late Paleocene–Early Eocene, Nigeria)

462 *Kallosphaeridium parvum* Jan du Chêne 1988 (Early Paleocene, Senegal)

463 *Kallosphaeridium yorubaense* Jan du Chêne & Adediran 1985 (Late Paleocene–Early Eocene,  
464 Nigeria)

465

466 **Provisionally accepted species:**

467 These species are provisionally accepted because the presence of the middorsal (1a/3') plate on  
468 the attached operculum has not been confirmed.

469

470 *Kallosphaeridium? circulare* (Cookson & Eisenack 1971) Helby 1987 (Late Cretaceous,  
471 Australia)

472 *Kallosphaeridium? coninckii* Burger 1980a (Late Cretaceous, Australia)

473 *Kallosphaeridium? hypornatum* Prauss 1989 (Middle Jurassic, Germany)

474 *Kallosphaeridium? inornatum* Batten & Lister 1988 (non Prauss 1989) (Early Cretaceous, UK)

475 *Kallosphaeridium? neophytensum* (Ioannides et al. 1977) comb. nov. herein (Late Jurassic, UK)

476 *Kallosphaeridium? orchiesense* de Coninck 1975 (Early Eocene, Belgium)

477

478 **Reattributed and synonymised species:**

479 *Kallosphaeridium aspersum* (Jiabo 1978) Sarjeant & Stancliffe 1994, considered a taxonomic  
480 junior synonym of *Sentusidinium? reticuloidum* (Jiabo 1978) comb. nov herein.

481 *Kallosphaeridium callosum* Dodekova 1994, to *Sentusidinium* as *Sentusidinium callosum*  
482 (Dodekova 1994) comb. nov. herein.

483 *Kallosphaeridium dolomiticum* Torricelli 2000, considered a taxonomic junior synonym of  
484 *Sentusidinium aptiense* (Burger 1980a) Burger 1980b.

485 *Kallosphaeridium? granulatum* (Norvick 1976) Stover & Evitt 1978, considered a taxonomic  
486 junior synonym of *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov., herein.

487 *Kallosphaeridium? helbyi* (Lentin & Williams 1989) subsp. *helbyi* (autonym), to  
488 *Cyclonephelium* as *Cyclonephelium helbyi* comb. nov. herein.

489 *Kallosphaeridium helbyi* subsp. *psilatum* (Burger 1980a) Lentin & Williams 1989, considered a  
490 taxonomic synonym of *Sentusidinium explanatum* (Bujak in Bujak et al.) comb. nov. herein.

491 *Kallosphaeridium jiyangense* Xu Jinli et al. 1997, considered a taxonomic junior synonym of  
492 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989.

493 *Kallosphaeridium praussii* Lentin & Williams 1993 nom subst. pro *Kallosphaeridium*  
494 *inornatum* Prauss 1989, considered a taxonomic junior synonym of *Sentusidinium explanatum*  
495 (Bujak in Bujak et al.) comb. nov. herein.

496 *Kallosphaeridium reticuloidum* (Jiabo 1978) Sarjeant & Stancliffe 1994, to *Sentusidinium* as  
497 *Sentusidinium? reticuloidum* (Jiabo 1978) comb. nov. herein.

498 *Kallosphaeridium? ringnesiorum* (Manum & Cookson 1964) Helby 1987, to *Sentusidinium* as  
499 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

500 *Kallosphaeridium? romaense* (Burger 1980a) Burger 1980b, considered a taxonomic junior  
501 synonym of *Sentusidinium capillatum* (Davey 1975) Lentin & Williams 1981.

502 *Kallosphaeridium spongiosum* Batten & Lister 1988, to *Sentusidinium* as *Sentusidinium?*  
503 *spongiosum* (Batten & Lister 1988) comb. nov. herein.

504

Species Name	Reference	Definig Features	Size (S, I, L)	Age.	Location
<b>Accepted Species</b>					
<i>Kallosphaeridium biornatum</i>	Stover 1977	Subspherical, small attached operculum, with nontabular cones and short spines.	I	Early Oligocene	Blake Plateau, Atlantic Ocean
* <i>Kallosphaeridium brevibarbatum</i>	de Coninck 1969	Subspherical, small attached operculum, densely covered in hairlike structures.	I	Early Eocene	Belgium
<i>Kallosphaeridium capulatum</i>	Stover 1977	Subspherical, small attached operculum, with a granulate autophragm.	S-I	Mid to Late Oligocene	Blake Plateau, Atlantic Ocean
<i>Kallosphaeridium nigeriense</i>	Jan du Chêne et al 1985a	Subspherical, small attached operculum, looks similar to <i>K. biornatum</i> but is more spinose.	I	Late Paleocene to Early Eocene	Nigeria
<i>Kallosphaeridium parvum</i>	Jan du Chêne 1988	Subspherical, small attached operculum, with dense granular, coarse verrucae, which are variable in size.	S	Early Paleocene	Senegal
<i>Kallosphaeridium yorubaense</i>	Jan du Chêne and Adediran 1985	Subspherical, small attached operculum, thin wall, with numerous dense low thin projections	I	Late Paleocene to Early Eocene	Nigeria
<b>Provisionally Accepted Species</b>					
<i>Kallosphaeridium ? circulare</i>	Cookson and Eisenack 1971	Large subspherical cyst, with tubercles. Small attached operculum, however, 1a plate is not viable.	I-L	Mid Cretaceous	Western Australia
<i>Kallosphaeridium ? coninckii</i>	Burger 1980a	Subspherical, with a dense covering of short acicular spines. Operculum attached.	S-I	Early Cretaceous	Surat Basin, Australia
<i>Kallosphaeridium ? hypornatum</i>	Prauss 1989	Ellipsoidal, with rugulate, verrucate, baculate or scabrate ornamentation confined to the antapex. Large operculum attached.	I	Middle Jurassic	Northwest Germany
<i>Kallosphaeridium ? inornatum</i>	Batten and Lister 1988	Subspherical, with psilate to scabrate ornamentation. Large attached operculum. Fresh water species	S	Early Cretaceous	Sussex, UK
<i>Kallosphaeridium ? neophytensum</i>	Ioannides et al. 1977	Elongate, with a dense covering of short processes with a prominent apical long process.	S	Late Jurassic	Dorset, UK
<i>Kallosphaeridium? orchiesense</i>	de Coninck 1975	Subspherical cyst with a granular autophragm surmounted by small short spines. Small attached operculum, however, 1a plate is not viable.	I	Early Eocene	Belgium

505

506 Table 2 Accepted and provisionally accepted species for *Kallosphaeridium*. \* denotes the type species. Size guide S  
507 <50µm, I 50>100µm, L >100µm (Evvitt 1978, p. 57)

508

509

510 *Kallosphaeridium? coninckii* Burger 1980a (Burger 1980b)

511

512 1980a *Membranosphaera coninckii* Burger, p. 74, pl. 26, figs. 5, 6a–b.

513 1980b *Kallosphaeridium coninckii* (Burger 1980a) Burger, p. 277.

514

515 **Remarks:** *Kallosphaeridium? coninckii* was originally described from the Albian of the Surat  
516 Basin in eastern Australia by Burger (1980a), as having a subspherical outline and a dense  
517 covering of short acicular spines. It is considered here to be a provisionally accepted species of  
518 *Kallosphaeridium* because, although it has an attached operculum, it lacks evidence of a fifth  
519 apical or an anterior intercalary plate in the operculum.

520

521

522 *Kallosphaeridium? hypornatum* Prauss 1989

523

524 1989 *Kallosphaeridium hypornatum* Prauss, p. 40–41, pl. 6, figs. 1–4; text-fig. 16.

525

526 **Remarks:** The ellipsoidal Middle Jurassic species *Kallosphaeridium? hypornatum* from  
527 northwest Germany has a very distinctive antapex with baculate, rugulate, scabrate or  
528 verrucate, ornamentation. However, it is now only considered to be provisionally accepted, due  
529 to the lack of evidence of a fifth apical or an anterior intercalary plate in the attached operculum.

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532 *Kallosphaeridium? neophytensum* (Ioannides et al. 1977) comb. nov. herein

533

534 **Basionym:** *Pilosidinium neophytensum* (Ioannides et al. 1977) Courtinat 1989, p. 191.

535

536 1977 *Tenua neophytensa* Ioannides et al., p. 463, pl. 6, fig 5, 8–9.

537 1978 *Sentusidinium? neophytensum* (Ioannides et al. 1977) Sarjeant & Stover, p. 50.

538 1989 *Pilosidinium neophytensum* (Ioannides et al. 1977) Courtinat, p. 191.

539

540 **Remarks:** *Kallosphaeridium? neophytensum* originally described from the Kimmeridgian of  
541 southern England has an elongate outline with a dense covering of short processes and a

542 prominent apical spine. This species is now considered to belong to the genus *Kallosphaeridium*  
543 on the basis of its attached operculum. However, due to the lack of evidence supporting a fifth  
544 apical or an anterior intercalary plate in the attached operculum it is only provisionally accepted.

545

546

547 *Kallosphaeridium? orchiesense* de Coninck 1975

548

549 1975 *Kallosphaeridium orchiesense* de Coninck, p.101–102, pl.18, figs.15–17.

550

551 **Remarks:** *Kallosphaeridium orchiesense* was first described from the Lower Eocene of  
552 Belgium as having a subspherical cyst with a granular autophragm surmounted by small short  
553 spines. It also has a small attached operculum, however, the fifth apical or anterior intercalary  
554 plate is not visible, and as such, is only provisionally accepted in this genus.

555

556

557 Suborder UNCERTAIN

558 Family UNCERTAIN

559 Subfamily UNCERTAIN

560

561 **Genus *Pentafidia* Backhouse 1988**

562

563 **Type:** *Pentafidia charlottensis* Backhouse 1988

564

565 1988 *Pentafidia* Backhouse, p. 103–104.

566

567 **Original diagnosis:** Cysts subcircular to ovoid, paratabulation indicated only by archaeopyle.  
568 Autophragm smooth, punctate, or bearing fine non-tabular surface features. Archaeopyle apical,

569 type [tA], primary and accessory archaeopyle sutures indicating 5 precingular and 4 apical  
570 paraplates (Backhouse 1988, p. 103–104).

571  
572 **Comments:** *Pentafidia* is an acavate, ovoid, proximate, nontabular gonyaulacoid dinoflagellate  
573 cyst with an apical archaeopyle. Therefore, it closely resembles the other genera in the  
574 *Sentusidinium* complex. It is most akin to psilate representatives of *Sentusidinium*, which were  
575 previously assigned to *Escharisphaeridia*. However, according to Backhouse (1988), *Pentafidia*  
576 has five precingular plates, inferred from the number of accessory archaeopyle sutures between  
577 these plates. This situation is extremely unusual in that almost all other gonyaulacoid genera  
578 have six precingulars (Evitt 1985). It is possible that the number of precingular plates was  
579 misinterpreted (see section 5), since one well-preserved specimen of *Pentafidia charlottensis*  
580 appears to have six precingular plates (Backhouse 1988, p. 37, fig. 9).

581 There are two species of this genus, *Pentafidia charlottensis* and *Pentafidia punctata*. Both were  
582 described from the latest Jurassic–earliest Cretaceous (Tithonian–Berriasian) of the Perth Basin,  
583 Western Australia by Backhouse (1988, fig. 35).

584

585 **Accepted species:**

586 *Pentafidia charlottensis* Backhouse 1988 (latest Jurassic to earliest Cretaceous, Australia)

587 *Pentafidia punctata* Backhouse 1988 (latest Jurassic to earliest Cretaceous, Australia)

588

589

590 Suborder **GONYAULACINEAE** Autonym

591 Family GONYAULACACEAE Lindemann 1928

592 Subfamily UNCERTAIN

593

594 **Genus *Sentusidinium* Sarjeant & Stover 1978 emend. nov.**

595

596 **Type:** *Sentusidinium rioultii* (Sarjeant 1968) Sarjeant & Stover 1978

597

- 598 1978 *Sentusidinium* Sarjeant & Stover, p. 49–50.  
599 1980 *Escharisphaeridia* Erkmen & Sarjeant, p. 62–63.  
600 1989 *Sentusidinium* Sarjeant & Stover 1978, emend. Courtinat, p. 192.  
601 1989 *Barbatacysta* Courtinat, p. 185.  
602 1989 *Pilosidinium* Courtinat, p. 190.

603

604 **Original diagnosis:** Proximate to proximo-chorate cysts, subspherical to ellipsoidal; wall  
605 single-layered or apparently so, and bearing short, usually evenly distributed nontabular  
606 projections such as coarse granulae, tuberculae, verrucae, baculae, or spines with blunt,  
607 acuminate, capitate or branched tips. These surface features are generally isolate, but some  
608 adjacent projections may have confluent bases and/or interconnected tips. The length of the  
609 projections is consistently less than one-half, and typically less than one-third, of the shortest  
610 diameter of the cyst. Paratabulation is indicated mainly by the type A apical archaeopyle, whose  
611 principal suture is generally zigzag (although the angulation may not be readily apparent on  
612 uncompressed specimens). Short, longitudinally directed accessory archaeopyle sutures are  
613 frequently present, their positions denoting the anterior boundaries between precingular  
614 paraplates. The operculum is free, its constituent paraplates not differentiated. An equatorial  
615 alignment of some projections, delimiting a lightly ornamented or unornamented paracingulum,  
616 may sometimes be observed; but this is usually inconspicuous and may not be developed. Other  
617 indications of paratabulation are lacking. Overall size is generally less than 100  $\mu\text{m}$  (Sarjeant  
618 and Stover 1978, p. 49–50).

619

620 **Emended diagnosis:** Proximate to proximochorate, acavate gonyaulacacean dinoflagellate cysts  
621 with a subspheroidal to ovoidal central body. The autophragm may be psilate or bear densely,  
622 generally evenly distributed, nontabular sculptural elements that are usually of low to moderate  
623 relief and isolated. Archaeopyle apical, type (tA), normally with a detached operculum; deep  
624 accessory archaeopyle sutures between the six precingular plates are typically present.

625

626 **Emended description:** Small to intermediate gonyaulacacean dinoflagellate cysts which may  
627 be proximate or proximochorate. The outline in dorso-ventral view is subspherical, oval or  
628 elongate oval and the cyst organisation is acavate. The autophragm is variable in thickness and

629 is devoid of ornament or covered by numerous mostly isolated nontabular sculptural elements of  
630 low to medium relief. The ornamentation is highly variable between species: for example, the  
631 autophragm may be psilate, shagreenate, scabrate, granulate, papillate, postulate, verrucate,  
632 gemmate, tuberculate, pilate, clavate, baculate, echinate or setose (Williams et al. 2000, pl. 24).  
633 Smooth (psilate and shagreenate) forms are less common than ornamented forms. The  
634 ornamental elements are typically evenly distributed, nontabular and short. Rarely, the  
635 ornamentation may be concentrated locally. Occasionally the individual elements of the  
636 ornamentation may be proximally confluent; distal connections or trabeculae are extremely rare.  
637 Occasionally a kalyptra may be developed. The archaeopyle is apical, type (tA), with a free  
638 operculum, although in some cases the operculum does not always fully detach; accessory  
639 archaeopyle sutures between the precingular plates are typically well developed, particularly those  
640 of Late Jurassic age. The shapes of the archaeopyle and operculum and the angular principal  
641 archaeopyle suture are strongly indicative of the standard sexiform gonyaulaccean tabulation.  
642 Very rarely, the ornamentation may partially reflect and indicate the cingulum, but other  
643 indications of the tabulation are rarely if ever developed.

644

645 **Comments:** Sarjeant and Stover (1978, p. 49–50) derived the generic name *Sentusidinium* from  
646 the Latin *sentus*, meaning thorny. The genus was emended by Courtinat (1989, p. 192), who  
647 gave a more concise diagnosis than the original description of Sarjeant and Stover (1978) and  
648 presented a tabulation formula. Courtinat (1989) also stated that the ornamentation (he used the  
649 term processes) is both intratabular and sutural. In our view, sutural ornamentation in  
650 *Sentusidinium* is extremely rare; only a few species exhibit alignment of the ornamentation to  
651 indicate the cingulum (e.g. *Sentusidinium fibrillosum*). The overwhelming majority of the low-  
652 to-medium-relief elements on *Sentusidinium* are nontabular. Indeed, if tabulation is developed to  
653 any degree, assignment to another genus, such as *Meiourogonyaulax*, would be appropriate.

654 We regard the genera *Barbatacysta*, *Escharisphaeridia* and *Pilosidinium* as taxonomic junior  
655 synonyms of *Sentusidinium*. The genus *Escharisphaeridia* was described by Erkmen and  
656 Sarjeant (1980) for psilate forms previously included in *Chytroeisphaeridia* that clearly have an  
657 apical archaeopyle. We consider forms of the *Sentusidinium* complex that are smooth, and do  
658 not conform to the morphologies of *Pentafidia* or *Kallosphaeridium*, to be attributable to  
659 *Sentusidinium*.



660 *Barbatocysta* was erected by Courtinat (1989, p.185) for ‘bearded cysts’ with a granular or  
661 verrucate autophragm, which have conical, subconical, buccinate, tubular or evexate intratabular  
662 processes that are distally acuminate, capitate, bifurcate or foliate. Courtinat (1989, p. 190) also  
663 described *Pilosidinium*, distinguishing it on the presence of capitate or bifurcate conical granules  
664 or spines, which may be interconnected and/or sutural. However, a review of the species in this  
665 genus indicates that the processes are consistently isolated and nontabular. Consequently, we  
666 consider that the generic concepts of both *Barbatocysta* and *Pilosidinium* fall within the  
667 circumscription of *Sentusidinium*.

668 The synonymy of *Barbatocysta*, *Escharisphaeridia* and *Pilosidinium* with *Sentusidinium* has  
669 clearly necessitated the transfer of their constituent species into *Sentusidinium*. During the  
670 course of our taxonomic review, it became clear that many of the species in the newly expanded  
671 *Sentusidinium* are superfluous. As a consequence, 59 species are considered to be taxonomic  
672 junior synonyms of other species of *Sentusidinium*, the 38 species in *Sentusidinium* that we  
673 consider to be separate are discussed below. Of those 38, we consider that 34 belong  
674 unquestionably to *Sentusidinium* and four are problematical.

675 The 34 species that we include in *Sentusidinium* without question collectively have a  
676 stratigraphical range from the Jurassic to the Palaeogene; no exclusively Miocene species have  
677 been described. Most of the Jurassic species were described originally from Europe. However,  
678 all but one of the Cretaceous forms were described from Africa, Australia and North America;  
679 while most of the Palaeogene taxa were described from China and India.

680

681 **Comparison:** *Kallosphaeridium* has an attached, five-plate operculum, in contrast to the more  
682 conventional gonyaulacacean four-plate apical operculum of *Sentusidinium*. *Batiacasphaera* has  
683 a reticulate to rugulate ornament and generally lacks deep accessory archaeopyle sutures.  
684 *Pentafidia* apparently has five precingular plates rather than six.

685

686

687 **Accepted species:**

688 *Sentusidinium agglutinatum* (McIntyre & Brideaux 1980) comb. nov. herein (Early Cretaceous,  
689 Canada)

690 *Sentusidinium aptiense* (Burger 1980a) Burger 1980b (Early Cretaceous, Australia)

- 691 *Sentusidinium asymmetrum* (Fenton et al. 1980) Lentin & Williams 1981 (Middle Jurassic, UK)
- 692 *Sentusidinium baculatum* (Dodekova 1975) Sarjeant & Stover 1978 (Middle Jurassic, Bulgaria)
- 693 *Sentusidinium bellulum* (Jiabo 1978) Xu Jinli et al. 1997 (Eocene, China)
- 694 *Sentusidinium bifidum* (Jiabo 1978) He Chengquan et al. 1989 (Late Eocene, China)
- 695 *Sentusidinium callosum* (Dodekova 1994) comb. nov. herein (Late Jurassic–Early Cretaceous,
- 696 Bulgaria)
- 697 *Sentusidinium capillatum* (Davey 1975) Lentin & Williams 1981 (Late Cretaceous, Ghana)
- 698 *Sentusidinium capitatum* Cookson & Eisenack 1960 comb. nov. herein (Late Jurassic, Australia)
- 699 *Sentusidinium densicomatum* (Maier 1959) Sarjeant 1983 (Middle Oligocene, Germany)
- 700 *Sentusidinium echinatum* (Gitmez & Sarjeant 1972) Sarjeant & Stover 1978 (Late Jurassic, UK)
- 701 *Sentusidinium eisenackii* (Boltenhagen 1977) Fauconnier & Masure 2004 (Late Cretaceous,
- 702 Gabon)
- 703 *Sentusidinium euteichum* (Davey 1969a) comb. nov. herein (Late Cretaceous, France)
- 704 *Sentusidinium explanatum* Bujak in Bujak et al. 1980, comb. nov. herein (Middle Eocene, UK)
- 705 *Sentusidinium extravermiculatum* (Shaw Chenglong 1999) comb. nov. herein (Eocene, Taiwan)
- 706 *Sentusidinium fibrillosum* Backhouse 1988 (Early Cretaceous, Australia)
- 707 *Sentusidinium granulosum* (Cookson & Eisenack 1974) comb. nov. herein (Cretaceous,
- 708 Australia)
- 709 *Sentusidinium hirsutum* (Stover 1977) comb. nov. herein (Oligocene, North Atlantic)
- 710 *Sentusidinium macbethiae* (Mantle 2009) comb. nov. herein (Middle Jurassic, Timor Sea)
- 711 *Sentusidinium microcystum* (Bujak in Bujak et al. 1980) Islam 1993 (Late Eocene, UK)
- 712 *Sentusidinium micropapillatum* (Stover 1977) comb. nov. herein (Oligocene–Early Miocene)
- 713 *Sentusidinium millepedii* nom. subst. pro. *Sentusidinium? brevispinosum* (Jain & Milleped
- 714 1975) Islam 1993 (Late Cretaceous, Africa)
- 715 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989. comb. nov. herein (Palaeogene,
- 716 China)
- 717 *Sentusidinium myriatrichum* Fensome 1979 (Late Jurassic, Greenland)

- 718 *Sentusidinium perforoconum* (Yun Hyesu 1981) Islam 1993 (Late Cretaceous, USA)
- 719 *Sentusidinium pilosum* (Ehrenberg 1854) Sarjeant & Stover 1978 (Late Jurassic–Early  
720 Cretaceous, Poland)
- 721 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein (Late Cretaceous,  
722 Canada)
- 723 \**Sentusidinium rioultii* Sarjeant 1968 (Middle Jurassic, France)
- 724 *Sentusidinium sahi* (Khanna & Singh 1981) comb. nov. herein (Early–Middle Eocene, India)
- 725 *Sentusidinium separatum* McIntyre & Brideaux 1980 (Early Cretaceous, Canada)
- 726 *Sentusidinium setulosum* (Shaw Chenglong 1999) comb. nov. herein (Eocene, Taiwan)
- 727 *Sentusidinium sparsibarbatum* Erkmen & Sarjeant 1980 (Middle Jurassic, UK)
- 728 *Sentusidinium verrucosum* (Sarjeant 1968) Sarjeant & Stover 1978 (Middle–Late Jurassic,  
729 France)
- 730 *Sentusidinium villersense* (Sarjeant 1968) Sarjeant & Stover 1978 (Middle–Late Jurassic,  
731 France)
- 732
- 733 **Problematical species:**
- 734 These species are problematical due to the lack of evidence regarding the presence of an  
735 archaeopyle and/or the type.
- 736 *Sentusidinium? asymmetricum* (Pocock 1972) comb. nov. herein (Middle Jurassic, Canada)
- 737 *Sentusidinium? panshanensum* (Jiabo 1978) Islam 1993 (Palaeogene, China)
- 738 *Sentusidinium? reticuloidum* (Jiabo 1978) comb. nov. herein (Oligocene, China)
- 739 *Sentusidinium? spongiosum* (Batten & Lister 1988) comb. nov. herein (Early Cretaceous, UK)
- 740
- 741 **Reattributed and synonymised species:**
- 742 *Sentusidinium brachyspinosum* Zheng Yuefang & Liu Xuexian in Liu Zhili et al. 1992,  
743 considered a taxonomic junior synonym of *Sentusidinium bifidum* (Jiabo 1978) He Chengquan  
744 et al. 1989.

745 *Sentusidinium conispinosum* Xu Jinli et al. 1997, considered a taxonomic junior synonym of  
746 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989.

747 *Sentusidinium erythrocomum* Erkmen & Sarjeant 1980, considered a taxonomic junior synonym  
748 of *Sentusidinium aptiense* (Burger 1980a) Burger 1980b.

749 *Sentusidinium fungosum* Harding 1990, considered a taxonomic junior synonym of  
750 *Sentusidinium aptiense* (Burger 1980a) Burger 1980b.

751 *Sentusidinium minutum* He Chengquan 1991, considered a taxonomic junior synonym of  
752 *Sentusidinium sahi* (Khanna & Singh 1981) comb. nov. herein.

753 *Sentusidinium reticuloides* Xu Jinli et al. 1997, considered a taxonomic junior synonym of  
754 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989.

755 *Sentusidinium spatiosum* Dodekova 1994, considered a taxonomic junior synonym of  
756 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov. herein.

757 *Sentusidinium stipulatum* Mao Shaozhi & Norris 1988, considered a taxonomic junior synonym  
758 of *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989.

759

Species Name	Reference	Defining Features	Size (S, I, L)	Age	Location
<b>Accepted Species</b>					
<i>Sentusidinium agglutinatum</i>	McIntyre and Brideaux 1980	Subspherical, with granulate autophragm, surrounded by a kalyptra.	I	Early Cretaceous	Mackenzie, Canada
<i>Sentusidinium aptiense</i>	Burger 1980a	Elongate, with prominent hollow tubular spines.	S-I	Early Cretaceous	Western Australia
<i>Sentusidinium asymmetrum</i>	Fenton et al. 1980	Subspherical, with granulate to baculate ornamentation wich is reduced towards the apex.	I	Middle Jurassic	Dorset, UK
<i>Sentusidinium baculatum</i>	Dodekova 1975	Subspherical, with variable ornamentation. Irregular gemmae to baculae with sparse short spines either distally joined or closed.	I	Middle Jurassic	Northeastern Bulgaria
<i>Sentusidinium bellulum</i>	Jiabo 1978	Subspherical, with psilate autophragm surmounted by gemmae.	S	Eocene	Bohai Coast, China
<i>Sentusidinium bifidum</i>	Jiabo 1978	Subspherical, with granulate autophragm surmounted by tuberculae.	S-I	Late Eocene	China
<i>Sentusidinium callosum</i>	Dodekova 1994	Subspherical, with psilate to finely scabrate autophragm.	I	Late Jurassic - Early Cretaceous	North Bulgaria
<i>Sentusidinium capillatum</i>	Davey 1975	Subspherical, setose ornament with variable tips.	S-I	Late Cretaceous	Ghana
<i>Sentusidinium capitatum</i>	Cookson and Eisenack 1960	Elongate, short dense spines with acuminate to capitate tips.	S-I	Late Jurassic	Australia
<i>Sentusidinium densicomatum</i>	Maier 1959	Subspherical, with granulate autophragm, surmounted by long hair like, acicular projections.	I-L	Middle Oligocene	Germany
<i>Sentusidinium echinatum</i>	Gitmez and Sarjeant 1972	Subspherical, with echinate ornamentation.	S-I	Late Jurassic	Dorset, UK
<i>Sentusidinium eisenackii</i>	Boltenhagen 1977	Subspherical, with variable ornamentation, including hooks.	I	Late Cretaceous	Gabon
<i>Sentusidinium euteichum</i>	Davey 1969	Subspherical, with a thick wall and densely granular autophragm.	S-I	Late Cretaceous	Calais, France
<i>Sentusidinium extravermiculatum</i>	Shaw Chenglong 1999	Subspherical, with variable ornamentaion, giving a spongy apperance.	S-I	Eocene	Taiwan
<i>Sentusidinium fibrillosum</i>	Backhouse 1988	Subspherical, with fibrous ornamented autophragm, well defined cingulum. Occasionally ofset by a small antapical horn.	S	Early Cretaceous	South Perth, Australia
<i>Sentusidinium granulosum</i>	Cookson and Eisenack 1974	Elongate, small archeopyle, with granulate autophragm.	S	Cretaceous	Australia
<i>Sentusidinium hirsutum</i>	Stover 1977	Subspherical, with a covering of thin dense hairs.	S	Oligocene	Blake Plateau, Atlantic
<i>Sentusidinium macbethiae</i>	Mantle 2009	Subspherical, psilate to shagreenate autophragm with a prominent and visible inclusion body.	S-I	Middle Jurassic	Timor Sea, Australia
<i>Sentusidinium microcystum</i>	Bujak in Bujak et al. 1980	Elongate, with a shagreenate autophragm surmounted by long spines with capitate or bifid tips.	S	Late Eocene	Isle of Wight, UK
<i>Sentusidinium micropapillatum</i>	Stover 1977	Subspherical, with a thin wall and scabrate to papillate autophragm.	S	Oligocene - Early Miocene	Blake Plateau, Atlantic

760

761 *Table 3* Accepted species for *Sentusidinium*. Size guide S <50µm, I 50>100µm, L >100µm (Evitt 1978, p. 57)

Species Name	Reference	Defining Features	Size (S, I, L)	Age	Location
<b>Accepted Species</b>					
<i>Sentusidinium millepedii</i>	Jain and Millepied 1975	Subspherical, with setose ornamentation.	S-I	Early Cretaceous	Senegal basin, Africa
<i>Sentusidinium minus</i>	Jiabo, 1978	Subspherical, with a covering of sparse thin spines.	S	Paleogene	Bohai Coast, China
<i>Sentusidinium myriatrichum</i>	Fensome 1979	Subspherical, with thin, dense, fine short hairs covering the autophragm.	S-I	Late Jurassic	Langryggen, Eastern Greenland
<i>Sentusidinium perforoconum</i>	Yun Hyesu 1981	Subspherical, proximochorate cyst with distinctive conical to acuminate spines.	I	Late Cretaceous	USA
<i>Sentusidinium pilosum</i>	Ehrenberg 1854	Elongate, very dense short processes with variable tips.	S-I	Late Jurassic - Early Cretaceous	Podgorze, Kraków, Poland
<i>Sentusidinium psilatatum</i>	Burger 1980a	Subspherical, with psilate autophragm.	S-I	Early Cretaceous	Surat Basin, Australia
<i>Sentusidinium ringnesiorum</i>	Manum and Cookson 1964	Subspherical, with a pronounced granulate autophragm.	I-L	Late Cretaceous	Ellef Ringnes Island, Canada
* <i>Sentusidinium rioultii</i>	Sarjeant 1968	Subspherical, with a granular surface surmounted by well spaced projections with variable tips.	S-I	Middle Jurassic	France
<i>Sentusidinium sahilii</i>	Khanna and Singh 1981	Subspherical, with granulate autophragm surmounted by sarse long spines with variable tips.	S-I	Early–Middle Eocene	Simla Hills, India
<i>Sentusidinium separatum</i>	McIntyre and Brideaux 1980	Subspherical, proximochorate cyst, with a shagreenate autophragm surmounted by long hollow spines with closed, bifid and branched tips.	S-I	Early Cretaceous	Canada
<i>Sentusidinium setulosum</i>	Shaw Chenglong 1999b	Subspherical, with a densely setose autophragm.	S-I	Eocene	Taiwan
<i>Sentusidinium sparsibarbatum</i>	Erkmen and Sarjeant 1980	Elongate, with an echinate and granulate autophragm.	S-I	Middle Jurassic	Dorset, UK
<i>Sentusidinium verrucosum</i>	Sarjeant 1968	Subspherical, with dense irregular verrucate autophragm.	S-I	Middle - Late Jurassic	Normandy, France
<i>Sentusidinium villerense</i>	Sarjeant 1968	Subspherical, with granulate autophragm surmounted by well spaced spines with variable tips. At the antapex there is a short broad spine.	I	Middle - Late Jurassic	France

762

763 Table 3 continued. Accepted species for *Sentusidinium*. \* denotes the type. Size guide S <50µm, I 50>100µm, L >100µm  
764 (Evitt 1978, p. 57)

765

Species Name	Reference	Defining Features	Size (S, I, L)	Age	Location
<b>Provisionally Accepted Species</b>					
" <i>Sentusidinium ? asymmetricum</i> "	Pocock 1972	Subspherical, with setose autophragm and lateral projection. No proven apical archeopyle.	S	Middle Jurassic	Alberta, Canada
" <i>Sentusidinium ? panshanensum</i> "	Jiabo 1978	Subspherical, with long tubiform spines with variable tips. No proven apical archeopyle.	S	Paleogene	Bohai Coast, China
" <i>Sentusidinium ? reticuloidum</i> "	Jiabo 1978	Subspherical, with granulate ornamentation. No proven apical archeopyle.	S	Oligocene	Bohai Coast, China
" <i>Sentusidinium ? spongiosum</i> "	Batten and Lister 1988	Subspherical, with tabulation and granulate ornamentation surmounted by short pilate structures. Problematical operculum.	S	Early Cretaceous	Sussex, UK

766

767 Table 3 continued. Accepted species for *Sentusidinium*. \* denotes the type. Size guide S <50µm, I 50>100µm, L  
768 >100µm (Evitt 1978, p. 57)

769

770

771 *Sentusidinium agglutinatum* (McIntyre & Brideaux 1980) comb. nov.

772

773 1980 *Batiacasphaera agglutinata* McIntyre & Brideaux, p. 25, pl. 12, figs. 5–12.

774

775 **Remarks:** The species *Batiacasphaera agglutinata* was originally described from Valanginian  
776 strata of the Northwest Territories in Canada by McIntyre and Brideaux (1980). It is unusual in  
777 having a prominent kalyptra. This species is relatively large and the autophragm is granulate to  
778 sporadically rugulate. It does not conform to our concept of *Batiacasphaera*, thus necessitating  
779 its transfer from *Batiacasphaera* to *Sentusidinium*.

780

781

782 *Sentusidinium aptiense* (Burger 1980a) Burger 1980b

783

784 1980a *Tenua aptiense* Burger, p. 76, pl. 23, figs. 1, 5; pl. 24, fig. 1.

- 785 1980 *Sentusidinium erythrocomum* Erkmen & Sarjeant, p. 56, 58, pl. 2, fig. 11; pl. 3, figs. 1–6,  
786 8–11; pl. 4, fig. 5.
- 787 1980b *Sentusidinium aptiense* (Burger 1980a) Burger, p. 277.
- 788 1986a *Batiacasphaera aptiensis* (Burger 1980a) Kumar, p. 32.
- 789 1998 *Sentusidinium fungosum* Harding 1990 ex Harding in Williams et al., p. 557.
- 790 2000 *Kallosphaedridium dolomiticum* Torricelli, p. 261–262, pl. 4, figs. 9, 12.
- 791 2004 *Pilosidinium aptiense* (Burger 1980a) Courtinat in Fauconnier & Masure, p. 447.

792

793 **Remarks:** *Sentusidinium aptiense* was first described from the Early Cretaceous (Aptian) of the  
794 Surat Basin, Australia, by Burger (1980a) and is characterised by its cover of distinctive hollow  
795 spines. We consider *Kallosphaedridium dolomiticum*, *Sentusidinium erythrocomum* and  
796 *Sentusidinium fungosum* to be taxonomic junior synonyms of *Sentusidinium aptiense* as they  
797 also exhibit hollow nontabular spines and are similar in all other aspects. *Tenua aptiense* and  
798 *Sentusidinium erythrocomum* were both published during February 1980, but the former was  
799 published first on February 15<sup>th</sup> (Burger 1980a) and hence has priority over Erkmen and  
800 Sarjeant 1980, which was published on February 29<sup>th</sup> (Geobios, 13:1). The stratigraphical range  
801 of *Sentusidinium erythrocomum* as now constituted is Middle Jurassic (Callovian) to Early  
802 Cretaceous (Aptian) and has a global distribution.

803

804

805 *Sentusidinium asymmetrum* (Fenton et al. 1980) Lentin & Williams 1981

806

807 **Basionym:** *Tenua asymmetra* Fenton et al. 1980, p. 160, 162, pl. 16, figs. 1, 3, 5.

808

809 1980 *Tenua asymmetra* Fenton et al., p. 160, 162, pl. 16, figs. 1, 3, 5.

810 1981 *Sentusidinium asymmetrum* (Fenton et al. 1980) Lentin & Williams, p. 253.

811 2004 *Pilosidinium asymmetrum* (Fenton et al. 1980) Courtinat in Fauconnier & Masure, p.  
812 447.

813



814 **Remarks:** *Sentusidinium asymmetricum* is distinctive in having irregularly distributed ornament  
815 of low relief that is densest in the antapical region. In some specimens, the ornament is sparse in  
816 the middorsal and midventral areas, with intermediate amounts laterally (Fenton et al. 1980, p.  
817 16, figs. 3, 5). This species clearly belongs in *Sentusidinium*. The type material is from the latest  
818 Bajocian of Dorset, England, and the species is a reliable marker for the Bajocian–Bathonian  
819 transition (Fenton et al. 1980; Feist-Burkhardt and Monteil 1997). Prauss (1989) also reported  
820 *Sentusidinium* cf. *asymmetricum* from the Bajocian of northwest Germany.

821

822

823 *Sentusidinium baculatum* (Dodekova 1975) Sarjeant & Stover 1978

824

825 **Basionym:** *Tenua baculata* Dodekova 1975, p. 28-29, pl. 6, figs. 1–3; text-fig. 7.

826

827 1975 *Tenua baculata* Dodekova, p. 28–29, pl. 6, figs. 1–3; text-fig. 7.

828 1978 *Sentusidinium baculatum* (Dodekova 1975) Sarjeant & Stover, p. 50.

829 1978 *Tenua biornata* Jiabo, p. 52, pl. 22, figs. 21–29; pl. 23, figs. 1–4.

830 1981 *Kallosphaeridium biparatum* Lentin & Williams, p. 160.

831 1985 *Batiacasphaera biornata* (Jiabo 1978) Jan du Chêne et al., p. 15.

832 1988 *Batiacasphaera hystricosa* Mao Shaozhi & Norris, p. 40, pl. 8, figs. 17–20.

833 1989 *Barbatacysta baculata* (Dodekova 1975) Courtinat, p. 185.

834 1989 *Sentusidinium biornatum* (Jiabo 1978) He Chengquan et al., p. 67.

835 1989 *Batiacasphaera oligacantha* He Chengquan et al., p. 39, pl. 7, fig. 13.

836 1992 *Sentusidinium biornatum* subsp. *conspicula* Liu Zhili & Zheng Yuefang in Liu Zhili et  
837 al., p. 84–85, pl. 9, figs. 10–11.

838 2004 *Batiacasphaera biornata* subsp. *conspicula* (Liu Zhili & Zheng Yuefang in Liu Zhili et  
839 al. 1992) Fensome & Williams, p. 74.

840

841 **Remarks:** Dodekova (1975, p. 29) described the ornamentation of *Sentusidinium baculatum* (as  
842 *Tenua baculata*) from the Middle Jurassic of Bulgaria, as follows: The processes are rare, short,  
843 and of varying types.(also see Dodekova 1975, text-fig 7). Subsequently Sarjeant & Stover  
844 (1978) transferred it to *Sentusidinium*, and we retain it as such herein. Courtinat (1989)  
845 transferred the species to *Barbatacysta*, which we consider a taxonomic junior synonym of  
846 *Sentusidinium*. We consider *Sentusidinium baculatum* to be the senior synonym of  
847 *Batiacasphaera biornata*, *Batiacasphaera biornata* subsp. *conspicula*, *Batiacasphaera*  
848 *hystricosa* and *Batiacasphaera oligacantha*. The stratigraphical range of *Sentusidinium*  
849 *baculatum* is Middle Jurassic (Bathonian) to Late Eocene.

850

851

852 *Sentusidinium bellulum* (Jiabo 1978) Xu Jinli et al. 1997

853

854 1978 *Tenua bellula* Jiabo, p. 51, pl. 23, figs. 14–16.

855 1981 *Kallosphaeridium?* *bellulum* (Jiabo 1978) Lentin & Williams, p. 160.

856 1985 *Batiacasphaera?* *bellula* (Jiabo 1978) Jan du Chêne et al., p. 15.

857 1989 *Batiacasphaera gemmata* Head et al., p. 488, pl. 9, figs. 1–4.

858 1997 *Sentusidinium bellulum* (Jiabo 1978) Xu Jinli et al., p. 46.

859 1997 *Pyxidinoopsis consolidata* Pan Zhaoren in Xu Jinli et al., p. 72, pl. 37, fig. 12; pl. 38,  
860 figs.11,16; name not validly published, as there was no English or Latin description.

861 1997 *Sentusidinium?* *verrucatum* Xu Jinli et al., p.47, pl.35, figs.12a–b, 13a–b, 15a–b, 16a–b,  
862 17–20, 21a–b; name not validly published, as there was no English or Latin description.

863 2009 *Pyxidinoopsis consolidata* Pan Zhaoren in Xu Jinli et al. 1997 ex He Chengquan et al. 2009,  
864 p.648.

865 2009 *Batiacasphaera verrucatum* Xu Jinli et al. 1997 ex He Chengquan et al. p. 650.

866

867 **Remarks:** *Sentusidinium bellulum* is distinguished by its relatively sparse covering of  
868 prominent gemmae. It therefore cannot be accommodated in *Batiacasphaera*. We consider  
869 *Batiacasphaera gemmata* and *Batiacasphaera consolidata* to be junior synonyms of *Sentusidinium*

870 *bellulum*. As now circumscribed, *Sentusidinium bellulum* ranges from the Oligocene to the  
871 Miocene.

872

873

874 *Sentusidinium bifidum* (Jiabo 1978) He Chengquan et al. 1989

875

876 **Basionym:** *Tenua bifidis* Jiabo, p.51–52, pl. 22, figs. 7–16.

877

878 1970 *Batiacasphaera baculata* Drugg, p. 814, fig. 6F.

879 1978 *Tenua bifidis* Jiabo, p.51–52, pl. 22, figs. 7–16.

880 1978 *Tenua biornata* subsp. *crassa* Jiabo, p. 52, pl. 23, figs.1–4.

881 1981 *Kallosphaeridium biparatum* subsp. *crassum* (Jiabo 1978) Lentin & Williams, p. 160.

882 1981 *Tenua kutharensis* Khanna & Singh, p. 389–390, figs. 1.3, 1.5; text–fig. 1.

883 1981 *Cleistosphaeridium bifide* (Jiabo 1978) Lentin & Williams, p.48.

884 1989 *Batiacasphaera biornata* subsp. *crassa* (Jiabo 1978) Lentin & Williams 1989, p. 34.

885 1989 *Sentusidinium? bifidum* (Jiabo 1978) He Chengquan et al., p. 66–67, pl. 16, figs. 17–23.

886 1992 *Sentusidinium brachyspinosum* Zheng Yuefang & Liu Xuexian in Liu Zhili et al., p. 85,  
887 pl. 18, figs. 12–17.

888 1993 *Batiacasphaera kutharensis* (Khanna & Singh 1981) Lentin & Williams, p. 55.

889

890 **Remarks:** The earliest name for this species is *Batiacasphaera baculata* which Drugg 1970  
891 described from the Late Eocene of Mississippi. However, this name cannot be transferred to  
892 *Sentusidinium* because the name is already preoccupied by *Sentusidinium baculatum* (Dodekova  
893 1975) Sarjeant & Stover 1978. Among the names that we consider synonymous with  
894 *Batiacasphaera baculata* Drugg, the earliest is *Tenua bifidis* Jiabo 1978, now *Sentusidinium?*  
895 *bifidum* (Jiabo 1978) He Chengquan et al. 1989. We agree that this species belongs in  
896 *Sentusidinium* because it has an autophragm ornamented with relatively low density, short  
897 baculae rather than a reticulum, and we accept it in that genus without question. In our view

898 *Batiacasphaera baculata* Drugg, *Batiacasphaera biornata* subsp. *crassa*, *Sentusidinium*  
899 *brachyspinosum* and *Batiacasphaera kutharensis* are all taxonomic synonyms of *Sentusidinium?*  
900 *bifidum* based on their respective type materials. The species is confined to the Palaeogene.

901

902

903 *Sentusidinium callosum* (Dodekova 1994) comb. nov.

904

905 1994 *Kallosphaeridium callosum* Dodekova, p. 22–23, pl. 4, figs. 7–9.

906

907 **Remarks:** This species was first described from the Late Jurassic of Bulgaria by Dodekova  
908 (1994). The absence of an anterior intercalary plate precludes its attribution to  
909 *Kallosphaeridium*, and from its general morphology it clearly belongs in *Sentusidinium*.  
910 *Sentusidinium callosum* closely resembles *Sentusidinium explanatum*, both species having a  
911 smooth autophragm. However, Dodekova (1994, p. 22) noted coarse ornamentation on some  
912 specimens of *Sentusidinium callosum*, which she termed ‘uncertain foveolae’, and interpreted  
913 this as possibly representing bacterial activity. Therefore, we retain *Sentusidinium callosum* due  
914 to this uncertainty.

915

916

917 *Sentusidinium capillatum* (Davey 1975) Lentin & Williams 1981

918

919 1975 *Tenua capillata* Davey, p. 155–156, pl. 2, figs. 4, 7.

920 1977 *Canningia spumosa* Brideaux, p. 12, pl. 3, figs. 9–14.

921 1980a *Membranosphaera romaensis* Burger, p. 74, pl. 27, figs. 1–3.

922 1980b *Kallosphaeridium? romaense* (Burger 1980a) Burger, p. 277.

923 1981 *Sentusidinium capillatum* (Davey 1975) Lentin & Williams, p. 253.

924 1981 *Batiacasphaera spumosa* (Brideaux 1977) Below, p. 26.

925 1983 *Sentusidinium filiatum* Davies, p. 29–30, pl. 10, figs. 5–6, 8–9; text–fig. 27.

- 926 1989 *Pilosidinium filiatum* (Davies 1983) Courtinat, p. 191.  
927 1992 *Pilosidinium cactosum* Quattrocchio & Sarjeant, p. 91–92.  
928 2004 *Pilosidinium capillatum* Courtinat in Fauconnier & Masure 2004, p. 448.

929  
930 **Remarks:** *Sentusidinium capillatum* is subcircular to subvoidal in outline and normally thin-  
931 walled. The autophragm is setose, being very densely covered by short (c. 2 µm), slender spines.  
932 We consider *Sentusidinium capillatum* to be a taxonomic senior synonym of *Batiacasphaera*  
933 *spumosa*, *Kallosphaeridium? romaense*, *Pilosidinium cactosum* and *Pilosidinium filatum*. The  
934 absence of a reticulate autophragm and an anterior intercalary plate excludes *Sentusidinium*  
935 *capillatum* from *Batiacasphaera* and from *Kallosphaeridium* respectively. The overall  
936 stratigraphical range of *Sentusidinium capillatum* is Late Jurassic to Late Cretaceous.

937

938

939 *Sentusidinium capitatum* (Cookson & Eisenack 1960) comb. nov.

940

941 **Basionym:** *Hystrichosphaeridium capitatum* Cookson & Eisenack 1960, p. 252, pl. 39, fig. 9.

942

943 1960 *Hystrichosphaeridium capitatum* Cookson & Eisenack, p. 252, pl. 39, fig. 9.

944 1971 *Prolixosphaeridium capitatum* (Cookson & Eisenack 1960) Singh, p. 342.

945 1972 *Tenua capitata* (Cookson & Eisenack 1960) Gitmez & Sarjeant, p. 189.

946 1980 *Batiacasphaera capitata* (Cookson & Eisenack 1960) Dörhöfer & Davies, p. 40.

947 1980 *Sentusidinium creberbarbatum* Erkmen & Sarjeant, p. 52–54, fig. 2.

948 1989 *Barbatacysta creberbarbata* (Erkmen & Sarjeant 1980) Courtinat, p. 186.

949 2005 *Barbatacysta capitata* (Cookson & Eisenack 1960) Schrank, p. 548.

950

951 **Remarks:** *Sentusidinium capitatum* is distinctive in its elongate outline and possesses a dense  
952 cover of short spines that are distally capitate at their terminations. Morphologically this species  
953 belongs in *Sentusidinium* rather than *Batiacasphaera* or *Barbatacysta*. We consider

954 *Sentusidinium creberbarbatum* to be a taxonomic junior synonym. *Sentusidinium capitatum* has  
955 a stratigraphical range throughout the Late Jurassic.

956

957

958 *Sentusidinium densicomatum* (Maier 1959) Sarjeant 1983

959

960 1959 *Galea densicomata* Maier, p.307–308, pl. 29, figs. 7–8.

961 1961 *Baltisphaeridium densicomatum* (Maier 1959) Gerlach, p. 193.

962 1966 *Impletosphaeridium densicomatum* (Maier 1959) Morgenroth, p. 33.

963 1983 *Sentusidinium densicomatum* (Maier 1959) Sarjeant, p. 111.

964 2004 *Pilosidinium densicomatum* (Maier 1959) Courtinat in Fauconnier & Masure 2004, p.  
965 448

966

967 **Remarks:** *Sentusidinium densicomatum* was first recorded from Oligocene and Miocene  
968 sediments of Germany (Maier 1959). It is characterised by its distinctive granular autophragm  
969 and hair-like projections. Specimens of this species are intermediate to large and subspherical in  
970 shape. We retain this species in *Sentusidinium* as it is now considered to be the taxonomic senior  
971 synonymy of *Pilosidinium*.

972

973

974 *Sentusidinium echinatum* (Gitmez & Sarjeant 1972) Sarjeant & Stover 1978

975

976 1972 *Tenua echinata* Gitmez & Sarjeant, p. 190, pl. 1, figs. 1,9.

977 1978 *Sentusidinium echinatum* (Gitmez & Sarjeant 1972) Sarjeant & Stover, p. 50.

978 1980 *Batiacasphaera echinata* (Gitmez & Sarjeant 1972) Dörhöfer & Davies, p. 40.

979 1989 *Pilosidinium echinatum* (Gitmez & Sarjeant 1972) Courtinat, p. 190.

980

981 **Remarks:** *Sentusidinium echinatum* is readily identifiable on the basis of its subspherical shape  
982 and echinate ornamentation. Gitmez and Sarjeant (1972) described this species from the Late  
983 Jurassic of southern England and likened it to a “prickly ball”. We retain the species in  
984 *Sentusidinium*, since *Batiacasphaera* has a rugulate to reticulate autophragm and we consider  
985 *Pilosidinium* to be a taxonomic junior synonym of *Sentusidinium*.

986

987

988 *Sentusidinium eisenackii* (Boltenhagen 1977) Fauconnier & Masure 2004

989

990 1977 *Tenua eisenackii* Boltenhagen, p. 56–58, pl. 5, figs. 5–8.

991 1977 *Tenua eisenackii* var. *eisenackii* (autonym); (see Boltenhagen, p. 56–58, pl. 5, figs. 5, 6).

992 1977 *Tenua eisenackii* var. *vermiculata* Boltenhagen, p. 57–58, pl. 5, figs. 7, 8.

993 1981 *Sentusidinium eisenackii* (Boltenhagen 1977) Lentin & Williams, p. 253.

994 1981 *Sentusidinium eisenackii* subsp. *eisenackii* (autonym).

995 1981 *Sentusidinium eisenackii* subsp. *vermiculatum* (Boltenhagen 1977) Lentin & Williams, p.  
996 253.

997 2004 *Sentusidinium eisenackii*? subsp. *vermiculatum* (Boltenhagen 1977) Courtinat in  
998 Fauconnier & Masure, p. 487.

999

1000 **Remarks:** *Sentusidinium eisenackii* is a relatively large subspherical form originally described  
1001 from the Late Cretaceous of Gabon by Boltenhagen (1977). It possesses a granular autophragm  
1002 surmounted by a distinctive dense covering of low-relief elements, which can be particularly  
1003 variable in width. Many of the elements are distally-hooked or recurved, and others may  
1004 coalesce. The ornamentation is similar to that of *Sentusidinium baculatum*, but the latter species  
1005 lacks hooked and recurved elements. We consider that the two subspecies, *Tenua eisenackii*  
1006 subspecies *vermiculatum* and *Tenua eisenackii* subspecies *eisenackii*, are synonymous and do  
1007 not warrant separation. The synonymy of *Sentusidinium spiculatum* Yu Jingxian and Zhang  
1008 Wangping 1980 with *Sentusidinium eisenackii* by Courtinat in Fauconnier and Masure (2004) is  
1009 not followed here because the former species has more simple ornamentation. We consider  
1010 *Sentusidinium spiculatum* to be synonymous with *Sentusidinium millepedii* (see below).

1011

1012

1013

*Sentusidinium euteichum* (Davey 1969a) comb. nov.

1014

1015 **Basionym:** *Chytroeisphaeridia euteiches* Davey 1969a, p. 141, pl. 3, figs. 8–9.

1016

1017 1969a *Chytroeisphaeridia euteiches* Davey, p. 141, pl. 3, figs. 8–9.

1018 1979 *Batiacasphaera euteiches* (Davey1969a) Davey, p. 217.

1019 1987 *Batiacasphaera asperata* Backhouse, p. 215, figs. 10A–C, 14E.

1020

1021 **Remarks:** *Sentusidinium euteichum* is subspherical and has a thick autophragm surmounted by  
1022 granular ornamentation. Therefore, it cannot be accommodated in *Batiacasphaera* due to its lack  
1023 of a reticulum. We consider *Batiacasphaera asperata* to be a taxonomic junior synonym of  
1024 *Sentusidinium euteichum*, which thus now has a stratigraphical range of Early to Late  
1025 Cretaceous.

1026

1027

1028

*Sentusidinium explanatum* Bujak in Bujak et al. 1980, comb. nov.

1029

1030 **Basionym:** *Chytroeisphaeridia explanata* Bujak in Bujak et al. 1980, p. 44, pl. 13, figs. 13–14.

1031

1032 1980a *Canningia minor* Cookson & Hughes 1964 var. *psilata* Burger, p. 71, pl. 25, figs. 5–11.

1033 1980 *Chytroeisphaeridia explanata* Bujak in Bujak et al., p. 44, pl. 13, figs. 13–14.

1034 1983 *Batiacasphaera explanata* (Bujak in Bujak et al. 1980) Islam, p. 235.

1035 1985 *Chytroeisphaeridia minor* (Cookson & Hughes 1964) Morgan 1980 subsp. *psilata*  
1036 (Burger 1980a) Lentin & Williams, p. 58.

1037 1986b *Escharispharidia psilata* Kumar, p. 383, 385, pl. 2, fig. 2; text-fig. 3.



- 1038 1988 *Escharisphaeridia laevigata* Smelror, p. 152–153, figs. 10G–H.
- 1039 1989 *Kallosphaeridium? helbyi* Lentin & Williams 1989 subsp. *psilatum* (Burger 1980a)
- 1040 Lentin & Williams, p. 206.
- 1041 1989 *Kallosphaeridium inornatum* Prauss, p. 41–42, pl. 5, figs. 4–6; pl. 6, fig. 18; text-fig. 17
- 1042 (an illegitimate name; see below)
- 1043 1993 *Kallosphaeridium praussii* Lentin & Williams, p. 365.
- 1044 1997 *Batiacasphaera laevigata* (Smelror 1988) Feist-Burkhardt & Monteil, p. 40.

1045

1046 **Remarks:** This taxon was first described from the Lower Cretaceous of the Surat Basin, eastern

1047 Australia by Burger (1980a) as a variety of *Canningia minor*. It was elevated to subspecies

1048 status by Lentin and Williams (1985). It was raised to species rank by Kumar (1986b), but not

1049 before other species had been proposed that we consider synonymous with it. Among these

1050 synonyms, the earliest at specific rank is *Chytroeisphaeridia explanata* Bujak in Bujak et al.

1051 1980, which we therefore transfer to *Sentusidinium* as the correct name for this taxon at specific

1052 rank. (*Canningia minor* var. *psilatum* and *Batiacasphaera explanata* were both published in

1053 1980; the former in a paper issued February 15<sup>th</sup> and the latter in December; but the latter name

1054 has priority at species rank.)

1055 *Sentusidinium explanatum* has a distinctive psilate to finely scabrate autocyst, with a

1056 subspherical to slightly elongate outline. We consider the species to be the taxonomic senior

1057 synonym of *Batiacasphaera laevigata* (as first proposed by Poulsen 1996, p. 80) and

1058 *Kallosphaeridium praussii*, (a substitute name for *Kallosphaeridium inornatum* Prauss) as well

1059 as *Canningia minor* var. *psiliata* (= *Escharisphaeridia psilata*); all of these taxa lack

1060 ornamentation.

1061 The stratigraphical range of *Sentusidinium explanatum* is Middle Jurassic (Aalenian) to Late

1062 Eocene and the species has a global distribution.

1063

1064

1065 *Sentusidinium extravermiculatum* (Shaw Chenglong 1999) comb. nov.

1066

1067 **Basionym:** *Batiacasphaera extravermiculata* Shaw Chenglong 1999, p. 183–185, figs. 87–95.

1068

1069 1999 *Batiacasphaera extravermiculata* Shaw Chenglong, p. 183–185, figs. 87–95.

1070 1999 *Batiacasphaera granulata* Shaw Chenglong, p. 186, figs. 78–81.

1071

1072 **Remarks:** *Sentusidinium extravermiculatum* is a spherical dinoflagellate cyst from the Eocene  
1073 of Taiwan. It is characterised by its sponge like appearance owing to its extremely dense  
1074 covering of clava and bacula. Because of the nature of its ornamentation, we transfer the species  
1075 to *Sentusidinium*. Moreover, we consider *Batiacasphaera granulata* to be a taxonomic junior  
1076 synonym of *Sentusidinium extravermiculatum*.

1077

1078

1079 *Sentusidinium fibrillosum* Backhouse 1988

1080

1081 1988 *Sentusidinium? fibrillosum* Backhouse, p. 107–108, pl. 41, figs. 3–6.

1082

1083 **Remarks:** *Sentusidinium fibrillosum* is a subspherical cyst, described from the Early Cretaceous  
1084 of South Perth, Australia. It has an autophragm surmounted by interlocking fibres and truncate  
1085 spines, and is characterised by its distinct cingular ridges. *Sentusidinium fibrillosum* is no longer  
1086 considered a problematical species due to the expansion of the original description by Courtinat  
1087 (1989) to include sutural ornamentation (see comments under *Sentusidinium*).

1088

1089

1090 *Sentusidinium granulosum* (Cookson & Eisenack 1974) comb. nov.

1091

1092 **Basionym:** *Palaeostomocystis granulosa* Cookson & Eisenack 1974, p. 79, pl. 28, fig. 10.

1093

1094 1974 *Palaeostomocystis granulosa* Cookson & Eisenack, p. 79, pl. 28, fig. 10.

1095 1978 *Fromea granulosa* (Cookson & Eisenack 1974) Stover & Evitt, p. 48.

1096 1989 *Batiacasphaera granulosa* (Cookson & Eisenack 1974) Jansonius, p. 67.

1097 1991 *Batiacasphaera granospina* He Chengquan, p. 53, pl. 6, figs, 22–23.

1098

1099 **Remarks:** The species *Sentusidinium granulorum* is characterised by an elongate ovoidal  
1100 outline, with a narrow apical archaeopyle and dense granular ornament. This ornamentation  
1101 precludes *Sentusidinium granulorum* from being retained in *Batiacasphaera* due to its lack of a  
1102 reticulum. Owing to the markedly similar morphology of *Batiacasphaera granospina*, this  
1103 species is considered here to be a taxonomic junior synonym of *Sentusidinium granulorum*.  
1104 Therefore, the stratigraphic range of *Sentusidinium granulorum* is now Lower Cretaceous to  
1105 Paleocene (Cookson and Eisenack 1974; He Chengquan 1991).

1106

1107

1108 *Sentusidinium hirsutum* (Stover 1977) comb. nov.

1109

1110 **Basionym:** *Batiacasphaera hirsuta* Stover 1977, p. 72–73, pl. 1, figs, 1–3.

1111

1112 1977 *Batiacasphaera hirsuta* Stover, p. 72–73, pl. 1, figs, 1–3.

1113 1999 *Batiacasphaera deheinzelinii* Louwye, p. 177, pl. 2, figs. 1–7.

1114

1115 **Remarks:** *Sentusidinium hirsutum* is a small dinoflagellate cyst first described from the  
1116 Oligocene of the North Atlantic. It is defined by its subspherical cyst body which is covered by  
1117 dense, thin, hair-like projections. The species is transferred to *Sentusidinium* because it has a  
1118 non-reticulate autophragm. *Batiacasphaera deheinzelinii*, a Miocene species from Europe,  
1119 appears to be morphologically indistinguishable from *Sentusidinium hirsutum* and hence we  
1120 consider these two species to be synonyms.

1121

1122 *Sentusidinium macbethiae* (Mantle 2009) comb. nov.

1123

1124 2009 *Batiacasphaera macbethiae* Mantle, p. 100–101, pl. 8; figs. 1, 3–5.

1125

1126 Remarks: *Sentusidinium macbethiae* was first described from the Middle Jurassic of the Timor  
1127 Sea, off northern Australia. It has a psilate to finely scabrate autophragm, with a subspherical to  
1128 slightly elongate outline and closely resembles *Sentusidinium explanatum*. However,  
1129 *Sentusidinium macbethiae* has a distinctive, centrally located accumulation body (Mantle 2009),  
1130 which *Sentusidinium psilatatum* lacks. Due to the absence of a reticulate autophragm, this species  
1131 cannot be retained in *Batiacasphaera*.

1132

1133

1134 *Sentusidinium microcystum* (Bujak in Bujak et al. 1980) Islam 1993

1135

1136 1980 *Tenua microcysta* Bujak in Bujak et al., p.88, 90, pl. 22, figs. 2–5.

1137 1981 *Cleistosphaeridium microcystum* (Bujak in Bujak et al. 1980) Lentin & Williams, p. 49.

1138 1993 *Sentusidinium microcystum* (Bujak in Bujak et al. 1980) Islam, p. 88.

1139 2004 *Pilosidinium microcystum* (Bujak in Bujak et al. 1980) Courtinat in Fauconnier &  
1140 Masure 2004, p. 448.

1141

1142 **Remarks:** *Sentusidinium microcystum* is a small elongate dinoflagellate cyst. The autophragm  
1143 is covered by short slender hollow spines which have capitate distal terminations. The species  
1144 should be retained in *Sentusidinium*, as we consider *Pilosidinium* to be a junior synonym of  
1145 *Sentusidinium*.

1146

1147

1148 *Sentusidinium micropapillatum* (Stover 1977) comb. nov.

1149

1150 **Basionym:** *Batiacasphaera micropapillata* Stover 1977, p. 73, pl. 1, figs. 7–8.

1151

1152 1977 *Batiacasphaera micropapillata* Stover, p. 73, pl. 1, figs. 7–8.

1153 1983 *Tectatodinium minutum* Matsuoka, p. 127, pl. 5, fig. 6, pl. 6, figs. 7a–b.

1154 1992 *Batiacasphaera minuta* (Matsuoka 1983) Matsuoka & Head, p. 167.

1155

1156 **Remarks:** *Sentusidinium micropapillata* has a small cyst with a subspherical outline and a  
1157 papillate to granulate autophragm. The absence of a rugulate to reticulate autophragm precludes  
1158 its retention in *Batiacasphaera*. We concur with Head in Head and Wrenn (1992, p. 3), who  
1159 considered *Batiacasphaera minuta* to be a possible junior synonym of *Batiacasphaera*  
1160 *micropapillata* and here complete the transfer. This species has a stratigraphical range of  
1161 Oligocene to Miocene (Stover 1977; Matsuoka 1983).

1162

1163

1164 *Sentusidinium millepedii* Fensome & Williams 2004 nom. subst. pro *Sentusidinium?*

1165 *brevispinosum* (Jain & Milleped 1975) Islam 1993

1166

1167 1975 *Cleistosphaeridium brevispinosum* Jain & Milleped, p. 150, pl. 5, figs. 80–82.

1168 1993 *Sentusidinium brevispinosum* (Jain & Milleped 1975) Islam, p. 87.

1169 2004 *Sentusidinium? millepedii* Fensome & Williams, p. 601 nom. subst. pro *Sentusidinium?*

1170 *brevispinosum* (Jain & Milleped) Islam.

1171

1172 **Remarks:** This species is relatively small with a narrow archaeopyle and apparently a small  
1173 antapical concavity (Jain and Milleped 1975, pl. 5, figs. 80, 81). It was originally described  
1174 from the Lower Cretaceous of Senegal and was transferred to *Sentusidinium* by Islam (1993, p.  
1175 87). However, the combination *Sentusidinium brevispinosum* was a junior homonym of  
1176 *Sentusidinium brevispinosum* Courtinat in Courtinat and Gaillard 1980. Therefore, Fensome and  
1177 Williams (2004, p. 601) proposed the substitute name *Sentusidinium? millepedii*. It is no longer  
1178 considered to be a problematical species because it fulfills our generic criteria

1179

1180

1181 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al. 1989

1182

1183 1978 *Tenua hystrix* Eisenack 1958 subsp. *minor* Jiabo, p. 52–53, pl. 23, figs. 5–7.

1184 1981 *Kallosphaeridium? minus* (Jiabo 1978) Lentin & Williams, p. 161.

1185 1981 *Tenua simlaensis* Khanna & Singh, p. 389–390, fig. 1, nos. 8–9; text-fig. 2.

1186 1988 *Sentusidinium stipulatum* Mao Shaozhi & Norris, p. 40–41, pl. 8, figs. 21–22.

1187 1989 *Batiacasphaera sinensis* Lentin & Williams, p. 36.

1188 1989 *Sentusidinium minus* (Jiabo 1978) He Chengquan et al., p. 68.

1189 1993 *Batiacasphaera? simlaensis* (Khanna & Singh 1981) Lentin & Williams, p. 56.

1190 1997 *Kallosphaeridium jiyangense* Xu Jinli et al., p. 100, pl. 18, fig. 11; pl. 20, fig. 7; name  
1191 not validly published: no English or Latin description.

1192 1997 *Sentusidinium conispinosum* Xu Jinli et al., p. 47, pl. 34, figs. 6a–b; pl. 35, figs. 14a–b,  
1193 16a–b; pl. 36, figs. 15a–b; name not validly published: no English or Latin description.

1194 1997 *Sentusidinium reticuloides* Xu Jinli et al., p. 47, pl. 16, figs. 3–4; pl. 17, figs. 3–4; pl. 18,  
1195 figs. 12–15; pl. 19, figs. 7–9; name not validly published: no English or Latin  
1196 description.

1197 2009 *Kallosphaeridium jiyangense* Xu Jinli et al. 1997, ex He Chengquan et al., p. 656.

1198 2009 *Sentusidinium conispinosum* Xu Jinli et al. 1997, ex He Chengquan et al., p. 662.

1199 2009 *Sentusidinium reticuloides* Xu Jinli et al. 1997, ex He Chengquan et al., p. 662.

1200

1201 **Remarks:** *Sentusidinium minus* is a subspherical cyst with an apical archaeople and is from the  
1202 Palaeogene of China. It has a distinct foveolate/granular autophragm, from which arise  
1203 numerous spines. The spines are thin, hollow or solid, up to 10 µm in length and with varying  
1204 terminations. Jan du Chêne et al. (1985, p. 15) transferred *Kallosphaeridium? minus* to  
1205 *Batiacasphaera* (as *Batiacasphaera minor*). However, this combination was illegitimate, being a  
1206 junior homonym of *Batiacasphaera minor* (Cookson and Hughes 1964) Dörhöfer and Davies  
1207 1980. So, Lentin and Williams (1989) erected *Batiacasphaera sinensis* as a substitute name. Its  
1208 lack of a reticulate autophragm means that the species cannot be accommodated in  
1209 *Batiacasphaera*. He Chengquan et al. (1989) retained it in *Sentusidinium*, which accords with  
1210 our views. The species *Batiacasphaera? simlaensis* from northern India, and *Kallosphaeridium*

1211 *jiyanense*, *Sentusidinium conispinosum*, *Sentusidinium reticuloides* and *Sentusidinium*  
1212 *stipulatum* from China, are all morphologically indistinguishable from *Sentusidinium minus*.  
1213 Hence, we treat all five species as taxonomic junior synonyms of *Sentusidinium minus*.

1214

1215

1216 *Sentusidinium myriatrichum* Fensome 1979

1217

1218 1979 *Sentusidinium myriatrichum* Fensome, p. 12–13, pl. 2, fig. 7; text-fig.5A.

1219 1989 *Pilosidinium myriatrichum* (Fensome 1979) Courtinat, p. 191.

1220

1221 **Remarks:** *Sentusidinium myriatrichum* was first described from the Late Jurassic of East  
1222 Greenland. It is subspherical with a distinctive dense covering of small fine simple hairs. We  
1223 retain this species in *Sentusidinium*, since we consider *Pilosidinium* to be a taxonomic junior  
1224 synonym of the former genus.

1225

1226

1227 *Sentusidinium perforoconum* (Yun Hyesu 1981) Islam 1993

1228

1229 1981 *Cleistosphaeridium perforoconum* Yun Hyesu, p. 43, pl. 15, figs. 1–4.

1230 1993 *Sentusidinium perforoconum* (Yun Hyesu 1981) Islam, p. 88.

1231

1232 **Remarks:** *Sentusidinium perforoconum*, described from the Late Cretaceous of the USA (Yun  
1233 Hyesu 1981), has a spherical cyst body, with a microgranulate autophragm. The autophragm is  
1234 covered with distinctive, prominent, conical to acuminate spines, 6–8 µm in length.

1235

1236

1237 *Sentusidinium pilosum* (Ehrenberg 1854) Sarjeant & Stover 1978

1238

- 1239 1854 *Xanthidium pilosum* Ehrenberg, pl. 37, fig. 8, no. 4.
- 1240 1937 *Hystrichosphaeridium pilosum* (Ehrenberg 1854) Deflandre, p. 79.
- 1241 1961 *Baltisphaeridium pilosum* (Ehrenberg 1854) Sarjeant, p. 101.
- 1242 1968 *Tenua pilosa* (Ehrenberg 1854) Sarjeant, p. 231.
- 1243 1978 *Sentusidinium pilosum* (Ehrenberg 1854) Sarjeant & Stover, p. 50.
- 1244 1980 *Batiacasphaera pilosa* (Ehrenberg 1854) Dörhöfer & Davies, p. 40.
- 1245 1989 *Barbatacysta pilosa* (Ehrenberg 1854) Courtinat, p. 187.

1246

1247 **Remarks:** *Sentusidinium pilosum* is elongate to ovoidal in outline with a dense covering of  
 1248 short, slender projections that have variable terminations (Erkmen and Sarjeant 1980, pl. 1). We  
 1249 do not accept the transfer of *Sentusidinium pilosum* to *Batiacasphaera* by Dörhöfer and Davies  
 1250 (1980). Since we consider *Barbatacysta* to be a taxonomic junior synonym of *Sentusidinium*, we  
 1251 retain this species in the latter genus. *Sentusidinium pilosum* ranges from the Late Jurassic to the  
 1252 Early Cretaceous (Sarjeant 1968).

1253

1254

1255 *Sentusidinium ringnesiorum* (Manum & Cookson 1964) comb. nov.

1256

1257 **Basionym:** *Canningia ringnesii* Manum & Cookson 1964, p. 15, pl. 2, fig. 10.

1258

1259 1964 *Canningia ringnesii* Manum & Cookson, p. 15, pl. 2, fig. 10.

1260 1968 *Chytroeisphaeridia pocockii* Sarjeant, p. 230, pl. 3, fig. 9.

1261 1972 *Chytroeisphaeridia mantelli* Gitmez & Sarjeant, p. 186, pl. 1, figs. 3–4; pl. 12, fig. 3.

1262 1972 *Meiourogonyaulax dicryptos* Gitmez & Sarjeant, p. 225–226, pl. 7, fig. 6; text fig. 22.

1263 1975 *Batiacasphaera macrogranulata* Morgan, p. 162, pl. 2, figs. 3a–d.

1264 1976 *Lithodinia dicrypta* (Gitmez & Sarjeant 1972) Gocht, p. 334.

1265 1976 *Membranosphaera granulata* Norvick, p. 79–80, pl. 11, fig. 9; pl. 12, fig. 3.



- 1266 1978 *Kallosphaeridium? granulatum* (Norvick 1976) Stover & Evitt, p.59.
- 1267 1979 *Lithodinia pocockii* (Sarjeant 1968) Davey, p. 217.
- 1268 1980 *Escharisphaeridia pocockii* (Sarjeant 1968) Erkmen & Sarjeant, p. 62.
- 1269 1980 *Batiacasphaera ringnesiorum* (Manum & Cookson 1964) Dörhöfer & Davies, p. 40.
- 1270 1980 *Chytroeisphaeridia ringnesiorum* (Manum & Cookson 1964) Morgan, p. 19.
- 1271 1980a *Membranosphaera norvickii* Burger, p. 73–74, pl. 26, figs. 7–8.
- 1272 1980 *Chytroeisphaeridia rugosa* Courtinat in Courtinat & Gaillard, p. 15–16, pl. 1, fig. 12; pl.  
1273 2, fig. 1; text fig. 2d.
- 1274 1980 *Chytroeisphaeridia granulata* Courtinat in Courtinat & Gaillard, p. 13–14, pl. 1, figs. 4,  
1275 6; text fig. 2b.
- 1276 1981 *Kallosphaeridium norvickii* (Burger 1980a) Lentin & Williams, p. 161.
- 1277 1981 *Canningia dicrypta* (Gitmez & Sarjeant 1972) Below, p. 31.
- 1278 1983 *Escharisphaeridia rudis* Davies, p. 28, pl. 10, figs. 7, 10–18; text fig. 25.
- 1279 1987 *Escharisphaeridia granulata* (Courtinat in Courtinat & Gaillard 1980) Stover &  
1280 Williams, p. 89.
- 1281 1987 *Kallosphaeridium? ringnesiorum* (Manum & Cookson 1964) Helby, p. 324–325.
- 1282 1988 *Escharisphaeridia senegalensis* Jan du Chêne, p. 155, pl. 15, figs. 1–8.
- 1283 1989 *Escharisphaeridia mantelli* (Gitmez & Sarjeant 1972) Courtinat, p. 180.
- 1284 1989 *Batiacasphaera norvickii* (Burger 1980a) Lentin & Williams, p. 35.
- 1285 1989 *Escharisphaeridia rugosa* (Courtinat in Courtinat & Gaillard 1980) Courtinat, p. 181.
- 1286 1989 *Escharisphaeridia gaillardii* Courtinat, p. 178–179, pl. 17, fig. 7; pl. 20, figs. 5, 8; pl. 21,  
1287 fig. 10; pl. 22, fig. 13; pl. 23, figs. 2, 7–8; text fig. 78A.
- 1288 1989 *Batiacasphaera henanensis* He Chengquan et al., p. 38, pl. 7, fig. 10.
- 1289 1990 *Batiacasphaera mica* Harding, p. 48, pl. 25, figs. 10–19 ex Harding in Williams et al.,  
1290 1998, p. 67.
- 1291 1991 *Batiacasphaera sparsa* He Chengquan, p. 53–54, pl. 6, fig. 4.
- 1292 1991 *Batiacasphaera tuberculata* He Chengquan, p. 54, pl. 6, fig. 2.

- 1293 1993 *Batiacasphaera xinjiangensis* Lentin & Williams, p. 57.
- 1294 1993 *Escharisphaeridia dicrypta* (Gitmez & Sarjeant 1972) Williams et al., p. 57.
- 1295 1994 *Sentusidinium spatiosum* Dodekova, p. 33, pl. 5, figs. 6–8, 11.
- 1296 1997 *Batiacasphaera granofoveolata* Pan Zhaoren in Xu Jinli et al., p. 43, pl. 39, fig. 1; name  
1297 not validly published, as there was no English or Latin description.
- 1298 2009 *Batiacasphaera granofoveolata* Pan Zhaoren in Xu Jinli et al. 1997, ex He Chengquan et  
1299 al., p. 649.
- 1300 2009 *Batiacasphaera macropyla* He Chengquan et al., p. 644, pl. 56, fig. 6.

1301

1302 **Remarks:** *Sentusidinium ringnesiorum* was first described, as *Canningia ringnesii*, from the  
1303 Late Cretaceous of Arctic Canada by Manum and Cookson (1964). (The epithet is correctly  
1304 rendered as "*ringnesiorum*", rather than "*ringnesii*", because the species was named avowedly  
1305 for the Ringnes brothers, not for an individual.) This species has a subcircular outline and highly  
1306 irregular granular ornamentation (Davies 1983, fig. 25). Typically, the autophragm is relatively  
1307 thick and robust. The species, and its synonyms, have been attributed to a total of nine  
1308 genera. These are: *Batiacasphaera*; *Canningia*; *Chytroeisphaeridia*; *Escharisphaeridia*;  
1309 *Kallosphaeridium*; *Lithodinia*; *Meiourogonyaulax*; *Membranosphaera*; and *Sentusidinium*.  
1310 *Sentusidinium ringnesiorum* has proved to be the most taxonomically complex of this review  
1311 because we consider 19 other species names as taxonomic junior synonyms. These are:  
1312 *Batiacasphaera granofoveolata*, *Batiacasphaera henanensis*, *Batiacasphaera macrogranulata*,  
1313 *Batiacasphaera macropyla*, *Batiacasphaera mica*, *Batiacasphaera norvickii*, *Batiacasphaera*  
1314 *sparsa*, *Batiacasphaera tuberculata*, *Batiacasphaera xinjiangensis*, *Escharisphaeridia dicrypta*,  
1315 *Escharisphaeridia gaillardii*, *Escharisphaeridia granulata*, *Escharisphaeridia mantellii*,  
1316 *Escharisphaeridia pocockii*, *Escharisphaeridia rudis*, *Escharisphaeridia rugosa*,  
1317 *Escharisphaeridia senegalensis*, *Kallosphaeridium? granulatum* and *Sentusidinium spatiosum*.  
1318 After reviewing the the descriptions and illustrations of these species in detail, we consider that  
1319 they cannot be consistently separated. *Sentusidinium ringnesiorum* belongs in the genus  
1320 *Sentusidinium* since it lacks a reticulum and an anterior intercalary plate, precluding its  
1321 assignment to *Batiacasphaera* and *Kallosphaeridium* respectively. As circumscribed here  
1322 *Sentusidinium ringnesiorum* has a long stratigraphical range of Jurassic to Eocene, reflecting its  
1323 simple morphology and probable polyphyly.

1324

1325

1326

*Sentusidinium sahii* (Khanna & Singh 1981) comb. nov.

1327

1328 **Basionym:** *Hexagonifera sahii* Khanna & Singh 1981, p. 391–393, fig. 2, nos. 1–3; fig. 4, no. 4;  
1329 text-figs. 4–5.

1330

1331 1981 *Hexagonifera sahii* Khanna & Singh, p. 391–393, fig. 2, nos. 1–3; fig. 4, no. 4; text-figs.  
1332 4–5.

1333 1984 *Kallosphaeridium curiosum* Bujak, p. 188, pl. 2, figs. 17–20.

1334 1985 *Batiacasphaera curiosa* (Bujak 1984) Jan du Chêne et al., p. 15.

1335 1991 *Sentusidinium minutum* He Chengquan, p. 59, pl. 15, fig 4.

1336 1993 *Batiacasphaera? sahii* (Khanna & Singh 1981) Lentin & Williams, p. 56.

1337

1338 **Remarks:** *Sentusidinium sahii* was first described from the Eocene of the Simla Hills in  
1339 northern India by Khanna and Singh (1981), as *Hexagonifera sahii*. It was transferred to  
1340 *Batiacasphaera?* by Lentin and Williams (1993). This species is characterised by its  
1341 subspherical to ovoidal cyst body, which is densely granular, and sparse, randomly distributed  
1342 longer spines. The non-reticulate autophragm means that *Batiacasphaera* is an inappropriate  
1343 assignment, but the species falls within the circumscription of *Sentusidinium*, to which we  
1344 transfer it. We consider the Eocene species *Batiacasphaera curiosa* from the North Pacific and  
1345 *Sentusidinium minutum* from China to be morphologically indistinguishable from *Sentusidinium*  
1346 *sahii* and hence to be taxonomic junior synonyms.

1347

1348

1349

*Sentusidinium separatum* McIntyre & Brideaux 1980

1350

1351 1980 *Cleistosphaeridium separatum* McIntyre & Brideaux, p. 19–20, pl. 6, figs. 4–5, 7–8.

1352 1981 *Sentusidinium separatum* (McIntyre & Brideaux 1980) Lentin & Williams, p. 254.

1353

1354 **Remarks:** The Early Cretaceous (Valanginian) species *Sentusidinium separatum* is a small  
1355 subspherical, proximochorate dinoflagellate cyst. Its distinguishing feature is the thin granulate  
1356 autophragm, which is surmounted by a moderately dense covering of long (2–8 µm) spines, with  
1357 closed, bifid or branched distal terminations.

1358

1359

1360 *Sentusidinium setulosum* (Shaw Chenglong 1999) comb. nov.

1361

1362 **Basionym:** *Batiacasphaera setulosa* Shaw Chenglong 1999, p. 182, figs. 72–77, figs. 84–86.

1363

1364 1999b *Batiacasphaera setulosa* Shaw Chenglong, p. 182, figs. 72–77, figs. 84–86.

1365 1999b *Batiacasphaera setulosa* var. *setulosa* (Autonym; see Shaw Chenglong, p. 182, figs. 72–  
1366 77).

1367 1999b *Batiacasphaera setulosa* var. *minima* Shaw Chenglong, p. 182, figs. 84–86.

1368

1369 **Remarks:** *Sentusidinium setulosum* was described from the Eocene of Taiwan by Shaw  
1370 Chenglong (1999). It is a small to intermediate dinoflagellate cyst with a subspherical outline.  
1371 The autophragm is covered in setose ornamentation, with elements 2–3 µm long. *Batiacasphaera*  
1372 *setulosa* var. *minima* appears to be morphologically identical to *Sentusidinium setulosa* var.  
1373 *setulosa* and hence we consider the two varieties synonymous. We transfer the species from  
1374 *Batiacasphaera* to *Sentusidinium* because it lacks a reticulate autophragm.

1375

1376

1377 *Sentusidinium sparsibarbatum* Erkmen & Sarjeant 1980

1378

1379 1980 *Sentusidinium sparsibarbatum* Erkmen & Sarjeant, p. 54–56, pl. 2, figs. 2–8; pl. 6, fig. 9;  
1380 text-figs. 4a–c.

1381 1980 *Sentusidinium brevispinosa* Courtinat in Courtinat & Gaillard, p. 60, pl. 9, figs. 4, 7, 11;  
1382 text-fig. 10e.

1383 1989 *Barbatacysta brevispinosa* (Courtinat in Courtinat & Gaillard 1980) Courtinat, p. 185.

1384

1385 **Remarks:** *Sentusidinium sparsibarbatum* is subspherical to elongate in outline and is  
1386 characterised by its distinct granular autophragm which is covered in short spines, with blunt,  
1387 capitate or bifurcating distal terminations. The elongate morphotypes (e.g. Erkmen and Sarjeant  
1388 1980, text-fig. 4b, pl. 2, fig. 2, 3, 6) are especially distinctive. We consider that the distinctive  
1389 ornamentation common to *Sentusidinium sparsibarbatum* and *Sentusidinium brevispinosum*  
1390 warrants treating the two species as synonyms. Both were described in the same year, with  
1391 Erkmen and Sarjeant 1980 appearing prior to Courtinat in Courtinat and Gaillard (1980). Hence  
1392 *Sentusidinium sparsibarbatum* has priority. The stratigraphical range of *Sentusidinium*  
1393 *sparsibarbatum* is Middle to Late Jurassic (Callovian–Oxfordian); the species has only been  
1394 recorded from Europe.

1395

1396

1397 *Sentusidinium verrucosum* (Sarjeant 1968) Sarjeant & Stover 1978

1398

1399 1968 *Tenua verrucosa* Sarjeant, p. 232, pl. 1, fig. 17; pl. 2, figs. 3, 6.

1400 1978 *Sentusidinium verrucosum* (Sarjeant 1968) Sarjeant & Stover, p. 50.

1401 1979 *Sentusidinium pelionense* Fensome, p. 13–15, pl. 1, figs. 5–9; text-fig. 5B.

1402 1980 *Batiacasphaera verrucosa* (Sarjeant 1968) Dörhöfer & Davies, p. 41.

1403 1989 *Barbatacysta verrucosa* (Sarjeant 1968) Courtinat, p. 187.

1404 1989 *Barbatacysta pelionensis* (Fensome 1979) Courtinat, p. 187.

1405 1989 *Pilosidinium fensomei* Courtinat, p. 190–191, pl. 21, figs. 2–3, 5, 7; pl. 23, fig. 15.

1406

1407 **Remarks:** *Sentusidinium verrucosum* is a subspherical dinoflagellate cyst, characterised by its  
1408 distinct irregular verrucae set on a granular autophragm. We consider it to be a taxonomic senior  
1409 synonym of *Barbatacysta pelionensis* and *Pilosidinium fensomei*, both of which exhibit the  
1410 same characteristics. *Sentusidinium verrucosum* should be retained in *Sentusidinium* as it lacks a  
1411 reticulum: its stratigraphical range is Middle to Late Jurassic (Bajocian–Oxfordian).

1412

1413

1414 *Sentusidinium villersense* (Sarjeant 1968) Sarjeant & Stover 1978

1415

1416 1968 *Tenua villerense* Sarjeant, p. 231–232, pl. 1, fig. 16; pl. 2, figs. 5–10.

1417 1978 *Sentusidinium villersense* (Sarjeant 1968) Sarjeant & Stover, p. 50.

1418 1980 *Batiacasphaera villersensis* (Sarjeant 1968) Dörhöfer & Davies, p. 41.

1419

1420 **Remarks:** *Sentusidinium villersense* was first recorded from the Jurassic (Callovian–Oxfordian)  
1421 of France by Sarjeant (1968). It has a spherical outline and a granular autophragm surmounted  
1422 by numerous distinctive, well-spaced spines, with distally-expanded terminations: at the antapex  
1423 there is there is a short broad spine. We retain the species in *Sentusidinium* as it lacks a reticulate  
1424 autophragm.

1425

1426

#### 1427 **Problematical species:**

1428 The following four species, which have been referred to *Sentusidinium*, all lack an unequivocal  
1429 apical archaeopyle hence are deemed to be problematical taxa.

1430

1431 *Sentusidinium? asymmetricum* (Pocock 1972) Jansonius 1986

1432

1433 1972 *Leiosphaeridia asymmetrica* Pocock, p. 107, pl. 26, figs. 29–30.

1434 1986 *Sentusidinium asymmetricum* (Pocock 1972) Jansonius, p. 219.

1435 2004 *Pilosidinium asymmetricum* (Pocock 1972) Courtinat in Fauconnier & Masure, p. 447.

1436

1437 **Remarks:** *Sentusidinium? asymmetricum* is predominantly subspherical in outline. However, it  
1438 has a distinct lobe on one lateral side. The autophragm is covered in dense spines.

1439 *Sentusidinium? asymmetricum* is deemed to be a problematical species due to the lack of  
1440 evidence for an apical archaeopyle. Since we consider *Pilosidinium* to be a taxonomic junior  
1441 synonym of *Sentusidinium*, we retain the species in the latter genus. *Sentusidinium?*  
1442 *asymmetricum* was originally described from the Middle Jurassic of Alberta, Canada.

1443

1444

1445 *Sentusidinium? panshanensum* (Jiabo 1978) Islam 1993

1446

1447 1978 *Cleistosphaeridium panshanense* Jiabo, p. 63, pl. 22, figs 1–6.

1448 1989 *Sentusidinium densispinum* He Chegquan et al in He Chengquan et al, p. 67, pl. 17, figs,  
1449 1–3.

1450 1989 *Sentusidinium shenxianense* He Chegquan et al in He Chengquan et al, p. 68, pl. 17,  
1451 figs, 6–10; text-fig. 10.

1452 1993 *Sentusidinium panshanense* (Jiabo 1978) Islam, p. 88.

1453 2004 *Sentusidinium? panshanense* (Jiabo 1978) Islam 1993. Courtinat in Fauconnier &  
1454 Masure, p. 487.

1455

1456 **Remarks:** *Sentusidinium? panshanensum* was described from the Palaeogene of China by Jiabo  
1457 (1978). It is small, subspherical and densely covered in tubiform spines. We consider two  
1458 species, *Sentusidinium densispinum* and *Sentusidinium shenxianense*, to be taxonomic synonyms  
1459 of *Sentusidinium? panshanensum*. The lack of evidence of an apical archaeopyle makes it a  
1460 problematical species.

1461

1462

1463 *Sentusidinium? reticuloidum* (Jiabo 1978) comb. nov.

1464

1465 **Basionym:** *Baltisphaeridium reticuloidum* Jiabo 1978, p. 115–116, pl. 31, figs. 18–19.

1466

1467 1978 *Baltisphaeridium reticuloidum* Jiabo, p. 115–116, pl. 31, figs. 18–19.

1468 1978 *Filisphaeridium aspersum* Jiabo, p. 116, pl. 31, figs. 1–6; pl. 49, figs. 2–4.

1469 1985 *Filisphaeridium reticuloidum* (Jiabo 1978) Song Zhichen et al., p. 55–56.

1470 1994 *Kallosphaeridium? reticuloidum* (Jiabo 1978) Sarjeant & Stancliffe, p. 56.

1471 1994 *Kallosphaeridium? aspersum* (Jiabo 1978) Sarjeant & Stancliffe, p. 56.

1472

1473 **Remarks:** *Sentusidinium? reticuloidum* was described from the Oligocene of China (Jiabo  
1474 1978). It is subspherical in outline and has a pronounced granular autophragm, surmounted by  
1475 sparse, variable short projections. Due to the apparent lack of an anterior intercalary plate this  
1476 species cannot be retained in *Kallosphaeridium* and therefore is transferred to *Sentusidinium*.  
1477 However, the complete lack of evidence of an apical archaeopyle, makes it a problematical  
1478 species. *Kallosphaeridium? aspersum*, which also does not have a discernible archaeopyle, is  
1479 interpreted here as a taxonomic junior synonym of *Sentusidinium reticuloidum*.

1480

1481

1482 *Sentusidinium? spongiosum* (Batten & Lister 1988) comb. nov.

1483

1484 1988 *Kallosphaeridium? spongiosum* Batten & Lister, p. 344–345, figs. 4e–h.

1485

1486 **Remarks:** *Sentusidinium spongiosum* was described from Lower Cretaceous (Upper  
1487 Hauterivian) freshwater strata from Surrey, southern England. It is no longer considered to be  
1488 referable to *Kallosphaeridium* as there is no indication of an anterior intercalary plate.  
1489 Therefore, we transfer the species to *Sentusidinium?*. However, there is no evidence of a clear  
1490 apical archaeopyle and the autophragm exhibits tabulation, which explains why we consider this  
1491 to be a problematical species of *Sentusidinium*.

1492



1493

1494

Subfamily LEPTODINIOIDEAE Fensome et al. 1993

1495

1496

### Genus *Meiourogonyaulax* Sarjeant 1966

1497

1498 **Type:** *Meiourogonyaulax valensii* Sarjeant 1966

1499

1500

*Meiourogonyaulax? angularis* (Stevens & Helby 1987) comb. nov.

1501

1502 1987 *Batiacasphaera angularis* Stevens & Helby, p. 165–166, figs. 2A–I, 3A–B.

1503

1504 **Remarks:** This earliest Cretaceous species from offshore northern Australia is highly variable in  
1505 morphology. Typically, it is somewhat elongate, has equatorial bulges and is rounded  
1506 heptagonal to subvoidal in outline. The autophragm is variably ornamented and occasionally  
1507 possesses low sutural ridges, which indicate a gonyaulacacean tabulation (Stevens and Helby  
1508 1987, figs. 2A–I). We do not consider this species assignable to *Batiacasphaera* because it lacks  
1509 a reticulate autophragm and is angular-elongate in outline. The occurrence of rare specimens  
1510 with tabulation means that this species has a greater affinity with *Meiourogonyaulax*. However,  
1511 we questionably include the species in *Meiourogonyaulax*, because the holotype lacks sutural  
1512 ridges (Stevens and Helby 1987, figs. 2A–B).

1513

## 1514 5. Phylogenetic affinities

1515 Due to their simple morphology, and the lack of full tabulation details, the phylogenetic  
1516 affinities of the four genera in the *Sentusidinium* complex are difficult to assess. The complex as  
1517 a group is clearly polyphyletic, as too may be the genera *Sentusidinium* and *Batiacasphaera*. It  
1518 is clear that all four genera belong to the Gonyaulacales because of their apical archaeopyles  
1519 (Fensome et al. 1993), but further assignment to family and subfamily is more difficult.

1520 *Kallosphaeridium* is perhaps the best phylogenetically constrained of the four genera, with its  
1521 distinctive extra climactal plate (climactal plates are apical plus anterior intercalary plates).

1522 Fensome et al. (1993) placed *Kallosphaeridium* questionably in the subfamily  
1523 Cribroperidinioideae of the family Gonyaulaceae based on the similarity of its tabulation to that  
1524 of *Lingulodinium*, which is based on cyst-theca relationships (Dodge 1989, text-fig. 1I, showing  
1525 a climactal plate configuration practical identical to that of *Kallosphaeridium*). However,  
1526 *Kallosphaeridium* exhibits no evidence of dextral torsion, which mitigates against the attribution  
1527 of this genus to the subfamily Cribroperidinioideae.

1528 *Pentafidia* also shows a characteristic tabulation feature in the reported presence of five  
1529 precingular plates. As noted above, it is possible that this number represents a misinterpretation,  
1530 or perhaps reflects a fusion of two plates. However, if the number of precingulars is confirmed,  
1531 the only other gonyaulacoid dinoflagellates with five precingular plates belong to the  
1532 exclusively extant family Ceratocoryaceae (Fensome et al. 1993); the morphology of the  
1533 Ceratocoryaceae is so distinctive that without further evidence to support such an affinity,  
1534 considering *Pentafidia* to be a ceratocoryacean would be overly speculative. The Jurassic–  
1535 Cretaceous genus *Atopodinium* was originally thought to have five precingular plates (Drugg  
1536 1978), but this was later convincingly shown to be a misinterpretation due to partial suppression  
1537 of parasutures (Masure 1991). Perhaps it is best for now to consider *Pentafidia* as a member of  
1538 the order Gonyaulacales of uncertain family assignment.

1539 Similarly, the tabulation reflected by the archaeopyle outline of the type of *Batiacasphaera*,  
1540 *Batiacasphaera compta*, is unclear although some other species of the genus reflect a more  
1541 conventional apical tabulation. Hence based on the type, and like Fensome et al. (1993), we  
1542 retain *Batiacasphaera* as a member of the order Gonyaulacales of uncertain family assignment.

1543 The conventional apical tabulation of *Sentusidinium*, as indicated by the archaeopyle margin,  
1544 confirms its affinity with the family Gonyaulacaeae, although in the absence of knowledge of  
1545 the hypocystal tabulation, the subfamilial assignment must remain uncertain. It is possible that  
1546 more than one gonyaulacean subfamily developed cysts with a relatively simple  
1547 “*Sentusidinium*” morphology.

1548

## 1549 **6. Conclusions**

1550 The Mesozoic-Cenozoic *Sentusidinium* complex is a polyphyletic group of gonyaulacacean  
1551 dinoflagellate cysts with a relatively simple morphology. They are acavate and generally  
1552 subspheroidal, and have an apical archaeopyles and relatively low ornamentation. As a result of  
1553 this detailed review, we consider that all the species with this morphology can be assigned to

1554 one of four genera: *Batiacasphaera*, *Kallosphaeridium*, *Pentafidia* and *Sentusidinium*. Through  
1555 extensive synonymising of forms with very closely similar to identical morphologies, we have  
1556 reduced the number of species from xxxx to yyyy , and have eliminated infraspecific taxa.

1557 *Sentusidinium* is the most diverse genus in the complex and has the longest stratigraphical range.  
1558 The archaeopyle in *Sentusidinium* normally has a free operculum and exhibits accessory  
1559 archaeopyle sutures. The 34 accepted species of this genus collectively range from the Jurassic  
1560 to the Neogene (Miocene); there are no known post-Pliocene species. The majority of the  
1561 Jurassic *Sentusidinium* species were originally described from Europe. By contrast, all but one  
1562 of the Cretaceous species are from Africa, Australia and North America. Six of the nine  
1563 Palaeogene taxa were described from Asia (Table 3). The oldest representatives of the genus are  
1564 from the Late Toarcian of northern England (Riding 1984), and were originally attributed to  
1565 *Escharisphaeridia* sp. This material may now be attributable to *Sentusidinium ringnesiorum*.  
1566 However, the genus is absent from the Toarcian of Australia (Riding and Helby 2001). The  
1567 oldest occurrence of the *Sentusidinium* complex in Gondwana may be that of *Kallosphaeridium?*  
1568 *hypornatum* from the Bajocian of Australia (Mantle and Riding 2012). The *Sentusidinium*  
1569 species with the oldest type is *Sentusidinium asymmetrum*, from the latest Bajocian of southern  
1570 England (Fenton et al. 1980).

1571 *Pentafidia* is an unusual gonyaulacoid genus, in that it apparently only has five precingular  
1572 plates. It comprises two species, both from the Jurassic-Cretaceous transition from Western  
1573 Australia (Backhouse 1988).

1574 The 17 accepted species of *Batiacasphaera* have a reticulate to rugulate autophragm, and  
1575 consistently lack deep accessory archaeopyle sutures. The stratigraphical range of  
1576 *Batiacasphaera* is Early Cretaceous to Miocene (Table 1). Most Cretaceous species are from the  
1577 former Gondwanan continents, while the Miocene species are predominately of North Atlantic  
1578 affinity.

1579 The principal characteristics of the six accepted species of *Kallosphaeridium* are a ventrally  
1580 attached operculum and a five-plate archaeopyle which has accessory archaeopyle sutures. All  
1581 the six accepted species of this genus were originally described from Palaeogene strata around  
1582 the North Atlantic (Table 2).

1583

1584 Notes:

1585

1586

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1594

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